

MODELLING AND SIMULATION  
OF THE MESOSCALE MOSAIC STRUCTURE  
OF THE LOWER MARINE TROPHIC LEVELS

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ABSTRACT

Marine ecology deals with biological and chemical processes in interaction with their aquatic environment. The possibility of using more of the products of the sea as human food has created at present a keen interest in the study of marine plankton. It is of importance to understand the production of phytoplankton and the predator-prey relationships between phyto- and zooplankton, the path by which the organic matter produced finally reaches the fish.

In the sea, plankton populations are almost entirely at the mercy of water movement. In spite of this diffusive process, these populations display a spatio-temporal structure.

The spectral analysis of the spatial organization of phytoplankton populations exhibits two main classes of behaviour depending on the range of spatial scale. Below 5 km, the phytoplankton behaves as a passive scalar

- i) from zero to 100 m, the spatial variability of phytoplankton is controlled by turbulence and its spectrum is similar to the spectrum of homogeneous and spatially isotropic turbulence according to Kolmogorov's theory,
- ii) from 100 m to 5 km, the coherence between chlorophyll and temperature are high. Beyond 5 km and until 100 km, the phytoplankton dynamics in promoting patchiness, i.e. mesoscale spatial heterogeneity, dominates over that of the physical diffusive processes in eroding it.

A model is proposed to explain the mechanism of this mosaic structure. The partial differential equations take into account advection, shear and eddy diffusivity and non-linear ecological interactions. The properties of the solutions of these equations are studied by simulation of simplified sub-models dealing with asymptotic behaviour of the ecological system. The horizontal structure is generated by local spatial instabilities. The most important characteristic is the disposition of the ecosystem to amplify microscopic excitations (fluctuations) to a macroscopic level leading to the emergence of new space and time patterns.

## I. INTRODUCTION

The possibility of using more of the products of the sea as human food has created at present a keen interest in the study of marine plankton. The plankton is considered a potential source of human food. It is of importance to understand the production of phytoplankton and the relationship between phytoplankton and zooplankton, the path by which the organic matter produced finally reaches the fish.

Rather different views of the problems connected with marine plankton have been referred from time to time. Without in any way attempting to review the study of plankton as a whole we may here consider one particular problem very important for budget evaluations of primary and secondary production, the so-called patchiness effect. In the sea, plankton populations such as phytoplankton and herbivorous zooplankton are in a prey-predator relationship. Plankton populations are almost entirely at the mercy of water movement. In spite of the diffusive process, plankton populations display spatially heterogeneous patterns. This paper deals with physical and mathematical modeling of interaction of fluid flow with such biological and chemical processes.

As plankton can be considered as small organisms of identical size embedded in a turbulent flow (Pielou (1969)), their number is sufficiently large so that only statistical properties can be possibly studied. The characteristic time of ecological response is of the order of

$$\omega^{-1} = (k_1 k_3)^{-1/2}$$

where  $k_1$  and  $k_3$  are respectively the rates of natality-mortality of phytoplankton and herbivorous zooplankton. From experimental values, one finds that the characteristic time is of the order of a few days.

Hence, if we average the evolution equations over a time which is short compared to the characteristic time of ecological response but still cover several tidal periods we smooth out the effects of oscillation and fluctuations of the sea without affecting significantly the process under study.

Let  $\underline{U}$  be the horizontal component of the average velocity (residual currents),  $U_z$  its vertical component and  $C_i$  the average concentration of species  $i$  at position  $\underline{r}$  and time  $t$ , respectively. The general equation of the distributions of species  $i$  can be written

$$\partial C_i / \partial t + \underline{U} \cdot \nabla C_i + U_z \partial C_i / \partial z = \langle f_i \rangle + \nabla \cdot (\tilde{K} \nabla C_i) + \partial (k \partial C_i / \partial z) \quad (1)$$

where  $\nabla$  is the horizontal differential vector operator, i.e.  $\nabla \equiv \underline{1}_x \partial / \partial x + \underline{1}_y \partial / \partial y$ ,  $\langle f_i \rangle$  the time-averaged chemical and biological interactions, and  $\tilde{K}$  and  $k$  the turbulent diffusivity.

It may be noted that in marine systems, the horizontal and vertical spatio-temporal physical, chemical and biological properties are characterized by completely different scales. In considering the case of the Southern North Sea, it is generally sufficient to consider the average concentrations over the depth. A depth-averaged interactions model may be governed by equations derived from the three-dimensional ones (eq. 1) by depth integration.

The depth-averaged motion is described in terms of the mean velocity  $\underline{u}$

$$\underline{u} = H^{-1} \int_{-h}^{\zeta} \underline{U} dz \quad (2)$$

where  $H$  is the total depth, i.e.  $H = h + \zeta$  where  $h$  is the depth and  $\zeta$  the surface elevation.

One defines the mean vertical concentration

$$N_i = H^{-1} \int_{-h}^{\zeta} C_i dz \quad (3)$$

The local deviations around the means are given by

$$\underline{U} = \underline{u} + \underline{w} \quad (4)$$

$$C_i = N_i + c_i \quad (5)$$

the depth-averaged  $\underline{w}$  and  $c_i$  being zero.

The depth-averaged equation is then written

$$\partial N_i / \partial t + \underline{u} \cdot \nabla N_i = \langle F_i \rangle + \nabla \cdot (K \nabla N_i) \quad (6)$$

where  $K$  is a new dispersion coefficient. Indeed, for hydrodynamic models concerned with the circulation over extended regions of the sea, the combined effect of the turbulent and shear dispersions can be simply taken into account by adjusting the diffusion term in modifying the values of the dispersion coefficient.

It is rather remarkable to point out that the depth-averaged model (eq. 6) is quite similar to the precedent one (eq. 1) by just dropping the derivatives with respect to  $z$  in eq. 1 (in appendix the demonstration is made). Moreover, in eq. 1 the divergence of the velocity vector is zero, i.e.  $\nabla \cdot \underline{u} + \partial U_z / \partial z = 0$  meanwhile for the depth-averaged velocity vector, one has  $\nabla \cdot (\underline{u} H) = 0$ . Due to the fact that the depth  $H$  is a function of the considered region,  $\nabla \cdot \underline{u} \equiv -H^{-1} \underline{u} \cdot \nabla H \neq 0$  which is not zero.

## 2. THE THREE SPATIAL SCALES OF PATCHINESS

### a. The turbulent patchiness

At very small spatial scale (from zero to 100 m) the turbulent diffusivity is the main source of dispersion. In this case, plankton population behaves as a passive scalar and the spectrum of its spatial variability (controlled by turbulence) is similar to the spectrum of turbulence. The turbulent diffusivity depends on the horizontal scale of the phenomenon, i.e.

$$K \sim \ell^{4/3} \quad (7)$$

Experimentally this conclusion was pointed out by Platt et al. (1975).

### b. The shear effect patchiness

At small spatial scale (from 100 m to 5 km) the shear effect will be the main source of dispersion. But now, contrary to the preceding case the shear effect diffusivity does not depend on the horizontal scale and may be taken as a constant (Ronday 1974), i.e.

$$K \sim \text{constant} \quad (8)$$

Here also plankton population behaves as a passive scalar but its spatial variability is not controlled by the shear effect coefficient, because it remains constant in the full spatial scale. In this case the spatial variability depends on the temperature fluctuations

spectrum (see below the temperature dependence of ecological parameters in the model). This conclusion is also in agreement with Platt et al. (1975) experimental data : from 100 m to 5 km, they found high coherences between chlorophyll (i.e. phytoplankton concentration indicator) and temperature.

c. The eddy diffusivity patchiness

Beyond 5 km and until 100 km, eddy diffusivity is predominant. The diffusivity  $K$  may be expressed by (Joseph and Sendner, 1958)

$$K \sim P\ell \quad (9)$$

where  $P$  is the diffusion velocity and  $\ell$  the characteristic length of the horizontal variations. As plankton dynamics in promoting spatial heterogeneity dominates over that of the physical diffusive processes in eroding it, an optimal value of the diffusivity  $K$  is calculated in taking into account the fact that (i) an optimal numerical value of the diffusion velocity  $P$  is of the same order as the residual currents

$$P \sim \|\underline{u}\| \quad (10)$$

and (ii) the characteristic length  $\ell$  of the horizontal variations of plankton concentration is of the same order as the Dubois' (1975) critical spatial wavelength

$$\ell \sim 2\pi (2K/\omega)^{1/2} \quad (11)$$

where  $\omega^{-1}$  is the characteristic time of the ecological response. So, ecological interactions and dispersion are competitive and a "natural selection" by resonance of fluctuations due to advective currents (residual circulation) leads to space-time patterns.

The mechanism of this mesoscale patchiness is based on the fact that the spatio-temporal structures are generated by local spatial instabilities characterized by a critical wavelength  $\lambda_c$  meanwhile the whole ecosystem exhibits a global spatial stability which prevents it from destruction. In general, the same type of pattern appears quasi-periodically with a period  $T = 2\pi/\omega$ . The most important characteristic is the disposition of the ecosystem to amplify microscopic excitations (fluctuations) to a macroscopic level leading to the emergence of new space and time patterns. Moreover, the ecosystem behaves like a filter ; perturbations with a wavelength smaller than  $\lambda_c$  are smoothed out by the diffusive processes meanwhile perturbations of greater wavelength are amplified by the non-linear interactions. The primitive master equations (model II) showed that the physical mechanism of patchiness is characterized by a continuous generation of ecological waves.

One can refer to them as dissipative structures (Glansdorff, P. and Prigogine, 1971). These structures (ecological waves) are far from equilibrium and their maintenance requires a steady supply of energy. The production of entropy which corresponds to a degradation of the energy is compensated continually by an exterior input of energy under the form of light and nutrients (coefficient  $k_1$ ). The earliest example of dissipative structure dealt with the chemical basis of morphogenesis (Turing, 1952).

A regular spatial distribution of structures can also be generated by a process of random structures initiation. Indeed, the process of structuration is initiated by these random fluctuations which are afterwards amplified by the activatory field, i.e. the prey population which behaves like an activator. With a time lag, a growing zone of inhibition is established by the predator population which behaves like an inhibitor. This spreading inhibitory field prevents new structures formation during a time corresponding to its refractory period. Activatory and inhibitory fields are transmitted by diffusion transport and the meeting of two active waves leads to their annihilation. A statistical mechanics of these expanding fields can be made to obtain more information on the mean number of structures by using methods as described by Glass et al, 1973.

Finally, in view of pointing out some global information about this statistics of ecological waves, the concept of diversity can be used. Margalef, 1967, has introduced the Shannon-Weaver entropy  $H$  of the information content of a collection of species as an index of diversity. This formula is identical to the definition of entropy in statistical mechanics. Moreover entropy constitutes a criterion of stability for closed systems of particles around an equilibrium state, i.e. the Boltzmann H-theorem which states that at equilibrium entropy is maximum. When the system is slightly perturbed from its equilibrium state, entropy decreases of a quantity  $\Delta H > 0$ . In these conditions, entropy is a criterion of stability in the sense of Lyapunov (Zubov, 1964). But these conclusions are only available for closed systems and we know that ecological systems are open systems far from equilibrium maintained at a steady state through an input of energy flow (Morowitz, 1968). This steady state is no more characterized by a maximum of entropy. Nevertheless, a Lyapunov function  $D_0$  can be deduced (Dubois, 1973) from the index of diversity in calculating the second variation of entropy around a reference state. For small fluctuations around

the reference state, this function  $D_0$  looks like a weighted variance. We suggested to call such a function an index of fluctuations. Diversity, stability and structuration through fluctuations are narrowly related. Recently a model was presented which relates disturbance to pattern: "hypotheses concerning the relation between pattern and diversity translate immediately into relationships between disturbance and diversity" (Levin and Paine, 1974). We arrive at the same conclusion from the concept of index of fluctuations in a quite general framework.

### 3. MASTER EQUATIONS FOR PHYTO-ZOOPLANKTON PATCHINESS

Explicit expression of the interaction term  $\langle F_1 \rangle$  is given in the case of prey-predator plankton populations.

For the phytoplankton, one can write

$$\langle F_1 \rangle = k_1 N_1 - k'_2 \left[ 1 - \exp(-\delta(N_1 - N'_1)) \right] N_2 \quad (12)$$

where  $N_1$  and  $N_2$  are respectively phyto- and zooplankton biomasses expressed in their organic carbon content per unit volume ( $\text{mg C m}^{-3}$ ),  $k_1$  the rate of growth of phytoplankton. The coefficient of  $N_2$  is a modification (Parsons et al, 1967) of an expression due to Ivlev (1945) and represents the rate of ingestion per unit concentration of grazer at phytoplankton concentration,  $k'_2$  is the maximum rate of ingestion attainable by the zooplankters,  $\delta$  is a constant defining the rate of change of ingestion with food concentration, and  $N'_1$  is the concentration of phytoplankton at which feed-food concentration, and  $N''_1$  is the concentration of phytoplankton at which feeding begins. The growth of phytoplankton is related to temperature, sunlight intensity and nutrient concentration. Averaging over the depth  $H$  and over time,  $k_1$  can be written (O'Connor et al, 1973)

$$k_1 = K_1 T \exp(K_e H)^{-1} (\exp(-\alpha_1) - \exp(-\alpha_0)) N / (K_N + N) \quad (13)$$

where  $K_1$  is the slope of the maximum growth rate versus temperature,  $T$  the temperature,  $e$  the base of the natural log,  $K_e$  the extinction coefficient,  $H$  the depth,  $f$  the fraction of daylight,  $N$  the nutrient concentration,  $K_N$  the half saturation constant for the nutrient  $N$ ,  $\alpha_1 = \alpha_0 \exp(-K_e H)$  with  $\alpha_0 = I_{av}/I_s$  where  $I_{av}$  is the mean daily incident solar radiation and  $I_s$  the optimal light intensity. It may be noted that the extinction coefficient is an important component in the growth rate expression which is related to a number of physical and biological

variables : turbidity due to the inorganic composition of the water and the self-shading of the growing phytoplankton. This last effect can be taken into account using the correlation developed by Riley (1963), i.e.  $K_e = K_e' + 0.008N_1 + 0.054N_1^{2/3}$ , where  $K_e'$  is the extinction coefficient without the phytoplankton-related extinction and  $N_1$  is the phytoplankton chlorophyll *a* content (in  $\text{mg m}^{-3}$ ).

For the herbivorous zooplankton, the interaction function  $\langle F_2 \rangle$  is written

$$\langle F_2 \rangle = -k_3 N_2 + \beta k_2' \left[ 1 - \exp(-\delta(N_1 - N_1')) \right] N_2 \quad (14)$$

where  $k_3$  is the rate of decay of zooplankton as a function of temperature and predation of the higher trophic levels, and  $\beta$  is the ratio of phytoplankton carbon ingested to zooplankton carbon produced (utilization coefficient). In first approximation  $k_3$  can be expressed as a linear function of temperature, i.e.  $k_3 = K_3' T + k_3''$ .

Substituting eqs. (10) and (12) in eq.(16) for  $i = 1, 2$ , the master equations for phyto-zooplankton horizontal structuration are written

$$\begin{aligned} \partial N_1 / \partial t + \underline{u} \cdot \nabla N_1 = & K_1 T \exp(K_e H)^{-1} \left( \exp(-\alpha_1) - \exp(-\alpha_0) \right) N / (K_N + N) \\ & - k_2' \left[ 1 - \exp(-\delta(N_1 - N_1')) \right] N_2 + \nabla \cdot (K \nabla N_1) \end{aligned} \quad (15)$$

$$\begin{aligned} \partial N_2 / \partial t + \underline{u} \cdot \nabla N_2 = & - (k_3' T + k_3'') N_2 \\ & + \beta k_2' \left[ 1 - \exp(-\delta(N_1 - N_1')) \right] N_2 + \nabla \cdot (K \nabla N_2) \end{aligned} \quad (16)$$

These general master equations are quite original. Their properties can be pointed out in considering asymptotic solutions. For this, several simplified models can be deduced (from eqs. (15) and (16)) which exhibit most aspects of the spatial structuration mechanism of phyto- and zooplankton populations.

(i) *Model I :*

When the behaviour of phyto- and zooplankton populations are only considered on a short period of time, parameters like  $T$ ,  $f$  and  $I_{AV}$  do not change drastically. To take into account the variation of the extinction coefficient and nutrient concentration with the concentration of phytoplankton, a logistic law can be used to approximate the growth rate  $k_1$ , i.e.

$$k_1 = k_1' (1 - N_1 / N_1'') \quad (17)$$

where  $N_1''$  is the maximum concentration of phytoplankton which can be



found in the sea. Obviously,  $N_1''$  is large as compared to the mean concentration of phytoplankton.

With these assumptions, eqs. (15) and (16) are written

$$\partial N_1 / \partial t + \underline{u} \cdot \nabla N_1 = k_1' (1 - N_1 / N_1'') N_1 - k_2' \left[ 1 - \exp(-\delta(N_1 - N_1')) \right] N_2 + \nabla \cdot (K \nabla N_1) \quad (18)$$

$$\partial N_2 / \partial t + \underline{u} \cdot \nabla N_2 = -k_3 N_2 + \beta k_2' \left[ 1 - \exp(-\delta(N_1 - N_1')) \right] N_2 + \nabla \cdot (K \nabla N_2) \quad (19)$$

(ii) Model II :

When the physical mechanism of patchiness is assumed working in the linear region of the grazing, the term  $\exp(-\delta(N_1 - N_1'))$  can be developed in series. Knowing that  $N_1' < k_3 / \beta k_2' \delta \ll N_1''$ , eqs. (18) and (19) become

$$\partial N_1 / \partial t + \underline{u} \cdot \nabla N_1 = k_1 N_1 - k_2 N_1 N_2 + \nabla \cdot (K \nabla N_1) \quad (20)$$

$$\partial N_2 / \partial t + \underline{u} \cdot \nabla N_2 = -k_3 N_2 + \beta k_2 N_1 N_2 + \nabla \cdot (K \nabla N_2) \quad (21)$$

where  $k_2 = k_2' \delta$ .

These equations exhibit a non-zero stationary solution uniformly distributed in space (with  $\underline{u} = 0$ )

$$N_{10} = k_3 / \beta k_2 \quad (22)$$

$$N_{20} = k_1 / k_2 \quad (23)$$

and we see that  $N_1' < N_{10} \ll N_1''$ . For small fluctuations of populations around  $(N_{10}, N_{20})$ , analytical solutions of eqs. (20) and (21) are given in the one-dimensional case (Dubois, 1975). The stationary spatial structuration is characterized by a wavelength given by

$$\lambda_c = 2\pi(2K/\omega)^{1/2} \quad (24)$$

where  $\omega = (k_1 k_3)^{1/2}$  is the frequency of the ecological response.

Eqs. (20) and (21) were simulated on computer in one and two spatial dimensions (Dubois, 1975). The basic mechanism of a spatial structuration of prey-predator was well exhibited. Three fundamental "laws" for the space and time behaviour of this structuration were deduced :

- a) the creation of a prey-predator wave,
- b) the propagation of this wave with constant intensity and velocity,
- c) the annihilation of two meeting waves.

A remarkable property is that this wave looks like an all-or-none

response (active wave), the prey behaving like an activator and the predator like an inhibitor (with a refractory period during which the generation of a new wave cannot occur). In two dimensions, the wave exhibits a ring structure the radius of which increases with time.

Taking into account the transport by advection due to the residual circulation, eqs. (20) and (21) were integrated on computer to simulate the spatial structuration of a patch of prey-predator plankton populations in the Southern Bight of the North Sea (Dubois and Adam, 1975). During its drift in the Southern Bight, the horizontal structuration of the patch is given by a growing circular disc which loses its centre (ring structure) and breaks into segments. Due to advection, the highest densities lie in a series of areas surrounding the empty region. In other words, the initial patch transforms into a series of patches surrounding an empty region (initial patch). The same succession of events was observed experimentally in following patches during a few weeks (Wyatt, 1973).

(iii) Model III :

When the grazing is saturated,  $\exp(-\delta(N_1 - N_1''))$  drops in eqs. (18) and (19). One obtains

$$\partial N_1 / \partial t + \underline{u} \cdot \nabla N_1 = k_1' N_1 (1 - N_1 / N_1'') - k_2' N_2 + \nabla \cdot (K \nabla N_1) \quad (25)$$

$$\partial N_2 / \partial t + \underline{u} \cdot \nabla N_2 = (-k_3 + \beta k_2') N_2 + \nabla \cdot (K \nabla N_2) \quad (26)$$

Eq. (26) shows that the zooplankton is no more feedbacking with the phytoplankton and its behaviour is essentially due to a balance between its decay rate and grazing, i.e.  $(-k_3 + \beta k_2')$ . The temperature and predation on zooplankton can become command parameters for the survival of plankton populations. When  $k_3$  is greater than  $\beta k_2'$ , the zooplankton population decreases and as a consequence the quantity of phytoplankton reaches its saturation point,  $N_1''$ . One can then assist to the phenomenon of "red tide" for patches where these dramatic conditions hold. When  $k_3$  is smaller than  $\beta k_2'$ , the zooplankton population increases and eq. (25) shows that the phytoplankton population will decrease leading to a non-saturated grazing. In this case, zooplankton controls phytoplankton behaviour. The spatial pattern of the growth of zooplankton is characterized by a critical length  $L_c$  deduced from a study of the stability of eq. (26) (The same type of equation was considered by Kierstead et al (1953), but for phytoplankton), i.e.

$$L_c = \pi \{K / (-k_3 + \beta k_2')\}^{1/2} \quad (27)$$

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