International Council for the
Exploration of the Sea

C.M.1974/L:6
Plankton Committee

Critical length-scales in phytoplankton populations

by

Trevor Platt*

June, 1974.

Prepared for presentation to the Plankton Committee at the 62nd Statuatory Meeting of the International Council for the Exploration of the Sea, Copenhagen, September, 1974.

Summary

A theoretical analysis is given of the critical length-scales of phytoplankton concentrations which may be conserved under various conditions of phytoplankton growth rate, horizontal turbulent diffusion, and grazing by zooplankton. The importance of wind-stress and water column stability is also discussed.

* * * * * *

We begin with the Kierstead and Slobodkin (1953) equation which describes the growth or decay in time of a given fluctuation in the plankton distribution in terms of cell-division and turbulent diffusion:

$$\frac{\partial b}{\partial t} = D_H \frac{\partial^2 b}{\partial x^2} + kb ,$$

where $b = b(x,t)$ is the concentration of phytoplankton, D_H is the coefficient of turbulent diffusion in the horizontal, and k

---

*Fisheries & Marine Service
Marine Ecology Laboratory
Bedford Institute of Oceanography
Dartmouth, Nova Scotia, Canada

is the exponential growth-rate of the phytoplankton within the water-mass encompassed by the fluctuation; the growth rate outside is assumed to be zero. If we introduce the non-dimensional variables B, X and T, defined by

$$b = \beta B$$

$$x = \xi X$$

$$t = k^{-1} T$$

Where β, ξ and k^{-1} are characteristic scales for the problem, we can rewrite the equation as

$$\frac{\xi^2 k}{D_H} \frac{\partial B}{\partial T} = \frac{\partial^2 B}{\partial X^2} + \frac{k \xi^2}{D_H} B$$

This representation allows us to identify the characteristic length scale for the problem (that is, the value of ξ which makes the two right-hand terms equal in magnitude) as

$$\xi_c \sim (D_H/k)^{\frac{1}{2}}$$

To within a factor of π, this is equal to the exact solution obtained by Kierstead and Slobodkin for the critical size of the fluctuation: for scales greater than ξ_c, reproduction dominates and fluctuations would grow; for scales less than ξ_c, turbulent diffusion dominates and fluctuations would be damped out.

To extend the analysis beyond the simple case treated by Kierstead and Slobodkin we should consider the influence on the phytoplankton of grazing by zooplankton. Mortality of phytoplankton by grazing modifies the exponential growth constant k. If the grazing can be considered to be linear in the availability of phytoplankton then the Kierstead-Slobodkin equation still applies, with the growth coefficient now reduced and equal to the difference between the exponential growth constant and an exponential mortality constant due to grazing.

There is, however, a substantial body of evidence which indicates that grazing is definitely a non-linear function of the food supply. A suitable representation of the empirical relationship is the modified Ivlev curve given by Parsons *et al* (1967):

$$m(b) = R_{max}\{1-e^{-\lambda(b-b_0)}\}, \quad b>b_0$$

or

$$m(b) = 0 \text{ , } b \leq b_0 .$$

In this equation the grazing mortality $m(b)$ is seen to be zero below a certain threshold b_0 of food availability, to increase with food supply for phytoplankton concentrations greater than b_0 at a rate determined by the constant λ, and finally to saturate for high food supplies at a value R_{max} representing the maximum ration required by the zooplankton population existing in the area. Clearly R_m depends both on the size and on the kind (turnover time) of the zooplankton population.

With this modification, the Kierstead-Slobodkin equation may now be written in the form (Platt, 1973)

$$\frac{\partial b}{\partial t} = D_H \frac{\partial^2 b}{\partial x^2} + kb - R_m \{1 - e^{-\lambda(b-b_0)}\}.$$

This is a non-linear equation for which we have no exact solutions. We can, however, express the grazing term as a series expansion such that the equation becomes, upon scaling:

$$\frac{k\xi^2}{D_H} \cdot \frac{\partial B}{\partial T} = \frac{\partial^2 B}{\partial X^2} + \frac{\xi^2}{D_H}(k-R_m\lambda)B + \frac{\xi^2}{D_H}R_m\lambda B_0 + \frac{\xi^2}{D_H\beta}R_m \cdot \left|\begin{matrix}\text{terms in} \\ \lambda^2\beta^2(B-B_0)^2 \\ \text{and higher order}\end{matrix}\right|$$

If $B>>B_0$ such that the first two terms on the right hand side dominate, this gives a characteristic length-scale for the problem of

$$\xi_c \sim \left|\frac{D_H}{k-R_m\lambda}\right|^{\frac{1}{2}} ,$$

to be interpreted as before.

In view of the above, it seems essential that we should try to improve our practical knowledge of the magnitudes of the diffusion coefficients in a variety of marine situations and environmental conditions, involving a broad range of scales of, for example, wind stress, surface currents, stability of the water column, proximity to coastline, and so on.

To give but one instance of a pertinent study in which such information was lacking, but thought, nevertheless, to be important, we may refer to the enigmatic results of Platt and Filion (1973). In this work, an attempt was made to assess the spatial homogeneity of the ratio productivity:biomass (that is, $b^{-1}db/dt$) for the phytoplankton community of a small marine basin using direct *in situ* methods. The measurements, which were carried out on ten different days during the four-month summer period, were well-replicated and gave, for a marine situation, reasonably-good statistical resolution. It was found that, 40% of the time, the basin could be considered spatially uniform with respect to the productivity:biomass ratio. For 60% of the time, however, important differences could be detected in the size of this ratio over distances of only hundreds of meters. The difference between these two modes of behaviour is thought (although not proved) to be due to differences in wind stress on the basin during the period (say 36 hours) prior to measurement. Calm conditions are thought to be conducive the accentuation of local fluctuations in productivity:biomass ratio such that adjacent stations tend to become more different from one another, and the basin more structured biologically. High wind stress leading to stronger turbulent diffusion is thought to be responsible for damping out any possible local fluctuations in productivity:biomass such that adjacent stations become more similar, and biological structure in the surface layer tends to be eroded.

We can make a first attempt at quantifying this balance between phytoplankton growth and (horizontal) turbulent diffusion by computing the appropriate dimensionless number $\Lambda \equiv k\xi^2 D_H^{-1}$. Following the work of Okubo (1971) we can write $D_H(\text{cm}^2\text{sec}^{-1}) = 0.0103\xi^{1.15}$ where ξ is in cm and the fit is for all the data which were available to Okubo and which covered a range of length-scales from 10m to 100km. Then,

$$\Lambda = \frac{k\xi^2}{0.0103\xi^{1.15}} \simeq 10^2 k\xi^{0.85}$$

The critical length scale ξ_c of fluctuations in phytoplankton biomass is the value of ξ which makes $\Lambda = 1$. Fluctuations on scales greater than ξ_c will tend to grow in size; fluctuations on scales smaller than ξ_c will tend to be damped out by turbulent diffusion. The best available estimate for ξ_c is then

$$\xi_c \simeq (10^2)^{-1.18}, \; k \text{ in sec}^{-1} .$$

Using a realistic range of magnitudes for k, we find ξ_c to be of order 10-75m, with a typical value of 30m for a cell-division rate of once per day.

If grazing is taken into account, the appropriate expression for ξ_c is

$$\xi_c \simeq (10^2[k-R_m\lambda])^{-1.18} ,$$

and it is valid for situations where the phytoplankton abundance is well above the grazing threshold. The critical length-scale is little modified by grazing under most conditions, for example a grazing rate ($R_m\lambda$) equal to $0.1k$ increases ξ_c by only 12% above the value obtained for no grazing.

In cases where phytoplankton growth and grazing are very nearly balanced, however, the situation is altogether different and ξ_c increases rapidly as equilibrium between these two processes is approached. By way of example, ξ_c is equal to 1000m when grazing is $0.94k$ and k is 10^{-5} sec^{-1}. It is thought that this is by no means an uncommon occurrence in the sea, especially during the period immediately following the spring phytoplankton bloom.

Unfortunately, there is as yet no reliable equation, theoretical or empirical, relating D_H to wind stress. When such an equation becomes available, we can calculate the corresponding values of ξ_c. We know that, in general, ξ_c will increase with increasing wind speed. But until we can specify ξ_c more closely than that, we will not know whether results such as those of Platt and Filion (1973), mentioned above, are indeed explainable in terms of the differences in the minimum sizes of fluctuations in phytoplankton abundance which can be conserved under different wind regimes. Clearly, this is one area in which biological oceanographers are waiting eagerly for progress to be made in physical oceanography.

A similar case could be made for the promotion of research on the relationship between D_H and the stability of the water column. A particularly interesting study could be made of the evolution with time of ξ_c during the rise and decline of the spring phytoplankton bloom. Here the coupling between the physical and biological systems is of crucial importance. Onset of the bloom is generally believed to be consequent on the establishment of the incipient thermocline (Sverdrup, 1953). Development of the phytoplankton population increases the optical attenuation coefficient which in turn promotes increased vertical stability (Denman and Miyake, 1973). Finally, the rapid growth of the zooplankton population towards the end of the phytoplankton bloom, together with the reduced growth rate of the phytoplankton as nutrients become exhausted will make the term $(k-R_m\lambda)$ very small such that there will be a large and rapid increase in ξ_c.

References

Denman, K.L. and M. Miyake.	1973	Upper layer modification at ocean station PaPa: Observations and simulation. *J. Physical Oceanogr.* 3(2): 185-196.
Kierstead, H. and L.B. Slobodkin.	1953	The size of water masses containing plankton blooms. *J. Mar. Res.* 12: 141.
Okubo, A.	1971	Oceanic diffusion diagrams. *Deep Sea Res.* 18: 789-802.
Parsons, T.R., R.J. LeBrasseur, and J.D. Fulton.	1967	Some observations on the dependence of zooplankton grazing on the cell size and concentration of phytoplankton blooms. *J. Oceanogr. Soc.* Japan. 23: 10-17.
Platt, T.	1973	The influence of physical processes on the spatial structure of phytoplankton populations. *Contribution to the NATO conference on Modelling of Marine Systems, Ofir, Portugal.*
Platt, T. and C. Filion.	1973	Spatial variability of the productivity:biomass ratio for phytoplankton in a small marine basin. *Limnology and Oceanography.* 18(5): 743-749.

Sverdrup, H.V. 1953 On conditions for the vernal blooming of phytoplankton. *J. du Conseil*. 18(3): 287-295.