
Diurnal variation and primary production in the ocean — preliminary results of a Lagrangian ensemble model

J.D. Woods and R. Onken

Institut für Meereskunde, Universität Kiel, Kiel, FRG

(Received January 1982; accepted May 1982)

Abstract. The diurnal variation of insolation influences the rate of primary production in the upper ocean in two ways. Firstly, light energy is only available for photosynthesis during the day, and secondly solar heating of the upper ocean during the day changes the depth of the surface mixed layer. The consequences of these physical changes have been investigated using a one-dimensional model in which the vertical motion and energy uptake of each member of an ensemble of phytoplankters is calculated deterministically on 3 min time steps. The depth change and energy uptake of a single plankter, and the depth distribution and total energy uptake of the ensemble of multiplying cells are described. Plankton become rapidly concentrated into a band centred just below the maximum depth of mixing in the previous 24 h. This provides a physical explanation for the depth of the maximum in measured chlorophyll profiles. The seasonal variation of production rate has been calculated, assuming no grazing, nutrient limitation or self shading. Sverdrup's classic explanation for the onset of the spring plankton bloom is re-interpreted, taking account of the diurnal cycle of insolation. It is argued that the *Lagrangian-ensemble* model of the growth of an ensemble of phytoplankters described in this paper is inherently better than *Eulerian-continuum* models, because it averages after integrating non-linear equations, rather than *vice-versa*. The model can easily be extended to investigate the consequences of physiological hypotheses not considered in this paper.

Introduction

The physical properties of the ocean that determine the onset of the spring plankton bloom, namely light and mixing, exhibit strong diurnal and seasonal variation. Most applications are concerned with the variation of primary productivity on time scales longer than a day, so attention has been focussed mainly on modelling the response of plankton to the seasonal change. For example, Sverdrup (1953) ignored the diurnal variation of mixed layer depth and light in his famous theory that showed how the date of the spring plankton bloom is controlled by the sharp decrease in mixed layer depth that occurs when the ocean starts to warm up each year. That seems a rather surprising omission when one considers the physiological processes that lead to cell division within individual plankters, and so determine the rate of development of the bloom as a whole. These processes are controlled by light intensity. They have time scales of order several hours and may therefore be expected to be sensitive to the diurnal change of daylight. There has even been some suggestion in the literature (e.g., Harris, 1980) that plankton physiology has adapted to the regular diurnal cycle of insolation, with a tendency for cell division to occur once per day. In this paper we present the results of an investigation into the response of phytoplankton to the diurnal variations of mixed layer depth and light at different times of year. The investigation uses a new method of modelling plankton growth on a computer.

In designing a model of primary production it is necessary to represent these

short time scale physiological processes taking place inside the plankter and its overall behaviour. Ideally that should be done deterministically, by keeping track of every plankter in the bloom. But their numbers are so large that the deterministic approach would require an impossible amount of computer time. The normal solution is to treat the development of the plankters statistically. In the jargon of computer modelling the unresolved details of the plankton bloom must be parameterized, that is to say, treated by terms in the model equations that are statistical in character. For example, the physical processes of turbulent mixing may be parameterized by means of a diffusion term in the equation for scalar concentration. In models of primary production it is normal to treat the cloud of individual plankters in terms of a *continuum* property of the seawater, such as organic carbon or chlorophyll concentration, which varies with position (just depth in a one-dimensional model) and time. This is a crucial step. Having taken it, the modeller is limited to describing the development of the plankton bloom in some sort of average way; no account is taken of the variability in the development of individual plankters. Let us call this the *Eulerian-continuum* method. It has been widely used by modellers. A recent example is the one-year integration by Kiefer and Kremer (1981).

The method successfully describes some of the main features of phytoplankton distributions, and has therefore been accepted as the basis for applied studies. But it suffers from a basic weakness that limits its usefulness and casts doubt on its predictions. The problem lies in the parameterization of the cloud of plankters by a continuum variable. That can lead to difficulties in modelling a highly non-linear process such as phytoplankton cell division. As is well known, averaging non-linear equations before integration does not give the same answer as averaging them after integration. The latter procedure is correct: the former is adopted in the *Eulerian-continuum* method of modelling primary production. It seems unlikely *a priori* that such a method can cope with the non-linear interaction between plankter physiology and the diurnal changes in mixed layer depth and light intensity. Happily, the steady increase in computer power has now reached the point where it is possible to adopt a less brutal approach to parameterizing the plankters in a bloom. It is now possible to design a model in which the individual histories of an ensemble (i.e., of a cloud) of (in our case 100) plankters are described deterministically, that is to say, the non-linear equations describing their growth are integrated step by step along their separate trajectories. The development of the bloom is estimated from the statistics of the ensemble. We call this the *Lagrangian-ensemble* method of modelling primary production.

We know of three earlier models in which the trajectories of individual plankters have been simulated. Ledbetter (1979) studied the redistribution of particles by Langmuir cells. Platt and Gallegos (1980) used a Markov method to explore the net effect on production of short-period adaptation on a cloud of particles moving randomly in a mixed layer. Falkowski and Wirick (1981) followed the random walks and non-linear growth of two particles in the mixed layer. Our implementation of the *Lagrangian-ensemble* method uses a combination of Langmuir circulation and random small-scale turbulence to displace the particles. The model has been used to investigate the influence of the diurnal cycle of mix-

ing and light on the initial (light-limited) stage of a plankton bloom.

The Model

The model is divided into two parts which do not interact. The first part describes the changing physical environment; its output is the vertical distribution of light as a function of wavelength and the mixed layer depth, for a given latitude, time of day, day of the year and weather. The second part describes the vertical motion and growth of a phytoplankter. An experiment consists of running the model 100 times for plankters with different initial depths in the mixed layer, but with the same physical forcing in the first part of the model. The output of such an experiment consists of a statistical description of the ensemble of 100 plankters. These statistics are intended to represent the much larger population in a natural plankton bloom.

Part 1: the physical environment

The model is a development of the one-dimensional mixed layer model of Kraus and Turner (1967). The main differences are that the solar spectrum is described by 27 spectral bands as in Woods (1980), and the mixed layer depth is calculated every time step by a sequence of routines designed to describe the following physical processes: heating by absorption of solar radiation, convective adjustment, convective penetration and wind-stress penetration. At the end of each time step, which is typically one hour long, the model predicts the temperature profile and the depth of the mixed layer. The terms used in the model are illustrated in Figure 1. For the present investigation it was assumed that there is no turbulence below the mixed layer.

Typical products of the model of the physical environment are illustrated in Figures 2–4. The vertical profile of the downward flux of solar energy in (i) the blue-green (400–700 nm wavelength) and (ii) the whole spectrum (Figure 2) are calculated on the assumption that the ocean acts like pure water, i.e., that the presence of plankton has no effect. The diurnal variation of mixed layer depth and temperature at different seasons is shown in Figure 3. The night-time period is shaded and noon is marked by a vertical line; note the change in day length with season. Figure 4a shows the annual cycle of mixed layer depth at noon and of the maximum depth achieved each day. The latter occurs at the moment when the rate of heating by the sun first exceeds the rate of surface cooling to the atmosphere about an hour after sunrise (see Figure 3). The annual maximum depth of the mixed layer occurs close to the spring equinox, on the day when the solar heat absorbed over 24 h first exceeds the heat lost to the atmosphere in the same period. The precise day depends on the weather; variation of cloud and wind can change it by as much as three weeks (Woods, 1982). Note the sharp rise in the daily maximum mixed layer depth once spring heating has begun. It is this rise that Sverdrup (1953) identified as being the main factor determining the onset of the spring plankton bloom.

A brief word about the definitions used in this paper. The diurnal thermocline is the layer that at any instant lies below the mixed layer but above the maximum mixed layer depth achieved during the previous 24 h. The seasonal thermocline is

the layer that at any instant lies below the diurnal thermocline but above the maximum depth attained by the mixed layer in the preceding twelve months. The flow in the mixed layer is turbulent, it is assumed to be laminar in the diurnal and

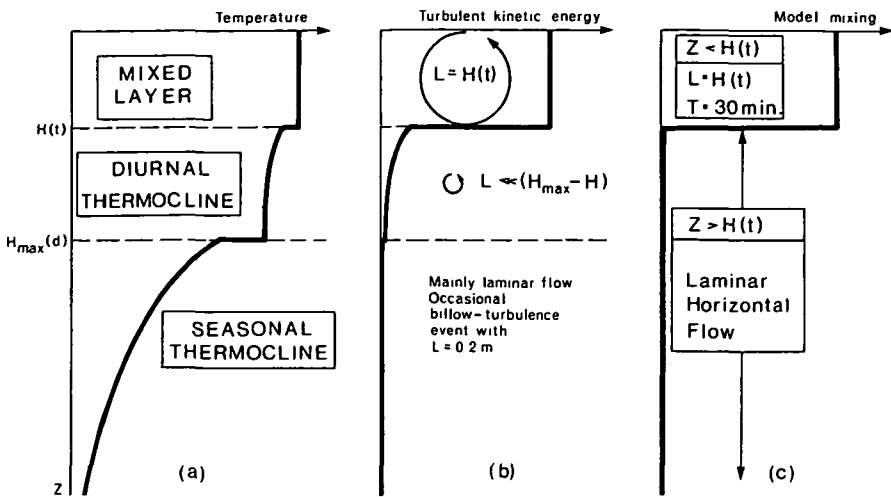


Fig. 1. The definition of terms used to describe the physical environment in the model. (a) The temperature profile. (b) The turbulent kinetic energy profile, showing the turbocline at the base of the mixed layer. Note the largest scale of overturning L , which is small below the mixed layer. (c) The simplified profile of mixing used in the model; the flow below the mixed layer is assumed to be horizontal and laminar.

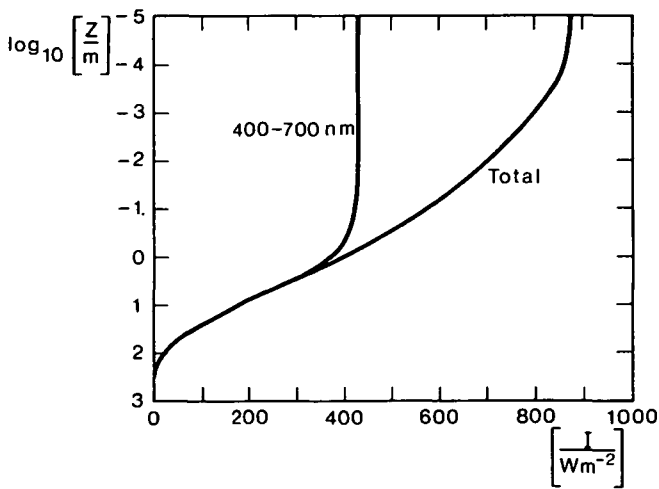


Fig. 2. Noon profiles of solar heating rate and downward flux of blue-green light on the summer solstice at 40°N .

seasonal thermoclines. The annual variation of the temperature profile is shown in Figure 4b. Note that the temperature profile in the seasonal thermocline is not a fossil record of the earlier deeper mixed layer, as is sometimes suggested (e.g., Kiefer and Kremer, 1981), but develops through the season in response to *in situ* solar heating.

Part 2: the plankton

The vertical displacement of a plankter is calculated every time step (3 min intervals) starting from its prescribed initial depth in the mixed layer. At every time step, the light flux in the 400–700 nm waveband is calculated for the plankter's depth at that time, using the radiation routine in part one of the model. The times of successive cell divisions in the plankter are then calculated according to a

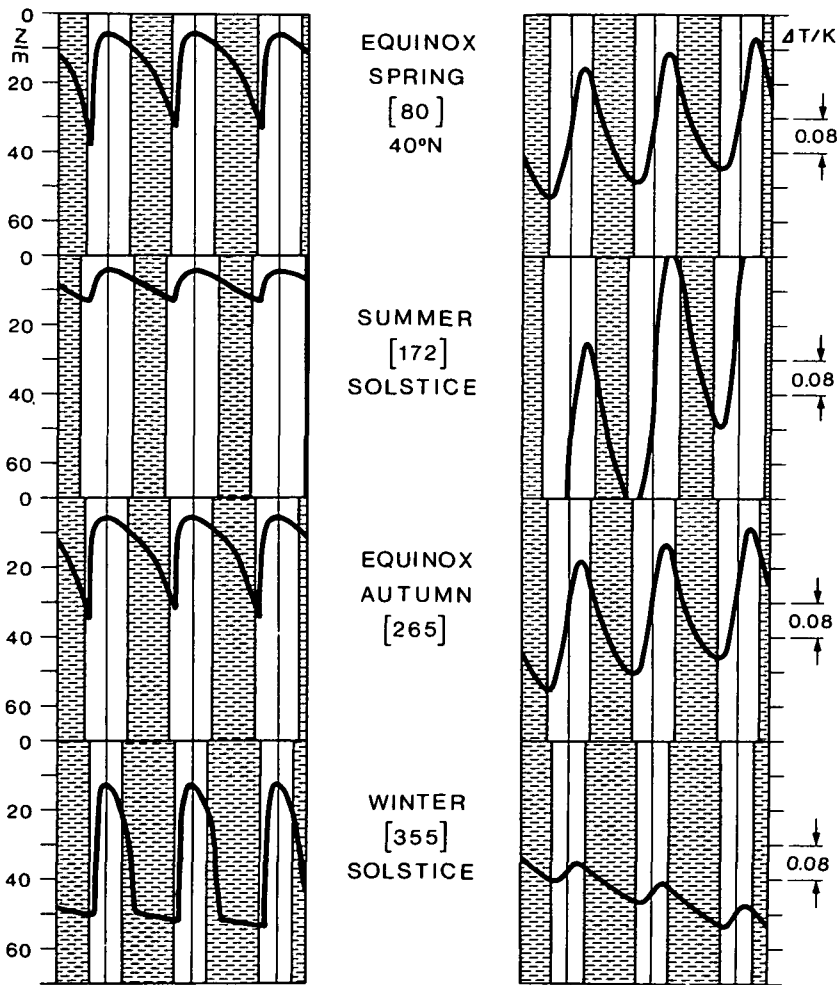


Fig. 3. The diurnal variation of mixed layer depth $H(t)$ and temperature at 40°N at the solstices and equinoxes.

physiological formula, which assumes a light-limited growth rate. A typical integration continues for five days in our investigation, but the duration is not limited by the model. The plankter's history of depth and cell number is stored. The calculation is repeated for each plankter in the ensemble (100 in our investigation). Each plankter starts with a different initial depth, the ensemble being uniformly distributed through the mixed layer. Statistical analysis of the set

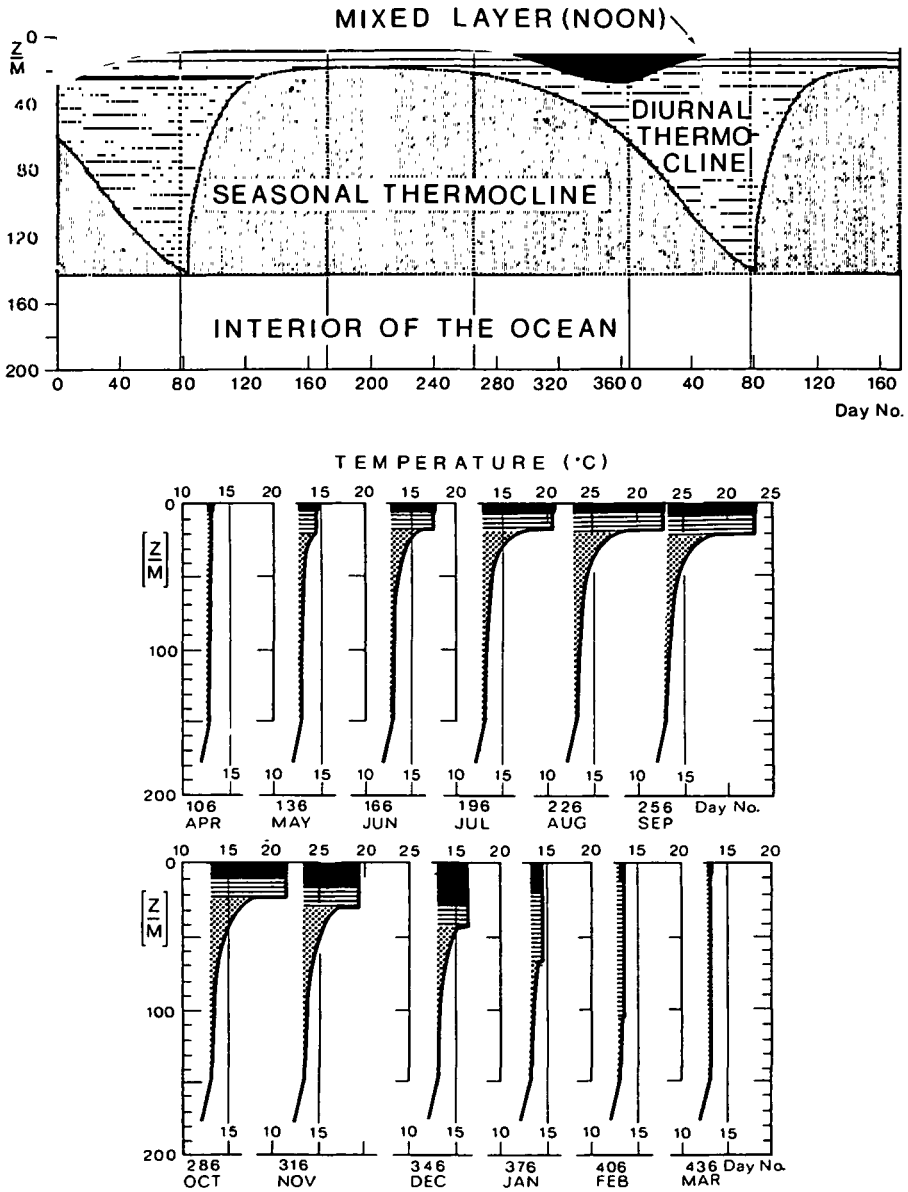


Fig. 4. (a) The variation with day number of minimum depth H_{min} (d) and maximum depth H_{max} (d) of the mixed layer at 40°N. (b) The noon temperature profile at the middle of each month.

of histories describes the plankton bloom. This brief summary will now be expanded to give details of the *Lagrangian-ensemble* method, which is also discussed in Onken (1981).

The vertical displacement of a plankter occurs in two ways. In the mixed layer it undulates somewhat erratically between the sea surface and the bottom of the layer. The motion is a combination of a sinusoidal undulation extending over the whole depth range with a period of 30 min, modulated by a small vertical displacement of random amplitude in the range ± 4 m every time step. These displacements represent the effect of the turbulent motion in the mixed layer. The large undulations simulate the energy-containing eddies, on the assumption they are like Langmuir circulations (Ledbetter, 1979); the random modulation simulates the smaller eddies. Tests showed that the model results are not very sensitive to the period of the undulations (Onken, 1981). The vertical speed of a plankter in the mixed layer is of order 1 m/min. Its much lower speed of sinking through the water (2 m/day in our investigation) is ignored in the mixed layer. But in the horizontal laminar flow below the mixed layer the sinking rate determines the particle's displacement at each time step. The mixed layer depth is changing continuously. A simple criterion determines whether a moving plankter that happens to be close to the bottom of the layer is entrained or detrained during the layer's vertical displacement in a 3-min time step. Remember that the imaginary horizontal interface at the bottom of the mixed layer is not a material surface: it marks the location of the boundary between turbulent and non-turbulent flow, it is a "turbocline" that presents no obstacle to the passage of particles.

Each plankter has one cell at the beginning of the model integration. Cell division occurs at intervals during the integration, which simulates five days in 3-min steps. The number of cells increase in the sequence $n = 1, 2, 4, 8, \dots$. All the daughter cells of each primary plankter move together; a simplification forced by limitations of computer power. It is assumed that the interval between cell divisions is independent of temperature, which is unlikely to change by much more than 1 K over 5 days. Nutrients and zooplankton are not represented in the model, so the emphasis of our investigation lies on the initial, light-limited growth of a plankton bloom (i.e., the Sverdrup problem).

The effective cross-section area A of each cell is constant ($A = \pi \cdot 10^{-8} \text{ m}^2$ in our calculations). The qualitative results do not depend on the particle size. In one time step dt , the energy $dE_i(t)$ absorbed by each cell of the plankter identified by the subscript i and having trajectory $z_i(t)$ depends on the photosynthetic efficiency P and the light flux $I(z_i, t)$, summed over the 400–700 nm waveband.

$$\text{i.e.,} \quad dE_i(t) = A P I(z_i, t) \cdot dt$$

All the cells in a plankter divide simultaneously after absorbing the prescribed unit of energy (100 mJ in the results illustrated in Figures 9 and 10; 30 mJ in Figures 11 and 12). The rate of cell division varies, but it lies typically in the range 1–3 per day in our calculations.

Bearing in mind that our main concern in the present investigation is to study the effect of diurnal changes in the physical environment, it seems appropriate to use the simplest possible formula for photosynthetic efficiency. On the other

hand, the power of the *Lagrangian-ensemble* method lies in its potential for testing the consequences of different hypotheses concerning the physiology and behaviour of plankters in a systematic and internally consistent way. We decided to illustrate this potential by repeating the calculations with three different formulae for P taken from the literature on *Eulerian-continuum* models (Platt *et al.*, 1977). In the first, P is a constant p .

$$(I) \quad dE_i(t) = A p I(z_i, t) \cdot dt$$

The second and third formula are based on the assumption that over the previous five days the cells have adapted to the ambient light, expressed by a reference light flux I_R (in the 400–700 nm waveband), as discussed by Platt *et al.* (1977) and Yentsch (1980). We have adopted the following definition of the reference light flux (Steele, 1962):

$$I_R = 0.5 \overline{I(0, t)} \text{ (preceding 5 days)}$$

The second formula is designed to represent the effect of saturation:

$$(II) \quad dE_i(t) = A p (1 + \beta I(z_i, t)/I_R)^{-1} \cdot I(z_i, t) \cdot dt$$

The value of $\beta = 2.0185$ was chosen for our calculations to minimize the difference between the mean production rates with formulae II and III (Dr. J. Steele, personal communication). The third formula, designed to represent the effect of inhibition (Steele, 1962) was the following:

$$(III) \quad dE_i(t) = A p I(z_i, t) \cdot \exp(-I(z_i, t)/I_R) \cdot dt$$

For simplicity we put $p = 1$ for our calculations. (The product $p A$ is a common factor of all the formulae, so if the reader objects that p should be less than unity, he is free to use the value of his choice and substitute the corresponding value of A to make $p A = \pi \cdot 10^{-8} \text{ m}^2$.) The formulae are illustrated in Figure 5.

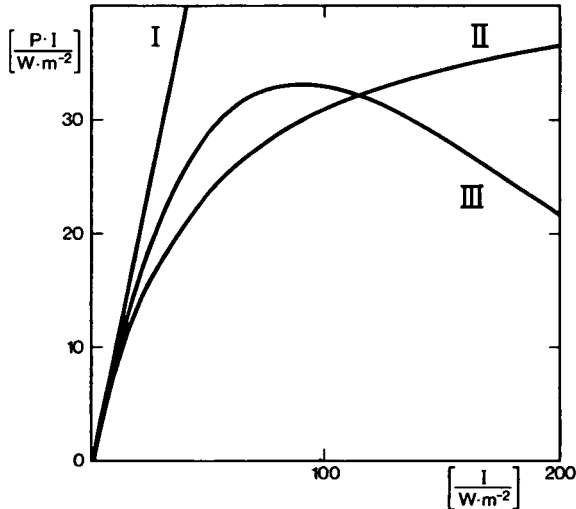


Fig. 5. The photosynthetic efficiency function used in the experiment.

$$(I) \quad \frac{\Delta E}{\Delta t} = p A I \quad (II) \quad \frac{\Delta E}{\Delta t} = \frac{p A I}{1 + \beta I/I_R} \quad (III) \quad \frac{\Delta E}{\Delta t} = p A I \exp(-I/I_R)$$

Results

The calculations performed so far with the model were designed to reveal the general character of particle motion and energy consumption during the diurnal cycle and to make a preliminary assessment of the effect of different photosynthetic efficiency formulae. To save computer time the diurnal variation of mixed layer depth was simplified; it was treated as a sawtooth curve with the same depths and times as the full calculation at the maxima and minima.

A single plankter

The depth variation of a typical plankter injected into the mixed layer is shown in Figure 6a. Note the rapid undulation while the particle remains in the mixed layer, its subsequent slow sinking through the diurnal thermocline during the day, and the return to undulations the next night after it has been entrained again by the descending mixed layer. The amount of energy consumed is shown in Figure 6c. Note that most of the energy is received while the plankter is below the mixed

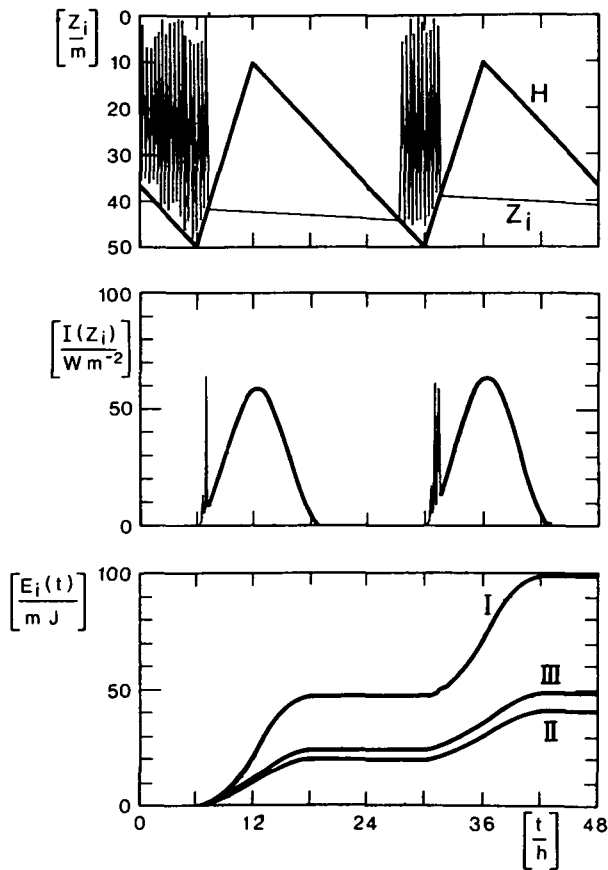


Fig. 6. (a) the depth variation (Z_i) of plankter i starting in the mixed layer (cloudless day number 95 at $40^\circ N$). (b) The variation of the energy flux $I(Z_i)$ in the waveband 400–700 nm at the depth of the plankter. (c) The energy consumed for the three photosynthetic efficiency functions.

layer and therefore not undulating. The amount of light received during this period depends on the depth at which the plankter happened by chance to be left behind by the rising mixed layer during the forenoon. It receives a little flickering energy while making its last undulations after dawn, but the sun is then low in the sky and the energy received is a small fraction of the 24-h total. The temperature of the particle does not vary very much. While in the mixed layer it follows the slow diurnal cycle of surface temperature (see Figure 3); during the day when it is in laminar flow below the mixed layer it is warmed slowly by the sun at a rate depending on its depth, and it cools as it slowly sinks through the diurnal thermocline.

If one morning the plankter happens to be left behind early in the ascent of the mixed layer, and therefore near its maximum depth, the particle may sink far enough to escape recapture by the mixed layer next night. This irreversible escape is illustrated in Figure 7. All plankters will eventually escape in this way provided the daily maximum depth of the mixed layer is decreasing or at least not increas-

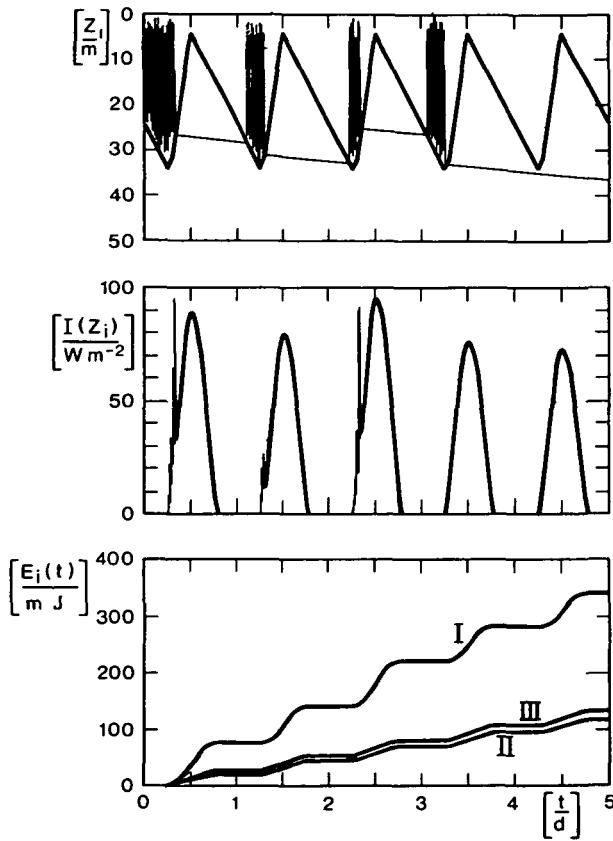


Fig. 7. (a) The depth variation of a plankter that is irreversibly lost from the mixed layer after the fourth night (day numbers 95 – 100 at 40°N). (b) The energy flux $I(Z_i)$ in the waveband 400 – 700 nm at the depth of the plankter. (c) The energy consumed for the three photosynthetic efficiency functions.

ing faster than the sinking speed of the plankters. This is the most important process revealed by the experiments with the *Lagrangian-ensemble* model.

An ensemble of plankters

The results of ensemble calculations are illustrated in Figures 8–12. Each calculation started with one hundred unicellular plankters distributed evenly through the mixed layer. The calculations were designed to reveal how the vertical distribution of plankters changes during the day at different seasons, and to discover how the seasonal changes in the physical environment influences the rate at which the total number of cells in the plankton ensemble increases in the early days of a plankton bloom (i.e., before grazing, self-shading and nutrient depletion become important). The calculations were repeated for the three different photosynthetic efficiency functions described above.

It was shown above that the slow sinking of a plankter relative to the water (at 2 m/day) eventually causes it to escape irreversibly from the mixed layer, assuming that the latter executes a regular diurnal cycle. Once a plankter has escaped from the mixed layer in this way its depth changes steadily and slowly. As successive plankters in an ensemble escape the mixed layer, they form a thin cloud just below the maximum depth attained by the mixed layer each day. Examples of such a concentration are to be found in Raymont (1980, Figures 6.24, 6.25, 6.26). During the spring, when the mixed layer progressively thins and during the early

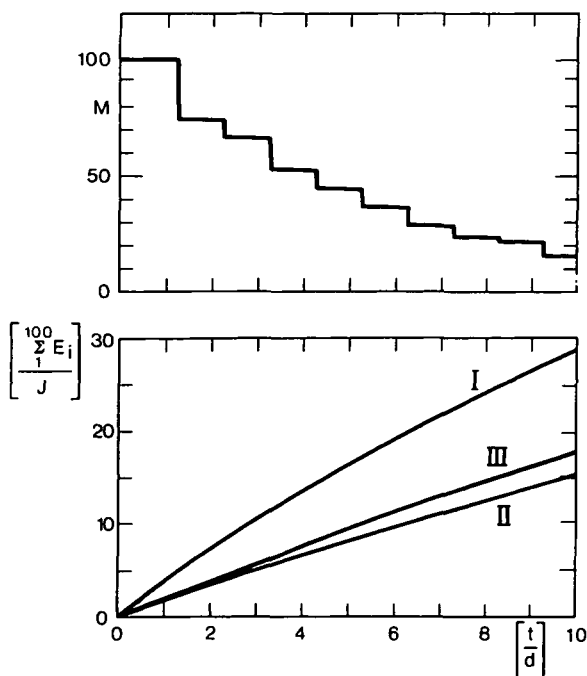


Fig. 8. The time variation of an ensemble of particles starting at different depths in the mixed layer on day number 95 at 40°N. (a) The number of particles M remaining in the mixed layer each night. (b) The total energy consumed by the ensemble for the three photosynthetic efficiency curves.

summer when it deepens less rapidly than the sinking speed of the plankters, it only takes a few days for all the plankters in an ensemble to accumulate in a cloud below the diurnal thermocline. The rate at which this happens is illustrated in Figure 8, which shows the progressive irreversible loss of plankters from the mixed layer over a period of ten days, each with a constant diurnal variation of mixed layer depth. The “mixed layer half-life” of an ensemble of plankters that start in the mixed layer is shortest in summer when the diurnal range of the mixed layer depth is smallest. The number of plankters in the mixed layer at any time since it last had a depth maximum is in principle proportional to the mixed layer depth. (Because there were only 100 plankters in our ensemble, individual model profiles deviate significantly from this ideal.)

But, if the plankton concentration in the mixed layer does not change during one diurnal cycle of the mixed layer depth, it is affected by the progressive dropping out of particles into the seasonal thermocline due to their sinking relative to the water. The tendency for the concentration in the mixed layer to decrease can be temporarily reversed in summer when a storm deepens the mixed layer below the climatological mean for a few days, and it is systematically reversed in autumn and winter when the climatological mean mixed layer depth steadily increases, as was shown in Figure 4.

These results help us to interpret the profiles of plankton cell concentration shown in Figures 9 and 10. The number of cells in each one metre depth range was calculated for every time step of the experiment. With only 100 plankters in the ensemble, these raw profiles do not provide a very good representation of the vertical distribution in a real plankton bloom. There was too much statistical noise, so the profiles were averaged over 3 h. The resulting average profiles may be compared with measured profiles of phytoplankton or chlorophyll concentration.

The diurnal variation is illustrated in Figure 9. The three-hourly mean profiles are shown for the fifth day of each calculations. In Figure 9a, for the late winter (day numbers 84–88), the mixed layer ranges between <10 and >120 m and very few of the plankters have escaped. There are between 0.1 and 1 cell/m in the mixed layer throughout the fifth day of the calculation. The situation is very different in the next model run (Figure 9b), for mid-summer, when the mixed layer depth varies only over a very narrow range (between 6 and 12 m). All the plankters have escaped from the mixed layer before the fifth day (day 180, shown in Figure 9b). They all lie in a thin cloud between 18 and 24 m. Their steady descent during day 180 is clearly visible. The concentration of cells in the cloud ranges from 100 to 6000 per m. Cell division in this summer calculation has been very much more vigorous than in the late winter one.

The third model run (Figure 9c) covered five days (280–284) in early autumn when the mixed layer depth ranged between 9 and 22 m. Most of the plankters have escaped the mixed layer by the fifth day, the few remaining being entrained and mixed up between the hours of 3 a.m. and 6 a.m. Their number is small and by chance they are all detrained below 19 m soon after 9 a.m. That is, of course, an artifact resulting from the model’s small number of plankters. In reality a finite plankton concentration would persist in the mixed layer throughout the

day. That is correctly shown in the fourth run (Figure 9d), which covers the early winter period (day number 360 to 364). The noon mixed layer depth is deepest at the winter solstice (see Figure 4a) with a value of 27 m; the maximum depth is 45 m. The cell concentration ranges from 0.1 to 1 per m in the mixed layer and 1 – 10 per m in the cloud below the diurnal thermocline.

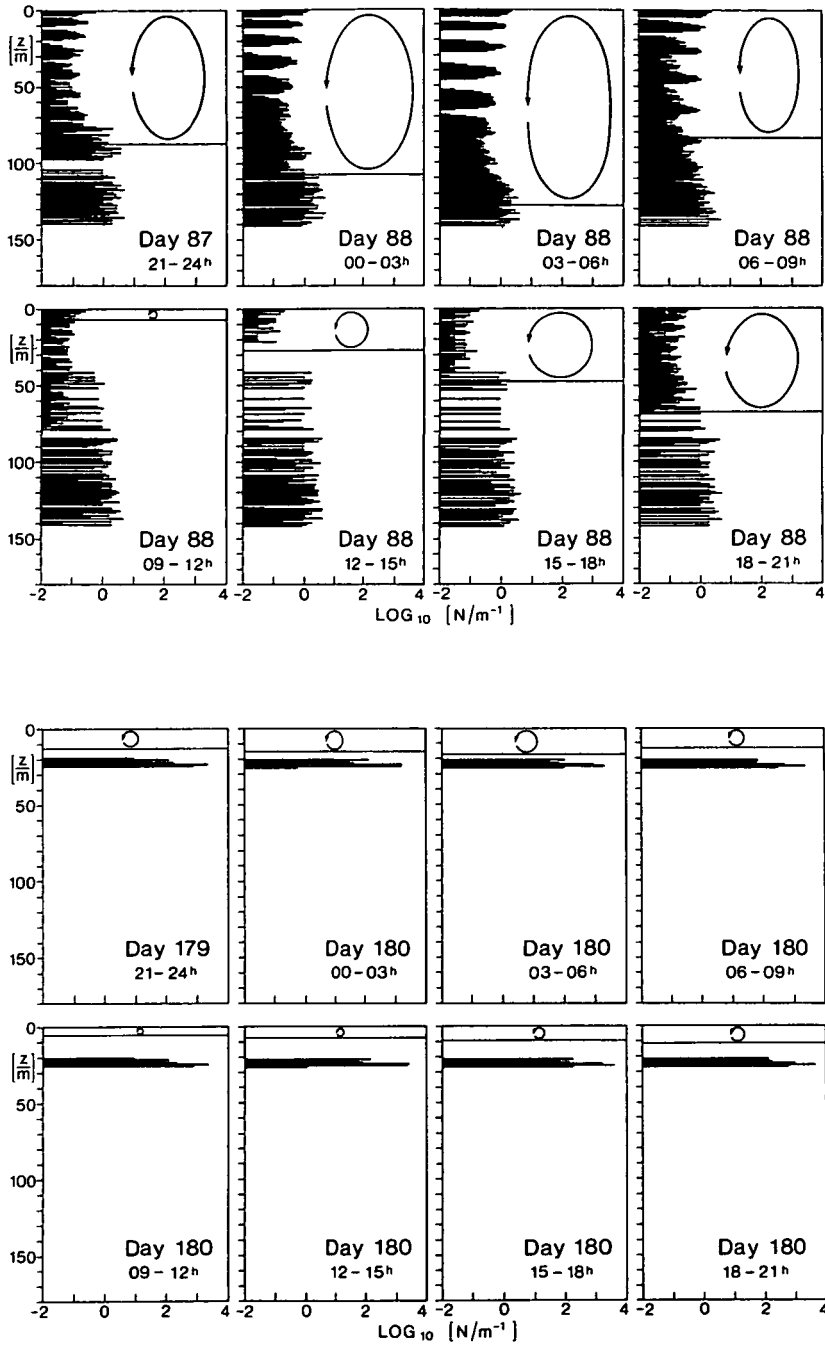
A more detailed picture of the seasonal variation of mid-day cell concentration is shown in Figure 10 by three-hourly mean profiles for the period noon to 3 p.m. on the mid-day of each month, that being in each case the last day of a separate five-day calculation. The concentration of the plankton into a thin cloud below the diurnal thermocline starts dramatically in spring. The cloud becomes thinner and shallower and contains an increasing number of cells through the spring and early summer months. Entrainment of plankton into the mixed layer is first seen in the November profile and continues through until March. This set of mid-month profiles vividly illustrates Sverdrup's theory that the onset of a spring plankton bloom coincides with the retreat of the (nocturnal) mixed layer towards the surface.

The rate of increase R of the cell population in the ensemble of 100 plankters on the fifth day in each of a set of calculations started at ten day intervals through the year is shown in Figure 11. The onset of the spring plankton bloom is clearly identified with the onset of spring heating and the rapid decrease of mixed layer depth that accompanies it. The figure shows the potential relative growth rate of a bloom starting at different times of the year. It does not show the actual growth of a plankton population from the start of the year.

Physiology

The effects of adaptation, saturation and inhibition are illustrated in Figure 6, 7, 8 and 11. There is a considerable difference between the productivity achieved with the linear efficiency formula (I), on the one hand, and the saturation (II) and inhibition (III) formulae, on the other. The value of the parameter β was chosen to minimize the difference between the productivity rates achieved by the saturation and inhibition formulae. But β was kept constant throughout the year, with the result that the ratio of the production rates R_{II} and R_{III} shows some response to the seasonal variation of the illumination of the plankton, which depend on their vertical distribution (i.e., on the daily maximum mixed layer depth) and the solar elevation. The result (Figure 11) is that the inhibition formula yields higher production rates throughout most of the year, with the ratio (R_{III}/R_{II}) having a maximum at the start of spring heating, and decreasing exponentially thereafter to a minimum at about the autumn equinox. This result suggests that, if it occurs in Nature as in our model, inhibition may contribute significantly to the sharp development of the plankton bloom as the ocean begins to warm in the spring. We make no claim that that is necessarily a true description of Nature, but it shows how the model can be used to investigate the implications of different assumptions about the physiology.

Both inhibition and saturation formulae assume that the plankters have adapted to the average illumination during the previous 5 days. The inclusion of adaptation significantly influences the form of curve III in Figure 11. We have us-



ed the simple assumption that all the plankters are adapted to half the 24-h mean surface light flux in the 400–700 nm waveband. Although computationally convenient, that does not really do justice to the phenomenon. It would be better to

Diurnal variation and primary production in the ocean

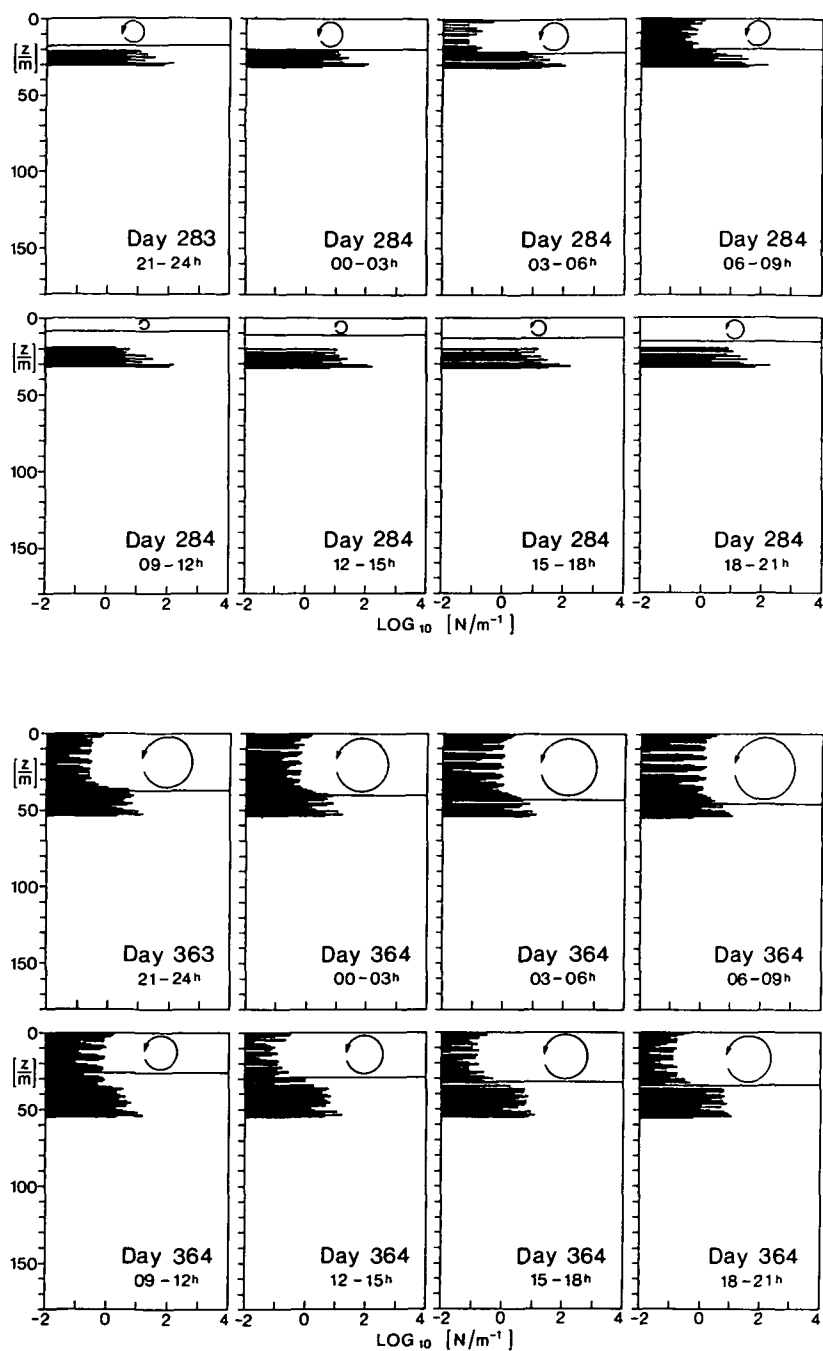


Fig. 9. The depth distribution of phytoplankton cells averaged over 3 h on the fifth day of an ensemble experiment at 40°N (no cloud), started on day number (a) 84 (b) 176 (c) 280 (d) 360. The mixed layer depth at the end of the 3 h period is shown by a horizontal line with an elliptical arrow to represent the "Langmuir" overturning.

allow each plankter to adapt to its own individual history of illumination, which, as was shown in Figure 7, can differ considerably from its neighbours in the

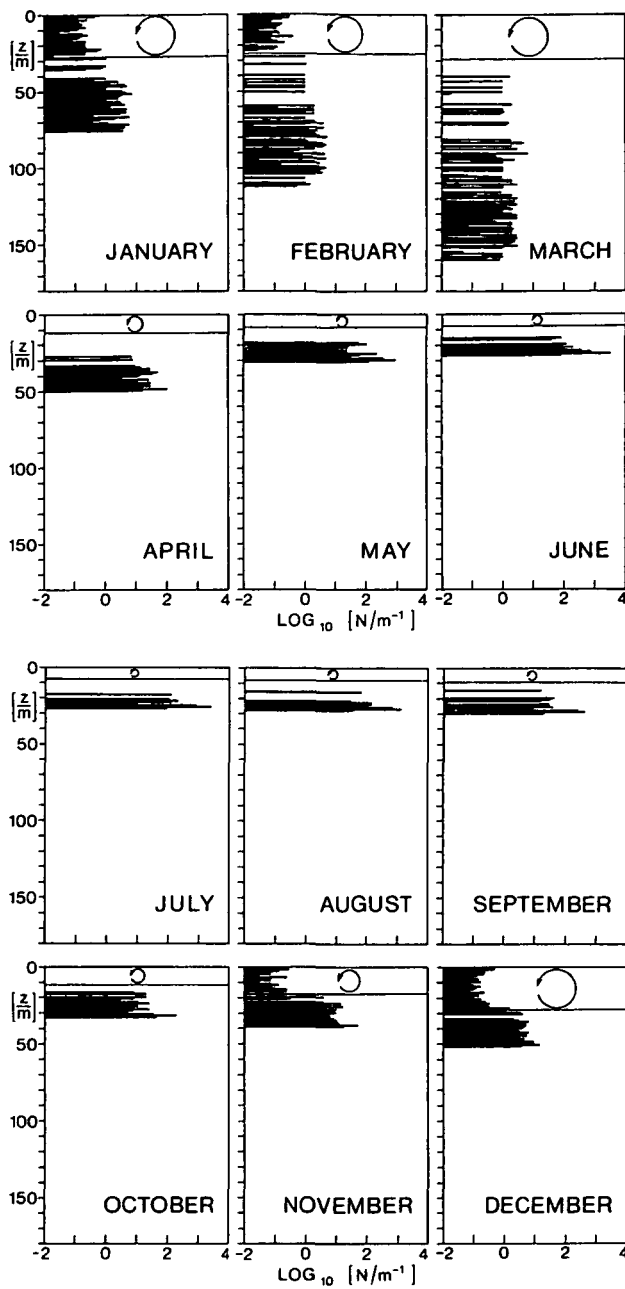


Fig. 10. Seasonal variation of the depth distribution of an ensemble of plankters, based on the experiment shown in Figure 9. The mean profile for the period 1200 – 1500 is shown for the mid-day of each month.

ensemble as a consequence of turbulence in the mixed layer. As Platt and Gallegos (1980) have shown with a constant mixed layer model, it is a simple matter to do so with the *Lagrangian-ensemble* method of modelling given longer integration than those reported in this paper, and we plan to do so in the future, after incorporating zooplankton and nutrients which influence the longer term development of a plankton bloom. Meanwhile, noting that most of the plankter ensemble congregates in a thin cloud at the top of the seasonal thermocline (Figures 9, 10), we propose that the reference light flux I_R used for adaptation in formulae II and III could be based on the depth of the top of the seasonal thermocline, as follows:

$$I_R = I(H_{\max}, t) \text{ (preceding 5 days)}$$

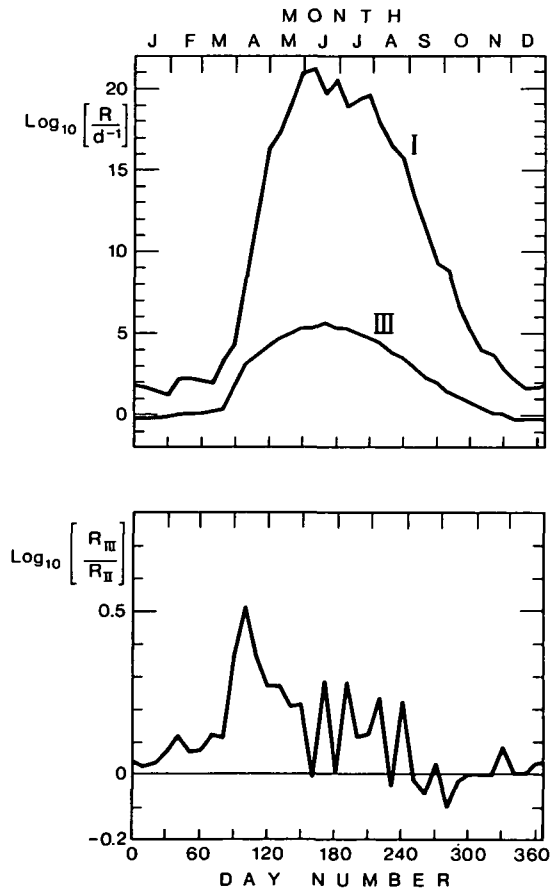


Fig. 11. (a) Seasonal variation of the productivity R of phytoplankton predicted by the model for the photosynthetic efficiency functions I and III.

$$R = \frac{N(5) - N(0)}{5N(0)}$$

$N(t)$ = Total number of cells in the ensemble after integration for t days. (b) Seasonal variation of the ratio of the productivities R_{II} and R_{III} achieved with the photosynthetic efficiency functions II and III.

The calculations leading to Figure 11 were repeated using this definition, with the result shown in Figure 12, where it is seen that the production rate is most sensitive to the choice of adaptation formula at the time of the spring plankton bloom.

Discussion

We had two aims in writing this paper. The first was to introduce a new method of modelling plankton growth. The second was to show how the new method could be used to clarify the role of turbulence in the surface mixed layer during the early stages of a plankton bloom, the problem analysed by Sverdrup (1953) in his classic paper. In order to simplify the problem we made a number of assumptions. These will now be considered and it will be argued that the new method of modelling lends itself to including the neglected effects in future experiments.

First, a few words about the method. The novel idea is to follow the trajectories of individual plankters as they rise and fall through the upper ocean, entering and leaving the mixed layer. The properties of the plankton bloom are then estimated from the statistics of an ensemble of plankters whose histories are first calculated individually. The method is similar to that used in modelling rain formation in clouds (see, for example, Mason, 1971). It is superior to the more common Eulerian method in which the cloud of plankters is modelled in terms of its changing concentration at fixed positions because it allows one to represent the non-linear effects of physical environment, cell physiology and plankter behaviour deterministically, before averaging rather than after. That does not mean that the results of contemporary Eulerian models are invariably wrong. Indeed they do seem to reproduce many of the observed features (see, for example, Kiefer and Kremer, 1981). Nevertheless, they do not describe specific effect of diurnal detrainment-entrainment into the mixed layer reported here. And by glossing over such details of the physics they leave one uncertain as to the validity

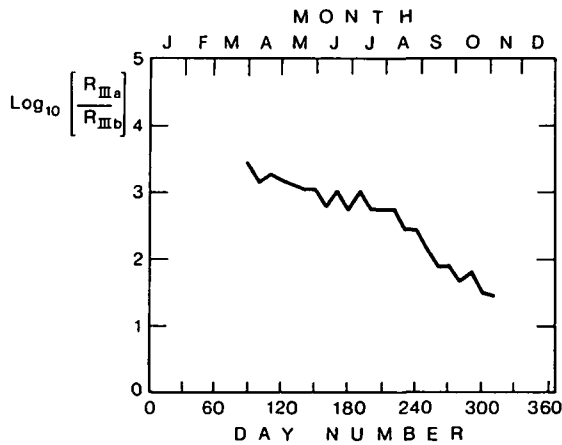


Fig. 12. Seasonal variation of the ratio of the productivities R_{IIIa} and R_{IIIb} achieved with the photosynthetic efficiency function III assuming

(a) $I_R = 0.5 \overline{I(0)}$ (5 preceding days)

(b) $I_R = \overline{I(H_{max})}$ (5 preceding days)

of their prediction about the effect of different parameterizations of the physiology. The *Eulerian* and *Lagrangian-ensemble* methods give different results because the processes controlling plankton growth are non-linear. In the experiments reported in this paper the non-linearity enters through the combination of vertical mixing, variation of light with depth and the variation of photosynthetic efficiency with light intensity. But that is only the tip of the iceberg. Some of the complexities that have been neglected so far will now be briefly discussed.

The effect of the plankton on the vertical distribution of light has been neglected. The concentration of plankters into a relatively thin cloud just below the diurnal thermocline simplifies the problem. First it means that the heating of the diurnal thermocline and mixed layer is virtually unaffected by plankton. But the change in blue-green light should be calculated. The availability of a profile of plankter concentration at every time step will simplify this task.

In the present investigation it has been assumed that the plankters sink at a constant rate (2 m/day) relative to the water while below the mixed layer. Smayda (1970) and Walsby and Reynolds (1980) have discussed the sinking and floating of plankton. The phenomenon is much more complicated than we have assumed. A plankter may vary its fall speed as it grows, or in response to the physical environment (e.g., light intensity). Different species vary their motion relative to the water in different ways. There has been speculation that such motion is an important factor in primary production (Hutchinson, 1967). It will be a rather straightforward matter to test such ideas with the *Lagrangian-ensemble* method.

The spring growth in the phytoplankton population rapidly consumes nutrients brought up to the surface by deep convection in winter. The rate of cell division eventually becomes limited not by the supply of light energy but by the nutrient concentration. That has not been considered in the present experiments, but it is not difficult to modify the model to take it into account. Similarly, it is possible to add a population of zooplankton to graze on the phytoplankton. The motion of the zooplankters must be prescribed; it may be influenced by the changing physical environment (e.g., light) or by the vertical distribution of the phytoplankton. A capture cross-section would have to be specified, as in meteorological models of cloud particle development. The addition of nutrients and grazing will greatly increase the non-linearity of the model, adding to the justification of using the *Lagrangian-ensemble* method.

Perhaps the ultimate use of the new method will be to study the effect on primary production of different assumptions concerning the physiology of phytoplankton. There are too many possibilities to list them here (for a recent review see Morris, 1980). But it is worth making the point that the *Lagrangian-ensemble* approach makes it possible to describe the different physiological hypotheses at the level of the individual cell.

Finally, returning to the role of the physical environment in primary production, there is the possibility of investigating the effects of coastal upwelling, internal waves and undulations of particles flowing along meandering frontal jets, all of which are believed to influence primary production. And, although the method has so far been used to describe only the vertical component of motion,

there is no reason why in principle it should not be used to follow the horizontal motion of plankters as well, and so explore the causes of plankton patchiness (Steele, 1978).

Conclusion

The *Lagrangian-ensemble* method of modelling is suitable for investigating the effect of diurnal changes in the physical environment on the development of a phytoplankton bloom. The investigation reported in this paper involved a number of simplifications and assumptions (see **The model**). It is therefore necessary to treat the results of our model calculations with some caution. They reveal some aspects of the early development of a plankton bloom. The predicted diurnal and seasonal variation of phytoplankton cell concentration can in principle be related to corresponding variations in observed profiles of chlorophyll concentration, but the latter may be influenced significantly by the effects left out of the model. Horizontal variability in plankton concentration poses sampling problems that must be overcome before one can collect a representative average vertical profile that can be compared with the prediction of a one-dimensional model.

Bearing in mind these limitations, the results of our computations suggest the following conclusions:

1. There is no diurnal cycle of phytoplankton concentration in the upper ocean.
2. Progressive change in the phytoplankton cell concentration during spring and summer is due to two opposing processes:

- a. the irreversible sinking into the seasonal thermocline of some of the plankters left each forenoon in the diurnal thermocline as the mixed layer recedes towards the surface,
- b. cell division, which may tend to become synchronized to the diurnal cycle of light (such synchronization was not featured in our experiments).

(Remember that grazing was not included in the model.)

3. The forenoon rise of the mixed layer leaves many of the plankters in laminar flow during most of the hours of day-light. So they do not experience significant variation of depth while illuminated by the sun.
4. During spring the climatological daily maximum depth of the mixed layer progressively decreases, and during most of the summer it increases more slowly than the (2 m/d) sinking rate of phytoplankters. During this period the plankters accumulate in a cloud just below the diurnal thermocline in laminar flow. The productivity is then greatest.
5. The effect of a spring storm has not been modelled, but it is clear from the computations that as the storm temporarily deepens the mixed layer the cloud of plankters that had sunk into the seasonal thermocline will be reentrained into the mixed layer. After the storm they will sink back into the seasonal thermocline with a half-life of a few days. The resulting cloud will tend to be shallower than the pre-storm one, which was laid down in spring when the climatological daily maximum depth of the mixed layer was deeper. So spring storms provide the mechanism for keeping the phytoplankton near the surface.
6. The model results support Sverdrup's (1953) conclusion that primary produc-

tivity rapidly increases when the ocean begins to warm in spring. They show that this is because of the associated decrease in the climatological daily maximum depth of the mixed layer, which occurs about an hour after sunrise. The date of the first day of spring heating varies from year to year because of differences in the weather. Our calculations show that typical variations of wind speed and cloud can change the date by up to 3 weeks. That may explain the observed inter-annual and spatial variation of the start of the spring plankton bloom (Cushing and Walsh, 1976).

7. The *Lagrangian-ensemble* method is capable of extension to include the effects not considered in the experiments reported in this paper.

Acknowledgements

This paper is dedicated to the memory of the late John Raymont, who first drew the attention of the senior author to the problem of modelling primary production. We thank Dr. D. Cushing and Dr. J. Steele for encouragement and helpful criticism of an earlier version. Our colleagues, A. Horch, V. Fiekas and K. Hofmann, helped with the model of the physical environment.

References

- Cushing, D.H. and Walsh, J.J. (eds.): 1976, *The Ecology of the Seas*, Blackwell, Oxford.
- Falkowski, P.G. and Wirick, C.D.: 1981, 'A simulation model of the effects of vertical mixing on primary productivity', *Mar. Biol.*, **65**, 69-75.
- Harris, G.P.: 1980, 'The measurement of photosynthesis in natural populations of phytoplankton', in I. Morris (ed.), *The Physiological Ecology of Phytoplankton*, Blackwell, Oxford, pp. 129-190.
- Hutchinson, G.E.: 1967, *A Treatise on Limnology*, Vol. 2, Wiley, New York.
- Kiefer, D.A. and Kremer, J.N.: 1981, 'Origins of vertical patterns of phytoplankton and nutrients in the temperate, open ocean: a stratigraphic hypothesis', *Deep-Sea Res.*, **28**, 1087-1105.
- Kraus, E.B. and Turner, J.S.: 1967, 'A one-dimensional model of the seasonal thermocline. II. The general theory and its consequences', *Tellus*, **19**, 98-105.
- Ledbetter, M.: 1979, 'Langmuir circulations and plankton patchiness', *Ecological Modelling*, **7**, 289-310.
- Lorenzen, C.J.: 1973, 'Diurnal variation in photosynthetic activity of natural phytoplankton populations', *Limnol. Oceanogr.*, **8**, 56-62.
- Mason, B.J.: 1971, *The Physics of Clouds*, (Second Edition), Oxford University Press.
- Morris, I. (ed.): 1980, *The Physiological Ecology of Phytoplankton*, Blackwell, Oxford.
- Onken, R.: 1981, 'Jahreszeitliche Veränderungen der Primärproduktion — ein numerisches Modell', Univ. of Kiel, diploma dissertation.
- Parsons, T.R., Takahashi, M. and Hargrave, B.: 1977, *Biological Oceanographic Processes*, (Second Edition), Pergamon, Oxford.
- Platt, T., Denman, K.L. and Jassby, A.D.: 1977, 'Modelling the productivity of phytoplankton' in Goldberg, E.D., McCave, I.N., O'Brien, J.J. and Steele, J.H. (eds.), *The Sea*, **6**, Wiley-Interscience, New York, pp. 807-856.
- Platt, T. and Gallegos, C.L.: 1981, 'Modelling primary production', in Falkowski, P.G. (ed.) *Primary Production in the Sea*, Plenum, pp. 339-362.
- Raymont, J.E.G.: 1980, *Plankton and Productivity in the Oceans*, (Second Edition), Pergamon, Oxford.
- Smayda, T.J.: 1970, 'The suspension and sinking of phytoplankton in the sea', *Annu. Rev. Oceanogr. Mar. Biol.*, **8**, 353-414.
- Steele, J.H.: 1962, 'Environmental control of photosynthesis in the sea', *Limnol. Oceanogr.*, **7**, 137-150.
- Steele, J.H. (ed.): 1978, *Spatial Pattern in Plankton Communities*, Plenum, New York.
- Sverdrup, H.U.: 1953, 'On conditions of vernal blooming of phytoplankton', *J. Cons. Exp. Mer.*, **18**, 287-295.

- Walsby, A.F. and Reynolds, C.S.: 1980, 'Sinking and Floating', in Mottid, I. (ed.), *The Physiological Ecology of Phytoplankton. Studies in Ecology*, Vol. 7, Blackwell Scientific Publications, Oxford, pp. 371-412.
- Woods, J.D.: 1980, 'Diurnal and seasonal variation of convection in the wind-mixed layer of the ocean', *Quart. J. R. Met. Soc.*, **106**, 379-394.
- Woods, J.D.: 1982, 'Climatology of the upper boundary layer of the ocean', Proc. JSC-CCCO Study Conference on 'Large-scale Oceanographic Experiments in the World Climate Research Programme.' A. Robinson (ed.) WMO, Geneva.
- Yentsch, C.S.: 1980, 'Light attenuation and phytoplankton Photosynthesis', in Morris, I. (ed.) *The physiological Ecology of Phytoplankton*, Blackwell, Oxford.