Sinking rate and pigment responses to light-limitation of a marine diatom: implications to dynamics of chlorophyll maximum layers

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Received 14/4/82, in revised form 8/7/82, accepted 27/7/82.

ABSTRACT

This work studied changes in sinking rates and various compositional characteristics of Thalassiosira weissflogii at six light levels ranging from 13.3 to 847 μE. m⁻². sec⁻¹. The intent was to examine the nature and magnitude of changes in both buoyancy and cellular pigment quotas as a function of light-limited conditions within the context of conditions prevailing at subsurface chlorophyll maxima. At each irradiance, sinking rate values acquired from two fundamentally different methods were not significantly (p>0.05) different from one another. Sinking rates were significantly (p<0.001) lower at light levels characteristic of the depth of subtropical chlorophyll maxima than rates at higher irradiances, characteristic of the overlying mixed layer. This behavior in vitro indicates that growth at low irradiance results in physiological changes which are manifested in changes in population buoyancy, and lends empirical support to the hypothesis that sinking rate deceleration can contribute to formation of subsurface chlorophyll maximum layers in the sea. Compositional characteristics varied continuously with changing light levels, whereas sinking rates displayed a step-function change. There was no apparent covariation of sinking rates with any of the compositional ratios, suggesting that the responsible physiological mechanism is independent of the cellular content of C, N, or ATP. Chlorophyll.cell⁻¹ and C.chlorophyll⁻¹ ratios varied by ca 4 x over the range of irradiances examined. The magnitude and direction of changes in these indices is consistent with the hypothesis that shade adaptation can be an important factor in the development of increased pigment concentrations at low light levels.

The relative importance of changes in sinking rates and cellular chlorophyll levels in creating deep chlorophyll maxima was examined theoretically. The results showed that shade adaptation alone could account for vertical pigment differences of the magnitude observed in subtropical waters. This is in agreement with observations that most of the phytoplankton biomass in such systems is of such a small cell size as to preclude sinking rate variations as the probable mechanism for the accumulation of chlorophyll. Both experimental and modelling results indicate: (a) little need to invoke sinking rate variability to explain maintenance of deep chlorophyll maxima in subtropical seas, and (b) sinking rate deceleration probably plays an important role in the development of subsurface chlorophyll maxima in temperate waters having a shallow mixed layer, a well-developed pycnocline and phytoplankton populations characterized by the abundance of larger-celled organisms.

Vitesse de sédimentation et réponse pigmentaire d'une diatomée marine en éclairement limitant. Conséquences sur la répartition verticale de la chlorophylle.

Ce travail examine les variations de la vitesse de sédimentation et de la composition biochimique de *Thalassiosira weissjogii* à six niveaux d'éclairement s'étendant de 13,3 à 847 μE·m⁻²·s⁻¹. L'intention était d'examiner la nature et l'importance des variations de la flottabilité et des quotas cellulaires de pigment lorsque la lumière limite la croissance, dans le contexte du problème des maxima subsuperficiels de chlorophylle en mer.

A chaque niveau lumineux, les valeurs des taux de chute obtenues par deux méthodes fondamentalement différentes ne différaient pas significativement (*p > 0,05*) l'une de l'autre. Les taux de chute étaient significativement (*p < 0,001*) plus lents aux faibles éclairages (comme ceux trouvés à la profondeur des maxima subtropicaux de chlorophylle) que les taux aux éclairages plus forts, comme ceux trouvés dans la couche de mélange. Ce comportement *in vitro* indique que la croissance aux faibles niveaux lumineux cause des changements physiologiques qui se traduisent par des changements de flottabilité de la population; d'où un appui empirique à l'hypothèse que le ralentissement des taux de chute peut contribuer à la formation de maxima de chlorophylle à une certaine profondeur en mer. Les paramètres biochimiques ont varié progressivement avec les changements d'éclairement, tandis que les taux de chute ont démontré un changement en paliers. On n'a pas observé de co-variation apparente des taux de chute avec aucun des quotients biochimiques, un fait qui suggère que le mécanisme physiologique en cause est indépendant des contenus cellulaires en C, N ou ATP.

Les concentrations de chlorophylle par cellule et les rapports carbone/chlorophylle ont varié approximativement de 1 à 4 dans les gammes d'éclairement utilisées. L'importance et le sens des variations de ces indices est en accord avec l'hypothèse que l'adaptation à l'ombre peut être un facteur important dans l'alimentation des concentrations en chlorophylle aux faibles éclairages. L'importance relative des changements du taux de chute d'une part, et des quotas cellulaires de chlorophylle d'autre part, comme causes possibles des maxima profonds de chlorophylle, a été ensuite examinée sous l'aspect théorique. Les résultats ont montré que l'adaptation à l'ombre pouvait expliquer les différences verticales telles qu'observées dans les eaux subtropicales. Ceci s'accorde avec l'observation générale selon laquelle la biomasse phytoplanctonique dans ces systèmes se compose de cellules tellement petites que l'hypothèse de variations du taux de chute est à exclure dans le mécanisme de l'accumulation de chlorophylle.

Les expériences comme le modèle indiquent que : (a) il n'est guère besoin d'invoquer la variabilité de taux de chute pour expliquer le maintien des maxima profonds de chlorophylle dans les mers subtropicales; et (b) le ralentissement du taux de chute est probablement important pour le développement des maxima subsuperficiels de chlorophylle dans les eaux tempérées dont la couche de mélange est peu profonde et la pycnocline bien marquée, et dont les populations phytoplanctoniques sont caractérisées par l'abondance des cellules de grande taille.


INTRODUCTION

In the open sea, the vertical distribution of chlorophyll is characterized by a layer of maximum concentration occurring between 60-120 m in subtropical waters and at more shallow depths in temperate regions. The persistence of the subsurface maximum in a given location (Bienfang, 1981a; Bienfang, Szyper, 1981), and the ubiquitous distribution of this pattern in stratified seas (Anderson, 1969; Saijo *et al.*, 1969; Hobson, Lorenzen, 1972; Revelante, Gilmartin, 1973; Venrick *et al.*, 1973; Kiefer *et al.*, 1976; Bienfang, Gundersen, 1977; Reid *et al.*, 1978; Shulenberger, 1978; Herbland, Voituriez, 1979; Cullen, Eppley, 1981), suggest some constancy in the dynamic balance of processes maintaining this feature. Cullen and Eppley (1981) present statistical analyses of profile physiography and compare the compositional character of maxima from a number of regions. The proposed mechanisms for maintenance of the chlorophyll maximum have been addressed by Riley *et al.* (1949), Steele and Yentsch (1960), Bienfang and Szyper (1981), and Cullen and Eppley (1981). These mechanisms include: 1) increased cell growth, stimulated by vertical nutrient supply;
2) increased amounts of chlorophyll per cell from shade adaptation to low light levels; 3) differential zooplankton grazing; and 4) biomass accumulation due to lower phytoplankton sinking rates in this depth region.

Observations have been made in support of all these mechanisms (and various combinations) including the deceleration of sinking rates near the floor of the photic zone. Work in waters off Hawaii (Bienfang, 1980) showed that the sinking rates of photosynthetically active phytoplankton taken from just above the chlorophyll maximum and retained by a 3 μm filter were significantly lower than those of similarly sized cells collected at two shallow depths. Although this observation provided empirical evidence that variations in phytoplankton buoyancy are associated with this layer, the prevailing size structure of the phytoplankton community (85% of the chlorophyll passed through a 3 μm filter) raised questions as to the potential for sedimentation processes to actually account for the increased levels of chlorophyll at the maximum.

As a laboratory complement to the above field work, the present study examined the sinking rate dynamics of a marine diatom grown under steady-state conditions over a range of light levels. In particular, we wanted to determine if the aforementioned buoyancy response would be mimicked in vitro due to physiological changes in cells growing at low light levels. In samples from nature, the compositional characteristics of phytoplankton per se are difficult to assess because of high and variable amounts of detrital material. This study describes changes in sinking rates and various compositional indices of Thalassiosira weissflogii (Grunow) Fryxell and Hasle (= T. fluviatilis Hustedt), a species which is particularly easy to grow in continuous culture and for which much information on growth rate and compositional characteristics is already available (Laws, Bannister, 1980). Studies were performed at six light levels ranging from near-surface irradiances (in subtropical regions) to <2% of these levels, a range encompassing conditions prevailing at the subsurface chlorophyll maximum.

MATERIALS AND METHODS

Populations were grown in a temperature controlled (20°C) continuous culture system described in detail by Bienfang (1975). Cultures were grown in FCRG medium, described in detail in Bienfang (1981b). Nitrate was the limiting nutrient at the highest light levels. The culture was illuminated by reflector-backed, ESR 40, incandescent lamps (75 W) set on a 10:14 L:D cycle. The growth chamber was enclosed in a jacket made of Rohm and Haas (#2424) blue plexiglas to simulate the spectral quality of submarine light. Steady states were produced at six different light levels by using neutral density filters and by varying the number of lamps used. The average irradiances simulated were chosen to approximate irradiance levels found between 5 and 110 m in the oligotrophic waters off Hawaii (Bienfang, Szyper, 1981). All light measurements were made using a quantum scalar irradiance meter (Biospherical Instruments Inc. Model QSL100) and calibrated against field measurements made with a QSP profiling quantum scalar irradiance meter.

The method of continuous culture used was a modified cyclostat approach. In a traditional cyclostat, the dilution rate of limiting substrate controls population growth rate. In our light-limited experiments, the growth rate affected only the population washout rate. Daily growth rates (μ) were calculated as the sum of the logarithm of the ratio of cell numbers on successive days and the known dilution rate (in days⁻¹), i.e. $\mu = \ln(N_{t+1}/N_t) + D$ where D is the dilution rate and $N_{t+1}$ and $N_t$ are cell concentrations on days $t+1$ and $t$ respectively. Desired cell concentrations were achieved by setting the dilution rate equal to the calculated growth rate. Only small adjustments in the dilution rate were necessary after that time to maintain constant cell numbers.

Cell density was monitored with a Celloscope electronic particle counter; the standard deviation (SD) of triplicate counts was typically <1% of the mean. The unit was calibrated for cell volume estimates using polystyrene spheres of known size. Chlorophyll a was analyzed by the fluorometric method for extracted (90% acetone) samples (Strickland, Parsons, 1972); the SD of triplicate analyses was <10% of the mean. Triplicate samples for particulate carbon and nitrogen were collected on precombusted glass fiber filters and analyzed with a Hewlett Packard Model 185B CHN analyzer; the SD was typically 5-15% of the mean. ATP was analyzed using methods described in Karl (1980); the SD of triplicates was ≤10% of the means. Subsamples for all aforementioned biomass parameters were taken within the last hour of both the light and dark periods and were designated as P.M. and A.M. samples respectively. Carbon fixation rates were determined by the 14C method (Strickland, Parsons, 1972). Subsamples were removed from the growth chamber, placed in 150 ml bottles, injected with 14C and incubated for three hours under light and temperature conditions identical to those of the parent populations. The procedures for calibration of working 14C activity, and sample handling/counting were identical to those detailed in Bienfang and Szyper (1981).

Sinking rates were measured by two different techniques. The homogenous-sample method (SETCOL) involves the use of settling columns initially containing a uniform distribution of cells. The population mean sinking rate is determined from the change in the vertical distribution of biomass after a given time. Complete details of the method and mathematical derivations are given in Bienfang (1981c). The discrete sample method (MARS) monitors the transit time of 14C-labelled cells through sinking columns of known height. The mean sinking rate is determined from the time-course of arrival times of cells at the bottom. The method, described in Rothwell and Bienfang (1978) and Bienfang (1979), has been used successfully in both laboratory and open sea (Bienfang, 1980) applications. Sinking rate measurements using the SETCOL and MARS methods were made on successive days. Measurements were started about three hours after the beginning of the 10-hour photoperiod. The duration of the SETCOL and MARS experiments was about 6 and 4 hours respectively.
RESULTS

Figure 1 shows semi-log plots of population sinking rates at the various light regimes. An analysis of variance (ANOVA) revealed no significant difference ($p>0.05$) in sinking rates calculated by the SETCOL and MARS methods, and the results obtained by the two methods have therefore been averaged in presenting the results. The ANOVA did however, reveal a significant effect of irradiance on sinking rate ($p<0.001$). The $a$ posteriori Student-Newman-Keuls test (Sokal, Rohlf, 1969), and Duncan’s multiple range test (Steel, Torric, 1960), were then used to determine which groups of sinking rates were not significantly different among themselves. Both tests indicated that the sinking rates measured for steady states 1-4 were not significantly different ($p>0.05$), and that sinking rates from steady states 5 and 6 were not significantly different ($p>0.05$). The sinking rates are therefore logically grouped into a high irradiance, high sinking rate set (steady states 1-4) and a low irradiance, low sinking rate set (steady states 5-6).

Compositional properties of the populations at the six steady-states are summarized in Table 1. Cell volume measurements ranged from 571 to 773 $\mu$m$^3$ cell$^{-1}$ during the study, and showed no systematic L : D periodicity or relationship to the various light regimes; thus, cell properties are treated only on a per cell basis. Mean cell quotas (averages of AM and PM values) of carbon were almost constant (range: 99-110 pg. cell$^{-1}$), but cell quotas of ATP were negatively correlated with irradiance. Chlorophyll cell quotas were negatively correlated with irradiance at light levels $\geq$64.7 $\mu$E. m$^{-2}$. sec.$^{-1}$, and positively correlated with irradiance at lower light levels. Nitrogen cell quotas were negatively correlated with irradiance at higher light levels $\leq$271 $\mu$E. m$^{-2}$. sec.$^{-1}$, but constant (range: 27-36 g. g$^{-1}$) at lower light levels. C : N ratios were positively correlated with irradiance. C : chlorophyll ratios were rather constant (range: 27-36 g. g$^{-1}$) at light levels $\leq$271 $\mu$E. m$^{-2}$. sec.$^{-1}$, but were positively correlated with irradiance at higher light levels.

Table 1

<table>
<thead>
<tr>
<th>Steady state number</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light intensity</td>
<td>847</td>
<td>515</td>
<td>271</td>
<td>64.7</td>
<td>27.4</td>
<td>13.3</td>
</tr>
<tr>
<td>(g. g$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Growth rate (H$^{-1}$)</td>
<td>0.023</td>
<td>0.020</td>
<td>0.018</td>
<td>0.016</td>
<td>0.005</td>
<td>0.002</td>
</tr>
<tr>
<td>Ambient nitrate concentration ((\mu)M)</td>
<td>0.37</td>
<td>0.50</td>
<td>2.52</td>
<td>5.39</td>
<td>8.01</td>
<td>13.5</td>
</tr>
<tr>
<td>A.M.</td>
<td>P.M.</td>
<td>A.M.</td>
<td>P.M.</td>
<td>A.M.</td>
<td>P.M.</td>
<td>A.M.</td>
</tr>
<tr>
<td>Cell concentration (10$^4$. ml$^{-1}$)</td>
<td>67.5</td>
<td>59.9</td>
<td>47.2</td>
<td>41.3</td>
<td>30.4</td>
<td>27.2</td>
</tr>
<tr>
<td>Chlorophyll a (pg. cell$^{-1}$)</td>
<td>0.68</td>
<td>0.85</td>
<td>1.11</td>
<td>1.72</td>
<td>2.83</td>
<td>3.43</td>
</tr>
<tr>
<td>Carbon (pg. cell$^{-1}$)</td>
<td>81.4</td>
<td>135.2</td>
<td>84.6</td>
<td>134.6</td>
<td>88.1</td>
<td>126.9</td>
</tr>
<tr>
<td>Nitrogen (pg. cell$^{-1}$)</td>
<td>9.7</td>
<td>11.2</td>
<td>15.1</td>
<td>17.1</td>
<td>20.5</td>
<td>22.3</td>
</tr>
<tr>
<td>ATP (pg. cell$^{-1}$)</td>
<td>0.149</td>
<td>0.174</td>
<td>0.181</td>
<td>0.164</td>
<td>0.292</td>
<td>0.222</td>
</tr>
<tr>
<td>C/Chl (g. g$^{-1}$)</td>
<td>119.0</td>
<td>159.0</td>
<td>79.9</td>
<td>78.2</td>
<td>31.1</td>
<td>41.4</td>
</tr>
<tr>
<td>C/N (g. g$^{-1}$)</td>
<td>8.42</td>
<td>12.10</td>
<td>5.68</td>
<td>7.88</td>
<td>4.37</td>
<td>6.38</td>
</tr>
<tr>
<td>C/ATP (g. g$^{-1}$)</td>
<td>546</td>
<td>804</td>
<td>466</td>
<td>823</td>
<td>302</td>
<td>639</td>
</tr>
</tbody>
</table>
Differences in population composition ratios between A.M. and P.M. samples varied with changes in the prevailing irradiance. The ratios chlorophyll : cell, C : cell, N : cell, C : N and C : ATP were generally decreasing with increasing light levels (Table 1). The ratios chlorophyll : cell, N : cell, C : N and C : ATP were generally decreasing with increasing light levels (Table 1). The ratios chlorophyll : cell, N : cell, C : N and C : ATP were generally decreasing with increasing light levels (Table 1).

Productivity/biomass (P/B) ratios, in terms of chlorophyll, particulate carbon, and ATP were well correlated with the prevailing irradiance (Fig. 2). In terms of chlorophyll a, P/B ratios (µg C·µg chlorophyll a⁻¹·h⁻¹) were linearly (r² = 0.987) related to irradiances (Fig. 2a, Table 2). The curves relating P/B ratios in terms of carbon (µg C·µg C⁻¹·h⁻¹) and ATP (µg C·µg ATP⁻¹·h⁻¹) showed decreasing slopes at higher light levels (Fig. 2b, c), indicating saturation kinetics. Rectangular hyperbolas, having the form \( Y = a(X + c)/(b + (X + c)) \) were fitted to these data, where \( Y \) is the P/B ratio, \( X \) is the irradiance, \( a \) is the asymptotic maximum P/B ratio, \( b \) is the half-saturation constant, and \( c \) is the X intercept. The calculated parameters for these three curves are given in Table 2. Differences in the absolute values of turnover rate estimates in Figure 2b and d, are due to the fact that the latter were calculated on a 24 hours basis, whereas the former involved production only during the light period.

**DISCUSSION**

The observation of significantly lower sinking rates of *Thalassiosira weissflogii* at the two lowest light levels lends empirical support to the hypothesis that sinking rate deceleration can be a contributing factor to the formation of subsurface chlorophyll maximum layers in the sea. This behavior in an *in vitro* culture indicates that growth at low light levels results in physiological changes which are manifest in buoyancy variation. Reduction in sinking rates was apparent using two fundamentally different methods of rate measurement (Bienfang et al., 1977), both of which showed good replicability at all light levels. The irradiances at which reduced sinking rates occurred were 1-3% of surface levels, and closely approximate the irradiances at the chlorophyll maximum in Hawaiian waters (Bienfang, Syzper, 1981).

Most compositional characteristics were either constant or varied monotonically with irradiance. The only exception to this observation was the chlorophyll cell quota. Chlorophyll bleaching at low light levels has been reported in several species (Falkowski, 1980), and is apparent in Table 1 at the two lowest light levels, where chlorophyll cell quotas were 25-30% lower at 64.7 µE·m⁻²·sec⁻¹. It is therefore tempting to hypothesize that a reduction in sinking rates is associated with chlorophyll bleaching at low light levels. However, C : chlorophyll ratios were almost constant between 13.3 and 271 µE·m⁻²·sec⁻¹. Thus whether or not one concludes that bleaching occurred at the two lowest light levels depends to a certain extent on...
whether one uses cell numbers or particulate carbon as a biomass normalizer. Because of this ambiguity, the hypothesis that sinking rate reductions are correlated with chlorophyll bleaching at low light levels must remain somewhat tentative.

There was no systematic co-variation between sinking rate and any of the other compositional characteristics over the range of light levels. The compositional characteristics varied continuously with changing light levels, whereas sinking rates displayed a step function change. Thus we may surmise that whatever aspect of physiological state was associated with the lower sinking rates, it was not reflected in the cellular content of carbon, nitrogen, or ATP. The principal controlling mechanism may be a dynamic process, the rate of which is not reflected in measurements of static parameters such as cell carbon or nitrogen.

The cause for the reduced sinking rates at low light observed by Bienfang (1980) in the field, and here (steady states 5 and 6) therefore remains unclear. It has been speculated that the sinking rate of cells may decrease as cells encounter the nutricline, but the results reported here argue against this explanation. Data (Fig. 1) show no evidence of a reduced sinking rate at steady states 3 and 4, where the ambient nitrate levels (Table 1) were almost certainly adequate to saturate uptake kinetics (Eppley et al., 1969). Although the reduced sinking rates observed here were found at low growth rates, low growth rates per se do not appear adequate to cause a reduction in sinking rates. Other laboratory studies (Bienfang, 1981b) failed to show a systematic relationship between sinking rate and growth rate in nutrient-limited, light-saturated populations. Our data suggest that not only slow growth, but slow growth at very low light levels, is the condition associated with populations having reduced settling rates.

The proposed mechanisms for maintenance of deep chlorophyll maximum layers are not mutually exclusive. Two pieces of information argue that the suspension behavior observed in this study, and with natural populations (Bienfang, 1980), cannot be taken to imply that sinking rate deceleration alone maintains the subsurface chlorophyll maximum. Firstly, the observed trend in cellular chlorophyll at light levels \( \geq 64.7 \mu \text{E. m}^{-2}. \text{sec}^{-1} \) (Table 1) is consistent with the hypothesis that increased chlorophyll. cell\(^{-1} \) can be a contributing factor to development of chlorophyll maximum layers. The data show that chlorophyll. cell\(^{-1} \) and carbon. chlorophyll\(^{-1} \) ratios varied by about 4x over the photic regimes examined (compared with a 2x variation in sinking rates). Similar observations were made by Laws and Bannister (1980).

The magnitude and direction of change in these ratios indicate that shade adaptation can produce substantially increased pigment levels at low irradiances; this adaptation would contribute to the observation of higher chlorophyll levels in field samples from depth regions of low light. The data (Table 1) suggest that increased cellular content of chlorophyll, possibly in association with a more favorable nutrient field, may play at least as important a role as sinking in the development of deep chlorophyll maxima in subtropical waters. Secondly, the size distribution of phytoplankton in oligotrophic seas shows that most of the biomass occurs as small cells; roughly 70% of the chlorophyll is contained in the \(<2\mu \text{m} \) size fraction (Bienfang, 1980; 1981a; Bienfang, Szyper, 1981; Takahashi, Bienfang, in prep.). Bienfang and Szyper (1981) found little difference in the concentration of cells less than \(5\mu \text{m} \) in diameter between the chlorophyll maximum layer and the overlying water column. Repeated sinking rate measurements (Takahashi, Bienfang, in prep.) failed to show any significant negative buoyancy (i.e., sinking rates were less than \(0.01 \text{ m. d}^{-1} \)) for this small size fraction. These observations in the face of a pronounced chlorophyll maximum composed primarily of \(<5\mu \text{m} \) cells, cast doubt on the role of sedimentation as the causative mechanism. Combining these observations with the results presented here, we conclude that the dynamics of sedimentation and shade adaptation probably play parallel roles in the development of increased chlorophyll levels at limiting irradiances. As noted by Cullin and Eppley (1981), the relative importance of these processes is likely to vary from one system to another, depending on factors influencing the depth of the mixed layer and the size structure of the resident phytoplankton populations.

Given results presented here, and additional information on phytoplankton composition as influenced by light and nutrients (Laws, Bannister, 1980) it is instructive to examine theoretically the relative importance of changes in cellular chlorophyll levels versus reduced sinking rates in creating the deep chlorophyll maximum. In the mixed layer, the mean irradiance \( I_m \) is given by the expression:

\[
I_m = \frac{I_0}{E_D} (1 - e^{-E_D}) \tag{1}
\]

where \( E \) is the extinction coefficient of visible light, \( D \) is the depth of the mixed layer, and \( I_0 \) is the surface irradiance. The irradiance just below the mixed layer \( I_m \) is of course equal to \( I_0 - e^{-E_D} \). As a cell sinks through the base of the mixed layer, the mean irradiance experienced by the cell therefore changes in a step function manner. The ratio of the mean irradiance just below the mixed layer to the irradiance in the mixed layer is:

\[
\frac{I_0}{I_m} = \frac{E_D}{e^{ED} - 1} \tag{2}
\]

In the oceanic waters near Hawaii, we can take the mixed layer depth to be 40 m (Bienfang, 1981a) and \( E \sim 0.04 \text{ m}^{-1} \) (Bienfang, Szyper, 1981); Equation 2 then gives the ratio \( I_0/I_m = 0.405 \). If the average radiation penetrating the first 1-2 m of the water column is \( I_0 = 850 \mu \text{E. m}^{-2}. \text{sec}^{-1} \) (Bienfang, Szyper, 1981; Bienfang, 1981a), then the mean irradiance in the mixed layer would be about \(424 \mu \text{E. m}^{-2}. \text{sec}^{-1} \), and the irradiance just below the mixed layer would be \((0.405) 424 = 172 \mu \text{E. m}^{-2}. \text{sec}^{-1} \). If we assume that growth rates just below the mixed layer are light-limited, then the data (Table 1) indicate that Thalassiosira weissflogii cells, growing just below the mixed layer,
would contain about 3.5 pg chlorophyll per cell. Within the mixed layer, growth rates are presumably limited by the supply rate of nutrients, and under these conditions compositional characteristics will depend both on the mean irradiance and the nutrient-limited growth rate (Hunter, Laws, 1981). At the relatively high nutrient-limited growth rate of 0.02 h⁻¹, and an irradiance of 515 μE m⁻² sec⁻¹, the chlorophyll cell quota of *Thalassiosira weissflogii* was about 1.4 pg cell⁻¹ \( \text{(Table 1)} \). Laws and Bannister (1980) found that at a similar nutrient-limited growth rate but with a 12 hours photoperiod irradiance of about 230 μE m⁻² sec⁻¹, the chlorophyll cell quota of *T. weissflogii* was about 1.3 pg cell⁻¹. Thus it seems reasonable to conclude that nutrient-limited *T. weissflogii* cells experiencing a mean photoperiod irradiance of 424 μE m⁻² sec⁻¹ would contain 1.3-1.4 pg cell⁻¹ chlorophyll if growing at 0.02 h⁻¹. This growth rate corresponds to a doubling time of 1.4 days, which is rather short compared to many estimated doubling times in oligotrophic areas (Sharp et al., 1980; Eppley, 1980). At long doubling times the cell quota of chlorophyll would be even lower (Shuter, 1979; Laws, Bannister, 1980). Thus the chlorophyll cell quota of *T. weissflogii* sinking through the bottom of the mixed layer could be expected to increase by at least a factor of about 3.5/1.35 = 2.6. This increase is comparable to or greater than the change in chlorophyll concentration observed for deep chlorophyll maxima of many oceanic areas.

Similar calculations for species other than *Thalassiosira weissflogii* would lead to qualitatively similar conclusions. The critical component of the model is that the mean irradiance experienced by the cells decreases in a step function manner as the cells sink through the bottom of the mixed layer. The critical experimental observation is that cell chlorophyll levels are strongly correlated with mean irradiances at light levels \( \geq I_k \) (Bannister, 1974; Shuter, 1979), where \( I_k \) is the irradiance at which growth rate is saturated. Thus, unless the mixed layer is so deep that the average irradiance \( I_k < I_k \), the sinking of cells through the bottom of the mixed layer can be expected to produce a step function increase in cell chlorophyll levels. Harris (1980) notes that for many phytoplankton, photosynthesis saturates at light levels of 50-120 μE m⁻² sec⁻¹. Data in Parsons and Takahashi (1973) show that light levels in the mixed layers of many oceanographic regions are high enough to saturate photosynthesis according to the threshold values of Harris (1980).

The importance of sinking rate changes in the formation of the deep chlorophyll maximum can be evaluated with the aid of a theoretical model slightly modified from one used earlier by Riley et al. (1949). If the distribution of phytoplankton cells is horizontally homogenous and in steady state, the vertical distribution of cells is governed by the differential equation:

\[
\frac{d^2P}{dx^2} - \frac{dP}{dx} - \frac{dP}{dx} + (U-G)P = 0.
\]

where \( P \) is the concentration of phytoplankton cells, \( \psi \) is the sinking rate of the cells, \( A \) is the vertical Austausch coefficient, \( U \) is the growth rate of the cells, \( G \) is the rate at which the cells are grazed by zooplankton, and \( x \) is the depth of the water column. The relationship between \( U-G \) and \( x \) is not well known, but studies of nutrient cycling in the ocean indicate that in oligotrophic areas the integral of \( U-G \) over the depth of the euphotic zone is approximately zero (Eppley, Peterson, 1979). For purposes of our model, we have set \( U-G \) equal to zero for all values of \( x \). In other words, we assumed that grazing losses exactly balance production at each depth in the euphotic zone. Within the mixed layer, we assume \( P \) to be constant with depth, due to mixing, and therefore confine our attention to the region just below the mixed layer. Experimental studies indicate that the value of \( A \) in this region is in the range 0.01 to 0.4 cm² h⁻¹ (Sharp, Church, 1981), and in our numerical solution to equation 3, we considered separate cases in which \( A \) was assigned values of 0.01 and 0.4 cm² h⁻¹. The depth dependence of \( \psi \) was modeled by assuming that \( \psi \) varied linearly with irradiance at light levels between 64.7 and 27.4 μE m⁻² sec⁻¹. The sinking rates at light levels greater than 64.7 and less than 27.4 μE m⁻² sec⁻¹ were assumed to be 0.22 and 0.11 m d⁻¹ respectively, based on the data in Figure 1. The irradiance at the surface was taken to be 850 μE m⁻² sec⁻¹, the visible light extinction coefficient to be 0.04 m⁻¹, and the depth of the mixed layer to be 40 m. Boundary conditions were established by setting \( P \) to an arbitrary value at the base of the mixed layer and \( dP/dx = 0 \) at the base of the euphotic zone. We assumed the compensation irradiance to be 5 μE m⁻² sec⁻¹ (Falkowski, Owens, 1980), and therefore took the depth of the euphotic zone to be 128 m. Equation 3 was then integrated numerically by approximating the derivatives with finite differences.

If \( U-G = 0 \) and if \( \psi \) is independent of depth, the given boundary conditions imply that \( P \) is constant between the base of the mixed layer and the base of the euphotic zone. However, if \( \psi \) is allowed to vary as indicated, \( P \) increases by a factor of 31-100% between 40 and 86 m. The magnitude of the increase is negatively correlated with the size of \( A \). Such increases are comparable to the increases in chlorophyll concentration reported in deep chlorophyll maximum layers (Revelante, Gilman, 1973; Venrick et al., 1973; Bienfang, Gundersen, 1977; Shulenberger, 1978; Bienfang, 1981; Bienfang, Szyperski, 1981). We conclude that reduced sinking rates probably play an important role in the maintenance of subsurface chlorophyll maxima in productive, high latitude waters having a shallow mixed layer, a well-developed pycnocline, and phytoplankton populations characterized by larger cells (Cullen, Eppley, 1981). However, both modeling and experimental data indicate little need to invoke sinking rate deceleration to explain formation of chlorophyll maxima in oligotrophic, subtropic waters.

This work was supported by National Science Foundation grants OCE-7819234 and OCE-8100679 to P. Bienfang.
REFERENCES


