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Light-shade adaptation and vertical mixing of marine phytoplankton: A comparative field study

by Paul G. Falkowski

ABSTRACT

The hypothesis is examined that the recent light history of phytoplankton contains information about vertical mixing processes in the euphotic zone. Chlorophyll/P700 ratios are used to estimate the degree of light or shade adaptation in natural phytoplankton communities. Along with information about the time- and light-dependent rates of change of chlorophyll/P700 ratios, a model is presented to estimate how recently populations at the surface were at the 1% light depth and vice versa. The model is based on first-order kinetics and employs a temperature correction. The model is used to estimate vertical displacement rates (i.e., piston velocities) on Georges Bank, in the New York Bight, and off the coast of Hawaii. The results suggest that vertical displacement rates vary by about two orders of magnitude (from ca. $3.8 \times 10^{-4}$ cm/sec to $1.1 \times 10^{-1}$ cm/sec). These values are in general agreement with theoretical calculations based on physical parameters.

1. Introduction

In phytoplankton dynamics the importance of vertical mixing processes for the availability of nutrients, light, and the distribution of biomass is qualitatively known (e.g., Sverdrup, 1953; Riley, 1965). Because of the difficulty in directly measuring vertical velocities, however, little progress has been made in quantitatively relating vertical mixing to phytoplankton production and distribution. Vertical eddy diffusivities can be estimated from vertical nutrient gradients and phytoplankton nutrient demands (Eppley et al., 1979; King and Devol, 1979); however, this approach cannot be used unless a nutricline is a prominent characteristic of the system. In this study, the hypothesis is presented that the recent light history of phytoplankton may provide information about vertical mixing processes.

Let us consider the light regimes experienced by marine phytoplankton in natural waters. First-order variations in the light regimes are influenced by the path of the sun (i.e., the diurnal photoperiod). Diurnal variations in light can be temporarily manifested in such properties as the diel periodicity of carbon/chlorophyll ratios.
Second-order variations in light regimes are primarily influenced by the vertical displacement of cells in the water column (Falkowski and Wirick, 1981). Second-order variations in light are spatially manifested in vertical variations in biochemical or physiological components of the cells. From these premises it can be inferred that vertical variations in biochemical or physiological components can be related to vertical displacement rates in situ.

**Theoretical considerations.** It is recognized that the light history of a phytoplankton community influences the empirical relationship between photosynthesis and irradiance (Steemann Nielsen and Hansen, 1959; Ryther and Menzel, 1959; Steemann Nielsen and Park, 1964; Beardall and Morris, 1976; Marra, 1978; Falkowski, 1980). The empirical relationship between photosynthesis and irradiance is mediated by physiological and biochemical adaptations, generally referred to as light-shade adaptation (Prezelin and Sweeney, 1979; Falkowski, 1980; Falkowski and Owens, 1980; Perry et al., 1981). Light-shade adaptation is characterized by changes in photosynthetic pigment content and photosynthetic response, and is often accompanied by changes in chemical composition, fluorescence characteristics, and cell volume (Myers and Graham, 1971; Falkowski and Owens, 1980).

Consider a vertical mixing process that displaces a cell on some time scale longer than the time it takes for the cell to become adapted to the difference in light regimes between depths $z_0$ and $z_1$. If the cells manifest some characteristic of adaptation to light, vertical variations in this characteristic would reflect the light history of the cell at depth $z_0$, and would be nonuniformly distributed vertically because of a new characteristic associated with the light regime at depth $z_1$. If the time scale of change in the adaptive variable is known, it is possible to estimate the maximum rate of vertical displacement of the cell in the water column. If mixing processes occur on a time scale shorter than the time it takes for the cells to adapt to the variations in the light regime, the vertical distribution of the light-dependent physiological characteristic would be expected to be more uniformly distributed. From knowledge of the time scale of change of the adaptive variable, a minimum vertical mixing rate can be estimated. Implicit in this hypothesis is that second-order variations in light-dependent physiological attributes are not masked by first-order variations.

One method that may be used to estimate vertical displacement rates is to estimate the recent light history of phytoplankton by generating $P$ vs $I$ curves from samples taken at known light depths (Steemann Nielsen and Hansen, 1961; Eppley and Brooks, unpubl. ms.). The assumption may be made that the differences in such photosynthetic parameters as the initial slopes of $P$ vs $I$ curves (i.e., the light utilization efficiency), $I_k$ values, or $P_{\text{max}}$ values reflect the light history of the sample. For example, differences in $P_{\text{max}}$ or $I_k$ values between samples collected at depths $z$ and $z \pm \Delta z$ might be used to estimate the degree to which two vertically separated phyto-
plankton populations are adapted to high or low light intensities. If kinetic coefficients of light-shade adaptation (vis-a-vis $P_{\text{max}}$ or $I_\perp$ values) are known, it is possible to estimate how far apart in time spatially separated samples are and thereby estimate an upper or lower bound for a vertical displacement rate.

This type of approach was taken by Steemann Nielsen and Hansen (1959) and Ryther and Menzel (1959) to qualitatively estimate the degree of vertical mixing. Eppley and Brooks (unpubl. ms.) attempted to semiquantitatively estimate mixing, using laboratory-derived coefficients for the time- and light-dependent rates of change in $I_\perp$ values. The validity of such estimations of vertical mixing rates, using $P$ vs $I$ parameters, depends upon (among other things) the length of the incubation period with radiocarbon. In some species (e.g., *Skeletonema costatum*), light-shade adaptation may occur within a few hours (Jørgensen, 1969; Riper et al., 1979), so that the $P$ vs $I$ parameters measured may not reflect the physiological state of the cells at the time of collection.

Changes in such photosynthetic parameters as light utilization efficiency, $P_{\text{max}}$, or $I_\perp$ values are thought to be brought about by changes in the size and/or numbers of photosynthetic units (cf. Herron and Mauzerall, 1971; Prezelin and Sweeney, 1979; Falkowski, 1980; Falkowski et al., 1981). This premise frames another approach that may be used to estimate the light history of phytoplankton. It is hypothesized that as cells become more shade adapted, the size of photosynthetic units increases. This hypothesis is supported by numerous laboratory studies on the characteristics of light- and shade-adapted unicellular algae (Myers and Graham, 1971; Falkowski and Owens, 1980; Falkowski et al., 1981; Perry et al., 1981).

A number of methods have been described for measuring the size of photosynthetic units (PSU) (Falkowski et al., 1980). In this study, photosynthetic unit (PSU) sizes were estimated by measuring the ratio of chlorophyll/$P_{700}$ using a spectrophotometric technique (e.g., Shiozawa et al., 1974; Falkowski and Owens, 1980). A diagram outlining the principle of this approach is given in Figure 1. As in the use of $I_\perp$ values to estimate light history, the ratio of photosynthetic unit sizes between two depths can be used as a relative index of the recent light history of a phytoplankton community within a given water column. This technique requires no incubation period, thereby preventing cells from adapting to a new light regime.

Using both chl/$P_{700}$ ratios and $P$ vs $I$ curves to estimate the light history of phytoplankton, a model is presented for the estimation of upper and lower bounds of vertical displacement rates in three contrasting regions: the southern portion of Georges Bank (GB), the New York Bight (NYB), and the subtropical Pacific (SP) at the site of a proposed OTEC plant off the coast of Hawaii. As a result of tidal mixing, GB is never stratified (Hopkins and Garfield, 1981); the NYB is vertically mixed in the winter but becomes intensely stratified in the summer (Bumpus, 1973; Beardsley et al., 1976); in the SP a permanent deep thermocline is present below the euphotic zone, and a shallow one develops seasonally.
Figure 1. Schematic representation of the changes that occur in a photosynthetic unit as a typical diatom undergoes light-shade adaptation. The photosynthetic unit may be conceived of as a dish antenna, the collecting area containing chlorophylls and accessory pigments. At the focus of the antenna is a reaction center—here represented by a $P_{700}$ molecule. As the cell becomes shade adapted the antenna size increases, leading to a proportional increase in chlorophyll/$P_{700}$ ratios. When shade-adapted cells are exposed to high light, the reverse phenomenon occurs (cf. Falkowski and Owens, 1980).

2. Materials and methods

Data used in this study were collected from five cruises between 1977 and 1979 (Table 1). Each day a productivity station was occupied at ca 0800 h local time. At these stations, light extinction coefficients were determined with a Lambda LI 192S quantum sensor interfaced with a ratio amplifier. A second sensor, placed on the deck, served as a reference. The ratios of surface light ($I_o$) to light at known depths

<table>
<thead>
<tr>
<th>Vessel</th>
<th>Region</th>
<th>Month</th>
</tr>
</thead>
<tbody>
<tr>
<td>R/V Kelez</td>
<td>NYB</td>
<td>March 1977</td>
</tr>
<tr>
<td>R/V Knorr</td>
<td>NYB</td>
<td>August 1977</td>
</tr>
<tr>
<td>R/V Atlantis II</td>
<td>NYB, GB</td>
<td>April 1978</td>
</tr>
<tr>
<td>R/V Atlantis II</td>
<td>NYB, GB</td>
<td>October 1978</td>
</tr>
<tr>
<td>R/V Kona Keoki</td>
<td>SP</td>
<td>October 1979</td>
</tr>
</tbody>
</table>
were output directly onto a recorder. Log $I/I_0$ values were plotted as a function of depth and extrapolated through the origin. Sampling depths were determined from the light extinction plots and corresponded to 100, 60, 30, 15, 5, 1, and 0.1% of $I_0$.

Samples were obtained with Niskin bottles. For $P/N$ curves, samples were drawn from selected light depths (usually 100 and 1%) and incubated with 5 $\mu$Ci of NaH$^{14}$CO$_3$ in screened bottles at 100, 60, 30, 15, 5, and 1% light. A dark bottle was run in parallel for each depth. These samples were incubated for 2 h in fluorescent light incubators at in situ temperatures. Temperatures were maintained with Neslab CFT 75 recirculating water baths. The sample bottles were mechanically rotated in the incubators at 6 rpm, and light was provided from two sides by VHO fluorescent tubes supplying 675 $\mu$E m$^{-2}$ sec$^{-1}$ (PAR).

Upon completion of the incubations, the samples were immediately filtered onto Millipore HA filters at 10 mm Hg vacuum pressure, fumed for 60 sec over concentrated HCl, and placed in scintillation vials to which 10 ml of Filter Solv (Beckman) was added. The samples were counted in a Beckman LS 3150T scintillation counter with an external standard. Dark bottle counts were subtracted from the corresponding light bottle counts in the productivity calculations (Strickland and Parson, 1972).

Chlorophyll $a$ was determined fluorometrically from 90% acetone extracts. Freshly drawn samples were filtered on Reeve Angel 984H glass fiber filters and ground in a tissue grinder with 90% acetone. The acetone extracts were filtered into clean graduated centrifuge tubes to remove the glass fibers, brought to a constant volume, and measured before and after acidification in a Turner Designs Model 10 fluorometer (Yentsch and Menzel, 1963) calibrated with pure chlorophyll $a$.

In situ measurements of in vivo chlorophyll fluorescence were made with a Turner Designs Model 10 fluorometer housed in a watertight pressure case. This instrument was also equipped with a thermistor and depth transducer, so that fluorescence, temperature, and depth (FTD) could be simultaneously measured.

To measure PSU unit sizes, 4- to 60-l samples were taken from selected depths with Niskin bottles (Fig. 2). The amount of water processed depended on the chlorophyll $a$ concentrations at the desired depths. Samples were either filtered directly on 4.7-cm Gelman AE glass filters (10 l or less) or continuously centrifuged to a small volume (ca 100 ml) and then filtered. Filtration or centrifugation was completed within 1 h of collection. The filters were homogenized under dim light in 2 ml of 50 mM ice-cold Tris-HCl buffer, pH 7.8, containing 0.01% Triton X-100. The suspensions, containing crude chloroplast membranes, were centrifuged at 2000 $\times$ g for 5 min to remove glass fibers and large cell debris. The supernatants were scanned with an opal glass filter (Shibata, 1958) and beam scrambler from 350 to 750 nm in the split beam mode of Aminco DW-2a spectrophotometer against distilled water. Chlorophyll $a$ was determined in the aqueous suspensions by subtracting the absorbance at 750 nm from that at 678 nm and using an absorptivity coeffi-
Figure 2. Flow diagram for the processing and measurement of chlorophyll/P₇₀₀ ratios in the field.

cient of 60 mM⁻¹ cm⁻¹ (Thornber et al., 1977). Solid methyl viologen and sodium ascorbate were added to the sample to final concentrations of ca 100 µM and 10 mM, respectively, and P₇₀₀ was measured in a 10 × 4-mm cuvette in the dual wavelength mode of the spectrophotometer by following the light-induced absorption changes at 697 nm relative to the isosbestic wavelength of 720 nm (Falkowski and Owens, 1980; Hiyama and Ke, 1972). Actinic illumination of 5 sec duration was provided by a focused 150-watt tungsten source filtered through two Corning 5543 filters (λₘₐₓ = 420 nm). The photomultiplier was protected by a single Corning 2030 blocking filter. Samples were held in the secondary sample position to eliminate chlorophyll fluorescence. Care was taken to ensure that the actinic source was suf-
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ficiently bright to achieve light saturation of $P_{700}$ photochemical activity. $P_{700}$ signals were averaged over 10 flashes for each sample. $P_{700}$ was calculated from the light-induced absorbance change using a difference absorptivity coefficient of $64 \text{ mM}^{-1} \text{ cm}^{-1}$ (Shiozawa et al., 1974). Typical absorption differences arising from the $P_{700}$ signal are small ($\approx 5 \times 10^{-4}$ o.d. units), requiring a high-sensitivity spectrophotometer; the coefficient of variation of the technique is $\pm 14\%$. The molar ratios of chlorophyll $a$ and $P_{700}$ were used to estimate the average size of PSUs from each of the sample depths.

Temperature was measured with reversing thermometers, salinity with a Guildline salinometer, and nutrients ($\text{NO}_3^-$, $\text{NO}_2^-$, $\text{NH}_4^+$, $\text{PO}_4^{3-}$, $\text{Si(OH)}_4$) with an AutoAnalyser (Whitledge et al., 1981). Phytoplankton samples were taken from desired depths, preserved with Lugol's iodine, and counted in Uttermohl chambers with an inverted microscope (Falkowski and von Bock, 1979).

3. Results and discussion

In 1960, Ryther and Hulburt suggested that a mixed layer as inferred from physical or chemical criteria is not necessarily mixed with respect to phytoplankton. This apparent anomaly is primarily related to two facts: (a) the density field does not provide information about the energy available for mixing at the time of observation, and (b) the distribution of phytoplankton is nonconservative. This principle is illustrated with a few specific examples.

Example 1. Consider two vertical profiles taken in the spring: one in April from the southern region of GB (Fig. 3a), the other in March from a similar isobath in the NYB (Fig. 4b). On GB both the density and chlorophyll fields are uniformly distributed with depth, suggesting that vertical mixing occurs on a relatively rapid time scale. Tidal stirring continuously provides enough energy and vertically distributes heat (Hopkins and Garfield, 1981) and chlorophyll such that vertical gradients in density or phytoplankton biomass do not form. At a similar isobath in the NYB, winter mixing processes are primarily driven by convective overturn and irregular wind events. In the absence of recent wind events, the density profile in this region is nonuniform, increasing by one $\sigma_T$ unit over the 30-m water column. It could be inferred from the vertical chlorophyll profile that little energy had been recently available for mixing; i.e., the phytoplankton appear to sink out of the water column faster than mixing processes redistribute them (Malone et al., 1983).

Example 2. The onshore-offshore gradient in mixing energy in the NYB in the spring is complicated by estuarine influences near the apex of the NYB and frontal systems near the shelf break. In the apex of the NYB, nutrient-rich water from the Hudson and adjoining estuaries is vertically separated from continental shelf water by a halocline. The plume of this estuarine system is characterized by high standing stocks of phytoplankton and high primary productivity (Malone, 1977). Vertical
profiles of the density fields in this region (Fig. 4a) suggest that a weak mixed layer extends to ca 8 to 10 m in March, about the same order of depth as the euphotic zone. The chlorophyll profile suggests that enough mixing energy is available in the upper mixed layer to evenly distribute phytoplankton in the euphotic zone, but not throughout the entire water column. At the shelf-slope front, however, the water column appears vertically stable (Fig. 4c) as a result of the interleaving of warm slope water with cold shelf water. At this frontal region the vertical chlorophyll profiles often reveal higher phytoplankton biomass near or at the surface, implying that growth rates exceed vertical mixing rates, at least within the upper 20 m (i.e., the euphotic zone).

Example 3. The southern portion of GB is vertically uniform at any one time and vertical profiles of $\sigma_t$ do not qualitatively change on seasonal time scales (Fig. 3a and b). Tidal stirring provides sufficient energy to prevent formation of a pycnocline in the warmer months, and the vertical chlorophyll distributions are qualitatively similar throughout the year. Phytoplankton species composition throughout the water column at any given time shows the same rank order abundance of floristic components (Falkowski and von Bock, 1979), which suggests that the vertical turnover of the water column is as fast as or faster than the mean growth rate of the phytoplankton.

In contrast, in the summer in the midshelf of the NYB warm shelf water overlays cold shelf water (the so-called “cold pool”; Bigelow, 1933; Ketchum and Corwin, 1964; Hopkins and Garfield, 1981), resulting in intense stratification (compare Fig. 4b and d). The turbulence in the upper mixed layer (between 5 and 10 m thick) is
Figure 4. Vertical profiles of density (●) and chlorophyll (△) in the New York Bight. (a) Near the mouth of the Hudson estuary in March 1977 (40°24' N, 73°53' W); (b) in the midshelf in March 1977 (30°39' N, 73°50' W); (c) at the shelf-break front in March 1977 (39°35' N, 72°25' W); and (d) in the midshelf in August 1977 (39°46' N, 73°46' W).

usually sufficient to maintain a uniform distribution of chlorophyll above the pycnocline. This mixed layer is often shallower than the euphotic zone (Falkowski et al., 1983). The pycnocline, a region of high vertical stability coupled with a high nutrient gradient, provides a region conducive to the growth and accumulation of phytoplankton (cf. Cullen and Eppley, 1981). A chlorophyll maximum, often coincident with the depth of the pycnocline, is normally found in this region. As in the Southern California Bight, the rank order abundance of phytoplankton species in the upper mixed layer of the NYB is, more often than not, completely different from the
Table 2. Estimations of vertical displacement rates and turnover of the mixed layer from Georges Bank, the New York Bight, and the subtropical Pacific.

<table>
<thead>
<tr>
<th>Region</th>
<th>Month</th>
<th>$T^*$ (°C)</th>
<th>$z_<em>^</em>$ (m)</th>
<th>$z_{**}$ (m)</th>
<th>$d\sigma_t/ dz$ (m$^{-1}$)</th>
<th>$\text{Chl}<em>t/\text{Chl}</em>{t\text{max}}$</th>
<th>(Chl/$P_{\text{co2}}$)$z_*$</th>
</tr>
</thead>
<tbody>
<tr>
<td>GB (Southern)</td>
<td>April 1978</td>
<td>4.5</td>
<td>45</td>
<td>15</td>
<td>$2.2 \times 10^{-2}$</td>
<td>0.93</td>
<td>725</td>
</tr>
<tr>
<td>GB (Southern)</td>
<td>October 1978</td>
<td>13.0</td>
<td>45</td>
<td>22</td>
<td>$1.0 \times 10^{-2}$</td>
<td>0.85</td>
<td>700</td>
</tr>
<tr>
<td>GB (Southern)</td>
<td>March 1977</td>
<td>4.1</td>
<td>7</td>
<td>7</td>
<td>$2.5 \times 10^{-1}$</td>
<td>0.84</td>
<td>400</td>
</tr>
<tr>
<td>GB (Southern)</td>
<td>August 1977</td>
<td>21.0</td>
<td>7</td>
<td>12</td>
<td>$1.4 \times 10^{-1}$</td>
<td>0.08</td>
<td>190</td>
</tr>
<tr>
<td>GB (Apex)</td>
<td>March 1977</td>
<td>3.0</td>
<td>35</td>
<td>21</td>
<td>$4.3 \times 10^{-2}$</td>
<td>0.39</td>
<td>220</td>
</tr>
<tr>
<td>GB (Apex)</td>
<td>August 1977</td>
<td>24.2</td>
<td>12</td>
<td>16</td>
<td>$2.1 \times 10^{-1}$</td>
<td>0.07</td>
<td>510</td>
</tr>
<tr>
<td>GB (Midshelf)</td>
<td>April 1978</td>
<td>3.7</td>
<td>50</td>
<td>30</td>
<td>$4.1 \times 10^{-2}$</td>
<td>0.56</td>
<td>520</td>
</tr>
<tr>
<td>GB (Midshelf)</td>
<td>August 1977</td>
<td>25.0</td>
<td>30</td>
<td>42</td>
<td>$8.3 \times 10^{-2}$</td>
<td>0.25</td>
<td>310</td>
</tr>
<tr>
<td>GB (Shelf break)</td>
<td>October 1979</td>
<td>27.0</td>
<td>~55</td>
<td>84</td>
<td>$1.8 \times 10^{-2}$</td>
<td>0.47</td>
<td>110</td>
</tr>
</tbody>
</table>

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1 — average temperature in upper mixed layer.

* — depth of mixed layer.

** — depth of euphotic zone.

*** — calculated over $Z_*$.

The qualitative comparison of the vertical density and chlorophyll fields can serve as the basis of a hypothesis: a comparison between the density field and some property of the chlorophyll assemblage found in the chlorophyll maximum (cf. Reid et al., 1978). These results suggest that the vertical exchange between the upper mixed layer and the pycnocline is slower than phytoplankton growth rates.

These and other examples of the lack of correlation between water column stability and mixing can be demonstrated by inspection of the data in Table 2. The degree of stability is proportional to $d\sigma_t/ dz$ while the degree of recent mixing can be represented by an “evenness” coefficient of chlorophyll distribution; i.e., the ratio of the maximum chlorophyll value to the minimum chlorophyll value in the euphotic zone (cf. Cullen and Eppley, 1981). In four cases the chlorophyll evenness index exceeds 0.8 (i.e., the water column is well mixed with respect to chlorophyll), however, these ratios span over four orders of magnitude of vertical stability.

**Effects of vertical mixing on phytoplankton light history.** The qualitative comparison of the vertical density and chlorophyll fields can serve as the basis of a hypothesis: a comparison between the density field and some property of the chlorophyll...
Consider the effects of turbulence on the light history of phytoplankton on GB and in the NYB (e.g., Example 3). If the vertically uniform distribution of chlorophyll and phytoplankton species composition on GB throughout the year is a consequence of continuous tidal stirring, it can be hypothesized that the mixing processes occur on a time scale that is as fast as or faster than that to which cells can adapt to variations in the light regimes influenced by turbulence. This hypothesis is supported by the evidence that chl/P_{700} ratios at the surface and 1% light depths usually differ by less than 5% between the two isolumes (Table 2). In the midshelf of the NYB in the winter (Fig. 4b) the chlorophyll distribution suggests that phytoplankton sinking rates exceed the rate of vertical mixing, so that a cell at the surface might become progressively more shade adapted as it sinks deeper in the water.
column. This hypothesis is further supported by the evidence that chl/P700 ratios at the surface and 1% light depths differ by fivefold.

In this qualitative way it is suggested that vertical mixing processes influence not only the distribution of the phytoplankton biomass but also the distribution of some physiological, or biochemical, properties of the cells. To estimate the rate of vertical displacement of phytoplankton in the water column from a physiological or biochemical attribute, a number of criteria must be met. First, the attribute must vary on some time scale that is compatible with an understanding of vertical mixing processes. Second, it must vary over such a dynamic range as to be applicable in a study of the upper ocean. Third, it should not be influenced by a material resource factor such as nutrient limitation. Finally, the attribute should not be limited by a cropping factor such as grazing.

Time scale of change in chl/P700 ratios. For chl/P700 ratios to be useful in understanding vertical mixing processes in the upper ocean, the time scale of change must be compatible with mixing processes and, ideally, insensitive to first-order variations in light (i.e., diel changes). In August 1977 a subsurface chlorophyll maximum was observed in the midshelf of the New York Bight (Fig. 4d). The phytoplankton in this layer were composed almost entirely of large Coscinodiscus spp., especially C. concinnus (83%) and C. centralis (16%). A 36-h time-series station, made at 39°46.0′ N and 073°46.0′ W, provided an opportunity to follow diel changes in chl/P700 ratios in situ.

The chl/P700 ratios are plotted as a function of time of day in Figure 6. These data suggest that PSU sizes did not systematically vary with diurnal variation in incident light in situ in the subsurface chlorophyll maximum. However, the possi-
Figure 6. Effects of day-night variations on chlorophyll/P_{700} ratios in situ in a natural phytoplankton community consisting overwhelmingly of *Coscinodiscus* spp.

bility that PSU sizes undergo diel periodicity cannot be completely ruled out. Owens *et al.* (1980) have presented evidence suggesting that there is a diel periodicity on C/chl ratios in situ in near-surface waters during a diatom bloom on the Long Island Shelf. They inferred that this periodicity was primarily influenced by variations in intracellular chlorophyll. As it has been suggested that variations in chl/cell in diatoms are primarily due to variations in chl/P_{700} ratios (Falkowski and Owens, 1980; Perry *et al.*, 1981), diel periodicities in PSU sizes may occur near the surface but not at low light depths. To avoid temporal anomalies in vertical profiles of PSU sizes, samples were obtained at all depths simultaneously between 1000 and 1400 hours local time, and processed as rapidly as possible.

The rate constants for light-shade adaptation can be estimated from time-course studies of changes in size of PSUs following the transfer of shade-adapted phytoplankton to high light intensities or of light-adapted phytoplankton to shade. During the August 1977 *Coscinodiscus* bloom, a large phytoplankton sample was obtained from the 1% light depth, and subsamples of these populations were incubated on deck in natural sunlight at sea-surface temperatures. Chl/P_{700} ratios were frequently measured over the next 48 h. These results are plotted as the function \( R \), which is the ratio of chl/P_{700} ratios at times \( T_0 \) and \( T_n \), versus time (Fig. 7a).

Time-course studies of light-shade adaptation suggest that changes in chl/P_{700} ratios can be approximated by first-order kinetics as a function of changes in light intensity (e.g., Falkowski, 1980; Rivkin *et al.*, 1982). If the initial chl/P_{700} ratio \( R_s \) is normalized to 1.0, the rate of change of chl/P_{700} ratios can be approximated by the equation:
Figure 7. (a) Time course of changes in chl/P700 ratios following light adaptation of a shade-adapted natural phytoplankton community, dominated by *Coscinodiscus* spp., in the New York Bight. (b) The same data replotted in the log form, suggesting that light-shade adaptation follows first-order kinetics.

\[
\frac{dR_t}{dt} = -k(R_o - R_\infty) e^{-kt},
\]

where, \(k\) is a first-order rate constant.

Integration of Eq. (1) yields

\[
-k_t = \ln \left( \frac{R_t - R_\infty}{R_o - R_\infty} \right),
\]

where \(R_t\) is the chl/P700 ratio at time \(t\), \(R_o\) is the chl/P700 ratio at time zero, and \(R_\infty\) is the chl/P700 ratio at infinite time after adaptation.
The data in Figure 7a are plotted in the integrated form in Figure 7b to estimate $k_1$. From these data, $k_1$ is estimated as $5.5 \times 10^{-2} \text{ h}^{-1}$ at $25^\circ C$ ($r^2 = 0.90$, $n = 11$). Similar rate constants for light-shade adaptation were calculated from changes in chl/cell for individual species from batch and turbidostat culture experiments, and these calculations are summarized in Table 3. In culture, changes in chl/cell are highly correlated with changes in PSUs (Falkowski and Owens, 1980; Perry et al., 1981). Laboratory data suggest that there is very little hysteresis between a light-to-shade transition and a shade-to-light transition (Falkowski, 1983), but it is not clear to what extent $k_1$ is itself a function of the magnitude of change in the light field. The data in Table 3 suggest that this effect may be small, but to avoid unnecessarily complicating the field data, only the surface and 1% light depths were analyzed.

The effect of temperature on the rate constants for light-shade adaptation is somewhat uncertain in natural systems. Owens et al. (1978) estimated a $Q_{10}$ for chlorophyll biosynthesis in the neritic diatom, *Skeletonema costatum*, as $ca 2.5$. The data of Hitchcock (1977) suggest a mean $Q_{10}$ in *S. costatum* and *Detonoma confervacea* of $ca 1.5$ for changes in cellular chlorophyll. The discrepancies between the various $Q_{10}$ values may indicate that the temperature coefficient of light-shade adaptation is species specific, and/or may reflect differences in sampling frequency by various researchers. Assuming, however, that the rate of change of chl/PSU ratios is dependent on the rate of enzymatic activity involved in chlorophyll metabolism, a generalized $Q_{10}$ of $ca 2.0$ is probably applicable in natural phytoplankton communities. If a $Q_{10}$ of $2.0$ is applied to the first-order rate constants calculated for light-shade adaptation given in Table 3, the average for $k_1$ at $15^\circ C$ is estimated as $(2.8 \pm 0.9) \times 10^{-2} \text{ h}^{-1}$.

Using this value of $k_1$, it is possible to calculate how far apart in time samples taken from depths $z$ and $z \pm \Delta z$ are by rearranging Eq. (2) and solving for $t$, such that

$$t = \frac{1}{-k_1} \ln \left[ \frac{(R_t-R_\infty)}{(R_\infty-R_\infty)} \right]. \quad (3)$$

The effect of temperature modification on $k_1$ can be modeled by the equation:

$$k_1 = 0.0099 e^{0.0097 T}, \quad (4)$$

where $T$ is in $^\circ C$.

**Dynamic range.** To solve Eq. (2) numerically, the dynamic range $(R_\infty-R_\infty)$ must be known. If we take the initial high light-adapted chl/PSU ratio $(R_\infty)$ of a given population to be 1.0, the dynamic range will be given by the maximum chl/PSU ratio measured in a shade-adapted population.

The primary environmental factor influencing chl/PSU ratios is light. Over a range of light intensities from 2000 to 20 $\mu E \text{ m}^{-2} \text{ sec}^{-1}$ (ca the range from 100 to 1% of full sunlight), the change in chl/PSU ratios is maximal (Falkowski and Owens,
Table 3. Estimation of first-order rate constants for light-shade adaptation in marine phytoplankton.

<table>
<thead>
<tr>
<th>Species</th>
<th>Light-regime</th>
<th>$T$ (°C)</th>
<th>$k_i$ (h⁻¹)</th>
<th>$k_i^{15}$ (h⁻¹)*</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Skeletonema costatum</em></td>
<td>14/10 LD (fluorescent)</td>
<td>15</td>
<td>$2.6 \times 10^{-2}$</td>
<td>$2.6 \times 10^{-4}$</td>
<td>Falkowski and Owens (1980)</td>
</tr>
<tr>
<td><em>Skeletonema costatum</em></td>
<td>12/12 LD (fluorescent)</td>
<td>20</td>
<td>$6.2 \times 10^{-2}$</td>
<td>$4.7 \times 10^{-4}$</td>
<td>Hitchcock (1977)</td>
</tr>
<tr>
<td><em>Detonula confervacea</em></td>
<td>12/12 LD (fluorescent)</td>
<td>10</td>
<td>$1.7 \times 10^{-2}$</td>
<td>$2.1 \times 10^{-4}$</td>
<td>Hitchcock (1977)</td>
</tr>
<tr>
<td><em>Phaeodactylum tricornutum</em></td>
<td>24 h (fluorescent, turbidostat)</td>
<td>20</td>
<td>$3.0 \times 10^{-2}$</td>
<td>$2.3 \times 10^{-4}$</td>
<td>Beardall and Morris (1976)</td>
</tr>
<tr>
<td>Natural populations</td>
<td>natural light (~14/10 LD)</td>
<td>25</td>
<td>$5.6 \times 10^{-2}$</td>
<td>$2.8 \times 10^{-4}$</td>
<td>this paper</td>
</tr>
<tr>
<td>(mostly <em>Coscinodiscus</em> spp.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dunaliella tertiolecta</em></td>
<td>24 h (fluorescent, turbidostat)</td>
<td>15</td>
<td>$2.2 \times 10^{-2}$</td>
<td>$2.2 \times 10^{-4}$</td>
<td>Falkowski (1983)</td>
</tr>
</tbody>
</table>

* $k_i^{15}$ is the rate constant calculated for 15°C from $k_i$ assuming a $Q_{10}$ of 2.0.
Below 20 \( \mu \text{E m}^{-2} \text{ sec}^{-1} \), cells tend to bleach, and there is a concomitant decrease in chl/P\(_{700}\) ratios. Over the range of light intensities a cell would experience in the euphotic zone, the ratio of chl/P\(_{700}\) obeys a log function of light intensity (Falkowski and Owens, 1980) and therefore would be expected to vary linearly with depth in the water column (Falkowski and Wirick, 1981). A minimum value for the ratio of chl/P\(_{700}\) values for fully light-adapted and fully shade-adapted cells, both in culture (see Falkowski and Owens, 1980; Perry et al., 1981; Ley and Mauzerall, 1982) and in the field, is ca 0.067; i.e., chl/P\(_{700}\) ratios at the 1% light depth do not appear to be more than fifteen times the chl/P\(_{700}\) ratio at the 100% light depth (Table 2). The value of \( R_a \) in Eq. (2) is taken to be 0.067, and thus \( (R_a - R_w) = 0.933 \).

Resource factors. Of the limiting resource factors potentially influencing the distribution of chl/P\(_{700}\) ratios, inorganic nitrogen and/or phosphate are likely to have the greatest influence. In the summer, in the upper mixed layer of the NYB, inorganic nitrogen is frequently undetectable; however, phytoplankton assimilation numbers are often maximal (Falkowski, 1981). In August 1977, whole natural seawater samples were taken in the midshelf of the NYB at 12 m, which corresponded to ca 5% light depth. These samples, containing less than 1.5 \( \mu \text{M} \) total dissolved inorganic nitrogen (\( \text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+ \)) and less than 0.50 \( \mu \text{M} \) PO\(_4^{3-}\), were enriched to 50 \( \mu \text{M} \) with \( \text{NO}_3^- \) and to 10 \( \mu \text{M} \) with PO\(_4^{3-}\). Over the next 72 h, the samples were incubated on the deck in 20-l polypropylene carboys at sea-surface temperatures. The carboys were screened to 5% light and incubated in natural sunlight while chl/P\(_{700}\) ratios were monitored.

In this experiment (Fig. 5) the chl/P\(_{700}\) ratios did not change significantly in nutrient enriched samples, as compared with unenriched samples, during the first 24 h, and increased thereafter. These results suggest that intracellular reserves of nutrients may be adequate to maintain the integrity of the size of PSUs for about a day.

Nutrient limitation may decrease the size of PSUs by forcing chlorosis (Falkowski, 1980). Off the coast of Hawaii, chl/P\(_{700}\) ratios are lower than those generally observed under similar temperature and nutrient regimes in the NYB. These results suggest that chl/P\(_{700}\) ratios may be influenced by nutrient limitation in oligotrophic regions.

Cropping factors. There are two major cropping factors influencing the distribution of phytoplankton: grazing and sinking. The ratio of the number of chlorophyll molecules to the number of P\(_{700}\) molecules is an intrinsic property of a given cell. Unlike phaeophytin/chlorophyll ratios, grazing stress is unlikely to alter chlorophyll/P\(_{700}\) ratios. While the vertical distribution of chlorophyll might be influenced by vertical variations in grazing pressure, the distribution of chl/P\(_{700}\) ratios within
the chlorophyll profile will not be affected; the chemical composition of the ungrazed cells is not influenced by those cells which have already been consumed.

Sinking rates are likely to affect the vertical distribution of chl/P_{700} ratios in the water column, as these ratios are influenced by changes in light intensity. As the vertical displacement of cells in a turbulent ocean is a balance between sinking and mixing, changes in chl/P_{700} ratios potentially can be used to estimate the net displacement rate at phytoplankton *in situ*.

**Estimating vertical mixing rates.** The data and arguments presented in the preceding sections suggest that chl/P_{700} ratios can fit the criteria required for estimating vertical mixing rates of phytoplankton in natural waters. If it is accepted that the effects of turbulence can influence the light regime experienced by a cell, and that a cell can adapt to variations in light regimes by altering the size of photosynthetic units (i.e., it can light-shade adapt via changes in chl/P_{700} ratios), it is possible to estimate the rate at which phytoplankton are translocated by vertical mixing processes from knowledge of the vertical variations in chl/P_{700} ratios.

By modifying Eq. (3), the rate at which phytoplankton at depth \( z \) are displaced to depth \( z \pm \Delta z \) is given by the equation:

\[
\frac{\Delta z}{\Delta t} = \frac{\Delta z(-k_i)}{\ln \left( \frac{R_t - R_m}{R_o - R_m} \right)}.
\]

Using Eq. (5), apparent maximum and/or minimum vertical displacement rates are estimated for various cases on GB, in the NYB, and in the SP (Table 2). These calculations are average displacement rates or piston velocities for the entire euphotic zone (i.e., to the 1% light depth) and include the temperature correction inferred from Eq. (4).

The results of these calculations suggest that vertical displacement rates vary by about two orders of magnitude in the regions studied (from ca 10^{-1} to 10^{-3} cm/sec). If the mean vertical displacement rates in the euphotic zone (\( Z_o \)) are applied to the upper mixed layer (\( Z_m \)), it is possible to estimate turnover times for mixed layer when \( Z_m > Z_o \). These estimates range from ca 0.1 d^{-1} to 10 d^{-1}.

Without direct simultaneous measurements of vertical mixing, it is difficult to verify these calculations with physical evidence. The least temporal variance in the estimated vertical displacement rates is observed on GB. The data (Table 2) suggest that mixing rates in this region are only about two times greater in the early spring than in the early fall. Although the region is continuously mixed by tidal stirring, the potential energy (positive buoyancy) of the water column increases as the water column heat content increases. In the fall, the water column on GB requires more kinetic energy to dissipate vertical heat gradients. As tidal energy available for mixing does not increase in warmer months, the rate at which density gradients are dissipated is decreased. The increased vertical stability on GB in the
early fall, associated with increased heat content, is physiologically reflected in the tendency of phytoplankton to become more shade adapted near the bottom of the euphotic zone; i.e., their apparent residence time at the bottom of the euphotic zone is increased. Thus, the ratio of PSU sizes between the surface and 1% light depths decreases from 0.95 in the spring to 0.78 in the fall. The vertical displacement rates on GB estimated by the PSU method described here agree well with estimations of vertical mixing based on heat flux calculations (Hopkins and Garfield, 1981).

Compared with GB, the vertical mixing rates in the NYB appear to be much more variable (a factor of ~30). On GB tidal stirring is a very predictable source of energy for mixing, while in the NYB the major energy sources for mixing are wind stress and convective overturn, which are much more stochastic forcing functions. It seems counter-intuitive that vertical mixing rates in the middle of March in the middle of the continental shelf of the NYB could be lower than in subtropical Pacific near Hawaii (Table 2). The results of the calculations presented here do not necessarily reflect the “average” vertical mixing condition for the season and region indicated. For example, on March 15, 1977, the day the midshelf station in the NYB was sampled, wind stress was very low (~0.1 dyne/cm²) and only a small portion of this wind energy is used for vertical mixing (Kullenberg, 1976). This relatively low wind stress, in combination with the early onset of thermal stratification (Fig. 4b), apparently resulted in low vertical mixing. Qualitatively low mixing rates could be inferred from the vertical chlorophyll profile. The phytoplankton were dominated by net plankton (> 20 μm) diatoms, which have sinking rates on the order of 10^{-8} cm/sec (Smayda and Boleyn, 1966; Bienfang, 1980). Vertical mixing rates greatly in excess of this sinking rate would tend to equalize the distribution of chlorophyll, while mixing rates equal to or less than this sinking rate would lead to an increase of chlorophyll near the bottom of the water column (Bienfang, 1980).

Of the vertical mixing calculations presented, probably the most unreliable is that for the SP. Because of extreme nutrient impoverishment at the surface and not at the 1% light depth, the dynamic range of the P_{700} technique was approached, such that the calculated mixing rate has to be taken as a maximum. It is highly likely that the actual mixing rates in this region were lower.

It is interesting to note that there is apparently a linear relationship between \( R_t \) and the ratio of \( P_{\text{max}}^B \) (in μg C μg chl\(^{-1}\) h\(^{-1}\)) values obtained at the surface and 1% light depths from \( P \) vs \( I \) curves. Based on this small data set (\( n = 6 \)), the correlation coefficient between \( R_t \) and the ratio of \( P_{\text{max}}^B \) values is 0.91 and \( [R_t = 0.97 \left( \frac{P_{\text{max}}^B Z_o}{P_{\text{max}}^B Z_e} \right) - 0.25]. \) These results suggest that the ratio of light-saturated assimilation numbers simultaneously obtained from the surface and 1% light depths in short-term incubations could be used to estimate vertical mixing in a fashion similar to that described for chl/P_{700} ratios.
Vertical mixing plays an important role in the regulation of primary production in each of the three regions examined. On GB, primary production is estimated as ca 450-500 g C m$^{-2}$ yr$^{-1}$ (Cohen et al., 1981; Falkowski, unpubl). On the shallow southeast portion of the Banks the critical depth almost always exceeds the bottom, and tidal stirring, along with the normal circulation around the region (Hopkins and Garfield, 1981), provides sufficient nutrient inputs to drive the high production. In the NYB, primary production is estimated at 250-300 g C m$^{-2}$ yr$^{-1}$, 40% of which occurs in the spring bloom (March to April). In the summer, strong vertical density gradients in the NYB prevent the vertical mixing of nutrient-rich water into the euphotic zone, which in turn leads to a reduced annual production compared with nearby GB. If, during the most productive times of the year, the water column is not mixed at a rate exceeding phytoplankton sinking rates, there will be a tendency for poorer coupling between primary and secondary pelagic production (Dagg and Turner, 1983). The less predictable mixing regime in the NYB may result in relatively large losses of phytoplankton due to sinking and subsequent export (Walsh et al., 1981).

4. Conclusions

In the early years of oceanography, phytoplankton ecologists used floristic evidence and their taxonomic skills to trace water masses. The data and arguments presented here suggest that, on a smaller scale, physiological features of phytoplankton can be used as means of understanding turbulence in the upper ocean. While the specific technique described here is hardly routine, in future years other simpler methods, such as fluorescence induction (Harris, 1980; Fujita, per. comm.), which also use light gradients and physiological responses, may be used more routinely to estimate vertical mixing.


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