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In situ response of phytoplankton fluorescence to rapid variations in light\(^1\)

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**Abstract**  
Phytoplankton chlorophyll \(a\) fluorescence responded to rapid fluctuations in light intensity in Lake Tahoe at three depths: 10, 35, and 60 m. Fluorescence yield was negatively correlated with surface irradiance at all depths, but there was a strong depth dependence in the intensity of this response. Phytoplankton at 35 m reacted more strongly to fluctuations than those at 10 or 60 m and therefore could show a noticeable response to more rapid variations. This may have been due to near-optimal light levels at 35 m, light inhibition at 10 m, and light limitation at 60 m.

Rapid fluctuations in irradiance may significantly affect both the process and measurement of photosynthesis (Galllegos et al. 1980). The amount of irradiance reaching a phytoplankton cell can vary due to fluctuations in the amount of solar radiation reaching the water surface (e.g., intermittent cloud cover: Marra 1980a), to surface waves (Dera and Gordon 1968), or to vertical motions within the water column (Marra 1980b). Such fluctuations, of the order of several minutes to a few hours, may increase net photosynthesis, presumably because photosynthesis would increase during constant high light conditions (Harris and Lott 1973; Harris and Piccinin 1977) or because of a time dependence of the photosynthesis-light relationship (Marra 1978a,b). This ability to respond to light fluctuations may be species-specific (Perry et al. 1981). The fluorescence system also responds to rapid changes in irradiance, as first described by Kautsky (Kautsky and Hirsch 1931; Kautsky et al. 1932). The Kautsky induction effect, in which changes in fluorescence are inversely proportional to changes in irradiance, has been shown for several phytoplankton populations from both cultures and natural waters (e.g., Kiefer 1973; Loftus and Seliger 1975; Heaney 1978). Fluorescence represents a loss of free energy that could otherwise be used in the electron transport system within photosynthesis, and its relationship to photosynthesis and associated time scales is discussed by Harris and Piccinin (1977) and Harris (1980).

We report here measurements of in situ fluorescence of natural phytoplankton populations in Lake Tahoe and concurrent measurements of solar radiation. The sky was partly cloudy so that the phytoplankton were subjected to a spectrum of light fluctuations of various durations. The effect of depth was also investigated during this experiment.

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**Methods**  
Lake Tahoe is on the California-Nevada border at 1,897 m and is ultraoligotrophic (avg Secchi depth 30 m: Smith et al. 1973). Our observations were made on 13 June 1980, at an anchor station in 115 m of water about 500 m from the west shore. Despite variable west winds (5–10 m·s\(^{-1}\)), the lake surface was dominated

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by small gravity (10 cm) and capillary waves because of the small fetch at this station. The fluctuations in incident light as clouds passed over the vessel were used to examine the response of phytoplankton fluorescence to fluctuating irradiance.

Light was measured with an Eppley model 8-48 flatplate radiometer mounted at the top of a mast about 5 m above the water surface. This type of measurement does not strictly represent the light climate at depth, as surface waves can create additional irradiance fluctuations (Dera and Gordon 1968; Snyder and Dera 1970; Fraser et al. 1980). However, with small waves these effects are confined to the top few meters even in clear water.

Fluorescence was measured with an in situ fluorometer system (Endeco model 815, Turner Designs model 10 fluorometer with red-sensitive photomultiplier tube) equipped with a pressure transducer and a thermost. The use of an in situ fluorometer minimized the problems of changes in light exposure that can occur during transit in a hose to a shipboard fluorometer (Loftus and Seliger 1975). The residence time in the fluorometer was <0.5 s. The measured fluorescence signal was therefore influenced by changes in natural light, rather than by phytoplankton response to a dark hose. The fluorescence, temperature, and light signals were sampled every 1.4 s and recorded on magnetic tape.

The fluorometer was held for 1 h at each of three depths, 10, 35, and 60 m, corresponding to approximately 50, 20, and 2.5% of incident surface radiation. Partly cloudy skies can significantly change the amount of light reaching a particular depth: light levels varied from about 0.75 to 0.25 ly·min⁻¹ at 10 m, 0.3 to 0.1 ly·min⁻¹ at 35 m, and 0.03 to 0.01 ly·min⁻¹ at 60 m (699.3 W·m⁻² = 1 ly·min⁻¹). Biological conditions differed between these three depths. Measurements at Lake Tahoe (Goldman 1974; Tilzer et al. 1975; Holm-Hansen et al. 1976) indicate that production is light inhibited at depths <20 m, at least under the conditions of fixed-depth bottle measurements. Primary production is maximal between 35 and 45 m, while a biomass maximum forms between 60 and 100 m (Richerson et al. 1978). The species compositions are also different at these three sampling depths (Lopez 1978).

Phase and squared-coherence functions between light and fluorescence were used to analyze the data (see Denman 1975; Bath 1974; Jenkins and Watts 1968). The response of fluorescence to light fluctuations of varying times, the presence of any delay time in the response, and the relationship of these responses to depth can be investigated with these techniques. Subsets of 2,048 points were selected from the time series and detrended with a least-squares fit. To minimize the nonstationarity in the fluctuating light signal imposed by the strong diurnal cycle, we made these measurements between 1030 and 1400 hours. The mean and variance from the three depth series were nearly identical.

Phase and squared-coherence spectra were calculated by the fast Fourier transform technique (Enochson and Otnes 1968) using a modified computer routine (Bergland 1969). From the 2,048 spectral estimates, 128 average estimates were formed from averages of 16 adjacent frequencies. This procedure increases the statistical reliability of each estimate but reduces the maximum time scale that can be resolved. A bias corrector (Benignus 1969) was applied to each squared-coherence estimate. Confidence limits (80%) from the χ² distribution were calculated for each squared-coherence estimate and variance spectrum estimate (Jenkins and Watts 1968).

Results

Figure 1 shows the average vertical structure of fluorescence and temperature during the experiment. Since we are interested in the physiological response to light variations, fluorescence values are presented rather than chlorophyll a concentrations. (On the basis of chloro-
phyll extractions, one fluorescence volt is about 1 mg·m⁻² Chl a.)

The time series of temperature, chlorophyll fluorescence, and light from 10, 35, and 60 m are shown in Fig. 2. Fluorescence generally declines with the increase in light over the sampling period at 10 m. There is also a negative relationship between the two variables at shorter time scales, for example between 20 and 25 min. However, there are several episodes of light variation where there is no apparent relationship. There are two differences between the series from 35 m and that at 10. First, the intensity of the fluorescence change with light fluctuations at 35 m is much stronger; second, the response of phytoplankton to shorter fluctuations of time scale in light is more apparent. The series from 60 m is similar to that from 10, although the changes in fluorescence seem to be smaller. Light fluctuations of long duration cause little change in fluorescence.

The frequency spectrum of light variations should be similar in all three sets of data if we are to compare the series properly. Figure 3 shows the spectra of light variations from 10, 35, and 60 m. The y-axis is the product of the frequency, \( k \), and the spectral estimate, \( S_k \). This representation differs from the usual log-log plots in that equal areas under the spectrum represent equal variances. The spectra from 35 and 60 m are nearly identical (within 80% confidence limits). However, the spectrum from 10 m is different at 0.007 Hz and from 0.012 to 0.015 Hz. At these frequencies the intensity of light fluctuations is lower than at the oth-
er two depths. However, this should not affect the coherence between light and fluorescence. Only if there is a complete absence of light fluctuations at a particular frequency or if the fluorescence fluctuations are below the noise level of the fluorescence signal should the coherence be affected, assuming that fluorescence can respond to variations at that particular time scale.

Table 1 lists the C.V. (SD : mean) of light and fluorescence for the three series. All three pairs of series had significant negative cross-correlation coefficients (−0.55 for 10 m and 60 m, −0.95 for 35 m), as expected from previous work on the Kautsky induction effect in phytoplankton. These values were determined from the cross-correlation function (ccf) and did not occur at zero lag. Rather, the maxima in the ccf occurred at about −15 to −40 s, indicating that changes in fluorescence lagged changes in light.

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>C.V. Light</th>
<th>C.V. Fluorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>0.66</td>
<td>0.12</td>
</tr>
<tr>
<td>35</td>
<td>0.59</td>
<td>0.10</td>
</tr>
<tr>
<td>60</td>
<td>0.54</td>
<td>0.03</td>
</tr>
</tbody>
</table>
We calculated the squared-coherence (Fig. 4) and phase spectra (Fig. 5) to find the strength of the correlation between light and fluorescence and their phase difference at each fluctuation frequency (0° represents positive correlation; 180° represents negative correlation). At 10 m there is significant coherence between light and fluorescence at time scales longer than about 0.011 Hz (90 s). At shorter scales no consistent pattern emerges, with coherence usually not significantly different from zero. The occasional significant peaks are probably spurious (80% confidence intervals suggest that one in five will appear significant by chance). Coherence is high at long time scales but becomes insignificantly different from zero at a scale of about 0.035 Hz (30 s) in the series at 35 m. Again, coherence is erratic at shorter scales. At 60 m,
the squared-coherence is significant at scales longer than 0.004 Hz (250 s),
though it might be significant to about 0.007 Hz (150 s) if we neglect the band
at 0.0045 Hz (220 s).

The behavior of the phase spectra (Fig. 5) supports our interpretations of the
squared-coherence spectra. A smoothly varying phase spectrum usually indicates
significant coherence while rapid fluctuations through 0° are typical of uncorrelated
series (Denman 1975). Such a criterion gives time scales for coherence similar to those
determined from the coherence spectra.

From these phase and squared-coherence spectra, we note that the effects of
lower intensity light fluctuations at 10 m are probably insignificant. At low fre-
cuencies, coherence is less than 10 than at 35 m, although the intensity of light fluc-
tuations is the same. At frequencies higher than 0.011 Hz and lower than
0.035 Hz, light and fluorescence are not coherent at 10 m but are coherent at 35
m. Again, the light variance spectra are identical at these frequencies. Therefore,
it seems unlikely that the lower light variance from 0.012 to 0.015 Hz at 10 m
is the reason for the lower coherence between fluorescence and light at 10 than
at 35 m.

Discussion

The data reported here may be the first field observations of the Kautsky fluo-
rescence induction effect in phytoplankton, which has been observed previously only
under controlled conditions (Loftus and Seliger 1975; Heaney 1978; Harris 1980).
Changes in fluorescence are negatively correlated with changes in surface light
and lag changes in irradiance by about 15–40 s, near the value measured by Kie-
fer (1973: fig. 6). In diatoms (Kiefer 1973; Harris and Piccinin 1977), this response
is due to conformational changes in the chloroplasts, affecting the fluorescence
yield of the cell and hence its photosynthetic rate. This induction effect and its
associated lag time is relatively unaffected by the wide range of light intensities
(0.01–0.75 ly·min⁻¹) over our measured depth range.

Our work bears on the effects of a naturally occurring broad frequency spec-
trum of irradiance fluctuations on this flu-
orescence response. First, despite the
lack of control over the light fluctuation
regime that there is in laboratory exper-
iments, we were able to detect fluores-
cence induction at several depths. Sec-
ond, there is a depth dependence of the
intensity of the fluorescence response
and the minimum time scale where flu-
orescence and light are coherent. The
most intense response (as determined by
the level of the squared-coherence func-
tion which is normalized by the product
of the variances of the two signals in each
frequency band) occurred at 35 m and the
minimum at 60 m. In addition, the more
intense response allows higher fre-
cuency fluctuations to be tracked by the phy-
toplankton. That is, at depths where the
response is small, high frequency fluo-
rescence fluctuations are not distinguish-
able from noise, and light and fluores-
cence are not coherent. Therefore, the
most intense fluorescence response has
the minimum significant fluctuation time
scale: 30 s at 35 m, 90 s at 10 m, and 150
s at 60 m. The similarity in delay times
for the three depths suggests that the flu-
orescence response is similar except in
its intensity.

Variations in the intensity of the fluo-
rescence induction effect observed by
Kiefer (1973), Loftus and Seliger (1975),
and Harris and Piccinin (1977) have been
explained by species differences, photo-
synthetic rate, and nutrient depletion.
Although there are species differences
with depth in Lake Tahoe (Lopez 1978),
we did not identify species during this
experiment. Both Kiefer and Loftus and
Seliger noted that the intensity of the flu-
orescence response increased with in-
creasing nutrient stress and decreasing
photosynthetic rates, but nitrate concen-
trations on 9 June 1980 from a station 1
km north of our sampling station were
constant, from the surface to 75 m, at 0.07
mmol·m⁻³ (C. Goldman pers. comm.).
Nor do depth-varying photosynthetic
rates seem to explain the observed depth dependence of fluorescence induction. Phytoplankton photosynthetic rates in Lake Tahoe are usually highest between 20 and 40 m (Tilzer et al. 1975; Holm-Hansen et al. 1976). Although photosynthesis was not measured during this experiment, it seems unlikely on the basis of previous work that phytoplankton at 10 and 60 m were photosynthesizing more rapidly than phytoplankton at 35 m, where the intensity of fluorescence induction was greatest. Thus, neither nutrients nor photosynthetic rates seem to explain the observed depth dependence.

A hypothesis relating the mean light regime and phytoplankton photosynthesis can be invoked to explain the observed fluorescence response as a function of depth. Phytoplankton at 10 m show some photosynthetic light inhibition (Tilzer et al. 1975) because intensities are high and therefore may be restricted in their ability to respond to fluctuations in irradiance. It seems unlikely that phytoplankton at 10 m were still recovering from exposure to high light before our experiment since the period before sampling had only brief sunny periods. After brief exposures to high irradiance, fluorescence recovers rapidly (Kiefer 1973). The fluorescence response of phytoplankton at 10 m is restricted by changes in the photosynthetic system during repeated daily exposure to inhibiting light intensities. Irradiance at 60 m on the other hand is <5% of the surface value, well below the level for optimal photosynthesis. A change in irradiance here has little effect on the photosynthetic system, which must capture as much irradiance as possible at low levels. The partitioning of energy to fluorescence and to the electron transport system will change only slightly with fluctuating irradiance. At 35 m, irradiance is 20% of the surface value and is likely to be near-optimal for phytoplankton photosynthesis. Phytoplankton at this depth are not restricted by high or low irradiance in their response to fluctuating light intensities and can react strongly to these fluctuations.

The reaction of phytoplankton to light fluctuations may be quite different in other situations. The biomass maximum in Lake Michigan is in the thermocline near the 1% light level (Brooks and Torke 1977). Low light populations could therefore frequently be subjected to near-optimal irradiance due to vertical displacement by internal waves. A comparison of data from a system having a shallow euphotic zone with the results from Lake Tahoe may elucidate the important physiological processes.

Our data confirm those of Harris (1980) in regard to the rapid variation of fluorescence due to fluctuations in irradiance. The comparison of fluorescence yield with photosynthetic rate is difficult because photosynthesis (with its slower response time) will reflect fluctuations on a longer time scale. Our results further suggest that rapid changes in fluorescence yield are also influenced by longer term changes in irradiance conditions.

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