

Survival of aphotic phytoplankton in Lake Tahoe throughout prolonged stratification

WARWICK F. VINCENT

With 1 figure and 3 tables in the text

Introduction

The deep aphotic zone of Lake Tahoe, California-Nevada, contains a large population of viable phytoplankton. A preliminary study by KIEFER et al. (1972) demonstrated that the greater proportion of algal biomass in Tahoe is located below the compensation depth, and in a subsequent extension of this work TILZER et al. (1977) described the controlling influence these deep living populations have on the extent of Tahoe's phytoplankton bloom each spring.

It is possible that viable aphotic populations in Lake Tahoe represent recent inocula from overlying euphotic waters and that aphotic conditions can be endured for only very short periods of time. In the pioneer work on Tahoe's aphotic zone by KIEFER et al. (1972) the distribution of deep living phytoplankton was related to the passive sinking of algal cells. To test this hypothesis, six phytoplankton species were brought into unialgal culture from 450 m water samples ($Z_{\max} = 500$ m) and settling velocities were determined experimentally on these isolates.

Chlorophyll data collected throughout 1976-1977 demonstrate that complete lake mixing did not occur in the winter of early 1976 and that consequently the residence time of deep aphotic populations might exceed 12 months. The present study examines the ability of these aphotic algae to begin photosynthesis upon re-exposure to euphotic light levels with particular reference to the rate at which dormancy is broken and photosynthesis initiated. As a further guide toward aphotic photosynthetic potential the activity of ribulose 1.5-diphosphate carboxylase (RuDPCase) was assayed down the water column. This enzyme catalyses the rate determining step of the dark reactions (reductive pentose phosphate cycle) of photosynthesis (KELLY et al. 1976) and data from these assays were therefore considered a useful supplement to chlorophyll data which specifically relate to the light reactions of photosynthesis.

Methods

Chlorophyll determinations were performed by fluorometric assay of acetone extracts (STRICKLAND & PARSONS 1968) from samples collected between December 1975 and April 1977 at approximately six weekly intervals. Sampling was with 30 liter Niskin bottles at a mid-lake station, every 50 m down the water column.

For the assay of dark reaction potential, four to eight liters of lake water were filtered under low (< 500 torr) vacuum pressure through 0.45 μm membrane filters. The filters were immediately placed on dry ice and RuDPCase activity assayed by the rapid-freeze technique of MUKERJI & MORRIS (1976). Cellular carbon was estimated by ATP assay (HOLM-HANSEN & BOOTH 1966).

To determine whether dormancy of aphotic phytoplankton is gradually broken, or whether algal cells are capable of fixing carbon at maximum rates immediately upon re-exposure to euphotic light levels, the following experiment was conducted. Water was collected at a mid-lake station in the middle of the night (no moon) to prevent any prior

light effects; subsamples were dispensed into 125 ml light and dark pyrex bottles and photosynthesis was measured by the $^{14}\text{C-HCO}_3^-$ technique (STEEMANN NIELSEN 1952, as modified by GOLDMAN 1963) over the first four hours exposure to light in the laboratory at 2500 lux, 5 °C. Further aliquots of the same water were dispensed into two liter translucent plastic bottles and subsampled after 4, 68 and 116 hours further exposure to light for similar photosynthetic rate measurements. Dissolved inorganic carbon was monitored in the two liter bottles by infra-red CO_2 analysis.

Aphotic phytoplankton were isolated from Lake Tahoe into unialgal culture by nutrient enrichment of 450 m water samples followed by streak plating on to defined inorganic media solidified with 2% agar (details in VINCENT 1977). Sedimentation velocities were determined on these isolates by a cell enumeration technique. Cells were first suspended in 0.45 μm membrane filtered lake water and dispensed into 10 100 ml measuring cylinders. At various intervals the upper 20 ml of duplicate cylinders were siphoned off and cell densities measured using a FUCHS ROSENTHAL haemocytometer. Settling rates (V) calculated as

$$V = \frac{1.85 \times 10^{-2} \text{ m}}{T_{50}}$$

where T_{50} is the time for cell densities in the top 20 ml to decrease by 50% and 1.85×10^{-2} m is the average distance a cell must sink to fall out of the upper 20 ml.

The sedimentation was performed in the dark at 5 °C.

Results

1. Chlorophyll levels in the aphotic zone

During lake mixing in February and March of 1976 the chlorophyll content of the 150—250 m stratum of Tahoe dramatically increased (Fig. 1), presumably as a result of down mixing of the chlorophyll rich waters of the deep chlorophyll maximum which normally lies between 90 m and 140 m. Over the next three months chlorophyll levels of this zone exponentially declined with a "half life" of 2.04 months. A slight increase between June and September was associated with the development of deep euphotic algal populations which achieved maximum population densities during this period. In November 1976 the effects of surface mixing were once again detectable in this region. In the 250—350 m stratum the effects of mixing are also apparent in 1976 and 1977, in both cases one to two months after they are detectable in the above stratum. Chlorophyll levels in the bottom-most 100 m stratum of the lake exhibited none of the fluctuations of the higher levels and between December 1975 and December 1976 the chlorophyll content of this zone remained statistically unchanged ($H_0: \beta = 0$, $t = 0.35$ $p > 0.5$). Therefore little exchange occurred between this stratum and overlying waters during surface mixing in the winter of 1975—1976.

2. Dark reaction potential of the aphotic zone

RuDPCase activity per liter decreased by almost a factor of 8 between 50 m and 250 m (Table 1). Between 250 m and 450 m there was no significant difference in enzyme levels ($F = 0.22$, $P > 0.25$). Per unit biomass, however, the maximum decrease in enzyme activity was by a factor of 3 between 50 m and 250 m ($F = 8.08$, $p = 0.05-0.1$) and there was no significant difference between 50 m and 450 m cellular levels ($F = 2.26$, $P > 0.1$).

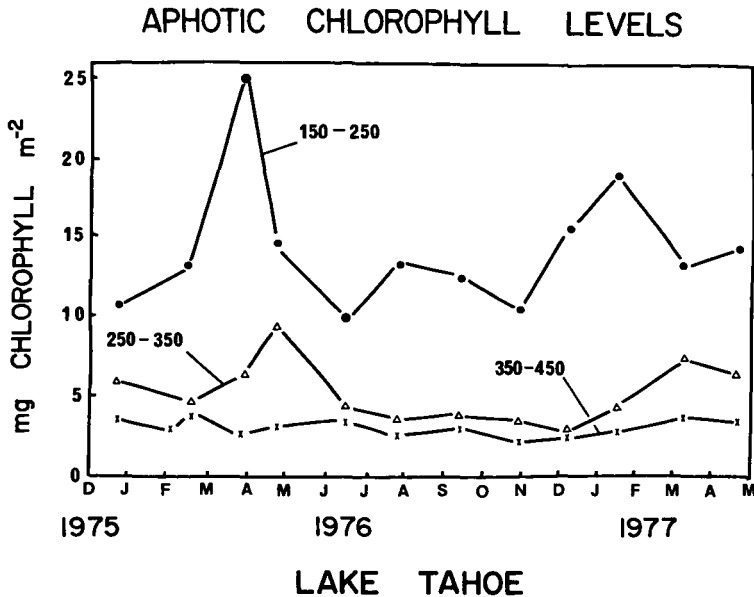


Fig. 1. Integral chlorophyll levels for 100 m strata in Lake Tahoe's aphotic zone between December 20, 1975 and April 22, 1977. Each curve is the trapezoidal integration of chlorophyll concentrations determined from discrete samples at 50 m intervals by fluorometric analysis of acetone extracts. Values phaeophytin corrected.

Table 1. Dark reaction potential down the water column as measured by RuDPCase activity, September 16, 1976. Each figure is the mean activity (nmoles CO_2 fixed hr^{-1}) of duplicates. Biomass carbon estimated by ATP.

Depth (m)	RuDPCase l^{-1}	RuDPCase ($\mu\text{g biomass C}$) $^{-1}$
50	0.241	0.044
250	0.031	0.015
450	0.040	0.028

3. Rate of photosynthetic initiation

Aphotic phytoplankton began photosynthesis immediately upon exposure to light and photosynthetic rates were not significantly increased by up to 116 hours further preincubation at 2500 lux (Table 2). The only significant different in the orthogonal comparisons [(0 hr light — 0 hr dark) — (116 hr light — 116 hr dark)] is a decrease in photosynthetic ability of 150 m water samples ($F = 5.14$, $p = 0.05-0.1$).

4. Sedimentation rates

Sinking velocities for all species examined are extremely low (Table 3). The highest recorded was 106.3 m yr^{-1} for *Fragilaria crotonensis*, stationary phase; the minimum recorded was 1.1 m yr^{-1} for *Choricystis* sp. For most species settling velocity varied greatly with growth phase.

Table 2. Photosynthetic rates ($\mu\text{g C m}^{-3} \text{ hr}^{-1}$) in water sampled at 02.00 hours, June 25, 1976 (no moon) immediately upon exposure to light and after 4, 68, or 116 hours preincubation in the light. Each figure is the difference between means of duplicate light and dark bottles incubated for four hours at 5 °C, 2500 lux cool white fluorescent.

Depth (m)	Hours of exposure to light prior to incubation			
	0	4	68	116
50	186.0	174.6	160.6	247.4
150	191.5	151.2	160.0	87.5
250	32.1	31.6	24.0	23.7
350	8.9	8.8	9.9	11.5
450	5.8	6.8	6.7	7.5

Table 3. Sedimentation velocities (m yr^{-1}) for six aphotic isolates at 5 °C in filtered lake water.

Isolate	Growth phase		
	Early exponential	Late exponential	Stationary
<i>Choricystis</i> sp.	1.7	1.1	1.6
Chlorosphaeralean	3.1	6.2	7.1
<i>Chlorella saccharophila</i> var. <i>saccharophila</i>	6.0	11.2	10.8
<i>Stichococcus chodati</i>	4.6	11.4	13.0
<i>Monoraphidium contortum</i>	30.1	15.4	23.9
<i>Fragilaria crotonensis</i>	73.6	72.0	106.3

Discussion

Lake Tahoe's aphotic zone contains phytoplankton which are photosynthetically primed for re-entry into euphotic waters and which are thereby not in a state of true physiological dormancy. Despite light intensities several orders of magnitude below compensation levels the cellular concentrations of the key dark reaction enzyme RuDPCase are statistically as high in the deep aphotic zone as they are in Tahoe's surface waters. These levels are particularly high in relation to cellular chlorophyll concentrations which decrease down the aphotic zone by about an order of magnitude (PAERL et al. 1976). It is unlikely that RuDPCase is active in algae residing in the aphotic zone since this enzyme requires light activation both directly, and indirectly by products of the light reaction of photosynthesis (HOCHACHKA & SOMERO 1973).

The dramatic decrease in overall aphotic chlorophyll levels subsequent to the onset of thermal stratification is possibly a result of environmental selection for those species capable of remaining for prolonged periods of time within the aphotic zone in a photosynthetically primed state. In the 350 m to 450 m stratum this selection may have occurred in the first few months after complete lake mixing in 1975.

It is unlikely that algae in Tahoe's deep aphotic zone are the result of constant inoculation from recently euphotic populations. Passive sedimentation rates

are too slow in relation to the magnitude of the aphotic community. Accelerated descent within zooplankton faecal pellets is unlikely for at least three of the smallest ultraplanktonic aphotic species which cannot be filtered out from dense suspension by the adult calanoid copepods that dominate Tahoe's zooplankton community (unpubl. data). It is therefore highly probable that viable, potentially photosynthetic phytoplankton reside deep in the aphotic zone of Lake Tahoe for periods in excess of 12 months between winters of complete lake mixing.

Summary

The chlorophyll content of the 350–450 m stratum of Lake Tahoe's aphotic zone remained statistically unchanged from December 1975 to December 1976, thereby demonstrating that exchange between the deep aphotic zone and overlying waters was minimal even throughout the period of surface mixing in early 1976. Algae collected from within this zone began photosynthesizing immediately upon re-exposure to euphotic light levels and photosynthetic rates were not increased with up to 116 hours further preincubation in the light. To supplement chlorophyll estimates of "light reaction potential" the enzyme catalysing the rate determining step of the dark reaction, ribulose 1,5-diphosphate carboxylase (RuDPCase) was assayed down the water column. RuDPCase levels per unit microbial biomass for deep aphotic populations were not statistically different from levels in the euphotic community. Settling velocities measured over a wide range of nutritional conditions for six aphotic algae isolated into unialgal culture were too slow to account for a recent euphotic origin of these cells by passive sedimentation.

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Author's addresses:

W. F. VINCENT, Institute of Ecology, University of California, Davis, California 95616, U. S. A.; at present: Dept. of Scientific and Industrial Research, Ecology Division/Freshwater Section, Taupo, New Zealand.