Arch. Hydrobiol./Suppl. 83 (Monographische Beiträge) | 2 | 175–196 | Stuttgart, Juni 1989

Comparison of surface and depth-integrated composite samples for estimating algal biomass and phosphorus values and notes on the vertical distribution of algae and photosynthetic bacteria in midwestern lakes[1]

By MATTHEW F. KNOWLTON and JOHN R. JONES

With 7 figures and 5 tables in the text

Abstract

Vertical profiles of temperature, dissolved oxygen and in vivo fluorescence and paired samples taken 1) at the surface or 2) as a composite from the oxygen saturated part of the water column, were collected from 48 lakes in Missouri, Iowa, Oklahoma, Kansas, and Arkansas during summers 1982–1983. Differences between surface and composite samples in chlorophyll and total phosphorus values were usually small (ca. 5%) but increased in water columns with surface temperature-clines where phytoplankton often formed subsurface layers. Differences between surface and composite samples were usually much less than temporal variation and can probably be neglected in large scale surveys intended to estimate seasonal averages. Fluorescence profiles showed diverse patterns in the vertical distribution of algal biomass but stable metalimnetic algal maxima were found only in Table Rock Lake, Missouri. Metalimnetic layers of green sulfur bacteria (Chlorobiaceae) were found in 9 reservoirs and seem to be the most common metalimnetic autotrophs in lakes in this region.

Introduction

Temporal and spatial variation in distribution of nutrients and phytoplankton in lakes complicate sampling programs designed to collect representative water quality data. Input and internal regeneration of nutrients can vary dramatically over time as can production and loss of phytoplankton. Point source inputs, sedimentation gradients, and concentration or dispersal of materials by wind and currents may also produce large differences among sampling sites in the same water body (GEORGE & EDWARDS 1976, GEORGE 1981, CARMACK & GRAY 1982, THORNTON et al. 1982, KENNEDY & WALKER, in press). Similar hydrodynamic processes together with active migration, passive accumulation, and in situ growth can produce substantial variation in the vertical distribution of algal biomass and

---

[1] Contribution of the Missouri Agricultural Experiment Station Journal Series No. 10505.

0341–2881/89/0083–0175 $ 5.50

associated nutrients (REYNOLDS & WALSBY 1975, GEORGE & HEANEY 1978, GEORGE 1981, VAN DEN AVYLE et al. 1982, MEFFERT & OVERBECK 1985). The relative magnitude of variation from these sources is an important consideration in planning sampling programs to estimate average values for purposes of water quality monitoring or interlake comparisons (KENNEDY et al. 1982, THORNTON et al. 1982, TRAUTMANN et al. 1982, KNOWLTON et al. 1984, KWIATKOWSKI 1985).

In midwest lakes, temporal variation is often large. In summer, concentrations of chlorophyll usually vary by >2.5 fold (maximum/minimum) at a given location and similar variation is often seen in total phosphorus (KNOWLTON et al. 1984). In large reservoirs, these parameters may vary at a given time by >9 fold along longitudinal gradients (THORNTON et al. 1982, JONES & NOVAK 1981, KNOWLTON & JONES 1989). Variation within the water column may be of similar importance, but we presently know little about vertical heterogeneity in these lakes.

To address this question, we collected in vivo fluorescence profiles from 48 midwest lakes during summer 1982 and 1983. Along with in vitro measurements of chlorophyll, these data provide an initial view of the vertical structure of photosynthetic pigments in these lakes and document metalimnetic peaks in the abundance of algae and photosynthetic bacteria. Concurrently, we measured total phosphorus and chlorophyll in surface samples and samples collected as a composite from the oxygen saturated portion of the water column. Past work in comparing lakes and developing empirical models has often relied on surface samples because the ease of their collection makes them amenable to large scale surveys (e.g. DEEVEY 1940, MOYLE 1956, SAKAMOTO 1966, CARLSON 1977, CANFIELD et al. 1984). Our principal objective here was to evaluate this practice as a potential source of error by comparing results obtained from surface samples with presumably more representative data from composites. By comparing the magnitude of differences between the two sample types with variation that occurs between sampling sites and over time we can evaluate, preliminarily, the relative importance of these sources of variation in sampling design. These data also allow us to describe general features of thermal stratification and vertical distribution of oxygen and autotrophs in these lakes.

Study area and methods

Collections were made from 14 reservoirs in Missouri in 1982. These waterbodies (Vandalia and Taneycomo Lakes excluded) and an additional 29 reservoirs and 5 natural lakes in Missouri, Iowa, Kansas, Oklahoma, and Arkansas were sampled in 1983. Profiles were taken at from 1–16 locations on the Missouri reservoirs and at 2 locations on the other lakes on from 1–5 dates during May through September. Morphological characteristics, the number of profiles per lake, and the depth range of sampling sites on each lake are presented in Table 1. Selected data from more recent sampling of Table Rock Lake, Missouri-Arkansas are also included in some examples (KNOWLTON & JONES 1989).

Temperature (Montedoro-Whitney Model TC-5C resistance thermometer), dissolved oxygen concentration (Yellow Springs Instrument Model 51) and in vivo chlorophyll fluorescence (IVF) were measured at 1 m intervals from the surface into the hypolimnion (to the bottom in unstratified lakes). In 1982, in situ measurements and discrete water samples were also taken at the Secchi depth. Fluorescence measurements were made using a Turner Designs Model 10 fluorometer equipped with a blue lamp (Turner Designs model 10-045), a Corning 5-60 excitation filter, Corning 3-66 reference filter, Kodak Wratten 70 and 16 emission filters, a red-sensitive photometer (Turner Designs, 1981) and a flow-through cell attached to a hose and submersible pump.

Surface samples were taken from about 10 cm. Composite and discrete-depth samples were collected from the outflow of the fluorometer. Composite samples were taken by quickly raising and lowering the sampling pump between the surface and oxycline (composite zone) while collecting the outflow. Care was taken to insure approximately equal sampling of all depths in this stratum. When no distinct oxycline was present or we were unable to take oxygen profiles, composite samples were taken from the mixed layer as determined from the temperature profile.

Surface and composite samples were analyzed for total phosphorus (PREPAS & RIGLER 1982) and chlorophyll *a*. Chlorophyll *a* was also measured at the Secchi depth (1982 only) and at some IVF peaks. Chlorophyll *a* (CHL) was measured fluorometrically using dimethylsulfoxide-acetone extracts of plankton concentrated on Gelman A-E filters (BURNISON 1980). Fluorescence of extracts (Turner Designs Model 10 fluorometer) was measured before and after acidification with HCl (KNOWLTON 1984). The fluorometer was calibrated using standards prepared from purified CHL (Sigma Chemical Co., St. Louis, Missouri). Spectral analysis of selected extracts was made using a Beckman Model 25 spectrophotometer. Selected surface samples were also analyzed for non-volatile suspended solids (HOYER & JONES 1983) and short-term biochemical oxygen demand (BOYD 1975). The short-term B.O.D. samples were incubated in an insulated box for 8–32 hours before analysis by a colorimetric version of the Winkler method (A.P.H.A. 1976).

Results

Physical characteristics and lake trophic state

Waterbodies sampled in this survey represent a broad range in size, depth and hydrology (Table 1). Surface area ranged from 6 ha (Cold Springs Lake, Iowa; Gopher Lake, Missouri) to 33863 ha (Eufala Lake, Oklahoma) and mean depth ranged from 1.2 m (Cottontail Lake, Missouri) to 18.9 m (Table Rock Lake, Missouri). All but 5 of these waterbodies are artificial impoundments (Table 1); several of which flush rapidly. Large reservoirs (>2000 ha) in this group had theoretical retention times ranging from about 15 days (Lake Hudson, Oklahoma) to about 1.7 years (Beaver Lake, Arkansas). For smaller reservoirs and natural lakes, retention times ranged from about 4 days (Taneycomo Lake, Missouri) to 20 years (Lake West Okoboji, Iowa). Water regimes in the larger reservoirs are managed through regulation of outflows and, in several cases, through control of inflows from other reservoirs upstream (Table Rock, Taneycomo, Truman, Lake of the Ozarks, Hudson, Fort Gibson, Spavinaw). Three lakes, Stanley Draper, Hefner, and Overholser, are water supply impoundments that receive substantial

Table 1. Name (county), surface area, mean depth, number of sampling visits, number of IVF profiles, depth range of sampling sites, theoretical hydraulic retention time, type of thermal stratification, and minimum depth at which anoxia was observed for 48 lakes sampled in 1982 and 1983.

	surface area (HA)	mean depth (M)	visits	IVF profiles	site depths (M)	hydraulic retention time[1] (years)	thermal stratification[2]	minimum depth of anoxia (M)
Missouri								
Blind Pony (Saline)	79	2.7	9	32	1–6	0.8	stable	3
Bodarc (Jackson)	17	2.2	5	4	4	1.9	stable	3
Coot (Jackson)	9	2.0	4	3	3–4	0.9	stable	3
Cottontail (Jackson)	11	1.2	4	3	2	1.3	stable	2
Gopher (Jackson)	6	2.2	4	3	3–4	3.3	stable	3
Lake of the Ozarks (Camden)	24170	9.8	7	21	4–19	0.3	stable	7
Little Dixie (Callaway)	83	3.0	9	43	2–8	1.3	very stable	3
Longbranch (Macon)	983	4.4	9	47	4–11	0.4	very stable	4
Montrose (Henry)	609	1.8	6	12	2–4	0.1	ephemeral	N[3]
Nell (Jackson)	13	2.5	4	3	3–4	1.5	stable	3
Paho (Mercer)	110	4.0	9	29	3–9	1.7	very stable	5
Pomme de Terre (Hickory)	3194	9.3	8	40	2–25	0.6	very stable	5
Pony Express (De Kalb)	97	3.3	9	39	3–9	1.3	stable	4
Smithville (Clay)	2890	6.1	9	42	4–15	1.3	very stable	5
Stockton (Cedar)	10031	10.9	8	44	2–28	1.2	very stable	2
Table Rock (Stone)	16794	18.9	9	75	6–50	1.1	very stable	5
Taneycomo (Taney)	700	3.5	2	3	4–9	0.01	very stable	N
Truman (Benton)	22510	6.6	8	52	3–22	0.2	very stable	4
Vandalia (Audrain)	18	2.4	4	14	2–4	0.7	stable	2
Iowa								
Anita (Cass)	74	3.7	2	4	5–6	2.2	ephemeral	N
Big Creek (Polk)	367	5.3	2	4	9–12	0.6	very stable	6
Black Hawk (Sac)[4]	295	1.7	2	4	2–3	0.6	unstratified	N
Clear (Cerro Gordo)[4]	1491	2.9	2	4	4–5	5.9	unstratified	N
Cold Springs (Cass)	6	2.1	2	3	3–4	–[5]	ephemeral	N
East Okoboji (Dickinson)[4]	743	3.2	2	4	4–6	1.1	unstratified	N
Green Valley (Union)	173	3.0	2	4	5–7	1.6	stable	6

Hawthorn (Mahaska)	72	3.8	2	4	5–8	???	very stable	3
Prairie Rose (Shelby)	83	3.1	2	4	5–6	1.1	ephemeral	5
Spirit (Dickinson)[4]	1688	5.3	2	4	6–7	4.8	unstratified	N
Viking (Montgomery)	55	4.6	2	3	3–10	2.3	very stable	5
West Okoboji (Dickinson)[4]	1558	11.5	2	3	7–39	20	very stable	20
Oklahoma								
Carl Blackwell (Payne)	1357	4.8	3	4	10–12	2.8	stable	7
Eucha (Delaware)	1172	8.4	3	4	4–10	0.3	very stable	6
Eufala (McIntosh)	33863	7.0	3	4	5–8	0.6	ephemeral	N
Ft. Gibson (Cherokee)	7904	5.7	3	4	9–15	0.08	ephemeral	7
Grand Lake (Delaware)	18990	10.8	3	4	10–21	0.3	stable	8
Hefner (Oklahoma)	1012	8.8	3	4	6–17	–[6]	ephemeral	N
Hudson (Mayes)	4412	5.6	3	4	5–11	0.04	ephemeral	N
Kaw (Kay)	7201	7.8	3	4	19–21	0.2	stable	10
Overholser (Canadian)	607	3.0	3	4	2–4	–[6]	ephemeral	N
Spavinaw (Mayes)	663	5.9	3	4	7–11	0.1	very stable	5
Stanley Draper (Cleveland)	1186	10.4	3	4	12–17	–[6]	very stable	N
Tenkiller Ferry (Sequoyah)	5061	15.4	3	4	3–35	0.6	very stable	10
Kansas								
Cheney (Reno)	3927	5.2	3	4	8–14	1.1	ephemeral	N
Melvern (Osage)	1619	5.4	3	4	13–19	0.7	very stable	10
Pomona (Osage)	1134	2.4	3	4	6–13	0.6	stable	6
Toronto (Woodson)	2805	6.8	3	4	2–4	0.06	ephemeral	N
Arkansas								
Beaver	11420	17.7	1	2	20–27	1.7	very stable	N

---

[1] Retention times obtained from U.S. Fish and Wildlife Service (unpublished data), JONES & BACHMANN 1976; BACHMANN et al. 1980 or calculated from catchment area and volume ratios assuming average annual runoff equal to average for region (U.S. Geol. Survey 1984)

[2] Stratification type: unstratified – no temperature gradients >0.8 C/m; ephemeral – gradients >0.8 C/m on one visit; stable – remained stratified for at least one month; very stable – stratified throughout study with little or no hypolimnetic warming

[3] N – anoxia not observed during study

[4] Natural lakes

[5] Receives substantial ground water input

[6] Water storage reservoir filled by pumping from other surface water sources

inputs via pumping or canals from waterbodies outside their catchment. Cold Springs Lake, Iowa, receives substantial inputs from springs.

Most of these waterbodies are productive with average CHL exceeding 30 µg/L and Secchi depth less than 1.2 m (Table 2). Only Beaver Lake and Stanley Draper Reservoir, had average CHL less than 5 µg/L. Excluding Beaver Lake, which was visited only once, no lake had an average transparency greater than 3.6 m. Several of these lakes are affected by high concentrations of abiogenic turbidity resulting from resuspension of bottom deposits or mixing of turbid inflows which contributed to their low average transparencies (Carper & Bachmann 1984, Nolen et al. 1985). Overall, Secchi depths were more highly correlated to concentrations of non-volatile suspended solids ($r = -0.89$, with double log transformation) than to CHL ($r = -.56$: Table 2) suggesting a pervasive influence of abiogenic turbidity on the light regimes of many lakes in this region (Hoyer & Jones 1983, Kirk 1985).

Table 2. Average limnological conditions of lakes in the survey[1].

	mean	range
surface area (ha)	4025	6.0 – 33683
mean depth (m)	5.8	1.2 – 19.1
secchi depth[2] (m)	1.2	0.3 – 5.5
chlorophyll *a* (µg/L)	32.2	3.3 – 95.7
total phosphorus (µg/L)	71.8	5.0 – 389.3
short-term B.O.D. (mg/L/day)	1.2	0.3 – 4.2
non-volatile suspended solids (mg/L)	7.1	0.8 – 37.4

[1] Averages for individual lakes were not weighted for differences in sampling frequency among individual sites.

[2] Secchi depth regressions:
$\log(\text{Secchi depth}) = -0.48 * \log(\text{chlorophyll}) + 0.66 \quad r = -0.56 \quad n = 312$
$\log(\text{Secchi depth}) = -0.65 * \log(\text{non-volatile suspended solids}) + 0.41 \quad r = -0.89 \quad n = 312$

Thermal stratification

About two thirds of these lakes were thermally stratified at one or more locations for at least a month during the study (Table 1). Of the lakes that did not stably stratify, most exhibited some degree of stratification on at least one sampling date. Over 96% of individual water columns sampled exhibited temperature gradients of at least 0.2 C/m at one or more depths. Of these, about 80% were strongly stratified with maximum temperature gradients 0.8–6.4 C/m. In about two thirds of the water columns with marked thermal stratification, temperature gradients near the surface were small and the epilimnion and metalimnion could be distinguished as a "knee" in the temperature-depth curve (e.g. Fig. 1c–e, g).

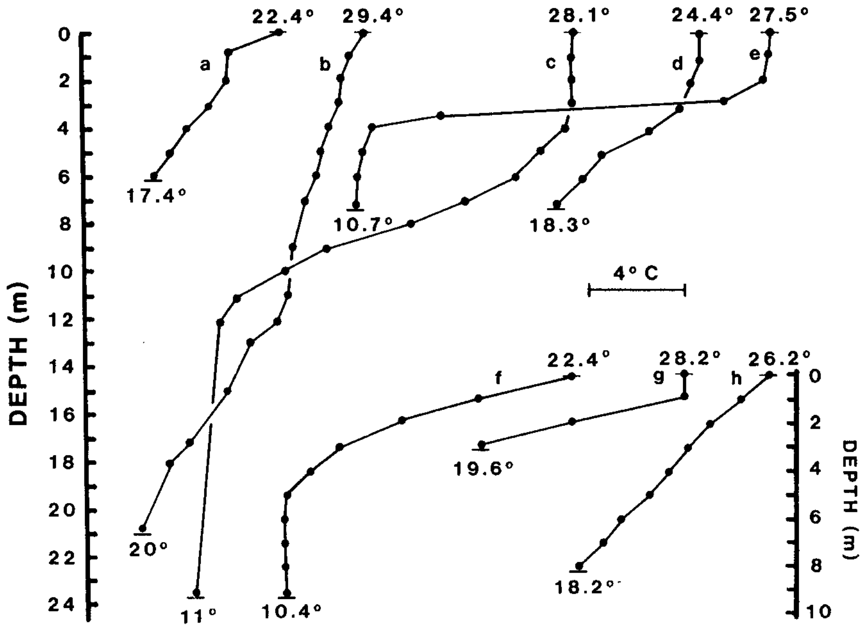

Fig. 1. Temperature profile examples. a – Longbranch, 17 June 1982; b – Kaw, 10 August 1983; c – Stockton, near dam, 29 August 1983; d – Longbranch, 2 July 1982; e – Table Rock, headwaters, 10 August 1986; f – Taneycomo, 10 August 1982; g – Vandalia, 2 July 1982; h – Stockton, headwaters, 28 June 1983.

The rest had moderate to large temperature gradients near the surface. Such profiles were usually encountered on hot, windless days when local heating produced high surface temperatures (e.g. Fig. 1a). In Lake Taneycomo, however, temperature gradients near the surface were a persistent feature (e.g. Fig. 1f) as the result of a cold (ca. 11 C) underflow from the hypolimnetic discharge of Table Rock Lake immediately upstream. Table Rock Lake also receives a hypolimnetic discharge from Beaver Lake which causes extreme temperature gradients (>14 C/m) in profiles taken in headwaters of the White River arm (Fig. 1e – data from more recent survey – Knowlton & Jones 1989). Advective water movements are probably also responsible for the indistinct stratification we observed in some rapidly flushed reservoirs (e.g. Kaw Lake – Fig. 1b), and the continuous surface to bottom temperature gradients we occasionally found in the headwater reaches of several others (e.g. Stockton Lake – Fig. 1h). We lack detailed information on volume and temperatures of inflows and discharge for most of these lakes but assume these factors play an important role in the development and maintenance of thermal stratification in many waterbodies in this region (Wunderlich 1971, Ford, in press).

Oxygen profiles

In 90% of the profiles oxygen declined at depths below the epilimnion or euphotic zone and two thirds of the lakes developed hypolimnetic anoxia at one or more locations. Sites with little or no thermal stratification usually had homogeneous oxygen concentrations or showed a steady decline in oxygen with depth (e.g. Fig. 2a). Abrupt oxyclines, however, were sometimes observed under near homothermal conditions (e.g. Fig. 2b). Short-term B.O.D. measurements on surface waters showed high average rates of oxygen consumption (mean = 1.2 mg/L/day – Table 2) so oxyclines could develop rapidly in unmixed and unilluminated layers. Sharp oxyclines were a regular feature of stably stratified lakes (e.g. Fig. 2c), and occurred at depths ranging from 1 to 13 m (mean 3.2 m; n = 498 profiles).

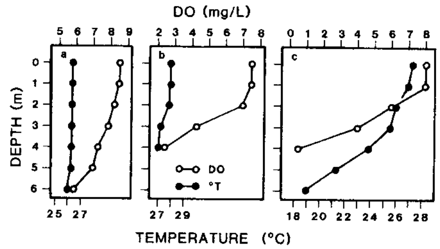

Fig. 2. Temperature and DO profile examples. a – Spirit, 23 August 1983; b – Anita, 21 August 1983; c – Paho, 3 August 1983.

In most profiles, the depth of the metalimnion was 2–4 times the Secchi transparency (mean = 3.2) and, as a result, we rarely observed metalimnetic dissolved oxygen maxima (HUTCHINSON 1957, EBERLY 1964). Only 13 of 620 oxygen profiles had dissolved oxygen peaks >10% above saturation at depths greater than 2 m. Ten of these occurred in Table Rock Lake in association with metalimnetic phytoplankton maxima.

Surface and composite samples

A practical concern in this study was to determine whether surface samples provide estimates of CHL and total phosphorus (TP) comparable to measurements from depth-integrated composite samples. In all, over 500 pairs of surface and composite samples were collected at 115 sampling locations in 47 lakes. Differences between these paired samples, expressed as coefficients of variation (CV) ranged from 0 to >70% for both CHL and TP (Table 3). As expected, differences between surface and composite samples generally reflected the degree of heterogeneity in the temperature profiles. In approximately 120 profiles where the composite zone was nearly homothermal (temperature gradients less than 0.1 degree/m – e.g.

Table 3. Comparison of surface and composite samples for chlorophyll *a* and total phosphorus from profiles with different temperature gradients in the composite zone using coefficients of variation (CV) and ratios (surface/composite) expressed as percents.

maximum temperature gradient	Chlorophyll *a*					Total Phosphorus				
		CV		surface/composite			CV		surface/composite	
	n	mean	range	mean	range	n	mean	range	mean	range
≤0.1/m	119	4.9	0–35.8	100.8	59.6–156.8	122	5.7	0–33.7	97.1[1]	61.5–144.4
intermediate	248	9.7	0–52.5	96.5[1]	48.9–218.3	269	7.1	0–32.6	95.0[1]	62.5–155.0
≥0.5/m	70	22.8	0–80.4	87.9[1]	37.9–363.8	74	11.5	0–70.7	89.8[1]	33.3–146.8
all profiles[2]	481	10.3	0–80.4	96.6[1]	37.9–363.8	510	7.2	0–70.7	94.8[1]	33.3–155.0

[1] $p < 0.05$ for paired t-test. Null hypothesis: mean = 100%

[2] Categories do not sum to total because temperature measurements were not made in several profiles

Fig. 3a), differences between surface and composite samples averaged 4.9% for CHL and 5.7% for TP – values similar to the average analytical precision of the methods used (average C.V. about ±5%). Differences greater than 20% were rare, occurring in only 8 profiles in this group. In contrast, about 70 profiles had large temperature gradients (e.g. Fig. 3b) in the composite zone (>0.5 C/m). For these profiles, differences between surface and composite samples averaged 22.8% for CHL and 11.5% for TP (Table 3). For profiles with intermediate temperature gradients (0.1–0.5 C/m), variation between surface and composite samples fell between these extremes.

Subsurface accumulations of phytoplankton were a frequent feature of lakes sampled during calm weather (e.g. Fig. 3b–d) and sometimes resulted in large

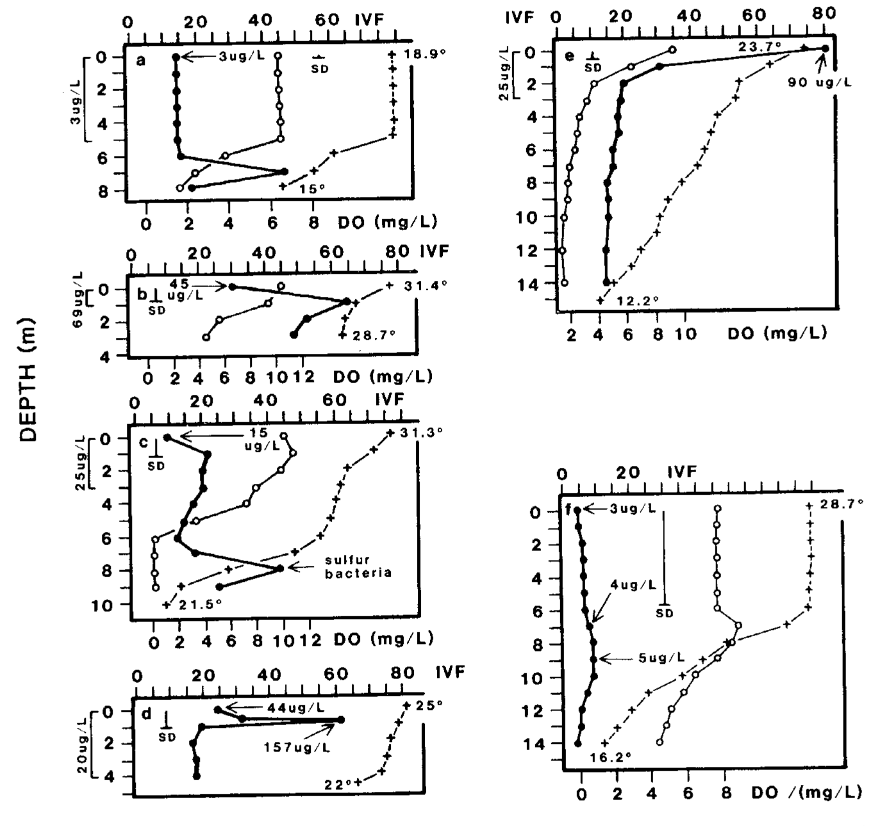

Fig. 3. Temperature, DO and IVF profile examples. a – Longbranch, 13 June 1983; b – Cold Springs, 21 August 1983; c – Pomme de Terre, 28 August 1983; d – Longbranch, 2 July 1982; e – Truman, 5 June 1983; f – Beaver, 17 August 1983. Solid circles – IVF, open circles – DO, crosses – temperature (C). Depth of composite zone and composite CHL is shown to the right of the depth scale. Discrete CHL measurements are shown by arrows. Vertical bars show Secchi depth (SD).

differences between surface and composite samples. Occasionally phytoplankton were compressed into thin plates with gradients of CHL with depth >100 μg/L/m (e.g. Fig. 3d). In a few profiles, CHL declined rapidly below the surface (e.g. Fig. 3e) probably as the result of surface blooms of blue-green algae. Such conditions, however, were rare and CHL usually increased slightly below the surface. In 1982, when discrete measurements of CHL were often made at the surface and Secchi depth, CHL increased by an average of about 10% between the two depths (mean = +10.4%, range = −64% to +189%, n=160). Only 7 of 160 profiles with both measurements showed >10% decrease between the surface and Secchi depth while 60 profiles showed >10% increase. This finding agrees with IVF data which seldom showed fluorescence maxima at the surface.

In most profiles with subsurface phytoplankton peaks, CHL and TP in composite samples were greater than those at the surface. For example, in those profiles with temperature gradients in the composite zone >0.5 C/m, subsurface phytoplankton peaks were common. Chlorophyll and TP in composite samples from these profiles exceeded those at the surface by an average of 12.1% and 10.2%, respectively (Table 3). In most lakes, however, subsurface CHL maxima were ephemeral and differences between seasonal means calculated using surface versus composite samples were small. For the entire data set, differences averaged 10.8% of the seasonal mean for TP and 16% for CHL (Table 4). In comparison, the range of surface values at individual sites over the entire sampling period averaged 45% of the seasonal mean for TP and 61.3% for CHL (Table 4). For

Table 4. Average differences between surface and composite samples (absolute values), among sampling sites and over time expressed as a percent of the seasonal average (surface-composite and temporal) or the mean of all sampling sites for that date (site-site). Seasonal and daily mean values were calculated with surface data.[1]

	surface-composite	site-site	temporal
CHL			
n	171	170	171
mean	15.5	44.8	61.3
S.D.	16.8	43.2	44.4
range	0.0–131.6	0.0–235.2	0.0–275.9
TP			
n	172	179	172
mean	10.8	36.7	45.0
S.D.	9.2	41.4	35.3
range	0.0–61.6	0.0–237.1	0.0–201.8

[1] Mean values for site-site and temporal variation calculated using composite, rather than surface data were: 42.6±40.4% and 56.9±37.9% for CHL and 36.8±41.1% and 43.4 ±82.8% for TP. In paired t-tests, average temporal variation of CHL was significantly less in composite than surface samples ($p - 0.026$). Other differences were not significant at the 5% level.

lakes sampled at two or more locations, the range of surface values among sites on a given day averaged 36.7% of the mean of all sites for TP and 44.8% for CHL. Temporal variation of CHL was significantly lower if calculated using data from composite, rather than surface sample (paired t-test, p = 0.026), but the average difference was only 4% of the surface mean (Table 4). Our data are not amenable to rigorous analysis of variance but these trends suggest that in estimating seasonal mean values variation over time and among sampling sites is of greater importance than variation with depth for the lakes considered here. Also, estimates of temporal and spatial variation are unlikely to differ greatly between surface and composite samples.

Metalimnetic chlorophyll maxima

Subsurface IVF maxima were found in about half the profiles taken from stratified water columns but many occurred at relatively shallow depths in association with ephemeral temperature gradients (e.g. Fig. 3b–d). In profiles with a distinct epilimnion, the metalimnion was usually 4–5 times the Secchi depth and at least partly oxygen-depleted. Of these profiles, 127 exhibited metalimnetic IVF peaks (e.g. Fig. 4a) at depths averaging 4 times the Secchi depth and with dissolved oxygen concentrations averaging less than 40% the surface concentration. An additional 98 profiles showed an increase in IVF in the last 1–2 m of the water column (e.g. Fig. 4b).

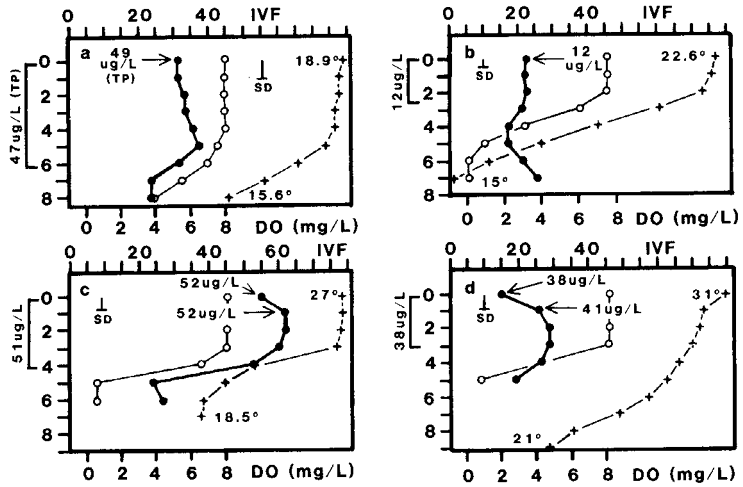

Fig. 4. Temperature, DO and IVF profile examples. a – Pony Express, 29 May 1983; b – Little Dixie, 13 June 1983; c – Smithville, 30 June 1982; d – Pomme de Terre, 24 July 1982. Solid circles – IVF, open circles – DO, crosses – temperature (C). Depth of composite zone and composite CHL (TP in "a") is shown to the right of the depth scale. Discrete CHL measurements (TP in "a") are shown by arrows. Vertical bars show Secchi depth (SD).

Because of the scope of the study we could not measure CHL in all IVF peaks encountered. Ratios of IVF to CHL ("R" values: Heaney 1978) can vary with depth as a result of photoinhibition or changes in the taxonomic or size composition of the phytoplankton community and sometimes complicate interpretation of IVF profiles (Kiefer 1973, Heaney 1978, Vincent 1983, Alpine & Cloern 1985). Values of R measured for metalimnetic IVF peaks in this study were usually greater than those at the surface (mean difference = 25%) so that IVF data tended to exaggerate the size of metalimnetic peaks (e.g. Fig. 4c–d).

Most metalimnetic IVF maxima were transient features observed only once at a given site and most were small with maximum IVF less than 20% larger than at adjacent depths (e.g. Fig. 4a). Because we took IVF measurements at discrete intervals our profiles could not resolve the fine structure sometimes seen at scales of a few centimeters in fluorescence or transmissometry studies of metalimnetic communities (Whitney 1938, Baker & Brook 1969, Fee 1976). This caveat aside, it is clear that these lakes rarely support large, metalimnetic phytoplankton communities.

Of the lakes sampled regularly, only Table Rock Lake developed large, persistent metalimnetic CHL maxima although the small metalimnetic maximum observed in Beaver Lake on our single visit (Fig. 3f) may be a persistent feature (Drury & Gearheart 1975) and large peaks of bacterial pigments were found in several lakes. We found metalimnetic CHL maxima in 58 of 75 profiles taken from Table Rock Lake. Ten of these profiles also had dissolved oxygen peaks located 1–2 m above the IVF maximum (e.g. Fig. 5a). In the less productive areas of the reservoir CHL maxima developed in early summer and were dominated numerically by *Fragilaria* and *Rhodomonas* species. In late summer, peaks at the

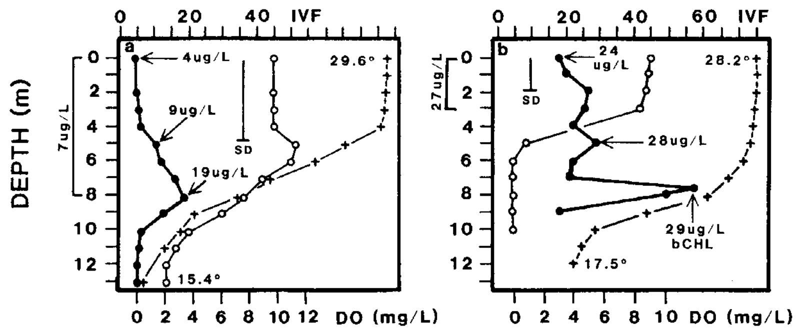

Fig. 5. Temperature, DO and IVF profile examples from Table Rock Lake. a) Long Creek arm, 26 July 1983; b) James River arm, 30 August 1983. Solid circles – IVF, open circles – DO, crosses – temperature (C). Depth of composite zone and composite CHL is shown to the right of the depth scale. Discrete CHL measurements are shown by arrows. In "b", estimated concentration of bacteriochlorophyll (bCHL) is shown at 7.5 m. Vertical bars show Secchi depth (SD).

same locations were dominated by *Achnanthes minutissima* which comprised up to 84% of total counts (Knowlton & Jones 1989). In the productive James River arm, metalimnetic peaks developed later in summer, often in anoxic water and sometimes included photosynthetic bacteria (e.g. Fig. 5b). Fluorescence maxima in all areas of Table Rock Lake usually occurred at depths undersaturated with oxygen (52 of 58 profiles with metalimnetic peaks).

Photosynthetic bacteria

We found several large IVF peaks in anoxic water, presumably due to photosynthetic bacteria, probably green sulfur bacteria (Chlorobiaceae). These peaks had unusually large R values averaging 5 times those measured concurrently at the surface (e.g. Fig. 5b). This may have resulted from the small size and extreme shade adaptation of photosynthetic bacteria (Pfennig 1978, Alpine & Cloern 1985). Spectral analysis of samples from these peaks revealed red absorbance maxima at 651–655 nm (compared to 663 nm for chlorophyll *a*). In acetone extracts, bacteriochlorophylls from green sulfur bacteria (bacteriochlorophyll *c*, *d*, and *e* – Jensen et al. 1964) have absorbance maxima at 647–663 nm (Stanier & Smith 1960, Gloe et al. 1975), so these samples may have contained a mixture of bacteriochlorophylls and perhaps some algal pigment. We did not find absorbance peaks indicating bacteriochlorophyll *a*, a major pigment in purple sulfur bacteria (Jensen et al. 1964).

Fluorescence acid ratios (fluorescence – before acidification/after acidification) in these samples ranged from 0.65–0.88. Pure chlorophyll *a* yields an acid ratio of 1.9 under the same conditions. These unusual acid ratios suggest the presence of bacteriochlorophyll e, a major pigment of the brown – colored varieties of Chlorobiaceae. This pigment has a Soret peak at 458 nm which is above the emission peak of the blue lamp/Corning 5–60 filter combination we used for fluorescence excitation (Fig. 6). Soret peaks of chlorophyll *a* and bacteriochlorophyll *c* and *d* lie below the excitation peak and shift further away on acidification causing reduced fluorescence and acid ratios >1. Acidification of bacteriochlorophyll e increases fluorescence by shifting the Soret peak nearer the excitation peak. From absorbance spectra (Stanier & Smith 1960, Gloe et al. 1975) we would expect pure bacteriochlorophyll e to have an acid ratio of about 0.5. The higher values we found presumably reflect the presence of other chlorophylls and pheopigments.

Metalimnetic maxima with recognizable bacterial pigments were found in 17 profiles from 9 lakes in 1983 – Pomme de Terre, Eucha, Spavinaw, Viking, Hawthorn, Table Rock, Truman, Stockton, Tenkiller Ferry (examples in Fig. 7). Bacterial layers were found at depths of from 3.5 to 12 m and from 3.0 to 6.7 times the Secchi depth. Pigment concentrations could not be determined accurately because the peaks presumably contained several pigments which we did not attempt to isolate and measure individually. But based on peak absorbances and the specific

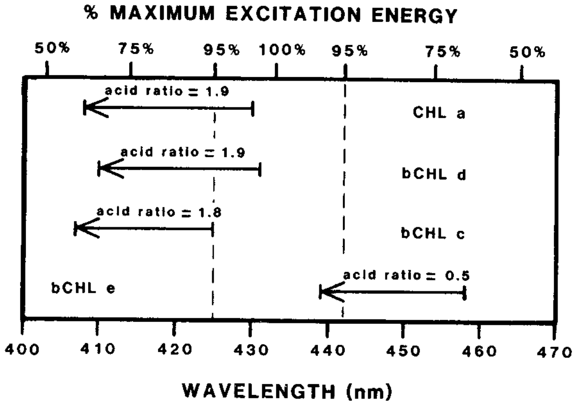

Fig. 6. Blue-shifts in Soret absorbance maxima caused by acidification of chlorophyll *a* and bacteriochlorophylls *c*, *d* and *e* shown in relation to the spectral distribution of light energy emmited by the lamp and filter used in fluorescence measurements (10-045 blue lamp and Corning 5–60 filter). Emmission values were calculated from separate lamp and filter spectral data provided by the manufacturer (Turner Designs, Mountain View, CA, USA). Soret peaks and the acid ratio of chlorophyll *a* were determined from purified chlorophyll *a* (Sigma Chemical Co., St. Louis, MO, USA). Soret peaks for bacteriochlorophylls and pheophytins were estimated from published spectra (Stanier & Smith 1960; Gloe et al. 1975) with minor changes to correct for differences between solvents used by original authors and in the present study. Acid ratios for these pigments were estimated from the overlap of Soret peaks of chlorophylls and pheophytins with the excitation energy spectrum. This approach provided accurate estimation of the acid ratio of chlorophyll *a* as measured directly.

absorption coefficient of bacteriochlorophyll *d* (Stanier & Smith 1960) we estimate total pigment concentrations within these layers varied from roughly 15 to 171 μg/L. In comparison, CHL in the surface waters ranged from 5.9 to 65.8 μg/L (Table 5). In Eucha, Spavinaw, and Pomme de Terre lakes, peaks were found at the same location on visits 4–5 weeks apart. In Table Rock Lake, photosynthetic bacteria were found in widely separated locations in the Long Creek and James River arms. At both locations, the bacterial peak lay below a metalimnetic algal layer in oxygenated water (Figs. 5b, 7c).

In addition to profiles where the presence of photosynthetic bacteria was confirmed by pigment analysis, about 100 IVF profiles exhibited peaks in anoxic water. Most of these were relatively small and only 5 were sampled for pigments. Acid ratios from these extracts ranged from 1.1 to 1.5. We would previously have interpreted these low acid ratios as evidence of pheophytin *a* and concluded that those peaks contained algal detritus. Instead, it seems that low acid ratios in anoxic peaks could result from a mixed population of sulfur bacteria or a mixture of bacteria and algae tolerant of low oxygen concentrations. Photosynthetic bacteria may have gone undetected in many profiles and may have been more important in others than suggested by our pigment analysis. Spectral data alone are not sufficient to distinguish algal from bacterial pigments because of the close similarity of

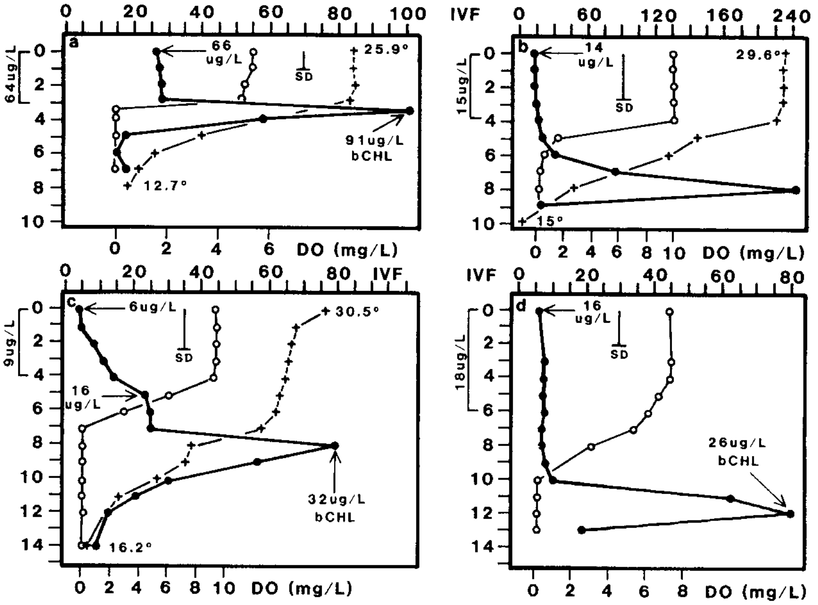

Fig. 7. Temperature, DO and IVF profile examples from lakes with photosynthetic bacteria. a – Hawthorn , 24 August 1983; b – Eucha, 7 August 1983; c – Table Rock, Long Creek arm, 29 August 1983; d – Tenkiller Ferry, 7 September 1983. Solid circles – IVF, open circles – DO, crosses – temperature (C). Depth of composite zone and composite CHL is shown to the right of the depth scale. Discrete CHL measurements are shown by arrows. Concentrations of bacteriochlorophyll (bCHL) were estimated without correction for interfering pigments from absorbance at the red maximum (Stanier & Smith 1960). Vertical bars show Secchi depth (SD).

Table 5. Characteristics of bacteriochlorophyll extracts and profiles in which bacterial IVF maxima were found.

	n	mean	range
extracts (n = 14)			
fluorescence acid ratio	9	0.75	0.65–0.88
red absorbance maxima (nm)	11	652.3	651.0–654.5
bacteriochlorophyll (µg/L)[1]	11	51.8	14.7–170.7
profiles (n = 17)			
surface chlorophyll *a* (µg/L)	17	19.9	5.9–65.8
depth of IVF peak (m)	17	7.2	3.5–12.0
peak depth / secchi depth	17	4.2	3.0– 6.7

---

[1] Bacteriochlorophyll concentrations estimated as red absorbance (1 cm cell) X 10.2 corrected for extract volume and volume of water filtered (after Stanier & Smith 1960). These calculations will underestimate concentrations of bacteriochlorophyll *c* and, if algal pigment is present, will overestimate bacteriochlorophylls *d* and *e*.

chlorophyll *a* and bacteriochlorophyll *c* (Jensen et al. 1964). The latter is present in several varieties of Chlorobiaceae and may be mistaken for algal pigment when extracts are analyzed without previous separation by chromatography (e. g. Steenbergen & Korthals 1982). Thus use of absorbance data to calculate concentrations of algal and bacterial pigments (Caraco & Puccoon 1986) may cause serious errors unless other evidence rules out the presence of bacteriochlorophyll *c* (Knowlton et al. 1989).

Discussion

This study was prompted by our desire to identify major limnological features of lakes in this region and evaluate our methods for measuring them. Results suggest that previous use of surface samples for measuring CHL and TP was commensurate with our goal of estimating seasonal averages for general comparisons. Assuming the present study has provided a reasonable estimate of vertical structure in these lakes, it seems that the effort required to collect composite samples would provide little improvement in resulting seasonal mean values of CHL and phosphorous for lakes in this region. Precision of these estimates depends more on the large temporal and spatial variation typically affecting these lakes and the low sampling frequency in our surveys (Knowlton et al. 1984). For example, in Table Rock Lake, average CHL and TP in different arms sometimes differ by more than 5 fold due to differences in nutrient loading from the various tributaries (Knowlton & Jones 1989). Similar conditions exist in most of the large reservoirs in the region (Jones & Novak 1981, Univ. Missouri, unpubl. data) and limit the value of data collected from single stations to characterize conditions in a given lake (George 1981, Thornton et al. 1982). Average spatial variation is less in smaller lakes, but temporal variation is often large. Two fold differences among samples taken at monthly intervals are common in these lakes and much larger differences often occur (Knowlton et al. 1984). Sampling programs intended to provide reasonable estimates of seasonal average conditions for these lakes should emphasize adequate spatial coverage and sampling frequency in preference to controlling for vertical heterogeneity. Composite samples, however, can be easily collected with pumps or tube sampling devices (e. g. Boyd 1979) and will sometimes provide more representative samples when the euphotic zone is not well mixed.

Although the water columns sampled tended to be homogeneous, many individual profiles showed considerable vertical structure in the distribution of CHL. Variation of phytoplankton densities with depth could result from depth-specific differences in growth or mortality, advective displacement from other areas, or vertical redistribution of existing phytoplankton (Reynolds 1984). Redistribution is probably the cause of many subsurface peaks found in this study. We would expect vertical heterogeneity to develop in any water column with too little turbulence to overcome the directional movements of motile algae and the negative or positive buoyancy of others. Flagellated phytoplankton often show marked vertical zonation in their distribution (e.g. FEE 1976, GEORGE & HEANEY 1978, VAN DEN AVYLE 1982, MEFFERT & OVERBECK 1985) as do buoyant cyanobacteria (REYNOLDS & WALSBY 1975, GEORGE & HEANEY 1978). On calm days many taxa move away from the surface, by active means or by passive sinking (REYNOLDS 1984). Such movements are the probable cause of most of the near-surface IVF "bulges" found in this study.

Vertical movements by phytoplankton are also a likely cause of many of the metalimnetic peaks encountered. Loss of phytoplankton from the epilimnion is a continuous but highly variable process in lakes (FORSBERG 1985). We would anticipate finding occasional metalimnetic peaks as result of crashes in epilimnetic populations (REYNOLDS 1984, MEFFERT & OVERBECK 1985) or accelerated entrainment of cells into the metalimnion during periods of low epilimnetic turbulence (REYNOLDS 1984). Active migrations might also be involved. Such peaks should be quite ephemeral so the stable metalimnetic peaks found in Table Rock Lake, and, rarely, in other lakes require more complex explanation. In some lakes, persistent metalimnetic phytoplankton peaks are common (EBERLY 1964, BAKER & BROOK 1969, FEE 1976, MOLL & STOERMER 1982, FAHNENSTIEL & SCAVIA 1987, COON et al. 1987) and are probably created and maintained by several mechanisms. In situ production certainly plays a role in growth and maintenance of some metalimnetic peaks (PRISCU & GOLDMAN 1983, KONOPKA 1983, FAHNENSTIEL & SCAVIA 1987, COON et al. 1987) but some are derived from the epilimnetic community and persist by maintaining low loss rates (PICK & NALEWJKO 1984), sometimes involving a reliance on heterotrophic metabolism (BIRD & KALFF 1987). The low light available to some metalimnetic populations stimulates the proliferation of CHL (e.g. BROWN & RICHARDSON 1968, FALKOWSKI & OWENS 1980) so that pigment concentrations may exaggerate the size of metalimnetic biomass peaks (CULLEN 1982, PICK et al. 1984).

Of the metalimnetic peaks found in this survey, only those caused by photosynthetic bacteria are unequivocably the result of in situ production. The large peaks found in some areas of Table Rock Lake may result from the entrainment of cells from above and their subsequent maintenance at near compensatory light levels. Similar peaks were not seen in other stratified lakes (Beaver Lake excluded) presumably because light penetration to the metalimnion was too weak to maintain entrained cells. With our present data, however, this conclusion remains speculative. More work is needed before reliable prediction of metalimnetic phytoplankton maxima is possible. It is nonetheless reasonable to assume that stable metalimnetic peaks will be rare in productive and turbid lakes like most of those in this study (MOLL & STOERMER 1982).

On the other hand, these lakes frequently support active metalimnetic populations of photosynthetic bacteria. In thermally stratified lakes, metalimnetic environments range from well lit and oxygen saturated to aphotic and anoxic depending largely on the clarity and thickness of the mixed layer. Along this continuum, photosynthetic bacteria are peculiarly adapted to the last niche available to metalimnetic autotrophs, the low light, anoxic environment in the metalimnia of eutrophic lakes (PFENNIG 1978). In such environments, these organisms probably contribute relatively little (<10%) to total photosynthesis (PARKIN & BROCK 1980), but scavenge the weak and chromatically altered light escaping epilimnetic algae and contribute to chemical cycling. In lakes of this region, these organisms may be the only widely distributed metalimnetic autotrophs exhibiting significant in situ production.

Summary

Chlorophyll and total phosphorus in surface samples from 48 midwestern lakes and reservoirs differed by averages of 10% and 7%, respectively, from values obtained from composites of the oxygen saturated portion of the water column (Table 3). Differences between the two sample types increased with variation in temperature profiles. Average differences were 2–5 times greater for lakes with secondary thermoclines near the surface than for sites with homothermal composite zones. Variation between surface and composite samples, averaged for individual sites, was one forth to one third as great as variation over time or among different sites in same basin (Table 4). Subsurface peaks of in vivo fluorescence (chlorophyll) were common in productive lakes on calm days, presumably because of settling or active migration of phytoplankton away from the surface (e.g. Fig. 3b–d) but some subsurface peaks may have occured from suppression of IVF near the surface (Fig. 4c). Large metalimnetic phytoplankton peaks were rare, occuring most frequently in Table Rock Lake where metalimnetic chlorophyll maxima persisted throughout the summer (Fig. 5). Large IVF peaks also occured in 9 reservoirs with metalimnetic populations of green sulfur bacteria (Fig. 7). High levels of algal and abiogenic turbidity in the epilimnia of these lakes limit the development of metalimnetic phytoplankton communities.

Acknowledgments

Support for this study was provided by the Missouri Agricultural Experiment Station, Missouri Department of Conservation, Sport Fishing Institute, Missouri Cooperative Fish and Wildlife Research Unit, University of Missouri Research Center and Paul K. Weihmiller Fellowship. We gratefully acknowledge KENT THORNTON who let us read a prepublication copy of "Reservoir Limnology: An ecological continuum". Thanks to TIMOTHY CANFIELD, GREG BUTHOLD and WILLIAM BARKLEY for help in sample collections and analysis and to ANN PAMPERL for counting phytoplankton samples. And special thanks to family and friends who fed and sheltered us during field trips to Iowa, Oklahoma and Kansas.

References

ALPINE, A. E. & CLOERN, J. E. (1985): Differences in in vivo fluorescence yield between three phytoplankton size classes. – J. Plank. Res. 7: 381–390.

American Public Health Association (1976): Standard methods for the examination of water and wastewater, 14ed. – Amer. Publ. Health Assoc., New York, NY. 1193 p.

Bachmann, R.W.; Johnson, M. R.; Moore, M. V. & Noonan, T. A. (1980): Clean lakes classification study of Iowa's lakes for restoration. Final Report. – Iowa Coop. Fish. Res. Unit and Depart. of Animal Ecol. 715 pp., Ames, Iowa.

Baker, A. L. & Brook, A. J. (1971): Optical density profiles as an aid to the study of microstatified phytoplankton populations in lakes. – Arch. Hydrobiol., **69:** 214–233.

Bird, D. F. & Kalff, J. (1987): Algal phagotrophy: Regulating factors and importance relative to photosynthesis in Dinobryon (Chrysophyceae). – Limnol. Oceanogr. **32:** 277–284.

Boyd, C. E. (1979): Water quality in warmwater fish ponds. – Agric. Exper. Station, Auburn Univ., Auburn, Alabama, 359 p.

Brown, T. E. & Richardson, F. L. (1968): The effect of growth environment on the physiology of algae: Light intensity. – J. Phycol. **4:** 38–54.

Burnison, B. K. (1980): Modified dimethyl sulfoxide (DMSO) extraction for chlorophyll analysis of phytoplankton. – Can. J. Fish. Aquat. Sci. **37:** 729–733.

Canfield, D. E., Jr.; Linda, S. B. & Hodgson, L. M. (1984): Relations between color and some limnological characteristics of Florida lakes. – Water Res. Bull. **20:** 323–329.

Caraco, N. & Puccoon, A. H. (1986): The measurement of bacteriochlorophyll and algal chlorophyll *a* in natural water. – Limnol. Oceanogr. **31:** 889–893.

Carlson, R. E. (1977): A trophic state index for lakes. – Limnol. Oceanogr. **22:** 361–369.

Carmack, E. C. & Gray, C. R. J. (1982): Patterns of circulation and nutrient supply in a medium residence-time reservoir, Kootenay Lake, British Columbia. – Can. Wat. Res. J. **7:** 51–69.

Carper, G. L. & Bachmann, R.W. (1984): Wind resuspension of sediments in a prairie lake. – Can. J. Fish. Aquat. Sci. **41:** 1763–1767.

Cullen, J. J. (1982): The deep chlorophyll maximum: Comparing vertical profiles of chlorophyll *a*. – Can. J. Fish. Aquat. Sci. **39:** 791–803.

Coon, T. G.; Lopez, M.; Richerson, P. J.; Powell, T. M. & Goldman, C. R. (1987): Summer dynamics of the deep chlorophyll maximum in Lake Tahoe. – J. Plank. Res. **9:** 327–344.

Deevey, E. S., Jr. (1940): Limnological studies in Connecticut. V. A contribution to regional limnology. – Amer. J. Sci. **238:** 717–741.

Drury, D. D. & Gearheart, R. A. (1975): Bacterial populations dynamics and dissolved oxygen minimum. – J. Am. Wat. Works Assoc.: 154–158.

Eberly, W. R. (1964): Further studies on the metalimnetic oxygen maximum, with special reference to its occurrence throughout the world. – Invest. Ind. Lakes Streams **6:** 103–139.

Fahnenstiel, G. L. & Scavia, D. (1987): Dynamics of Lake Michigan phytoplankton: The deep chlorophyll layer. – J. Great Lakes Res. **13:** 285–295.

Falkowski, P. G. & Owens, T. G. (1980): Light-shade adaptation. Two strategies in marine phytoplankton. – Plant Physiol. **66:** 592–595.

Fee, E. J. (1976): The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: Implications for primary production estimates. – Limnol. Oceanogr. **21:** 767–783.

Ford, D. E. (in press): Reservoir transport processes. [In:] Thornton, K.W. (ed.): Reservoir Limnology: An ecological continuum, ch. 2. – John Wiley & Sons, New York.

Forsberg, B. R. (1985): The fate of planktonic primary production. – Limnol. Oceanogr. **30:** 807–819.

George, D. G. (1981): The spatial distribution of nutrients in the South Basin of Windermere. – Freshwater Biol. **11:** 405–424.

George, D. G. & Edwards, R.W. (1976): The effect of wind on the distribution of chlorophyll *a* and crustacean plankton in a shallow eutrophic reservoir. – J. Applied Ecol. **13:** 667–690.

George, D. G. & Heaney, S. I. (1978): Factors influencing the spatial distribution of phytoplankton in a small productive lake. – J. Ecol. **66:** 133–155.

Gloe, A.; Pfennig, N.; Brockmann, H., Jr. & Trowitzsch, W. (1975): A new bacteriochlorophyll from brown-colored Chlorobiaceae. – Arch. Mikrobiol. **102:** 103–109.

Heaney, S. I. (1978): Some observations on the use of in vivo fluorescence technique to determine chlorophyll-*a* in natural populations and cultures of freshwater phytoplankton. – Freshwater Biol. **8:** 115–126.

Hoyer, M.V. & Jones, J. R. (1983): Factors affecting the relation between phosphorus and chlorophyll *a* in midwestern reservoirs. – Can. J. Fish. Aquat. Sci. **40:** 192–199.

Hutchinson, G. E. (1957): A Treatise on Limnology. I. Geography, Physics, and Chemistry. – 1015 pp., John Wiley & Sons, New York.

Jensen, A.; Aasmundrud, O. & Eimhjellen, K. E. (1964): Chlorophylls of photosynthetic bacteria. – Biochim. Biophys. Acta **88:** 466–479.

Jones, J. R. & Novak, J. T. (1981): Limnological characteristics of Lake of the Ozarks, Missouri. – Verh. Int. Verein. Theoret. Angew. Limnol. **21:** 919–925.

Kennedy, R. H.; Thornton, K. W. & Gunkel, R. C. (1982): The establishment of water quality gradients in reservoirs. – Can. Water Resour. J. 7 (1): 71–87.

Kennedy, R.H. & Walker, W.W. (in press): Reservoir nutrient dynamics. [In:] Thornton, K.W. (ed.): Reservoir Limnology: An ecological continuum, ch. 5. – John Wiley & Sons, New York.

Kiefer, D. A. (1973): Fluorescence properties of natural phytoplankton populations. – Mar. Biol. **22:** 263–269.

Kirk, J. T. O. (1985): Effects of suspensoids (turbidity) on penetration of solar radiation in aquatic ecosystems. – Hydrobiol. **125:** 195–208.

Knowlton, M. F. (1984): Flow-through microcuvette for fluorometric determination of chlorophyll. – Water Res. Bull. **20:** 795–799.

Knowlton, M. F.; Hoyer, M. V. & Jones, J. R. (1984): Sources of variability in phosphorus and chlorophyll and their effects on use of lake survey data. – Water Resour. Bull. **20:** 397–407.

Knowlton, M. F. & Jones, J. R. (1989): Summer distribution of nutrients, phytoplankton and dissolved oxygen in Table Rock Lake, a large midwestern reservoir. – Arch. Hydrobiol., Suppl. **83** (2): 197–225.

Knowlton, M. F.; Jones, J. R. & Perkins, B. D. (1989): A comment on "The measurement of bacteriochlorophyll and algal chlorophyll *a* in natural water" by Caraco & Puccoon (1986). – Limnol. Oceanogr. [in press]

Konopka, A. (1983): Epilimnetic and metalimnetic primary production in an Indian hardwater lake. – Can. J. Fish. Aquat. Sci. **40:** 792–798.

Kwiatkowski, R. E. (1985): Importance of temporal variability to the design of large lake water quality networks. – J. Great Lakes Res. **11:** 462–477.

Meffert, M. & Overbeck, J. (1985): Dynamics of chlorophyll and photosynthesis in natural phytoplankton associations. I. Seasonal and annual cycles of chlorophyll and phaeopigments, in relation to euphotic depth and their vertical distribution in small Northgerman lakes. – Arch. Hydrobiol. **104:** 219–234.

Moll, R. A. & Stoermer, E. F. (1982): A hypothesis relating trophic status and subsurface chlorophyll maxima of lakes. – Arch. Hydrobiol. **94:** 425–440.

Moyle, J. B. (1956): Relationships between the chemistry of Minnesota surface waters and wildlife management. – J. Wildl. Manag. **20:** 303–323.

NOLEN, S. L.; WILHM, J. & HOWICK, G. (1985): Factors influencing inorganic turbidity in a great plains reservoir. – Hydrobiol. **123:** 109–117.

PARKIN, T. B. & BROCK, T. D. (1980): Photosynthetic bacterial production in lakes: The effects of light intensity. – Limnol. Oceanogr. **25:** 711–718.

PFENNIG, N. (1978): General physiology and ecology of photosynthetic bacteria. [In:] CLAYTON, R. & SISTROM, W. (eds.): The Photosynthetic Bacteria: 3–18. – Plenum Press, New York.

PICK, F. R.; NALEWAJKO, C. & LEAN, D. R. S. (1984): The origin of a metalimnetic chrysophyte peak. – Limnol. Oceanogr. **29:** 125–134.

PREPAS, E. E. & RIGLER, F. A. (1982): Improvements in quantifying the phosphorus concentration in lake water. – Can. J. Fish. Aquat. Sci. **39:** 822–829.

PRISCU, J. C. & GOLDMAN, C. R. (1983): Seasonal dynamics of the deep-chlorophyll maximum in Castle Lake, California. – Can. J. Fish. Aquat. Sci. **40:** 208–214.

REYNOLDS, C. S. (1984): The ecology of freshwater phytoplankton. – 384 pp., Cambridge Univ. Press, Cambridge.

REYNOLDS, C. S. & WALSBY, A. E. (1975): Water blooms. – Biol. Rev. **50:** 437–481.

SAKAMOTO, M. (1966): Primary production by phytoplankton community in some Japanese lakes and its dependence on lake depth. – Arch. Hydrobiol. **62:** 1–28.

STANIER, R. Y. & SMITH, J. H. C. (1960): The chlorophylls of green bacteria. – Biochim. Biophys. Acta **41:** 478–484.

STEENBERGEN, C. L. & KORTHALS, H. J. (1982): Distribution of phototrophic microorganisms in the anaerobic and microaerophilic strata of Lake Vechten (The Netherlands). Pigment analysis and role in primary production. – Limnol. Oceanogr. **27:** 883–895.

THORNTON, K. W.; KENNEDY, R. H.; MORGAN, A. D. & SAUL, G. E. (1982): Reservoir water quality sampling design. – Water Res. Bull. **18:** 471–480.

TRAUTMANN, N. M.; MCCULLOCH, C. E. & OGLESBY, R. T. (1982): Statistical determination of data requirements for assessment of lake restoration programs. – Can. J. Fish. Aquat. Sci. **39:** 607–610.

Turner Designs (1981): Fluorometric Facts. Chlorophyll and pheophytin. Bulletin No. 101. – Turner Designs, Mountain View, California.

U. S. Geological Survey (1984): Water Resources Data for Missouri. U. S. Geological Survey Water-Data Reports MO-76-1 – MO-86-1. – U. S. Geol. Surv., Water Resources Div., Rolla, Missouri.

VAN DEN AVYLE, M. J.; ALLARD, D.W.; DREIER, T. M. & CLARK, W. J. (1982): Effects of diel phytoplankton migrations on chlorophyll *a* vertical profiles in a central Texas pond. – Texas J. Sci. **34:** 69–78.

VINCENT, W. F. (1983): Fluorescence properties of the freshwater phytoplankton: Three algal classes compared. – Br. J. Phycol. **18:** 5–21.

WHITNEY, L.V. (1938): Microstratification of inland lakes. – Trans. Wis. Acad. Sci. Arts Let. **31:** 155–173.

WUNDERLICH, W. O. (1971): The dynamics of density-stratified reservoirs. [In:] HALL, G. E. (ed.): Reservoir Fisheries and Limnology: 219–231. Spec. Pub. No. 8, Amer. Fish. Soc., Washington D. C.

Address of the authors:

MATTHEW F. KNOWLTON and JOHN R. JONES, School of Forestry Fisheries and Wildlife,
112 Stephens Hall, University of Missouri, Columbia, MO 65211.