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ECOLOGY OF THE CRYPTOPHYCEAE IN A NORTH TEMPERATE HARDWATER LAKE

By

William D. Taylor

A DISSERTATION

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ABSTRACT

ECOLOGY OF THE CRYPTOPHYCEAE IN A NORTH TEMPERATE HARDWATER LAKE

By

William D. Taylor

The Cryptophyceae is a poorly understood small class of single celled flagellate algae with a ubiquitous distribution, often cited for large contributions to phytoplankton biomass. Interest in cryptophyte ecology has recently increased as information on their nutritional quality, short turnover times and intermittent dominance has accumulated. The objectives of this research were to (1) characterize short-interval cryptophyte dynamics within the framework of the annual phytoplankton community structure, (2) measure _in situ_ cryptophyte productivity for comparison with total phytoplankton community productivity, and (3) evaluate the impact of grazing losses to the cryptophytes.

Routine limnological sampling was conducted biweekly while cryptophyte samples were collected daily over an annual period (1982-83) from phosphorus limited Lawrence Lake, Michigan. Only 20 of 121 species of algae contributed greater than 5% of the total biovolume at any particular time. Algal biovolume was often dominated by large unicellular species. Microflagellates (<10 μm) constituted ca. 80 percent of the total algal units annually but their contributions to algal volume were <10%. Cryptophytes

dominated the phytoplankton community during autumn (50% maximum by volume).

Two cryptophyte species dominated within the group; *Rhodomonas minuta* (≈70 μm^3) was abundant and unusually stable (100-300 cells$\cdot$mL^{-1} 80% of the time), *Cryptomonas erosa* (≈1600 μm^3) was less abundant (rarely >100 cells$\cdot$mL^{-1}). An analysis of observed growth rates based on 2-day sampling showed that growth and loss was negligible (i.e. ±G >7 days), 52% and 34% of the time for *Rhodomonas* and *Cryptomonas*, respectively. Few periods of sustained growth occurred by either species.

^{14}C productivity and zooplankton grazing studies were conducted during the summer and autumn, 1984. Cryptophyte species productivity was determined using track micro-autoradiography. Unexpectedly, cryptophyte contributions to productivity were relatively less than their contributions to phytoplankton biovolume and cryptophyte carbon-based growth rates were lower than the phytoplankton community growth rates. Mixotrophic cryptophyte nutrition and temporary spatial patches of refuge from predation resulting from simultaneous differential migration by zooplankton and cryptophytes were discussed to explain the persistance of cryptophytes under high cladoceran grazing pressure, minimal ^{14}C productivity and low growth rates.

To Karen and Kristen

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For two years I have been counseled and encouraged by Mississippi colleagues to complete this work. I greatly appreciate the support provided by Ms. Barb Kleiss, Mrs. Dwilette McFarland, Drs. Rex Chen and Mike Smart; special thanks to Dr. John Barko for his many efforts and patience on my behalf, and for support from the USACE, Waterways Experiment Station.

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CHAPTER 1

PHYTOPLANKTON COMMUNITY DYNAMICS IN LAWRENCE LAKE OF SOUTHWESTERN MICHIGAN

Introduction

An intensive and continuous limnological investigation of Lawrence Lake and its wetland areas was begun in 1967 and extended through 1986. During that period, extensive information was gathered, summarized, and synthesized, particularly regarding the interaction and functional role of wetlands and aquatic macrophytes in the productivity and carbon cycling of lakes. Wetzel (1975, 1983) used many of the data from Lawrence Lake during this extended period to illustrate functional processes within lakes. In so doing he also summarized and referenced many of the numerous publications resulting from research on the lake. The later volume (Wetzel 1983) contains a comprehensive summary of the limnology of Lawrence Lake.

A detailed study of the phytoplankton community and its seasonal dynamics over an annual period was undertaken in 1968 but remains unpublished in detail. Graffius (1963), in a comparative study of Lawrence Lake and a nearby acid bog, provided the first qualitative summary of algal species occurring in this water. In his treatment, species distributions within a variety of sampling sites in and around the lake were noted and subjective references were made to seasonality and abundance.

Where the phytoplankton are discussed in later studies, emphasis was placed on a few selected species of special interest (Wetzel et al. 1972, Manny 1972, McKinley and Wetzel 1979, Ward and Wetzel 1980a, Crumpton and Wetzel 1982, Stewart and Wetzel 1982) or detailed data were presented with minimal discussion (Stewart and Wetzel 1986). The phytoplankton data presented by Stewart and Wetzel (1986) were from studies conducted in 1967 and 1968 which makes them historically invaluable but not necessarily representative of current patterns. Taylor and Wetzel (1984) gave a more detailed discussion of phytoplankton community dynamics in Lawrence Lake but it covered only the period August through February and was restricted to the upper 4 m of the lake.

The present study was undertaken (1) to characterize the community structure and seasonal dynamics of phytoplankton in Lawrence Lake relative to the physical and chemical constraints of the habitat and (2) to establish the background with which to compare the results of high frequency sampling for selected cryptophyte taxa. A detailed discussion of the high frequency sampling has been relegated to Chapter II of the dissertation.

Site Description

Lawrence Lake is a small, dimictic, hardwater lake with low pelagic productivity in southwestern Michigan, U.S.A. The lake has been described with morphometric, chemical and biological data given in numerous sources (e.g. Rich et al. 1971, Wetzel et al. 1972, Wetzel 1983). A brief summary of these characteristics is presented in Table 1.1.

Materials and Methods

Phytoplankton samples were routinely collected and analyzed from one station over the central depression of the lake basin. Crumpton and Wetzel (1982) evaluated phytoplankton patchiness in Lawrence Lake and consistently found no greater variance among five stations than between replicates at a single station. Further periodic testing in this study at four stations supported their findings.

Vertically integrated phytoplankton samples were collected biweekly between 10:00 and 14:00 with a 4-m long Van Dorn-type sampler from 0-4, 4-8, and 8-12 m depths. These depths closely approximated the epi-, meta-, and hypolimnion during summer stratification. The sampler had an inside diameter of 5 cm with a total capacity of about 5 L. A water sample was poured into a bucket for mixing and a 130-mL subsample was immediately preserved with 1 mL of acid Lugol's solution (Vollenweider 1974).

Table 1.1. Morphometric[1] and limnological parameters for Lawrence Lake, Michigan.

Parameter	Value or Range
Surface Area (h)	4.96
Volume (m^3)	292,350
Maximum Depth (m)	12.6
Mean Depth (m)	5.89
Relative Depth (%)	5.01
$NO_3 + NO_2$ nitrogen[2] ($mg \cdot L^{-1}$)	1.5 - 5.0
NH_4 nitrogen[2] ($mg \cdot L^{-1}$)	0.25 - 0.30
Total Dissolved Phosphorus[3] ($mg \cdot L^{-1}$)	0.001 - 0.010
Soluble Reactive Phosphorus[3] ($mg \cdot L^{-1}$)	< 0.005
pH	7.6 - 8.4
Alkalinity ($meq \cdot L^{-1}$)	3.7 - 4.7
Conductivity ($\mu mhos \cdot cm^{-1}$, 25 °C)	400 - 571
SiO_2[2] ($mg \cdot L^{-1}$)	6 - 11
Secchi Disk Transparency (m)	1.8 - 10.9
Annual Mean Productivity[2,4] ($mgC \cdot M^{-2} \cdot day^{-1}$)	79.5 - 119.1 (93.3)
Chlorophyll-a[5] (corrected) ($\mu g \cdot L^{-1}$)	0.32 - 3.19

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[1] Morphometric values are from Wetzel et al. (1972).
[2] Wetzel 1983.
[3] Wetzel 1972.
[4] Fourteen-year range and (mean).
[5] Range of biweekly concentrations in the 0 to 8-m stratum (1982-1984).

Utermöhl's (1958) sedimentation method was used to prepare the samples for identification and enumeration. The recommendations of Lund et al. (1958) were followed for counting precision. In all cases, between 600 and 2000 total algal units were counted giving a counting error of less than ten percent for each sample. Complete transects of the chamber diameter were counted at several magnifications (360x, 180x, 90x); the magnification was dependent upon the size and abundance of the cells being evaluated. The entire chamber was used to enumerate large forms such as *Ceratium*. Species identification under oil immersion (900x) was routine. Counting and cell measurements were made with a Wild M40 inverted microscope. Twenty-five mL samples were settled for at least 15 h within a styrofoam insulated box to minimize convective currents caused by temperature fluctuations throughout the day.

Biovolumes were calculated for each species using formulae for solid geometric shapes most closely matching the cell shape. Mean cell volumes were based on individual cell volume calculations (Appendix A). Biovolumes were determined seasonally when changes in cell size were apparent (e.g. *Cyclotella* *bodanica* v. *affines*).

Light and temperature measurements were made at 1-m intervals with a LiCOR model L1-185 quantum photometer and a YSI 43JD thermistor, respectively. Samples for determination of conductivity, alkalinity, pH, alkaline phosphatase activity (APA), and chlorophyll a (Chla) were collected with an opaque 3-L Van Dorn bottle at 0,1,2,3,4,5,6,7,10 and 12-m depths. Primary productivity incubations were made at 0,1,2,3,5,7,10 and 12-m depths.

Biweekly sampling was standard throughout the study but Secchi disk transparency, light (as μEinst$\cdot$m$^{-2}\cdot$s^{-1} PAR) and particularly temperature were often measured at more frequent intervals. Temperature, for example, was measured daily from mid-October to mid-November 1982 during epilimnetic destratification and every other day from March through June 1983 during restratification.

Because phytoplankton samples were integrated over 4-m intervals, equivalent integrated values were determined for some of the parameters that were measured at discrete depths. Integral mean values, i.e. adjusted for differences in volume with depth, were calculated for primary productivity, APA and Chla for 0-4 and 4-8-m strata.

APA of whole lake water samples was measured by the enzymatic hydrolysis of non-fluorescent 3-0-methyl fluorescein phosphate mono-cyclohexylammonium to the fluorescent product, 3-0-,ethyl fluorescein as slightly modified from Hill et al. (1968) and Perry (1972) by Wetzel (1981).

The ^{14}C uptake method of Steemann Nielsen (1951, 1952) was used to measure primary productivity. Specific details of our methods are given in Wetzel and Likens (1979). One mL of ^{14}C as $NaH^{14}CO_3$ with known specific activity ranging from 5-8 $\mu Ci \cdot mL^{-1}$ (18.5-29.6 x 10^4 Bq) was injected into replicate 125-mL glass stoppered light bottles and non-replicated dark bottles. Samples were incubated in situ from about 10:00 to 14:00 at the depths from which the samples were collected. Fifty-mL aliquots were filtered onto HA Millipore filters (0.45-μm pore size) and analyzed by Geiger-Müller radioassay (Nuclear-Chicago D-47 of known counting efficiency).

Chlorophyll was measured using the trichromatic method of Strickland and Parsons (1968) as presented by Wetzel and Likens (1979). Samples of 500 to 750 mL were filtered onto AA Millipore filters (0.8-μm pore size) at a vacuum differential of less than 0.5 atm.

Alkalinity was determined by titration with H_2SO_4 using a mixed indicator. Conductivity was measured at 25°C with a Yellow Springs Model 31 conductivity bridge. A Coleman 38A pH meter was used to measure pH in the lab with samples at room temperature.

Results and Discussion

Temperature

Temperature patterns in Lawrence Lake were typical for north temperate dimictic lakes of moderate depth and surface area (Figure 1.1). The lake was highly stratified in August 1982 with epilimnetic deepening commencing in September.

Figure 1.1. Daily solar radiation (Photosynthetically Active Radiation, g cal$\cdot$cm$^{-2}\cdot$day^{-1} 400-700 nm)(upper) and depth-time isotherms (°C) (lower) over an annual cycle in Lawrence Lake, Michigan.

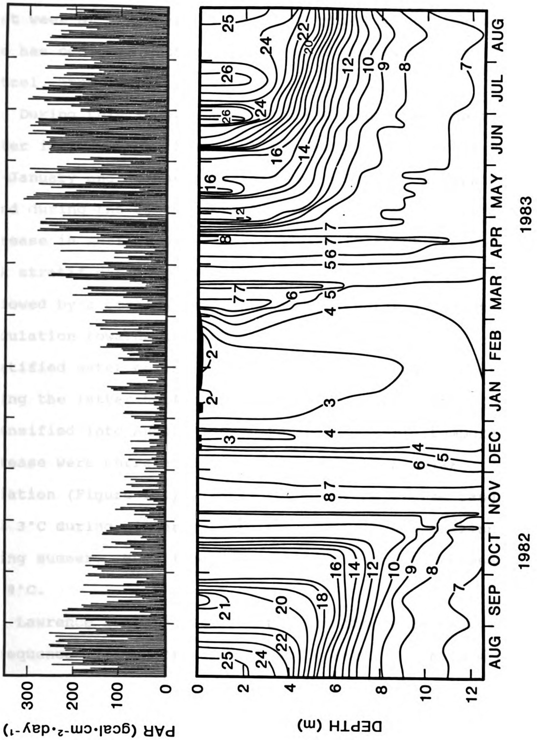

PAR (gcal·cm-2·day-1)
300
200
100
0
DEPTH (m)
0
2
4
6
8
10
12
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
1982
1983
25
24
22
21
20
18
16
14
12
10
9
8
7
87
6
5
4
3
2
77
56
26
24
22
20
16
14

Figure 1.1

The lake continued cooling until autumn turnover during the first week of November. Autumnal circulation of Lawrence Lake has occurred within ±1 week of 31 October since 1968 (Wetzel, unpublished).

During this study southwestern Michigan had the mildest winter in 50 years. Permanent ice cover did not form until mid-January and it was gone again by 3 March. A warming trend during the week before and after ice-out led to an increase in surface water temperatures to about 7°C with weak stratification. This thermal discontinuity was followed by a cooling period that resulted in a spring circulation towards the end of March. A persistent stratified water column followed an intense heating period during the latter half of April, that continued and intensified into August 1983. Periods of rapid temperature increase were correlated with periods of high solar radiation (Figure 1.1). Water column temperatures ranged from 3°C during winter to more than 26°C in the epilimnion during summer. Hypolimnetic temperatures varied between 4 and 8°C.

Lawrence Lake is deep relative to its surface area as a consequence of its origin as a kettle lake (Wetzel and Manny 1978). Relative depth (Z_r) is the formal mathematical expression for this relationship which gives the maximum depth as a percentage of the mean lake diameter (Wetzel 1983). Whereas most lakes have a Z_r of ca. 2 percent, in

Lawrence Lake it is 5.01 percent, a condition conducive to the development of the highly stable water stratification encountered there (Figure 1.2; cf. also Johnson et al. 1978). The epilimnion averaged about 4 m deep above a metalimnion in which temperatures declined as much as 14°C between 4 and 8 m. Vertical movement of water across such a thermal gradient is greatly restricted.

Light

Lawrence Lake was well illuminated throughout much of its depth during most times of the year (Figure 1.3). Secchi disk values were rarely less than 5 m and only in late June and July during epilimnetic decalcification and relatively high algal biovolume. About 89 percent of the lake volume is contained in the first 8 m, i.e. from the surface to the base of the metalimnion. The annual mean light reaching 8 m was 16.3 μEinst$\cdot$m$^{-2}\cdot$s^{-1}. There were, however, broad seasonal differences. During autumn and winter (August 1982 through February 1983) the average light reaching 8 m was 8.5 μEinst$\cdot$m$^{-2}\cdot$s^{-1}, while between February and June 1983 the average was about 30 μEinst$\cdot$m$^{-2}\cdot$s^{-1}. Annually between 0.55 to 8.1 percent of subsurface light reached 8 m.

Light extinction coefficients (η), calculated for the 0–4 and 4-8-m strata, were based on means of the percentage

Figure 1.2. Water temperature at 2 m and total heat content (upper) and Schmidt stability (lower) over an annual cycle in Lawrence Lake, Michigan.

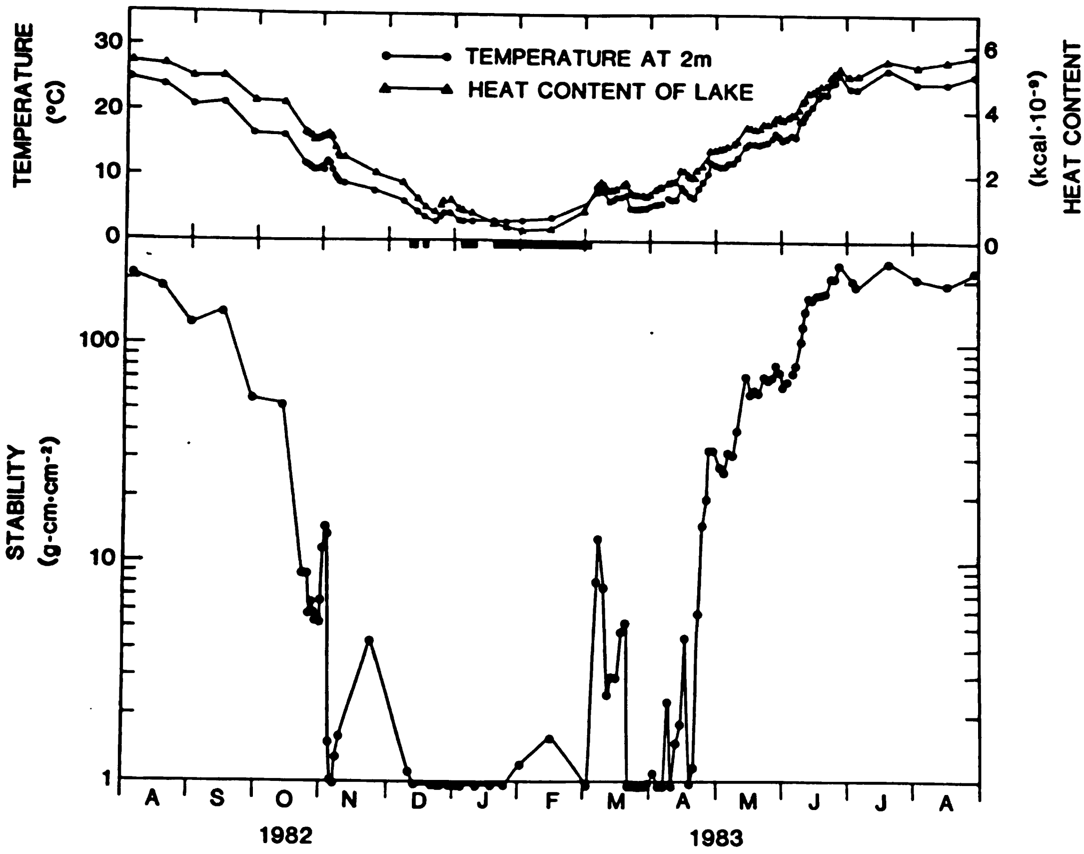

TEMPERATURE (°C)
30
20
10
0
TEMPERATURE AT 2m
HEAT CONTENT OF LAKE
(kcal·10⁻⁹) HEAT CONTENT
6
4
2
0
STABILITY (g·cm·cm⁻²)
100
10
1
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.2

Figure 1.3. Light characteristics over an annual cycle in Lawrence Lake, Michigan; (a) Monthly mean photosynthetically active radiation (PAR), (b) Secchi water transparency depth, (c) PAR and the percent of surface light at 8 m, (d) Light extinction coefficients (η) in two depth-strata.

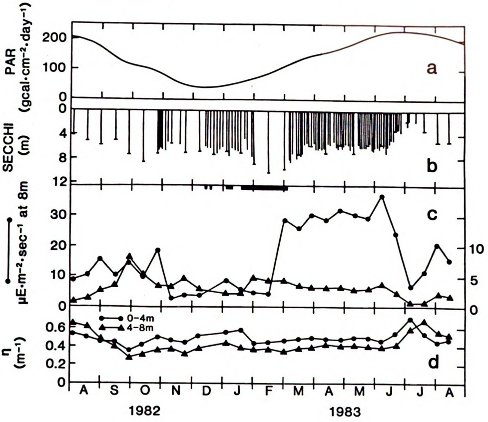

PAR (gcal•cm⁻²•day⁻¹)
200
100
0
a
SECCHI (m)
0
4
8
12
b
μE•m⁻²•sec⁻¹ at 8m
30
20
10
0
c
% I₀ at 8m
10
5
0
η (m⁻¹)
0-4m
4-8m
0.6
0.4
0.2
0
d
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.3

changes in light at 1-m intervals through each of the strata. Extinction coefficients varied from 0.279 to 0.711 m^{-1} which was well within the range for Lawrence Lake (Wetzel 1983). η was always greater in the surface waters than in the 4-8-m stratum except in July and August when greater Chla concentrations developed in the metalimnion. Historically, and in this study, increased phytoplankton productivity and to a lesser degree increased surface temperatures in June and part of July lead to massive precipitation of calcium carbonate (Otsuki and Wetzel 1974) which contributed to the observed increase in η.

From these data it is clear that light limitation was rare and that in Lawrence Lake as much as 90 percent of the lake volume was in a light regime adequate to support most photoautotrophs during much of the year. During the stable stratified period adaptation to lower metalimnetic light levels is likely common. Accumulation of phytoplankton in the metalimnion is largely dependent upon growth rates being greater than losses by sedimentation. Wetzel (1983 and unpublished) found oxygen, photosynthetic productivity and biomass (as chlorophyll) maxima in the metalimnion of Lawrence Lake for 18 years during July and August.

pH, conductivity, alkalinity

The hardwater character of Lawrence Lake is reflected in the pH, conductivity and alkalinity of its waters (Figure 1.4).

Figure 1.4. pH (upper), conductivity (center), and alkalinity (lower) at 2 m and 6 m over an annual period in Lawrence Lake, Michigan.

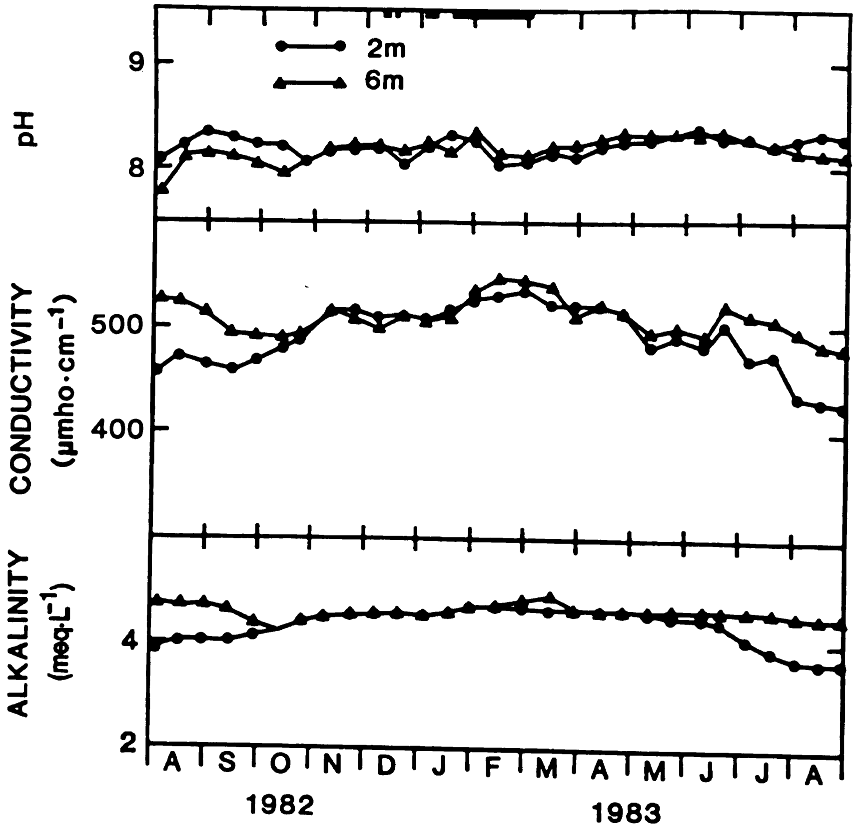

2m
6m
pH
9
8
CONDUCTIVITY
(µmho·cm⁻¹)
500
400
ALKALINITY
(meq·L⁻¹)
4
2
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.4

A detailed analysis of calcium and total alkalinity budgets and calcium carbonate precipitation in Lawrence Lake is given in Otsuki and Wetzel (1974).

During this study pH varied less than one unit throughout the year at 6 m and only about 0.3 pH units at 2 m. Usually pH was between 8.0 and 8.4 in water less than 8 m deep.

Although annual conductivity values were high (>400 μmho·cm^{-1}), significant variations occurred during the year and among depths. Conductivity was greatest in mid-winter (about 550 μmho·cm^{-1}) and began decreasing steadily at ice-out with the onset of the spring phytoplankton bloom. The surface water decrease in conductivity during June was largely due to the massive precipitation of calcium carbonate.

Alkalinity was predominately bicarbonate alkalinity and followed a pattern similar to conductivity (Figure 1.4). Small differences were observed between 2 m and 6 m until the onset of epilimnetic decalcification in June. Alkalinity ranged from 3.7-4.9 meq·L^{-1} at 2 m throughout the year while staying nearly constant at 4.5 meq·L^{-1} at 6 m.

Silica

Silica concentrations are high in Lawrence Lake and are never limiting to the growth of diatoms and other silica-dependent organisms. However, a significant biological reduction of silica occurred, particularly in the epilimnion (Wetzel 1983). Silica is transported by sedimenting diatoms out of the epilimnion to deeper water and ultimately to the sediments. Typical winter concentrations of 10-11 mg $SiO_2 \cdot L^{-1}$ were reduced to about 6 mg $SiO_2 \cdot L^{-1}$ by June in the surface waters.

Nitrogen

Nitrogen is a nutrient required in relatively large amounts by all living organisms. In Lawrence Lake inorganic nitrogen, mostly in the form of nitrate, is in great excess of that needed to support the normal phytoplankton biomass found in the lake (Wetzel 1983). The nitrogen inputs to Lawrence Lake occur largely as nitrates which leach from the calcareous till of the drainage basin. Annual concentrations of NO_3-NO_2 range from about 1.5 to 5 $mg \cdot L^{-1}$ in the upper water (0-8-m stratum). Ward and Wetzel (1980a) detected no N_2-fixation over the growing season between April and September. Their work showed that certainly NO_3 and possibly NH_3 (via diffusion from the hypolimnion) was adequate to supply all the nitrogen needs of the algae.

Phosphorus

Direct measurements of pelagic phosphorus were made infrequently during this study. In calcareous lakes such as Lawrence, much of the soluble phosphate and other essential micronutrients (i.e. iron and manganese) form highly insoluble compounds (Otsuki and Wetzel 1972, Wetzel 1972, 1983). During the period of relatively high productivity (June) these precipitates and seston settle rapidly from the trophogenic zone. The absolute concentrations of phosphorus compounds in Lawrence Lake are relatively constant and exhibited little correlation with changes in algal growth (Wetzel 1972). More relevant are turnover rates and availability.

Alkaline phosphatase activity (APA) was routinely measured to determine biological phosphorus stress and phosphorus availability in the system. APA was about 30x higher at its maximum in August than it was in February at its annual low point (Figure 1.5). APA was uniform within the lake until thermal stratification stabilized the water column in May (Figure 1.2). Thereafter, APA was greater in the 4-8-m stratum than in the 0-4-m stratum indicating either a higher demand for phosphorus or reduced availability from organic compounds in the metalimnion. These findings were consistent with higher productivity rates and Chla concentrations found in the metalimnion during the same period.

Further insight into phytoplankton phosphorus stress during the year is apparent with an examination of the ratio of APA to chlorophyll (Figure 1.5). During periods of greatest vertical stability to mixing, phosphorus stress per

Figure 1.5. Total alkaline phosphatase activity (unfiltered lake water) (upper) and the ratio of alkaline phosphatase activity to chlorophyll a concentration (lower) over an annual cycle in Lawrence Lake.

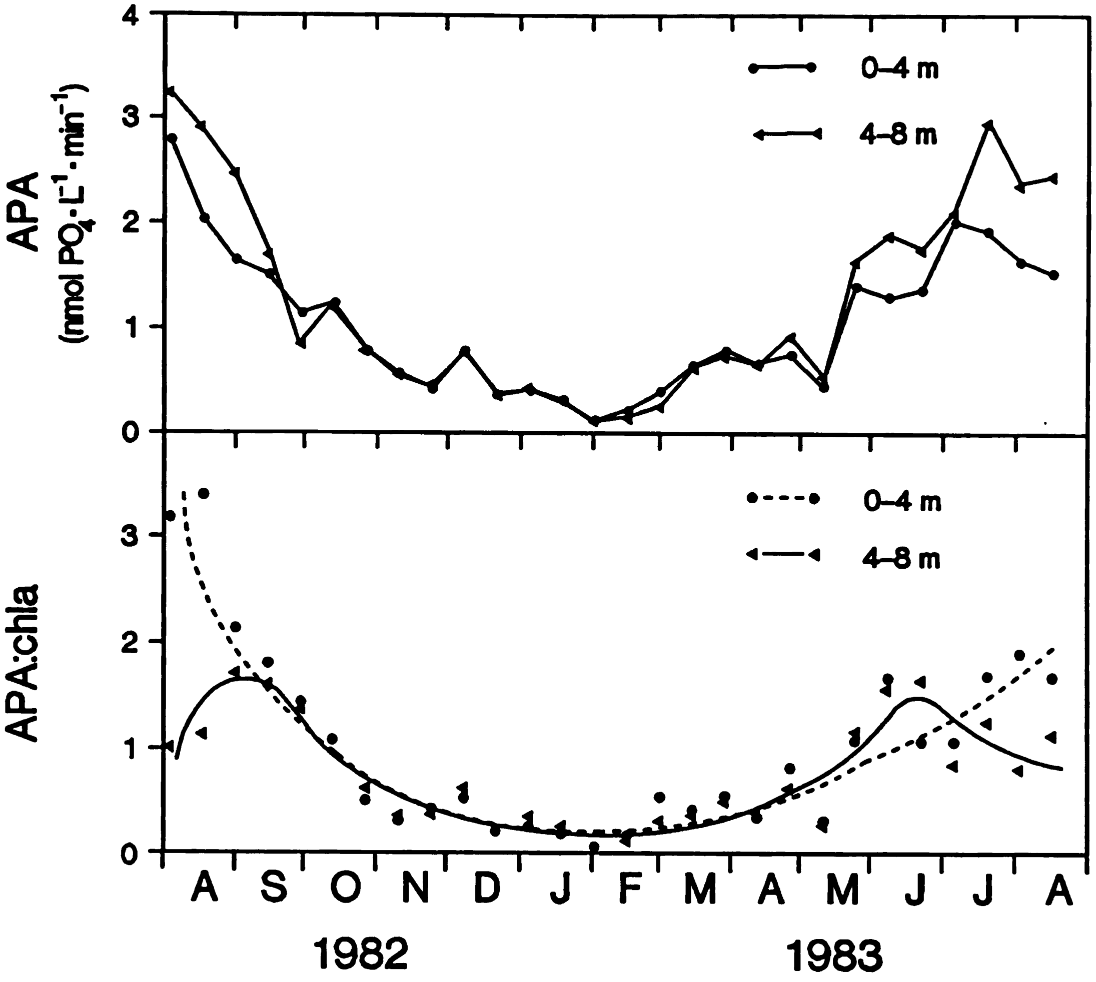

4
3
2
1
0
APA
(nmol PO$_4$·L^{-1}·min^{-1})
0–4 m
4–8 m
APA:chla
A S O N D J F M A M J J A
1982
1983

Figure 1.5

unit Chla was greater in the epilimnion than in the metalimnion. From the mixed winter period until epilimnetic decalcification in June the APA/Chla ratio was similar in both strata. The phosphorus stripping action of the annual decalcification event (precipitated by increased productivity) functioned to reduce available phosphorus to the epilimnetic phytoplankton during a period when replacement was least likely from internal and external loadings (Wetzel, in preparation).

The bacterioplankton can also be direct or indirect sources of phosphatase. Cembella et al. (1984) emphasized that APA may be derived in part directly from bacterial secretion or indirectly from bacterial degradation which would lead subsequently to high organic phosphorus production and induction of APA by bacteria and algae. Of the total dissolved and particulate APA, non-algal particulate APA can comprise a major component (15 to 73%) of the particulate pool (Wetzel 1981; Stewart and Wetzel 1982). During thermal stratification APA was always lowest in hypolimnetic water below 8 m where inorganic phosphorus was more readily available in the more reducing environment. During February APA was minimal, as was algal biomass, productivity, temperature, and available light.

Chlorophyll a

The oligotrophic status of Lawrence Lake was characterized by the low Chla concentrations (Figure 1.6). Mean Chla never exceeded 2 $\mu g \cdot L^{-1}$ in the 0-4-m stratum and did so only during July and August in the 4-8-m stratum. On most sampling dates concentrations were between 1 and 2 $\mu g \cdot L^{-1}$ in the upper 8 m of the lake. Chla concentrations declined during the period of ice-cover on the lake.

Minimal Chla concentrations of about 0.75 $\mu g \cdot L^{-1}$ were found in the upper 8 m just prior to ice-loss on 3 March. In general, Chla concentrations were slightly higher in the 0-4-m stratum during winter, but they were highest in the 4-8-m stratum during spring and summer. The elevated Chla concentrations in October and November were due to algal growth rather than upward mixing of metalimnetic algae during destratification, as has been noted elsewhere (Fee 1976). The excellent light conditions during October were conducive to the observed growth.

Primary productivity

Throughout the study period primary productivity (Figure 1.7) followed the pattern of annual solar radiation (Figure 1.1). The lowest rates occurred between November and ice-loss in early March when values were always less than 50 mg $C \cdot m^{-2} \cdot day^{-1}$. Primary productivity began to increase just prior to ice-loss, and continued until it

Figure 1.6. Chlorophyll *a* concentration (corrected for phaeophytin) over an annual cycle in Lawrence Lake.

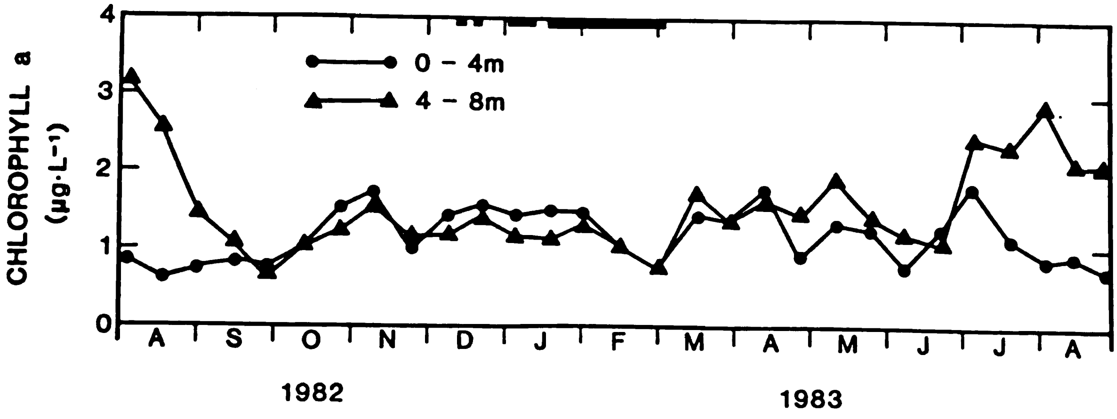


Figure 1.6

Figure 1.7. Primary productivity of phytoplankton over an annual cycle in Lawrence Lake, Michigan; integrated areal productivity in the 0-8-m stratum (upper), integrated volumetric productivity in the 0-4 m and 4-8-m strata (center), and percent of total 0-8 m carbon fixed in the 0-4 m and 4-8-m strata (lower). All points were corrected for depth-volume variations.

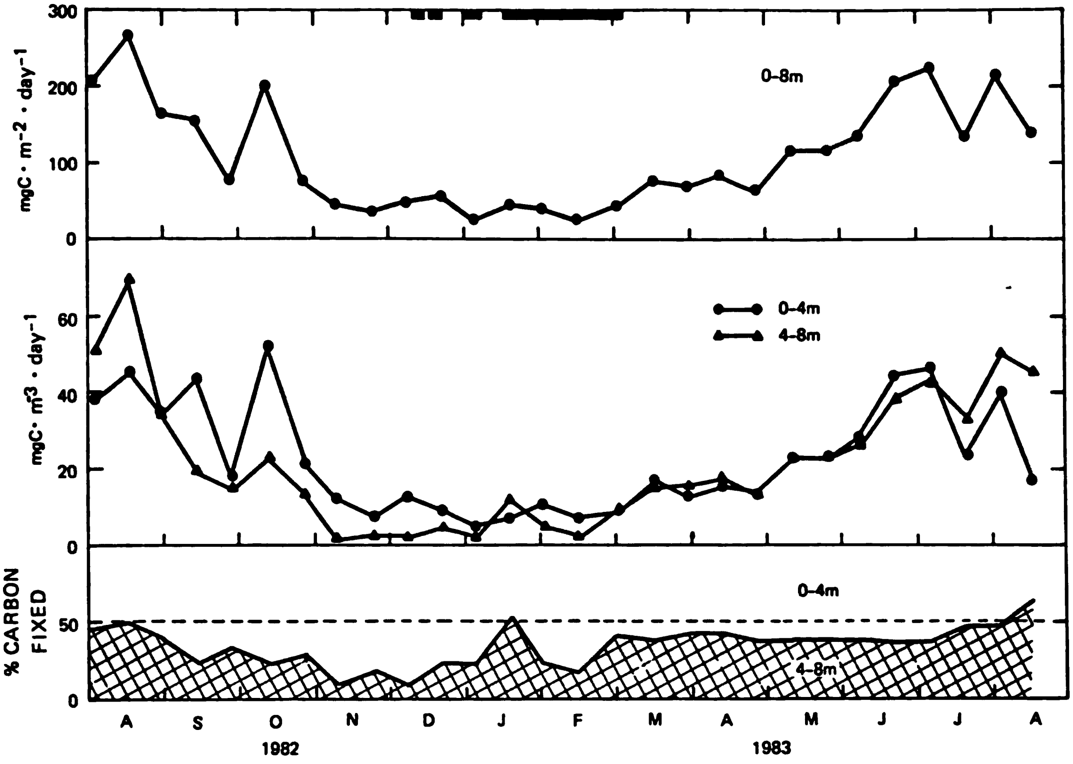

300
200
100
0
mgC · m-2 · day-1
0-8m
60
40
20
0
mgC· m3 · day-1
0-4m
4-8m
50
0
% CARBON FIXED
0-4m
4-8m
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.7

reached a maximum in July of 235 mg $C \cdot m^{-2} \cdot day^{-1}$. A slighter greater rate (269 mg $C \cdot m^{-2} \cdot day^{-1}$) was measured the preceding August.

Two radical departures from a smooth seasonal transition in productivity (Figure 1.7, upper panel) can be accounted for by changes in phytoplankton community structure via bursts of growth followed by rapid decline of selected taxa. In the fall of 1982, as the lake was undergoing epilimnetic deepening, a steep decline in productivity occurred through September, followed by a mid-October increase to about 200 mg $C \cdot m^{-2} \cdot day^{-1}$. This increase coincided with the annual cryptophyte biovolume maximum (details to follow). Thereafter primary productivity and cryptophyte biovolume simultaneously decreased sharply. In the second case, the precipitous decline in primary productivity on 19 July 1983 coincided closely with the collapse of the Stichogloea population, a colonial chrysophyte that accounted for 35-40 percent of the total phytoplankton volume at that time. Primary productivity briefly recovered from that decline by the next sampling date, largely as a result of blue-green algae.

Metalimnetic primary productivity (as mg $C \cdot m^{-3} \cdot day^{-1}$) was greater in 4-8 m than in 0-4 m during the stratified period in July and August (Figure 1.7). This difference was expected given the consistent occurrence of a metalimnetic Chla maximum during this time of year (Wetzel 1983, this study). During those months there was an average of 3.3 and 2.3 times as much Chla in the metalimnion as in the epilimnion in 1982 and 1983, respectively.

Primary productivity was greater in the 0-4-m than in the 4-8-m stratum during epilimnetic deepening and throughout most of the winter until ice-loss. This pattern most likely resulted from restricted light availability in the lower stratum. There was very little difference in primary productivity between these strata from ice-loss until well into the stratified period of July.

The distribution of fixed carbon between the epilimnion and the metalimnion during the year is illustrated in the lower panel of Figure 1.7. Even when metalimnetic productivity rates were higher than in the epilimnion it was rare for metalimnetic production to equal or exceed that in the epilimnion. About 51 and 38 percent of the lake volume are in the 0-4-m and 4-8-m strata, respectively. Metalimnetic productivity would have to be sufficiently great to exceed this difference in order to achieve greater production, as was the situation in mid-January during several days of relatively high light and no ice cover.

Phytoplankton community dynamics

One hundred twenty-one algal taxa were identified in the plankton samples examined in this study (Appendix A).

More species could have been identified if additional effort had been directed towards the rare diatoms.

Four phytoplankton groups (Cyanophyta, Chrysophyta, Bacillariophyceae and Chlorophyta) were represented by more than 20 species (Table 1.2). The Pyrrhophyta, Cryptophyta, and Euglenophyta were less well represented with 12, 8 and 3 species, respectively. Twenty species contributed more than five percent of the algal volume at some time during the study.

Five of the dominant species were large dinoflagellates with cell volumes ranging from 25200 to 84600 μm^3. Although these algae were always present in relatively low numbers when they occurred, dinoflagellates often represented a significant portion of the phytoplankton volume.

Another relatively large-celled form, *Cyclotella bodanica* var. *affines* Grunow, (about 5000 μm^3) was the single most important contributor to algal volume during the study and was present at all times. Similarly, *Cryptomonas* (the 1600 μm^3 size class) was a prominent biovolume contributor. *Mallomonas* species were about the same size as *Cryptomonas* but as a group they rarely attained dominance even though they occurred in many samples.

Microflagellates frequently accounted for about five percent of the algal volume. The cells in this artificial group crossed divisional lines and were placed in one of three size classes for enumeration, <3, 3-6 and 6-10 μm

Table 1.2. Number of phytoplankton species by major group, and dominant species during the annual cycle from August 1982 through August 1983.

Taxon	Number of Species	Dominant Taxa (> 5% total biovolume)
Pyrrhophyta	12	*Ceratium hirundinella* fa. *austriacum*, *Gymnodinium helveticum*, *Peridinium polonicum*, *P. gatunense*, *P. willei*
Cryptophyta	8	*Cryptomonas* '*erosa*-*ovata*', *Rhodomonas minuta* v. *nannoplanctica*
Cyanophyta	23	*Anabaena flos-aquae*, *Aphanocapsa*-*Aphanothece*, *Coelosphaerium palidum*, *Chroococcus limneticus*
Chrysophyta	27	*Chrysosphaerella longispina*, *Dinobryon divergens*, *Mallomonas* spp., *Stichogloea doederleinii*
Bacillariophyceae	23	*Asterionella formosa*, *Cyclotella bodanica* v. *affines*, *C. michiganiana*, *Fragilaria crotonensis*
Chlorophyta	26	*Crucigenia rectangularis*
Euglena	3	none
TOTAL	121	20

diameter. Most of the cells counted in these size classes were microflagellates but other nondescript cells were placed here as well.

With the exception of the small cryptophyte, Rhodomonas, the remaining dominant species were colonial. Cell volumes of the colonial species ranged from 4.2 μm^3 (Aphanocapsa-Aphanothece) to 890 μm^3 (Chrysosphaerella).

Phytoplankton data are commonly presented as either cells, biovolume or occasionally as algal units (particles) per unit lake volume. Each approach emphasizes a different aspect of the data and should be used accordingly. Each approach will be addressed in the following discussion to more fully characterize phytoplankton dynamics in Lawrence Lake.

Algal cell sizes varied over four orders of magnitude (4.2 μm^3 to 84600 μm^3). Cells at either end of the range can certainly not be considered physiological and/or ecological equivalents. It can therefore be misleading to compare seasonal dynamics of species using cell number. Cell volume has been coupled to rates of metabolic activity (Banse 1976) and when combined with cell numbers provides a more acceptable basis for comparing phytoplankton dynamics of mixed taxonomic units. The algal unit incorporates colonial morphology into the analysis giving each algal particle, single cell, or colony, equivalent weight. The algal unit is particularly useful for grazing studies since it is the unit encountered by grazers. The size, shape and abundance of particles may have profound effects on grazing rates and the structure of zooplankton populations (Gliwicz 1980). The arrangement of cell aggregation also effects light availability, e.g. it is well known that aggregates of cells such as those found in *Aphanizomenon* flakes intercept less light than the equivalent biomass of cells distributed more evenly and in smaller aggregates throughout the same water volume.

Total cell concentration

Annual patterns of cell concentration show that Cyanophyta (blue-greens) completely dominated the community from August through turnover at the end of October (Figure 1.8). Most of these cells were very small, non-heterocystis, and organized in high cell density colonies (e.g. *Aphanothece*). As is often the case with this morphological type, the relative importance of the blue-green algae may be exaggerated. This group accounted for as much as 90 percent of the cells in August and September. Blue-green cell numbers dominated until permanent ice formation in mid-January when they still accounted for nearly 20 percent of the total cells in the upper 8 m of the water column.

From autumnal turnover through winter, and until the lake stratified in mid-June, microflagellates and for a

Figure 1.8. Percentage of algal cells within major phytoplankton groups in the 0-4-m stratum (upper) and 4-8-m stratum (center), and total cell concentrations (lower) in those strata over an annual cycle in Lawrence Lake, Michigan.

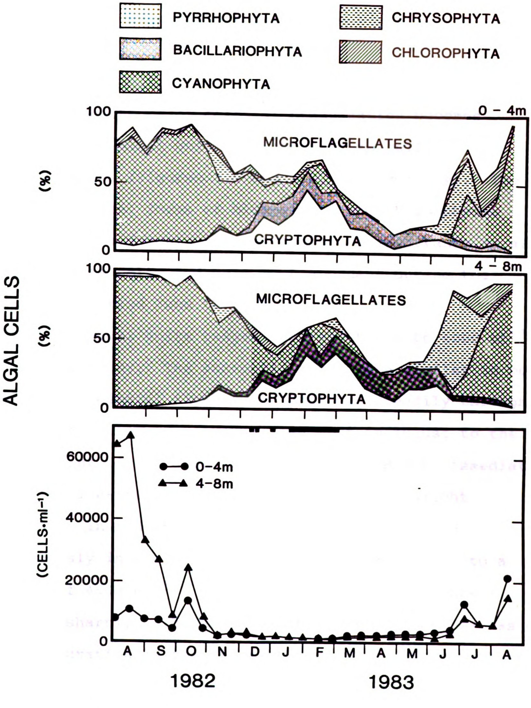

PYRRHOPHYTA
BACILLARIOPHYTA
CYANOPHYTA
CHRYSOPHYTA
CHLOROPHYTA
ALGAL CELLS
(%)
100
50
0
0 - 4m
MICROFLAGELLATES
CRYPTOPHYTA
4 - 8m
(CELLS·ml⁻¹)
60000
40000
20000
0-4m
4-8m
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.8

shorter period cryptophytes, were the overwhelming contributors of phytoplankton cells to the lake. Very few colonial forms were present during the winter months.

Total algal units

The importance of colonial organization becomes apparent when algal units are compared to cell concentrations (Figures 1.9 and 1.8, respectively). The largely colonial forms of blue-greens and chrysophytes decreased considerably in their relative importance as algal units than as cells and were most abundant during the stratified period June through August.

Total algal units ranged from about 600 to 4000 mL^{-1} during the study. The seasonal trends were similar in both strata. In general algal units declined steadily throughout autumn and winter from around 2300 mL^{-1} in August to the lowest point of 600 algal units$\cdot mL^{-1}$ on 1 March, immediately preceding ice-loss. With the exception of a slight depression in mid-June, algal units then increased continuously in the 0-4-m stratum until early July to a maximum of 4500 mL^{-1}. Thereafter epilimnetic values declined sharply. The rapid increase after ice-loss was of shorter duration in the 4-8-m stratum where concentrations leveled out after reaching 2000 mL^{-1} in early April. The June depression was more apparent in the metalimnion. The

Figure 1.9. Percentage algal units within major phytoplankton groups in the 0-4-m stratum (upper) and 4-8-m stratum (center), and total algal unit concentrations (lower) in those strata over an annual cycle in Lawrence Lake, Michigan.

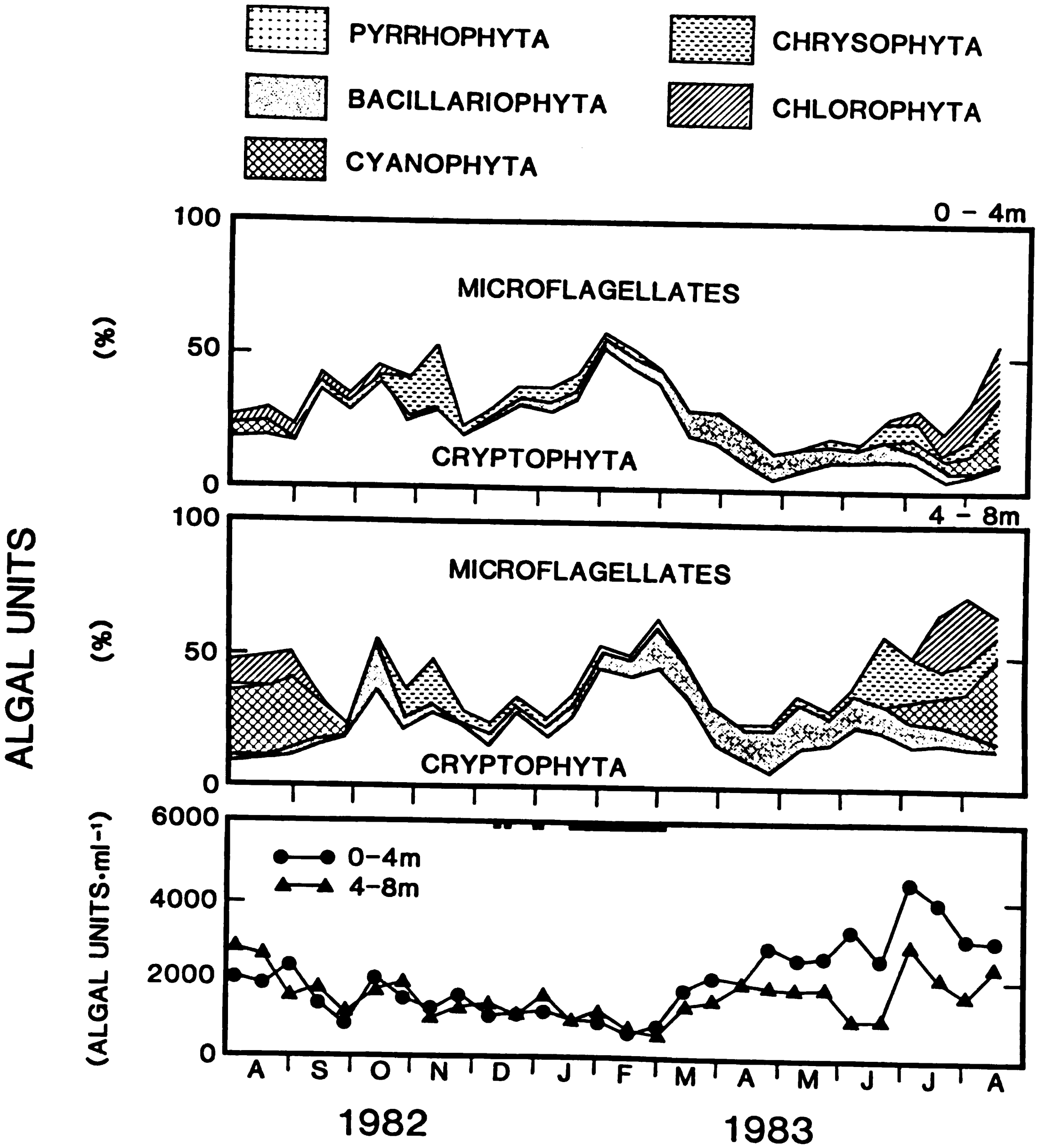

PYRRHOPHYTA
CHRYSOPHYTA
BACILLARIOPHYTA
CHLOROPHYTA
CYANOPHYTA
ALGAL UNITS
(%)
100
50
0
0 - 4m
MICROFLAGELLATES
CRYPTOPHYTA
4 - 8m
(ALGAL UNITS·ml⁻¹)
6000
4000
2000
0-4m
4-8m
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.9

metalimnetic maximum (2900 algal units mL^{-1}) occurred in the first week of July.

Microflagellates and cryptophytes, being single-celled and in great abundance, produced an overwhelming majority of the algal units present in the lake. On an annual basis the average daily contribution by microflagellates was near 60 percent in both strata (Figure 1.10). Cryptophytes were of lesser importance but still they accounted for most of the remaining algal particles in the lake (about 20% annually). Seasonal cryptophyte contributions were greatest during the winter months under ice (>40%), but they also contributed more than 20 percent throughout and beyond the period of destratification in October and November (Figure 1.9).

Important changes from the microflagellate-cryptophyte pattern of dominance occurred at the end of October in the 0-4-m stratum, when chrysophytes increased to 20 percent and in late August 1983 when cryptophytes, blue-greens, chrysophytes and greens accounted, about equally, for 50 percent of the total algal units (Figure 1.9). Seasonal patterns in the 4-8-m stratum differed. Blue-greens contributed about 25 percent in August 1982 and in late August 1983. Diatoms contributed 10-15 percent over an extended period from late February (ice-out) through July. Chrysophytes provided about 20 percent of the algal units during two periods, at turnover in early November and again in late June. Green algae made notable contributions in July and August of both years in the metalimnion.

Figure 1.10. Annual mean percentage of algal units by phytoplankton groups: Euglenophyta (EUG), Pyrrhophyta (PYR), Cryptophyta (CRYP), diatoms (DIA), blue-green algae (B-G), Chrysophyta (CHRY), Chlorophyta (CHL), microflagellates, <6.0 μm diameter (MF).

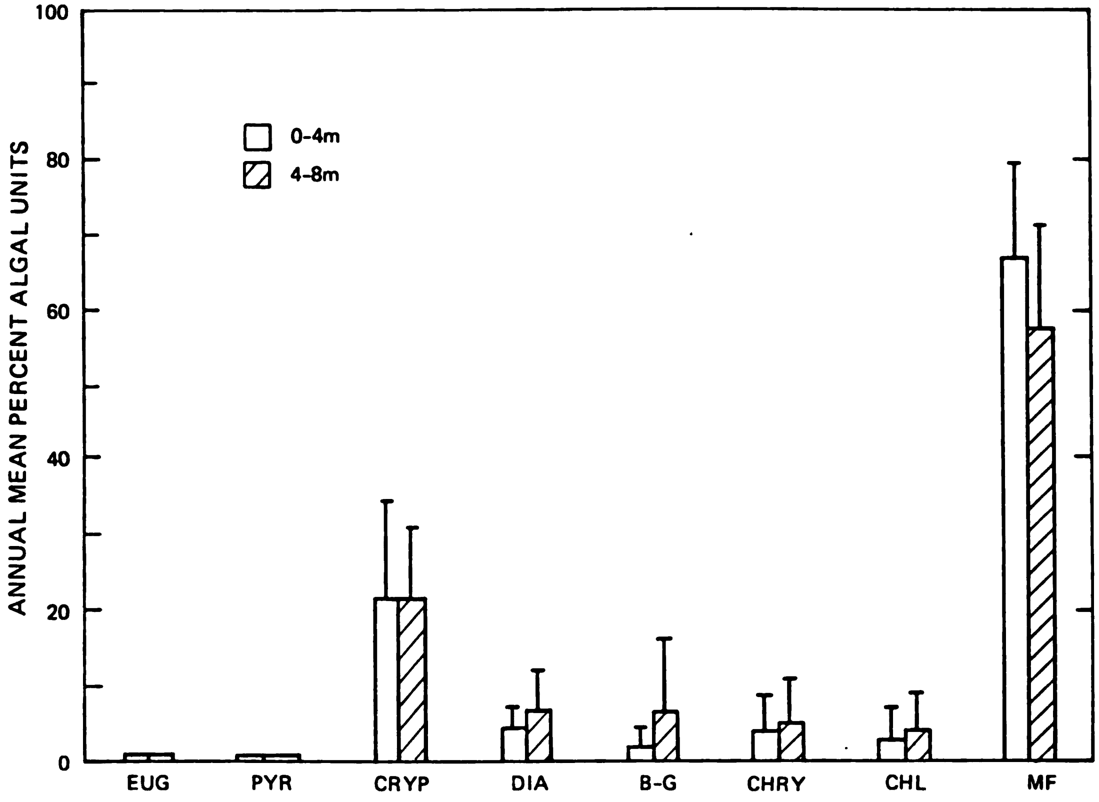

100
80
60
40
20
0
ANNUAL MEAN PERCENT ALGAL UNITS
☐ 0-4m
▨ 4-8m
EUG
PYR
CRYP
DIA
B-G
CHRY
CHL
MF

Figure 1.10

Total cell volume

Only minor seasonal differences were found in total cell volume between the 0-4-m and 4-8-m strata during the study with the exception of August 1982 (Figure 1.11). Volumes ranged from a low of about 250 $mm^3 \cdot m^{-3}$ in November 1982 to a maximum of about 2000 $mm^3 \cdot m^{-3}$ in early July 1983. On this basis Lawrence Lake would be classified as oligotrophic (Vollenweider 1974). The sharp increase in June and July resulted almost exclusively from the population development of the colonial chrysophyte *Stichogloea*.

Manny (1972) reported total cell volume maxima in Lawrence Lake more than four times those presented here. On about one-third of his sampling dates, during all seasons of the year, total cell volumes were greater than the annual maximum reported here. Several explanations are possible for such a large difference: 1) lake and phytoplankton conditions may have changed over a ten-year period, 2) variations between techniques used for counting and measuring cells, and in the formulae selected for calculating cell volumes, 3) the experience of individual microscopists varies, and 4) it may be that the variation between years is within normal limits for a lake such as Lawrence.

Figure 1.11. Percentage biovolume within major phytoplankton groups in the 0-4-m stratum (upper) and 4-8-m stratum (center), and total phytoplankton volume (lower) in those strata over an annual cycle in Lawrence Lake, Michigan.

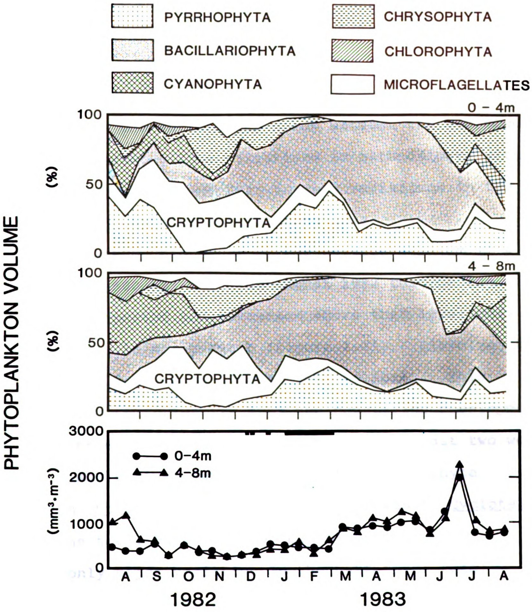

PYRRHOPHYTA
BACILLARIOPHYTA
CYANOPHYTA
CHRYSOPHYTA
CHLOROPHYTA
MICROFLAGELLATES
PHYTOPLANKTON VOLUME
(%)
0 - 4m
4 - 8m
CRYPTOPHYTA
100
50
0
3000
2000
1000
(mm³.m⁻³)
0-4m
4-8m
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.11

Productivity data (Table 1.1) and particulate organic carbon data (Wetzel 1983, Table 22-5 and unpublished) collected over 19 years do not support the notion of a major change in the trophic state of Lawrence Lake. Experience has indicated (e.g. Hobro and Willén 1977, Niemi et al. 1985) that large variations in estimated cell concentrations and phytoplankton volumes can be expected between laboratories. The variability noted between the two studies most likely resulted from variations in methodology, with individual experience and year to year variations in the phytoplankton community contributing less.

Phytoplankton biovolume of the surface stratum (0-4 m) was less than 500 $mm^3 \cdot m^{-3}$ from August 1982 through the entire winter period and increased above that level only after ice-loss in early March (Figure 1.11). Biovolume then doubled rapidly to about 1000 $mm^3 \cdot m^{-3}$ by April. This increase resulted primarily from the population development of the centric diatom Cyclotella. During the last two weeks in June a short-lived development in the chrysophyte population (Stichogloea) and continued growth by Cyclotella doubled the total phytoplankton biovolume.

The only major variation in the pattern of total biovolume dynamics between the epilimnion and metalimnion was in August 1982. At that time more than twice the algal biovolume was present in the 4-8-m stratum than the 0-4-m water. A metalimnetic maximum of algae, photosynthesis, and oxygen is common in lakes and has been reported as an annual event in Lawrence Lake (Ward and Wetzel 1980a & b, Wetzel 1983).

In August 1982 blue-green algae dominated the metalimnion and accounted for 40 percent of total cell volume (Figure 1.11). The remainder of the biovolume in that stratum was equally divided among dinoflagellates, diatoms, cryptophytes, and the green algae. In contrast the epilimnion was dominated by dinoflagellates which accounted for about 40 percent of the biovolume. During destratification blue-green, green and dinoflagellate biovolume contributions decreased while cryptophytes increased in relative numerical importance and in volume.

At turnover the cryptophytes were still dominating, diatom biovolume increased in relative importance with no actual volume change, and chrysophytes represented 25 to 35 percent of total biovolume following a late October growth increase.

At the time of permanent ice formation in mid-January the diatoms fully dominated phytoplankton biovolume (50-60 percent). This change resulted from a decline in cryptophyte and chrysophyte biovolume as well as the increase in diatom volume. A shift in dinoflagellate species, discussed below, led to their recovery so that they accounted for 25-30 percent of the biovolume by that time. Diatoms continued to dominate the lake waters through winter and spring until June when there was a 50 percent reduction in their biovolume. A bloom of chrysophytes followed within two weeks of the diatom collapse. Six weeks later the chrysophytes declined again to low levels. Diatom contributions continued to decrease through July and August, while the blue-greens increased and constituted 20-35 percent of the biovolume by mid-August. At that time the remaining biovolume was again nearly equally distributed between chrysophytes, diatoms, cryptophytes, and dinoflagellates. Epilimnetic chrysophytes, however, were especially prominent in mid-August.

Phytoplankton divisional dynamics

Euglenophyta

The euglenoids rarely contributed significantly to total algal volume above 8 m. On only one date, 16 August 1983, was *Euglena* observed in the 0-4-m stratum and then it accounted for less than one percent of the total volume. *Euglena*, when present, was in the form of relatively large cells (volume = 34,000 μm^3) but they were always few in number. Euglenoids never exceeded one cell mL^{-1} throughout the study and therefore were never appreciable as contributors of algal particles to the community. Stewart and Wetzel (1986) reported *Euglena* in very narrow depth-time strata at infrequent intervals in Lawrence Lake.

Pyrrhophyta

The dinoflagellates were important contributors to biovolume throughout much of the year but notable periodic fluctuations reduced their relative importance. Seasonal changes in dinoflagellate volume were very similar in the 0-4-m and 4-8-m strata (Figure 1.12). Their contributions to total algal volume averaged about 20 percent per day on an annual basis (Figure 1.13). The dinoflagellates made significant contributions to total algal cell volume at all times except during the later stages of destratification when they were nearly undetectable (Figures 1.11 and 1.12). By December the dinoflagellates increased again, and continued until March when their volume began fluctuating around 175 $mm^3 \cdot m^{-3}$. Between 24 May and 6 June a large decrease in total cell volume occurred with the population collapse of one species, *Peridinium willei*, followed by a steady increase back to earlier levels. By mid-August 1983 total dinoflagellate cell volume was down to about 100 $mm^3 \cdot m^{-3}$. Fluctuations throughout the year were more extreme in the 0-4-m stratum than in the 4-8-m stratum.

Dinoflagellates never exceeded 25 cells mL^{-1} throughout the study (Figure 1.14) and therefore were never of any relative value as contributors of algal particles to the community. The large cell sizes of the most important dinoflagellates compensated for the low cell numbers so that the group often made significant contributions to total volume.

Figure 1.12. Total dinoflagellate cell volume in two depth-strata over an annual cycle in Lawrence Lake, Michigan.

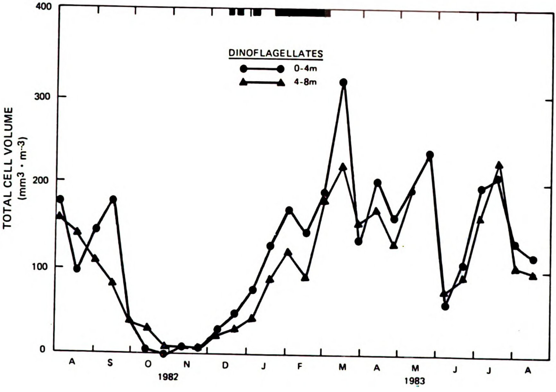

400
300
200
100
0
TOTAL CELL VOLUME
(mm³ · m⁻³)
DINOFLAGELLATES
0-4m
4-8m
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.12

Figure 1.13. Annual mean percentage cell volume by phytoplankton groups in two depth-strata over an annual cycle: Euglenophyta (EUG), Pyrrhophyta (PYR), Cryptophyta (CRYP), diatoms (DIA), blue-green algae (B-G), Chrysophyta (CHRY), Chlorophyta (CHL), microflagellates, <6.0 μm diameter (MF).

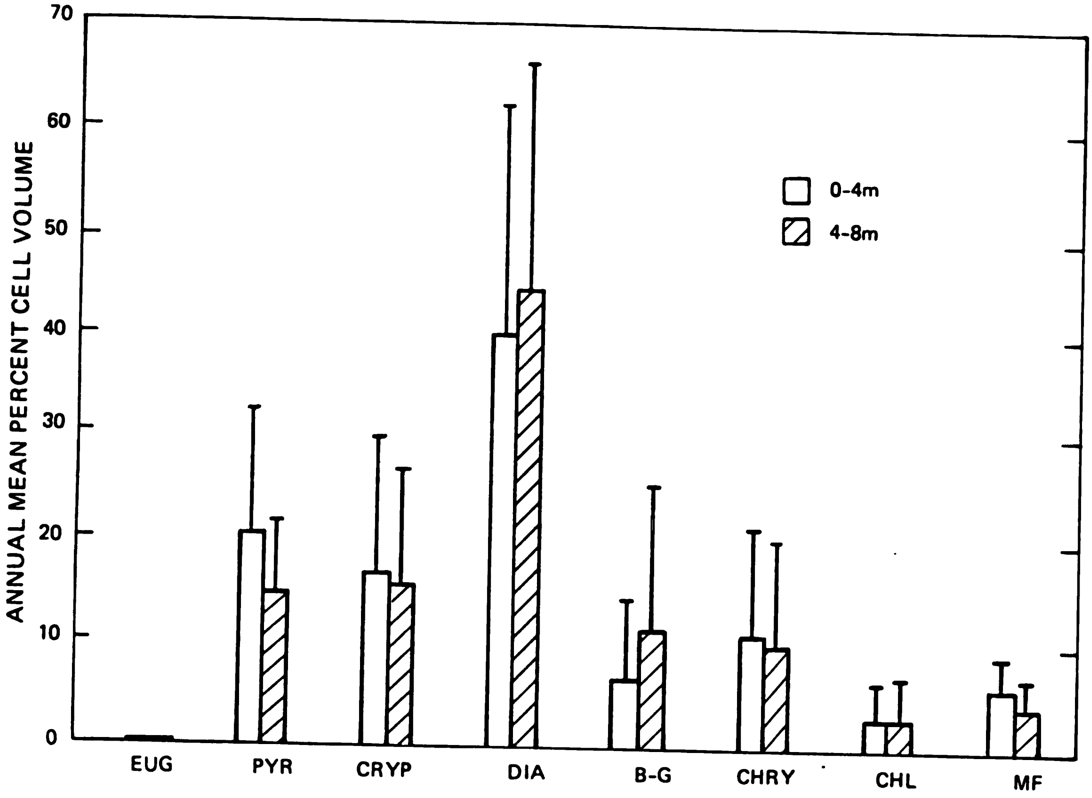

70
60
50
40
30
20
10
0
ANNUAL MEAN PERCENT CELL VOLUME
0-4m
4-8m
EUG
PYR
CRYP
DIA
B-G
CHRY
CHL
MF

Figure 1.13

Figure 1.14. Total dinoflagellate cell concentration in two depth-strata over an annual cycle in Lawrence Lake, Michigan.

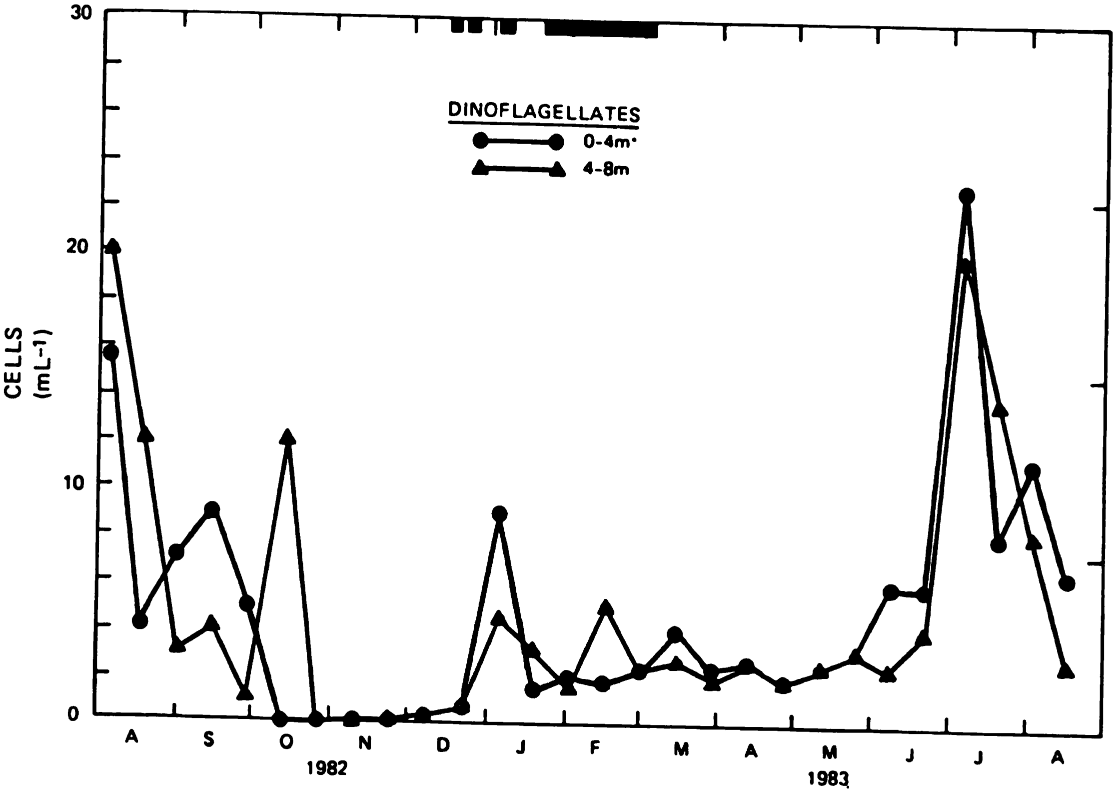

DINOFLAGELLATES
0-4m
4-8m
CELLS (mL-1)
30
20
10
0
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.14

The smallest of these, *Peridinium polonicum*, had a mean cell volume of 25000 μm^3 and the largest, *P. willei*, averaged 85000 μm^3 (Appendix A).

The seasonal dynamics of five dinoflagellate species are illustrated in Figure 1.15. *Ceratium hirundinella*, *Peridinium gatunense*, and *P. polonicum* were restricted to the period after mid-June, when temperatures exceeded about 16°C. These species declined in number with declining temperatures in September and were essentially gone when the temperature reached about 16°C in mid-October. In contrast, growth of *Peridinium willei* began shortly after turnover, continuing steadily through winter. A relatively constant population was maintained from ice-loss in March through May when it declined to very low levels by mid-June. The sharp decline was concurrent with a rapid increase in epilimnetic temperature (7°C) during the first week of June (Figure 1.1). *P. willei* was responsible for as much as 45 and 25 percent of the total winter and early spring algal volume in the 0-4-m and 4-8-m strata, respectively.

Gymnodinium helveticum was present during most of the year but in very low numbers (Figure 1.15). *G. helveticum* populations increased steadily at 4-8 m and attained a maximum near the end of June. This pattern closely followed that of *Cyclotella bodanica* (Figure 1.16).

Phagotrophy by *G. helveticum* on *C. bodanica* was observed numerous times during May and June. Whole cells of

Figure 1.15. Cell concentration of selected Pyrrhophyta species in two depth-strata over an annual cycle in Lawrence Lake, Michigan. The species are *Gymnodinium helveticum*, *Ceratium hirundinella* fa. *austriacum*, *Peridinum gatunensis*, *P. polonicum* and *P. willei*.

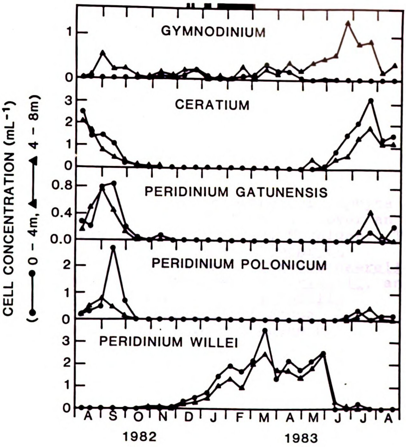

GYMNODINIUM
CERATIUM
PERIDINIUM GATUNENSIS
PERIDINIUM POLONICUM
PERIDINIUM WILLEI
CELL CONCENTRATION (mL⁻¹)
(● 0 - 4m, ▲ 4 - 8m)
1
0
3
2
1
0
0.8
0.4
0.0
2
1
0
3
2
1
0
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.15

Figure 1.16. Cell concentration of selected Chrysophyta and diatom species in two depth-strata over an annual cycle in Lawrence Lake, Michigan. The species of chrysophytes are *Dinobryon divergens*, *Mallomonas* spp., *Chrysosphaerella longispina* and *Stichogloea doederleinii*, and the species of diatoms are *Cyclotella michiganiana*, *Asterionella formosa*, *C. bodanica* and *Fragilaria crotonensis*.

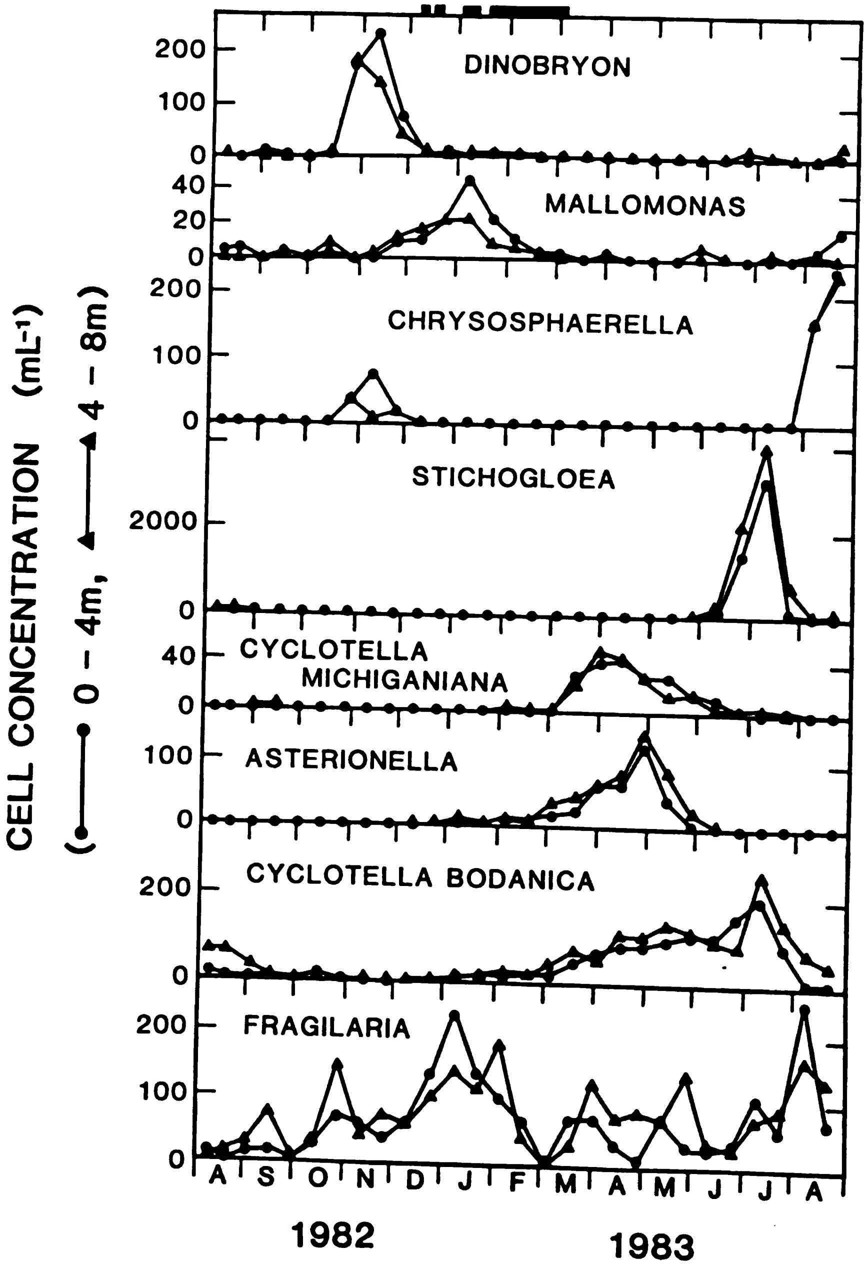

DINOBRYON
MALLOMONAS
CHRYSOSPHAERELLA
STICHOGLOEA
CYCLOTELLA MICHIGANIANA
ASTERIONELLA
CYCLOTELLA BODANICA
FRAGILARIA
CELL CONCENTRATION (mL⁻¹)
(● 0 - 4m, ▲ 4 - 8m)
200
100
0
40
20
0
200
100
0
2000
0
40
0
100
0
200
0
200
100
0
A S O N D J F M A M J J A
1982
1983

Figure 1.16

Cyclotella, in some cases nearly the diameter of G. helveticum, were enclosed within G. helveticum cells. All of those observations were made in 4-8-m samples where G. helveticum was most abundant. Similar reports of phagotrophy by this species have been made by others (Irish 1979, Popovsky 1982).

Cryptophytes

Cryptophytes were always present in the water column and they made a significant contribution to total phytoplankton volume with an annual average of about 16 percent (Figure 1.13). Seasonal changes in their total volume were quite similar in the 0-4-m and 4-8-m strata throughout the year (Figure 1.17). During the winter and early spring months (January through May) cryptophyte biovolume was relatively low, and rarely totaled more than 50 $mm^3 \cdot m^{-3}$ (mean = 40 $mm^3 \cdot m^{-3}$). Other periods in the study were characterized by greater but fluctuating biovolume. Maxima occurred on 5 July, 14 September and, the largest, on 12 October. The October maximum (254 $mm^3 \cdot m^{-3}$) developed within a sunny period with stable water temperatures during the first 10-12 days in October (Figure 1.1). In late September cloudy days resulted in rapid cooling of the epilimnion with the concurrent seasonal decline of the summer phytoplankton volume. Cryptophyte growth rapidly responded to the sudden shift to bright days and possibly to

Figure 1.17. Total cryptophyte cell volume in two depth-strata over an annual cycle in Lawrence Lake, Michigan.

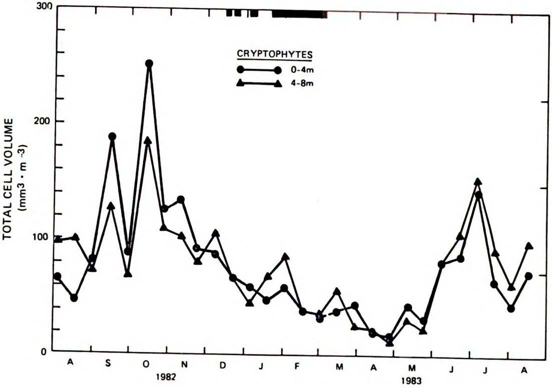

CRYPTOPHYTES
0-4m
4-8m
TOTAL CELL VOLUME
(mm3 · m -3)
300
200
100
0
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.17

nutrients released from the collapsing phytoplankton community or from mixing as the epilimnion was deepened. The cryptophytes declined quickly during the following cooling period with lower light levels and decreased lake stability.

The temporal dynamics of three species of cryptophytes are presented in Figure 1.18. *Cryptomonas*, as considered here, is a composite of *C. erosa*-like forms that were of similar size but difficult to differentiate during cell enumeration. Most of these cells were either *C. erosa* or *C. ovata*. Although *Cryptomonas* never attained exceptionally high cell concentrations, its contribution to total algal volume was important because of its large cell size. *Rhodomonas minuta* v. *nannoplanctica* is a small-celled cryptophyte that was always present and often abundant.

Ketablepharis ovalis, a colorless cryptophyte, was present in all but one of the samples examined (Figure 1.18). This species was just slightly smaller than *Rhodomonas* and never was observed at concentrations greater than 110 cells$\cdot$mL^{-1}. *K. ovalis* persisted throughout the year with relatively minor fluctuations in concentration. A much larger population developed in the epilimnion during August and September 1982. In contrast, that pattern did not reappear in August 1983.

Figure 1.18. Cell concentration of selected Chlorophyta and Cryptophyta species, and microflagellates (<6 µm dia) in two depth-strata over an annual cycle in Lawrence Lake, Michigan. The species of chlorophytes are *Botryococcus braunii*, *Sphaerocystis schroeteri*, *Planktonema lauterborni*, *Crucigenia rectangularis*, and of cryptophytes are *Cryptomonas 'erosa-ovata'*, *Rhodomonas minuta* v. *nannoplanctica* and *Ketablepharis ovalis*.

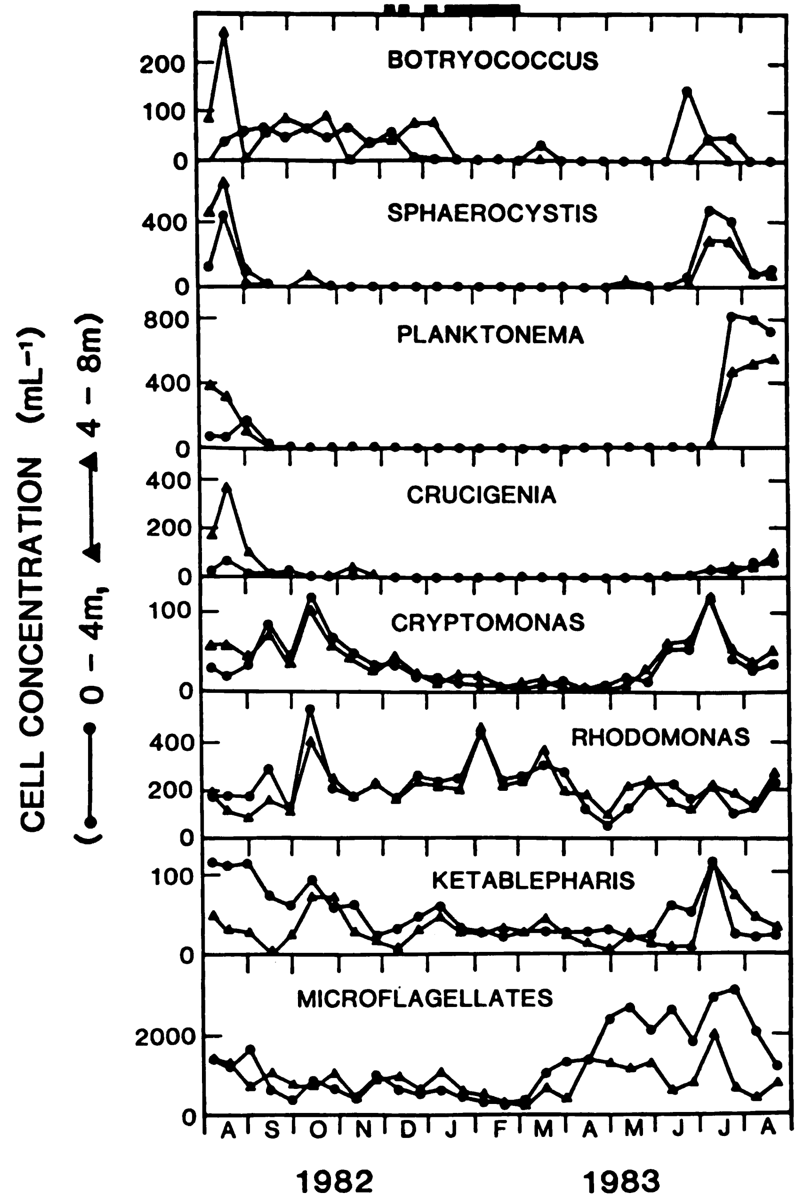

CELL CONCENTRATION (mL⁻¹)
(●—● 0 - 4m, ▲—▲ 4 - 8m)
BOTRYOCOCCUS
200
100
0
SPHAEROCYSTIS
400
0
PLANKTONEMA
800
400
0
CRUCIGENIA
400
200
0
CRYPTOMONAS
100
0
RHODOMONAS
400
200
0
KETABLEPHARIS
100
0
MICROFLAGELLATES
2000
0
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

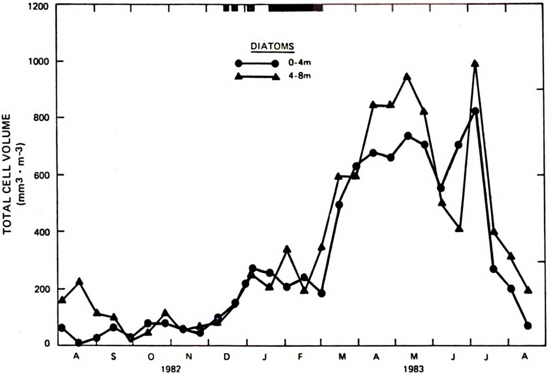
Figure 1.18

Diatoms

Diatoms dominated algal biovolume throughout the year except from August through the October period of destratification. There were only minor variations in relative importance between the 0-4-m and 4-8-m strata (Figure 1.11). Diatoms contributed more than ten percent of the total algal biovolume on all but a few days during the entire year in the upper 8 m of the water column. The annual mean biovolume contribution of diatoms was over 40 percent (Figure 1.13). The relative importance of diatoms increased continuously throughout the winter and spring, and reached a maximum in March when they constituted as much as 80 percent of the total biovolume. Once diatoms attained biovolume dominance in early December it was retained for eight months until the following July. This mid-winter dominance is at variance from the pattern during 1968-1969 described by Stewart and Wetzel (1986) and probably resulted from the exceptionally warm winter, late development of ice and greater than normal light availability.

The absolute contribution of diatoms to biovolume followed a different pattern (Figure 1.19). Total diatom cell volume remained near 100 $mm^3 \cdot m^{-3}$ from late August through December 1982, when it increased to over 200 $mm^3 \cdot m^{-3}$. Volume of this group remained at this plateau, under ice, through February when it began another sharp increase to nearly 1000 $mm^3 \cdot m^{-3}$ by mid-May. This maximum was due to

Figure 1.19. Total diatom cell volume in two depth-strata over an annual cycle in Lawrence Lake, Michigan.



TOTAL CELL VOLUME
(mm3 · m-3)
1200
1000
800
600
400
200
0
DIATOMS
0-4m
4-8m
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.19

co-dominance by *Cyclotella bodanica*, *C. michiganiana*, *Asterionella formosa* and to a lesser extent *Fragilaria crotonensis*. Diatom biovolume decreased rapidly to 400 $mm^3 \cdot m^{-3}$ by mid-June, largely from the decline of *C. michiganiana* and *Asterionella*. Diatom biovolume increased again to April levels in the first week of July from growth by *C. bodanica*. A rapid decline followed; by August 1983 values were again below the 200 $mm^3 \cdot m^{-3}$ levels.

Both single-celled and colonial diatom species commonly occurred either simultaneously or separately at various times during the year. As a result, differences between the annual distribution of diatom algal units and cell numbers were common (Figures 1.20 and 1.21, respectively). The general pattern for algal units was from a low (<50 mL^{-1}) in autumn and winter until ice-loss, followed immediately by an abrupt increase through the spring period. During this study two major peaks were observed, one on 10 May (about 300 algal units mL^{-1}) and a second lower one on 5 July (about 250 algal units mL^{-1}), with a major depression between these peaks to less than 150 algal units mL^{-1}. There was a final precipitous decline after July 5 to concentrations less than 50 algal units mL^{-1}. In contrast, cell numbers, largely from the filamentous *Fragilaria*, were relatively high under winter ice (Figure 1.21).

Four diatom species were selected for discussion because of their contribution to biomass or their

Figure 1.20. Total diatom algal units in two depth-strata over an annual cycle in Lawrence Lake, Michigan.

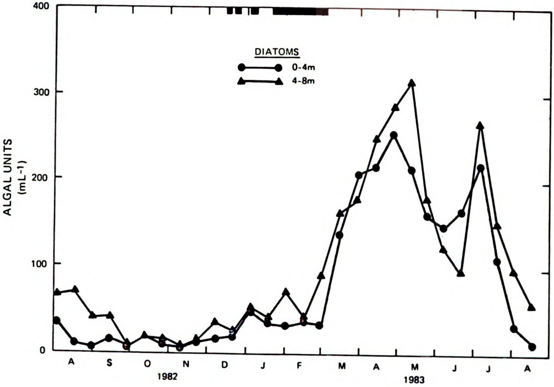

DIATOMS
0-4m
4-8m
ALGAL UNITS (mL-1)
400
300
200
100
0
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.20

Figure 1.21. Total diatom cell concentration in two depth-strata over an annual cycle in Lawrence Lake, Michigan.

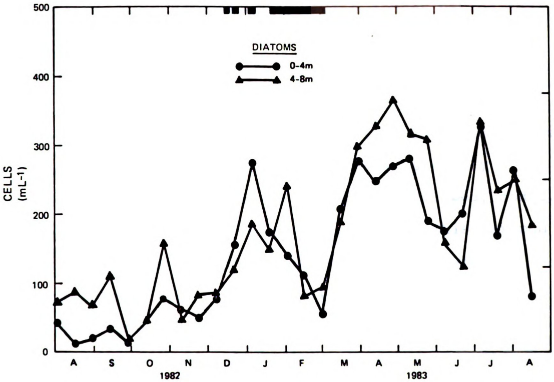

DIATOMS
0-4m
4-8m
500
400
300
200
100
0
CELLS (mL-1)
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.21

conspicuous occurrence during the year (Figure 1.16). Three species, Cyclotella michiganiana, C. bodanica var. affines and Asterionella formosa, started growing at or just prior to ice-loss. C. michiganiana reached its maximum in April, after just one month of growth from nearly undetectable levels. A. formosa grew steadily over a longer period and reached a maximum a month later at the end of April. These two species were essentially eliminated from the system by the end of June. Growth of C. bodanica var. affines was initiated under ice in January but at a very low rate. More rapid growth began at ice-loss and continued steadily through mid-May. An increase of net growth followed, and C. bodanica reached its annual high in mid-July. This maximum coincided with a chrysophyte bloom (detailed below). Thereafter, Cyclotella rapidly declined. Fragilaria crotonensis, although present at most times during the year (Figure 1.16), was a biovolume dominant only during the winter months. Cell numbers for this species fluctuated considerably during the year.

Significant differences in the successional patterns and timing were noted between this study and that of Crumpton and Wetzel (1982). The dominant species in their study during the summer of 1979 (i.e. Cyclotella michiganiana, C. comensis and Sphaerocystis schroeteri) were all present in this study but none of them attained dominance. Indeed, C. comensis, instead of reaching cell concentrations of 4000 cells mL^{-1} in August, was very rarely observed in 1982 and 1983. Whereas Crumpton and Wetzel found *C. michiganiana* to reach 1000 cells mL^{-1} in July, we found it at only 40 cells mL^{-1} and then only in April. Similarly, *S. schroeteri* never attained its earlier prominence in the year of this study.

Cyanophyta

Blue-green algae contributed significantly to total algal biovolume during the short period between August and mid-October particularly in the metalimnion (Figure 1.11). In the first week of August (1982 and 1983) blue-greens contributed about 25 percent of the total biovolume in the 0-4-m stratum and about 40 percent in the 4-8-m stratum. When present, blue-greens were always greater in the 4-8-m stratum than in 0-4 m (Figure 1.22). The difference was not as great in August 1983 as in August of 1982 when values were 4-5 times higher in the metalimnion. Blue-green algae were insignificant for more than half the year, November through June.

Important blue-green contributions to algal particle density occurred only during August and then it was restricted to the 4-8-m stratum (Figure 1.9). These algae accounted for a maximum of 25 percent and 33 percent of total algal units in August 1982 and August 1983, respectively.

Figure 1.22. Total Cyanophyta cell volume in two depth-strata over an annual cycle in Lawrence Lake, Michigan.

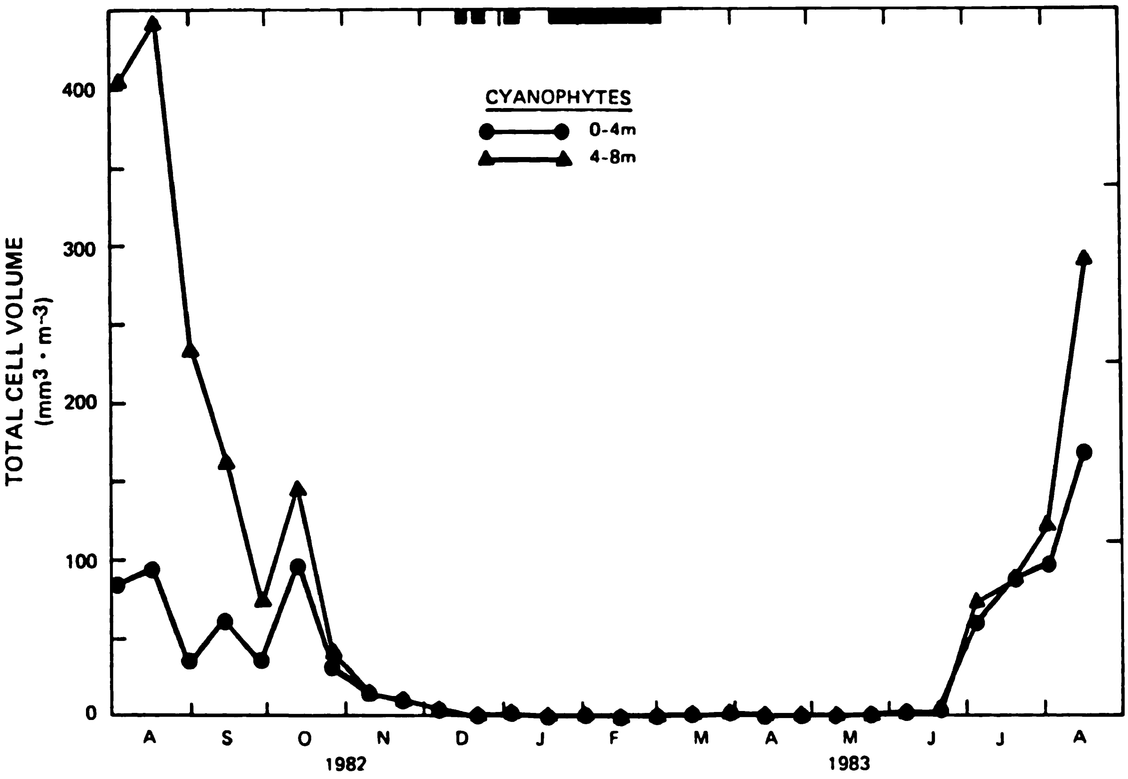

CYANOPHYTES
0-4m
4-8m
TOTAL CELL VOLUME
(mm3 · m-3)
400
300
200
100
0
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.22

Five species accounted for most of the blue-green biovolume during the study (Figure 1.23). Growth started late in June with biovolume peaking in late August or early September. Four of the five species were colonial coccoid forms; Anabaena flos-aquae was the most important filamentous species.

A notable form, assigned to Aphanothece nidulans P. Richter by Taylor and Wetzel (1984), is here referred to as Aphanocapsa-Aphanothece. The form was conspicuous in the summer phytoplankton community. Morphological variability of its cells and colonies precluded definitive identification. The colonies varied considerably in size as well as in the arrangement and compactness of the cells. The cells were often paired (Aphanocapsa) but spacing between pairs varied considerably. Cells varied in shape from spherical (Aphanocapsa) to ovate (Aphanothece). Numerous colonies or parts of colonies had cells arranged radially as those found in the genus Radiocystis. Since the extremes in variability were found in single colonies as well as in different colonies within the same collection, a definitive name was not assigned. Cell numbers of this form reached high levels, especially in the 4-8-m stratum (Figure 1.23).

Chroococcus limneticus most clearly illustrates the general trend for greater development or accumulation of blue-green biomass in the metalimnion. Some blue-green

Figure 1.23. Cell concentration of selected Cyanophyta species in two depth-strata over an annual cycle in Lawrence Lake, Michigan. The species are *Chroococcus limneticus*, *Coelosphaerium palidum*,*Gomphosphaeria aponina*, '*Aphanocapsa*-*Aphanothece*' and *Anabaena flos-aquae*.

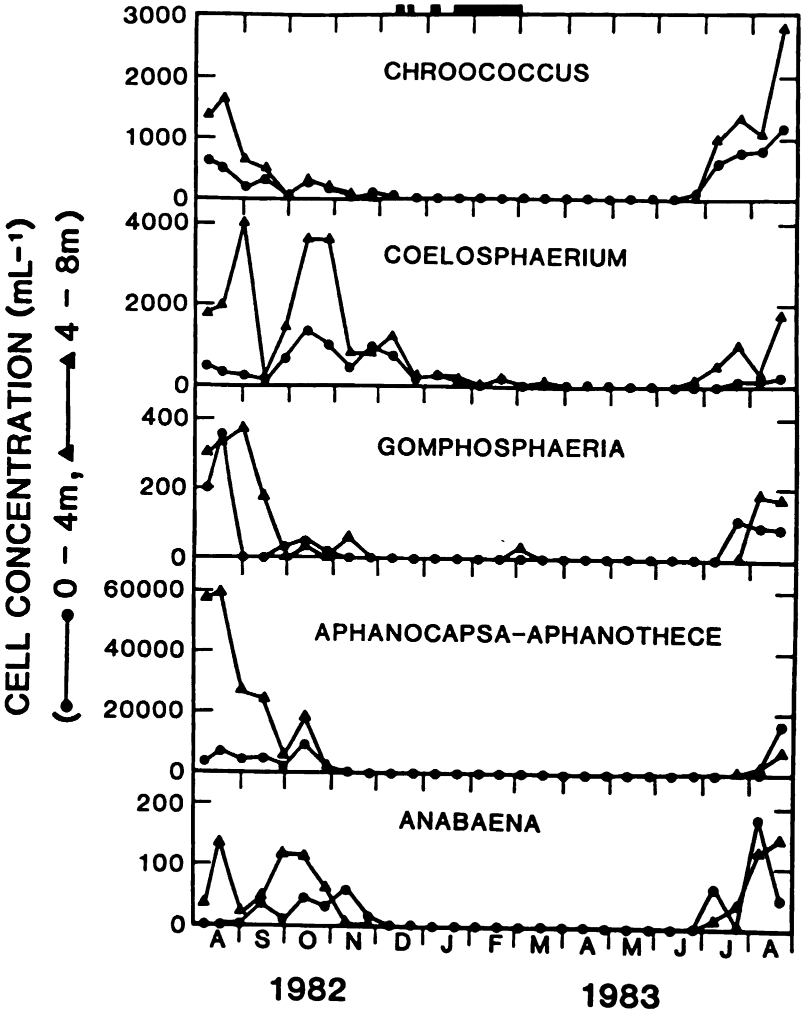

CELL CONCENTRATION (mL⁻¹)
(●——● 0 - 4m, ▲——▲ 4 - 8m)
CHROOCOCCUS
3000
2000
1000
0
COELOSPHAERIUM
4000
2000
0
GOMPHOSPHAERIA
400
200
0
APHANOCAPSA-APHANOTHECE
60000
40000
20000
0
ANABAENA
200
100
0
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.23

algae can utilize buoyancy regulating mechanisms to maintain favorable positions in the highly stable metalimnion, a region of high heterotrophic activity and nutrient regeneration. These factors and adequate light availability made the metalimnion highly suitable for positive net growth by phytoplankton. Another colonial blue-green, *Coelosphaerium palidum*, conspicuously occurred throughout most of the winter even though it was a minor biovolume contributor (Figure 1.23).

Chrysophyta

Chrysophytes were always present, usually in amounts less than 100 $mm^3 \cdot m^{-3}$ (Figure 1.24). The exception was in June and July when chrysophyte biovolume (mostly *Stichogloea*) rapidly increased to about 800 $mm^3 \cdot m^{-3}$ and accounted for 35 to 40 percent of the total biovolume in the 0-4-m and 4-8-m strata, respectively (Figure 1.11). The chrysophytes were also important biovolume components from October through January when total biovolume was lower, and accounted for about 35 and 20 percent in the 0-4-m and 4-8-m strata, respectively.

With few exceptions, chrysophyte contributions to algal particle density were minor (Figure 1.9). However, at turnover they accounted for 20 percent of the total in both strata. The chrysophytes did not approach that level again in the 0-4-m stratum. A ten-fold increase in chrysophyte

Figure 1.24. Total Chrysophyta cell volume in two depth-strata over an annual cycle in Lawrence Lake, Michigan.

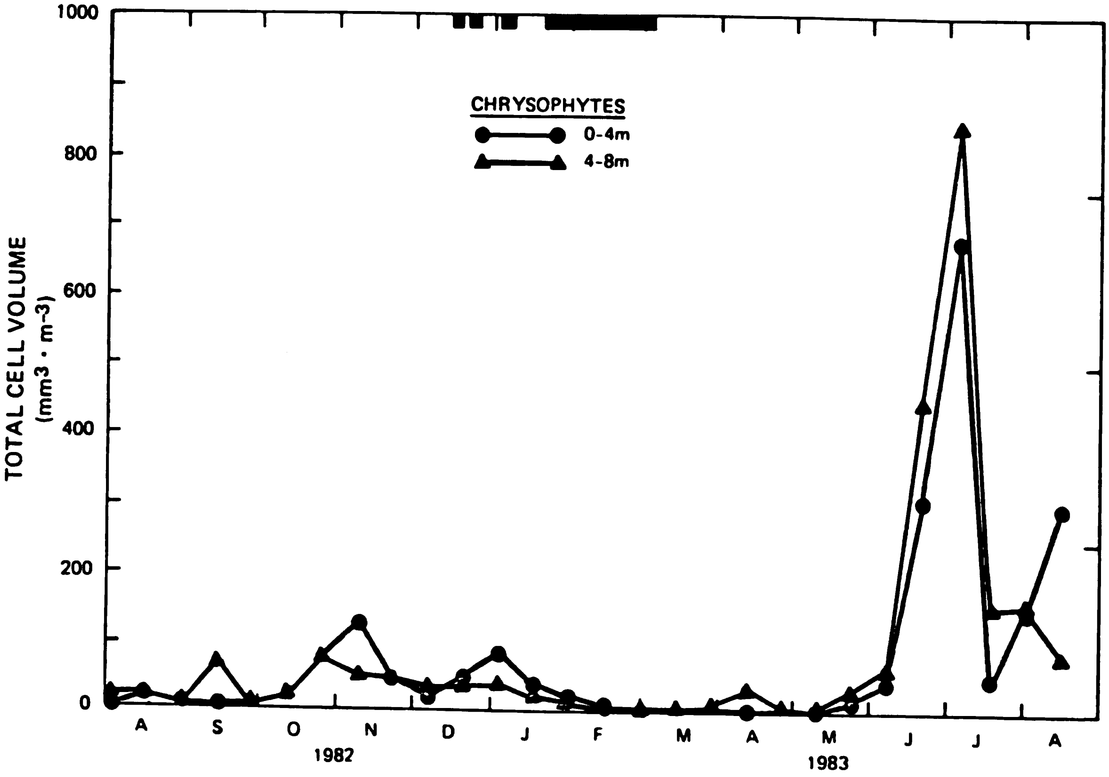

1000
800
600
400
200
0
TOTAL CELL VOLUME
(mm3 · m-3)
CHRYSOPHYTES
0-4m
4-8m
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

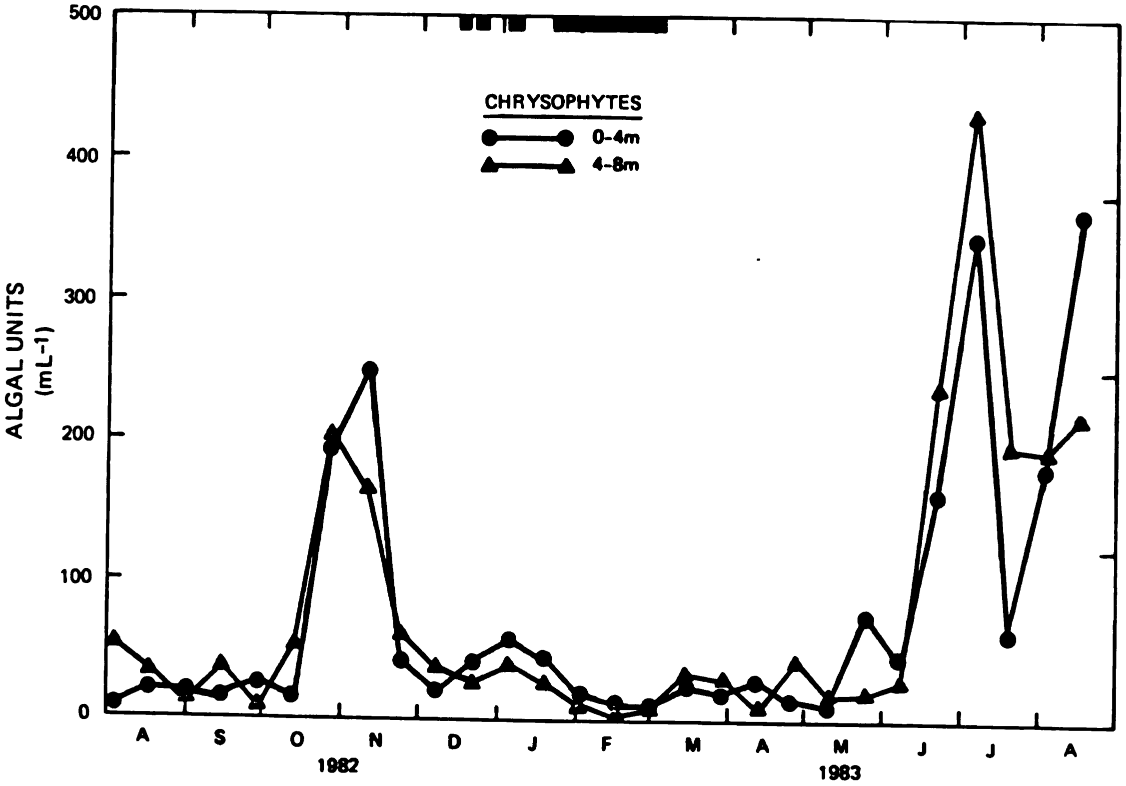
Figure 1.24

algal units occurred during a four-week period between 7 June and 5 July (Figure 1.25). Greater numbers of microflagellates in the epilimnion than in the metalimnion (Figure 1.18) decreased the relative value of the chrysophyte algal unit contribution in the epilimnion at that time.

Chrysophyte population dynamics were characterized by infrequent intense periods of growth followed by quick declines. Usually numerous species were present in very low numbers. Of four species of _Dinobryon_ identified in Lawrence Lake, only _D_. _divergens_ was notable (Figure 1.16). This species developed during the latter stages of destratification, reached a maximum in the same week as turnover, and then rapidly declined. Temperatures were less than 14°C during this period. The species was undetected once lake temperatures reached 4°C and ice first formed on the lake.

Chrysosphaerella _longispina_ followed a pattern similar to _Dinobryon_ in the autumn of 1982 but was less abundant, particularly at 4-8 m (Figure 1.16). A very large population developed in both strata, however, during August of 1983. Water temperature and stratification had little affect on the development of this species. During its occurrence nearly uniform epilimnetic temperatures ranged from 23 to 25°C, while the metalimnion was strongly stratified with temperatures ranging from 9 to 23°C (Figure 1.1).

Figure 1.25. Total Chrysophyta algal units in two depth-strata over an annual cycle in Lawrence Lake, Michigan.



CHRYSOPHYTES
0-4m
4-8m
ALGAL UNITS
(mL-1)
500
400
300
200
100
0
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.25

The Chrysosphaerella maximum in August 1983 closely followed the rapid decline of Stichogloea, another colonial chrysophyte (Figure 1.16).

Stichogloea doederleinii was present throughout much of the study in very low concentrations, but unlike other chrysophytes it bloomed during late June and early July (Figure 1.16). This species accounted for about 45 percent of the total biovolume between 0-8 m during the first week in July. The bloom occurred during an extended period of high solar input and rapidly increasing epilimnetic temperatures. The temperature structure in the highly stratified metalimnion was stable during this period (Figure 1.1). During the Stichogloea maximum, light penetration was reduced to the annual minimum by turbidity from epilimnetic decalcification and to a lesser degree high algal biovolume (Figure 1.3).

Development of Mallomonas spp. was concurrent with the decline of other chrysophytes, i.e. Dinobryon and Chrysosphaerella (Figure 1.16). Maximum cell concentrations of Mallomonas occurred under the sporadic ice-cover of early winter. Uniform vertical temperatures of 3-4°C were prevalent at that time. Solar radiation was then at its annual minumum (Figure 1.1).

Chlorophyta

Seasonal biovolume trends of the green algae closely followed those of the blue-green algae, i.e. peak development in June and August. The green algae never contributed more than about 16 percent of the total biovolume. Notable differences in biovolume between 0-4-m and 4-8-m strata occurred only in August 1982 where metalimnetic concentrations were four times the biovolume of the epilimnion (Figure 1.26).

The green algae added few particles to the community during the study. Again, as with the blue-green algae, their greatest contributions (between 4 and 23 percent) were in late July and August.

Four species of green algae were conspicuous components of the summer plankton community (Figure 1.18). *Sphaerocystis schroederi*, *Crucigenia rectangularis* and *Planktonema lauterborni* were restricted to July and August. *Botryococcus braunii* maintained a relatively stable population through December 1982 until permanent ice formed. *Planktonema* grew very quickly in July, doubling almost daily over a two-week period in the epilimnion. Overall, green algae were of minor importance in Lawrence Lake during this study.

Figure 1.26. Total Chlorophyta cell volume in two depth-strata over an annual cycle in Lawrence Lake, Michigan.

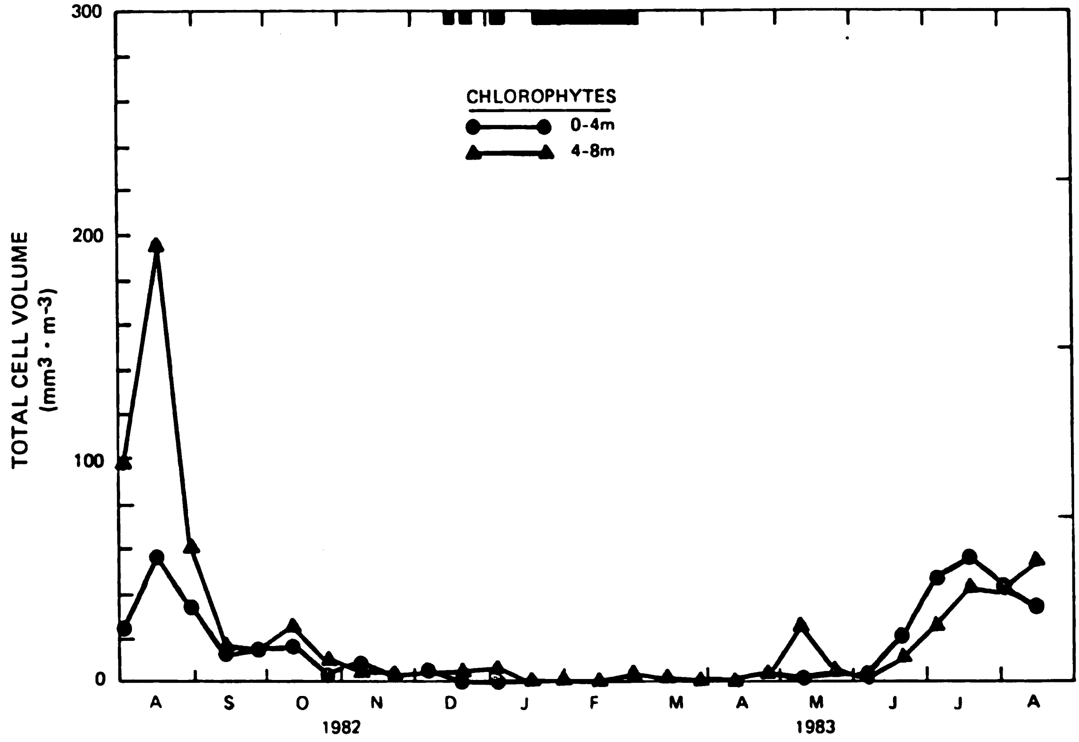

300
200
100
0
TOTAL CELL VOLUME
(mm3 · m-3)
CHLOROPHYTES
0-4m
4-8m
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.26

Microflagellates

Microflagellates were always present and often provided the greatest number of cells, and therefore particles per unit volume, of any group encountered. This group was composed largely of small *Ochromonas*-like cells but always contained *Chrysochromulina parva* as well. The latter species could not always be positively identified during routine counting and was therefore placed in the general category. Annual cell concentrations of microflagellates (<6 μm in diameter) are given in Figure 1.18.

The microflagellates rarely contributed more than 10 percent to the total biovolume and then only during the late autumn near the annual minimum (Figure 1.11). Their biovolume fluctuated frequently (Figure 1.27) with regular oscillations between about 15 and 40 $mm^3 \cdot m^{-3}$ from August through December 1982. A period of decline then followed through the end of February to the observed minimum for the group (6 $mm^3 \cdot m^{-3}$). During the August through February period there was no consistent pattern of microflagellate dominance in either the 0-4-m or 4-8-m strata. After ice-loss and the beginning of stratification in March, microflagellate biovolume increased faster and remained higher in the surface stratum. This pattern continued throughout the remainder of the study year. The microflagellate biovolume maximum was 78 $mm^3 \cdot m^{-3}$ in the 0-4-m on 5 July (Figure 1.27), but this accounted for less than 2 percent of the total algal biovolume at that time.

Figure 1.27. Total microflagellate (<6 μm dia) cell volume in two depth-strata over an annual cycle in Lawrence Lake, Michigan.

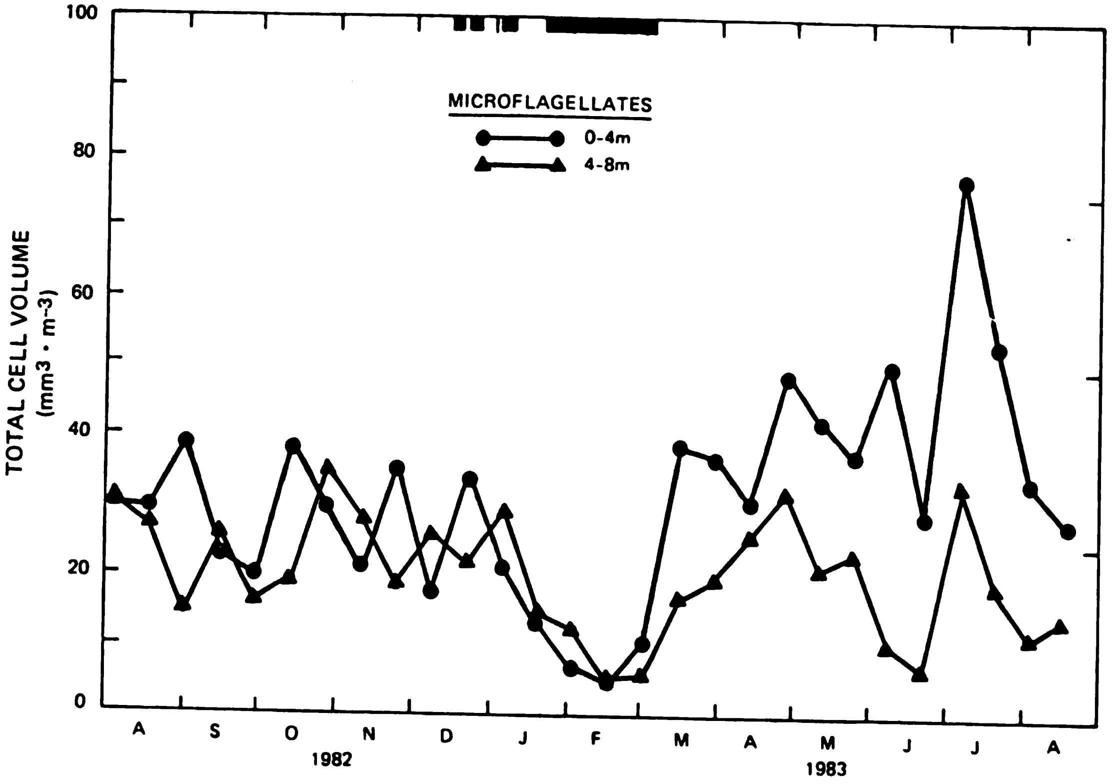

MICROFLAGELLATES
0-4m
4-8m
TOTAL CELL VOLUME
(mm3 · m-3)
100
80
60
40
20
0
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 1.27

Summary

1. One hundred twenty-one algal species of phytoplankton were identified from hardwater Lawrence Lake of southern Michigan during this study. Only 20 species contributed more than 5 percent of the total biovolume at any particular time. Biovolume was often dominated by relatively large single celled forms, i.e. Cyclotella bodanica var. affines (January through July), Ceratium hirundinella and Peridinium gatunensis (summer), P. willei (winter and spring) and Cryptomonas (autumn). Populations of the motile colonial forms Chrysosphaerella (late summer) and Dinobryon (autumn) developed and declined rapidly. Non-motile colonial forms varied in their occurrence, i.e. the short-lived development of Stichogloea (summer), the irregular fluctuations of Fragilaria throughout the year and the blue-green algae during summer (Aphanothece-Aphanocapsa, Gomphosphaeria, Chroococcus, Coelosphaerium). Small microflagellates (<6 μm) and Rhodomonas and Ketablepharis accounted for about 80 percent of the algal units in the lake throughout the year; their contributions to algal biovolume, however, was almost always less than 10 percent.

2. During this study a major phytoplankton biovolume maximum occurred in late June (about 2000 $mm^3 \cdot m^{-3}$). This maximum biovolume was largely the result of a bloom of

Chrysosphaerella. At other times biovolume ranged from about 250 $mm^3 \cdot m^{-3}$ to about 1000 $mm^3 \cdot m^{-3}$, only a fourfold factor. The oligotrophic status of the phytoplankton of Lawrence Lake was indicated by the low Chla concentrations (maximum =
3.2 $\mu g \cdot L^{-1}$), productivity rates (maximum <300 mg $C \cdot m^{-2} \cdot day^{-1}$), and biovolume.

3. Several potentially nuisance species of blue-green algae were present in low numbers (i.e. Microcystis aeruginosa, Anabaena flos-aquae and Aphanizomenon flos-aquae). Changes in community structure to where these species dominate could occur rapidly with nutrient enrichment and/or shifts in nutrient availability.

4. Only minor vertical stratification of species occurred during much of the study, which in part resulted from integration of portions of the water column by the sampling technique. However, even during the stratified period motile forms known to actively seek optimal strata or migrate vertically on a diel basis, e.g. Cryptomonas (Salonen et al. 1984) and Rhodomonas (Sommer 1982), did not appear to congregate in one stratum more than another. Other forms were clearly located in discrete strata, e.g. Gymnodinium helveticum was almost always found in the metalimnion and the microflagellates were usually twice as abundant in the surface water as they were in the metalimnion during the stratified period.

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CHAPTER 2

SHORT-INTERVAL CRYPTOPHYTE DYNAMICS AND GROWTH RATES OVER AN ANNUAL PERIOD

Introduction

In Chapter 1 of this work a description of the limnology and phytoplankton population dynamics in Lawrence Lake was presented for an annual period, August 1982 to August 1983. Those data were collected at two-week intervals. Important changes in populations of small algae (<30 μm) may be missed when seasonal phytoplankton studies employ sampling intervals much greater than the doubling times of the fastest growing forms. Under ideal conditions for growth, large species may have doubling times greater than three days (e.g., *Ceratium*), while smaller forms have the potential for dividing several times each day (e.g., *Chlamydomonas*) (Reynolds 1984). The purpose of this study was to determine short-interval population dynamics of selected cryptophyte species. The effects of sampling interval on seasonal population dynamics and estimates of daily net growth rate constants were evaluated for those species. The collections were made during 1982-1983, thus adding detail to the general discussion in Chapter 1.

Materials and Methods

Sample collection, preservation and counting methods were as described in Chapter 1. Integrated phytoplankton samples were collected at two-day intervals (one-day intervals during October) from three depth-strata (0-4, 4-8 and 8-12 m) at the central depression. The cryptophytes were dominated by two taxa, *Rhodomonas* (*Rhodomonas minuta*, as discussed by Willén et al. 1982) and *Cryptomonas* '*erosa*', a composite of mostly *C. erosa* but also *C. ovata*, two species often difficult to differentiate during cell enumeration. Between 100 and 450 *Rhodomonas* cells were counted per sample. Counting error (±1 std) varied between 9 and 20 percent (Lund et al. 1958). *Cryptomonas* '*erosa*' abundance estimates were based on counts of 30 to 120 cells per sample, and counting error ranged from 18 to 30 percent. *C. phaseolus* was very seasonal in its distribution and abundance in Lawrence Lake. In most samples during its growing-season at least 100 cells were counted.

Observed (net) growth rate constants (k_n) were calculated assuming exponential growth or decline between sampling intervals, a widely used practice by phytoplankton ecologists (Horn 1984, Braunwarth and Sommer 1985, Elser et al. 1987):

$$k_n = \ln(N_1/N_0)/(t_1-t_0), \qquad (1)$$

where, N_0 and N_1 are cell abundances at times t_0 and t_1, respectively. k_n will most closely estimate maximum growth rate when all factors required for growth are in excess and when losses are minimal, conditions rarely achieved or sustained in nature. Positive values indicate population growth while negative values indicate population decline. Doubling time (G), in days, was calculated as:

$$G = \ln 2/k_n. \qquad (2)$$

Results and Discussion

General cryptophyte dynamics

Rhodomonas and *Cryptomonas* '*erosa*' accounted for 76 to 98 percent (mean > 90 %) of the total cryptophyte cell volume throughout the year in the 0-8-m stratum. Cryptophyte contributions to total phytoplankton biovolume were greatest between September and December, reaching a maximum of 50 percent in the 0-4-m stratum (Figure 2.1). *Cryptomonas* '*erosa*' cell volumes were typically 20-fold greater than those of *Rhodomonas* cells, and usually resulted in a much larger contribution to total cell volume by *Cryptomonas* even though *Rhodomonas* was always more abundant.

Figure 2.1. Contribution of cryptophyte cell volume to total phytoplankton cell volume in 0-4-m (upper) and 4-8-m (center) strata, and total phytoplankton cell volume (lower) in Lawrence Lake, Michigan, at two-week sampling intervals.

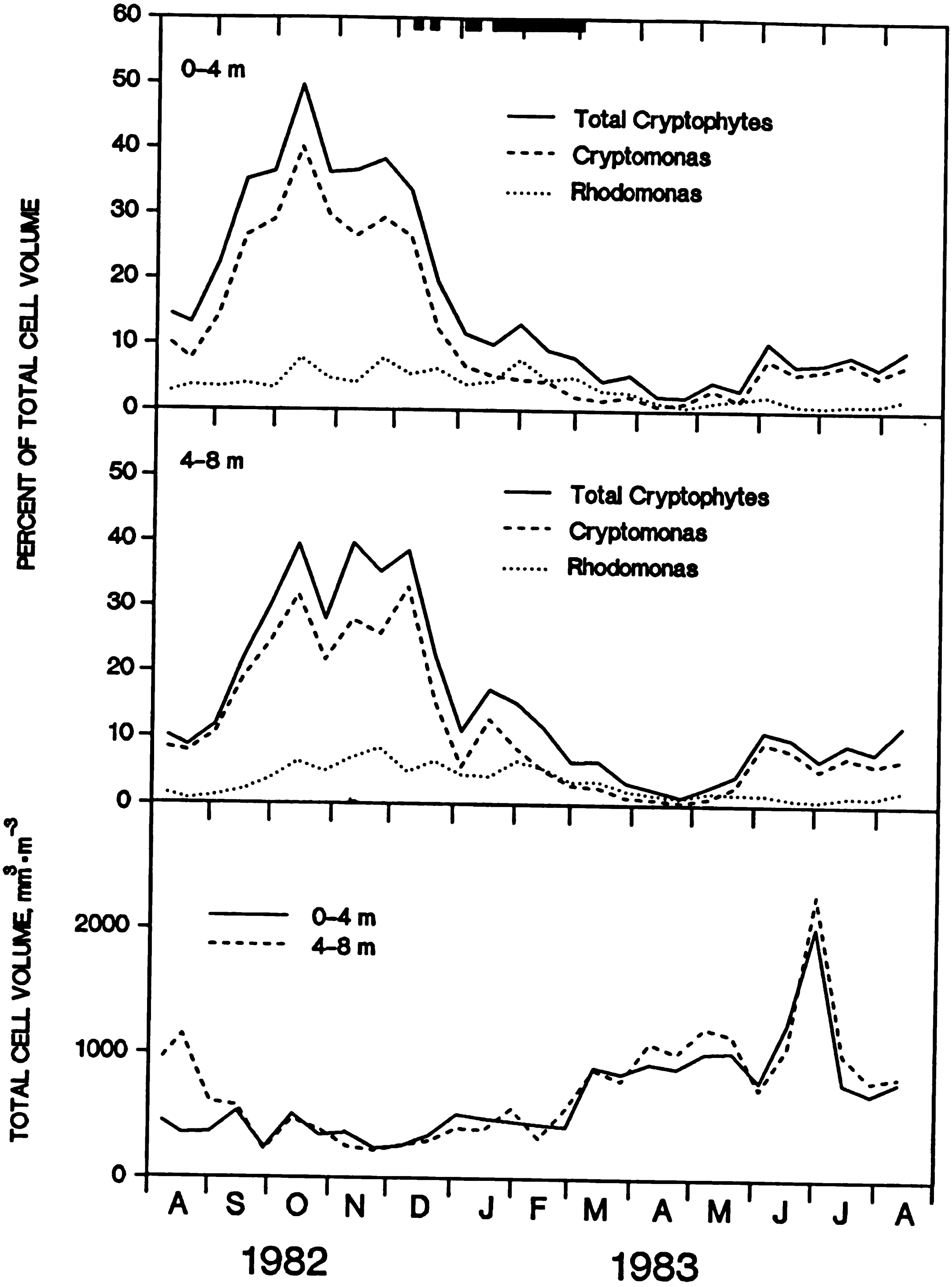
PERCENT OF TOTAL CELL VOLUME
0-4 m
Total Cryptophytes
Cryptomonas
Rhodomonas
4-8 m
Total Cryptophytes
Cryptomonas
Rhodomonas
60
50
40
30
20
10
0
TOTAL CELL VOLUME, mm³·m⁻³
0-4 m
4-8 m
2000
1000
0
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 2.1

Short interval cryptophyte dynamics

Population dynamics of Rhodomonas, Cryptomonas 'erosa' and C. phaseolus are presented by stratum at two-day intervals (one-day intervals during October) in Figures 2.2, 2.3 and 2.4, respectively. A complete list of cell abundances for Rhodomonas and Cryptomonas 'erosa' is given in Appendix B. Rhodomonas and Cryptomonas 'erosa' were observed continuously throughout the annual cycle. C. phaseolus was most frequently observed in summer and early autumn.

Rhodomonas abundance ranged from 33 cells$\cdot$mL^{-1} in the hypolimnion in August to 544 cells$\cdot$mL^{-1} in the epilimnion in October, representing only a 16-fold maximum difference within the lake during the year. Cell abundances between 100 and 300 cells$\cdot$mL^{-1} occurred in 80 percent of all samples examined from all depths, illustrating the highly stable nature of this population. These results are in marked contrast to the population dynamics of Rhodomonas in other north temperate lakes. Lund (1962) found Rhodomonas populations frequently reaching 1500-3000 cells$\cdot$mL^{-1} in several lakes and in one case in Blelham Tarn, 6000 cells$\cdot$mL^{-1}. Cell densities reached about 9000 cells$\cdot$mL^{-1} in a eutrophic bay of Lake Mälaren (Willén et al. 1982). Larger seasonal fluctuations, as illustrated in these examples, are more typically encountered in the literature

Figure 2.2. *Rhodomonas minuta* abundance by depth-strata in Lawrence Lake, Michigan.

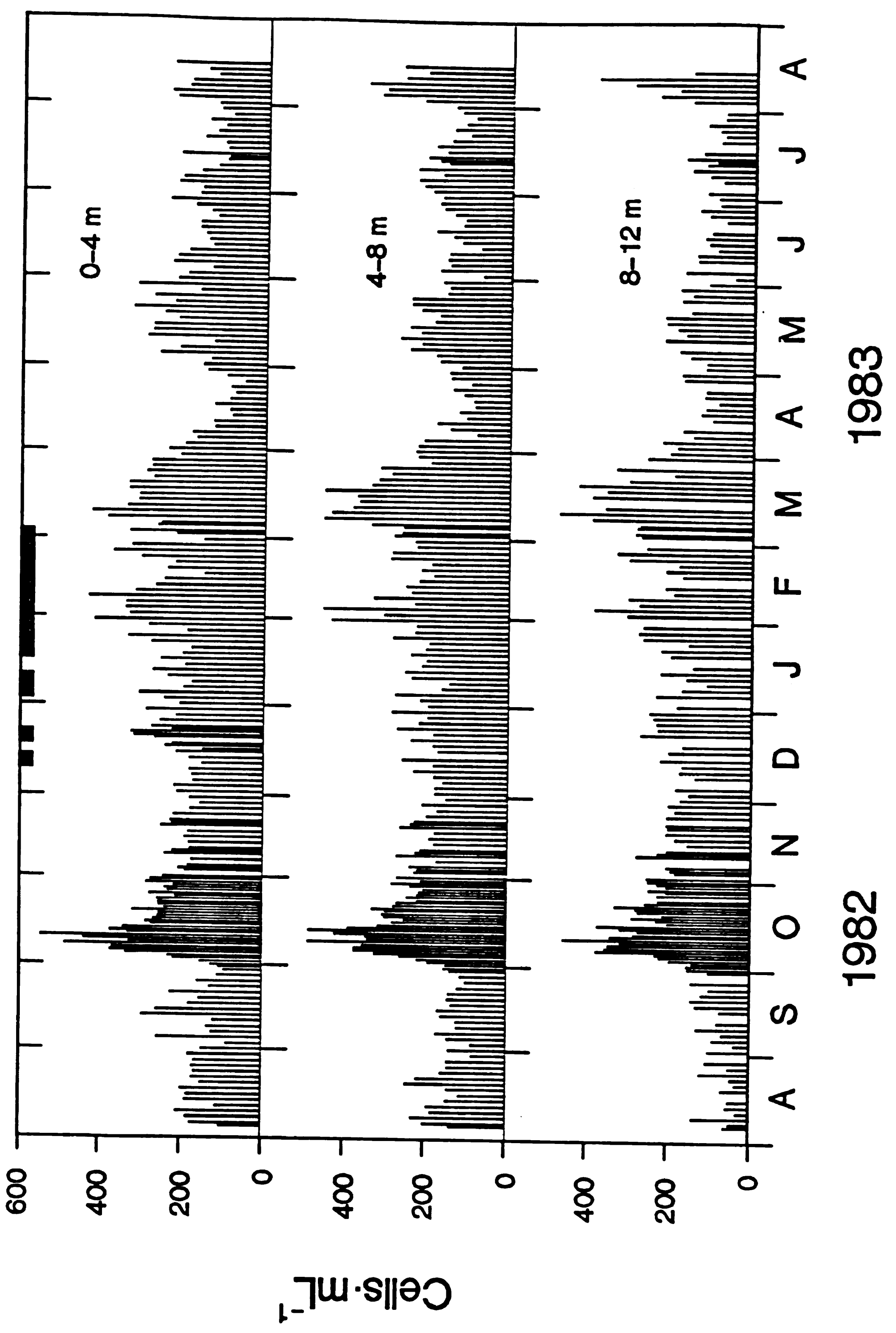
Cells·mL^{-1}
600
400
200
0
400
200
0
400
200
0
0–4 m
4–8 m
8–12 m
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 2.2

Figure 2.3. *Cryptomonas* '*erosa*' abundance by depth-strata in Lawrence Lake, Michigan.

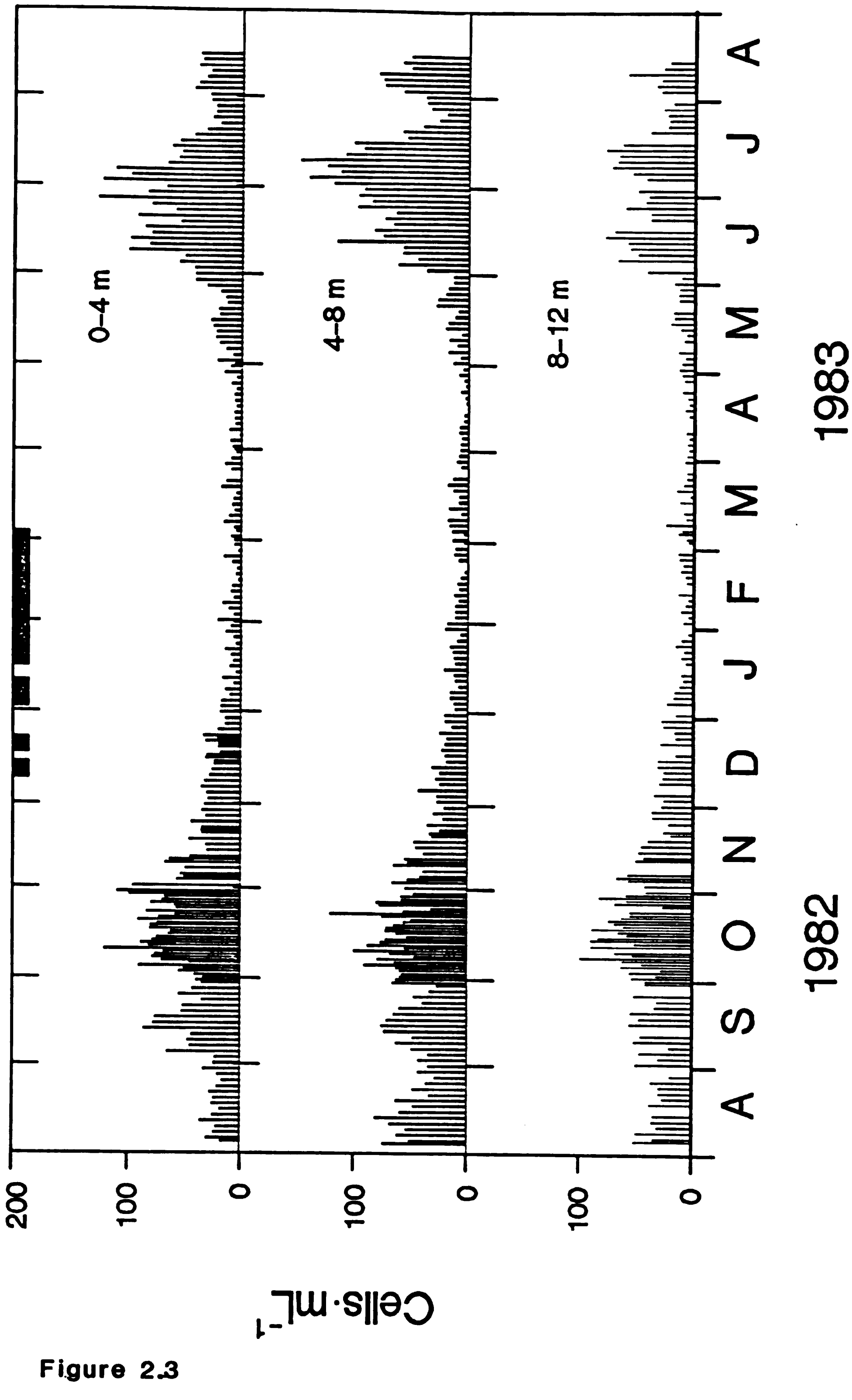
0–4 m
4–8 m
8–12 m
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983
200
100
0
100
0
100
0
Cells·mL⁻¹

Figure 2.3

Figure 2.4. *Cryptomonas phaseolus* abundance by depth-strata in Lawrence Lake, Michigan.

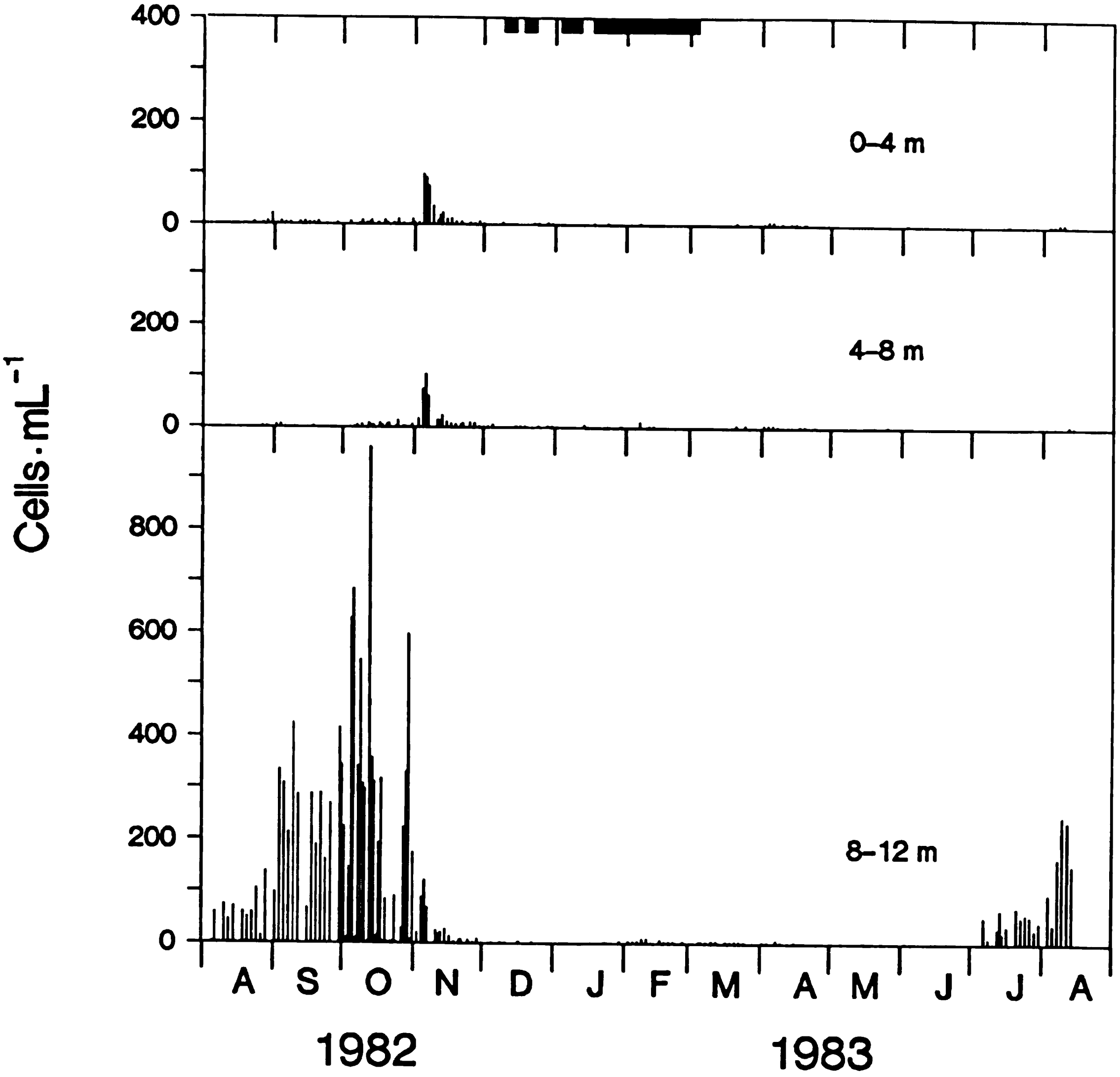
400
200
0
200
0
800
600
400
200
0
Cells·mL^{-1}
0–4 m
4–8 m
8–12 m
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 2.4

for a wide variety of phytoplankton species. The total autotrophic biovolume of Lawrence Lake varied by only eight-fold during this study (Figure 2.1). This level of community stability is similar to that described for total autotrophic biomass in tropical Lake Lanao (Lewis 1978). Rhodomonas was the only species observed with such a consistently stable population in Lawrence Lake.

The most abrupt population change occurred early in October with a five-fold increase during a ten-day period (Figure 2.2). A relatively large population was maintained under ice which, after ice-loss on 2 March, declined steadily over a six-week period to less than 100 cells$\cdot$mL^{-1}. The population increased again to about 300 cells$\cdot$mL^{-1} during a two-week period in May and then fluctuated between 100-200 cells$\cdot$mL^{-1} during the rest of spring and summer.

In contrast to Rhodomonas, Cryptomonas 'erosa' abundance maxima occurred as broad peaks in the autumn and in the early summer (Figure 2.3). Both peaks developed and declined slowly over extended periods. The population remained low (<20 cells$\cdot$mL^{-1}) throughout winter and spring. Cell abundances were rarely greater than 100 cells$\cdot$mL^{-1} during the annual cycle. Unlike Rhodomonas, the Cryptomonas population frequently occurred at very low cell abundances.

The third species, Cryptomonas phaseolus, formed a dense population in the hypolimnion during September and October (Figure 2.4). Hypolimnetic samples integrated over 8-12 m had abundances exceeding 600 cells$\cdot$mL^{-1}, while abundances in occasional grab samples from 11 m exceeded 6000 cells$\cdot$mL^{-1} indicating development of this species in thin strata. C. phaseolus has been noted for its association with nutrient-rich environments (Anton and Duthie 1981). Very large nearly unialgal populations of C. phaseolus were reported in a layer at the metalimnion where oxygen and sulfide were both at low concentrations (Pedrós-Alió et al. 1987). In Lawrence Lake the highest concentration of nutrients can be expected near the sediment-water interface during brief periods of anoxia. The development of this species coincided with the onset of anoxia at the sediment surface (early August). Although its decline was concurrent with the reintroduction of oxygen to the hypolimnion during autumnal turnover (early November), other factors such as decreasing light and lower temperatures may have been more important in its decline. Complete mixing of the lake can be seen in these data with the sudden introduction of C. phaseolus into the upper eight meters on 5 November.

Large day to day fluctuations in cell abundances of C. phaseolus were common in the hypolimnion. This phenomenon was thought to result from repeated minor vertical migrations by the population across the 12-m depth plane in response to changing light and nutrient regimes. Migration of the population below a depth of 12 m placed it beyond the 8-12-m sampling interval resulting in an apparent reduction in cell abundance in the hypolimnion. The maximum depth of the lake was 12.5 m, allowing the population a 0.5 refuge from the sampler.

Depth variations

Pronounced differences in cell abundance were found between depth-strata on numerous days (Appendix B) even though seasonal patterns in abundance appeared to be quite similar (Figures 2.2 and 2.3). Studies conducted under conditions of minimal turbulence demonstrated cell stratification by *Rhodomonas* and *Cryptomonas* along light gradients (Ruttner 1963, Wright 1964, Sommer 1982, 1986). In the present study, interpretation of daily differences in cell abundances among strata is difficult because of the potential variability associated with each datum. Variability may arise from vertical and horizontal patchiness, and cell enumeration. Variability resulting from vertical patchiness was reduced through the collection of 4-m-long integrated samples that masked stratification within the stratum when it was present. This sampling method restricted details to differences between major vertical strata. Crumpton and Wetzel (1982) tested for horizontal phytoplankton patchiness in Lawrence Lake and consistently found no greater variance among five stations than between replicates at a single station. Similar periodic testing during this study using *Rhodomonas* and *Cryptomonas* '*erosa*' as the test organisms support their findings.

In order to identify differences in abundance between strata, three-point running means were calculated for the *Rhodomonas* and *Cryptomonas* data sets (Figure 2.5). These calculations integrated information over six-day periods during the year except in October when integration covered three days. This treatment of the data reduced much of the day to day variability and thus smoothed the curves and clarified comparisons among strata.

Only minor variations in *Rhodomonas* abundance occurred with depth (Figure 2.5). Departures from vertical homogeneity in the *Rhodomonas* population were greatest during the period of thermal stratification. The largest depth differences were in August and September 1982 when *Rhodomonas* abundance below 8 m was about half that in the upper strata. From May through June *Rhodomonas* abundance was slightly stratified, high to low, from the surface downward. Just after photosynthetically induced epilimnetic decalcification in June, epilimnetic cell numbers declined relative to other strata, perhaps as a result of reduced nutrient (phosphorus) availability (Figure 1.5, Wetzel 1981).

Figure 2.5. Rhodomonas minuta and Cryptomonas 'erosa' cell abundance curves smoothed through the calculation of three-point running means.

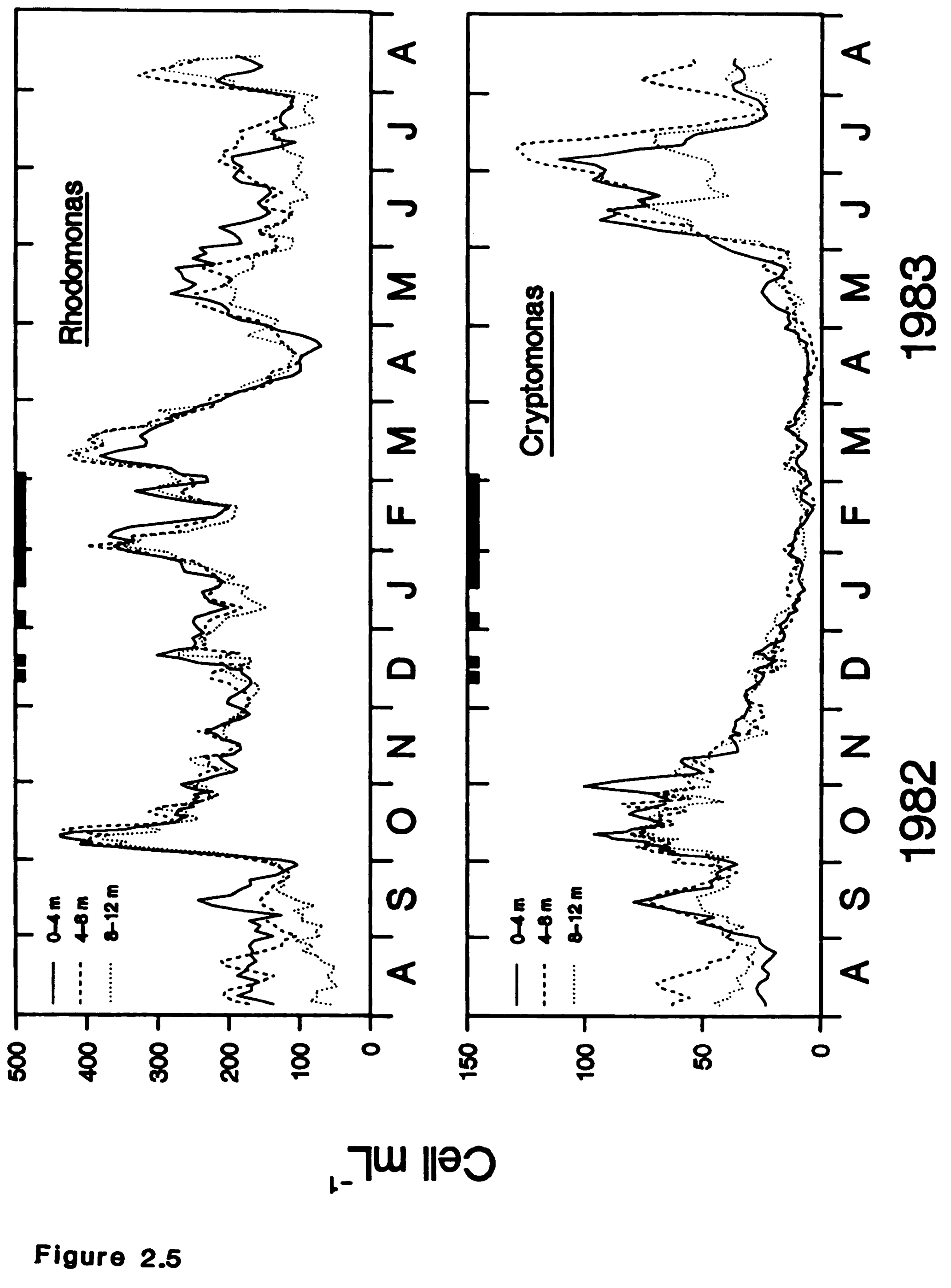
Rhodomonas
Cryptomonas
0–4 m
4–8 m
8–12 m
500
400
300
200
100
0
150
100
50
0
Cell mL⁻¹
A S O N D J F M A M J J A
1982
1983

Figure 2.5

By August, surface abundances of Rhodomonas were lower than in deeper strata. The slight surface depression during March may have been a response by low-light adapted cells to intense light following ice-loss. Similarly, the Cryptomonas population varied little with depth especially during winter and spring (Figure 2.5). Metalimnetic maxima occurred during July and August, the period of greatest density discontinuity from thermal stratification. Hypolimnetic Cryptomonas and Rhodomonas abundances were notably low in June and early July, possibly from reduced light during epilimnetic decalcification and its associated turbidity ("whiting") (Figure 1.3).

The remarkable constancy in temporal and vertical abundance of Rhodomonas and Cryptomonas in Lawrence Lake is difficult to explain given the dynamic physical, chemical and biological conditions normally associated with a dimictic temperate lake. This stability suggests that these populations may be tightly controlled. Control by environmental factors seems unlikely in view of the extremes in temperature and thermal stability (Figures 1.1 & 1.2), seasonally and vertically variable light (Figure 1.3) and nutrient regimes (Figure 1.5). Light, among these variables, appears to have been adequate for growth throughout much of the water column during the study. Lund (1962) suggested that Rhodomonas populations normally may be nutrient limited. Phosphorus limitation to phytoplankton productivity prevails in the pelagial zone of Lawrence Lake throughout the year (Wetzel 1981, 1983) and may contribute to the apparent threshold levels of *Rhodomonas* and *Cryptomonas* population development. Lawrence Lake supports an active grazer community (Haney and Hall 1975, Crumpton and Wetzel 1982) that may exert seasonal control in some depth strata. *Rhodomonas* and *Cryptomonas* are an optimal size for many zooplankton grazers (Porter 1973) and *Rhodomonas* is a preferred food item for rotifers (Pejler 1977). The grazers may be largely responsible for the maximal biomass levels of these species. Most likely, different factors are operating with depth to maintain population stability. The ubiquitous occurrence of these species in virtually all lake types and degrees of eutrophy underlie their ability to adapt to a wide range of conditions.

Effects of sampling interval on observed seasonal dynamics

Sampling interval can greatly modify the apparent seasonal dynamics of a phytoplankton community (Horn 1984). The close-interval data for the *Rhodomonas* population were used to examine this phenomenon by systematically increasing the sampling interval. Data were rejected to create subsets at 4-, 8-, 14- and 32-day intervals (Figure 2.6). The upper panel shows the complete data set at two-day sampling intervals. Randomly selected examples of curves for each

Figure 2.6. Seasonal dynamics of *Rhodomonas* in the 0-4-m stratum at sampling intervals ranging from 2 to 32 days. See text for discussion of different lines in each panel.

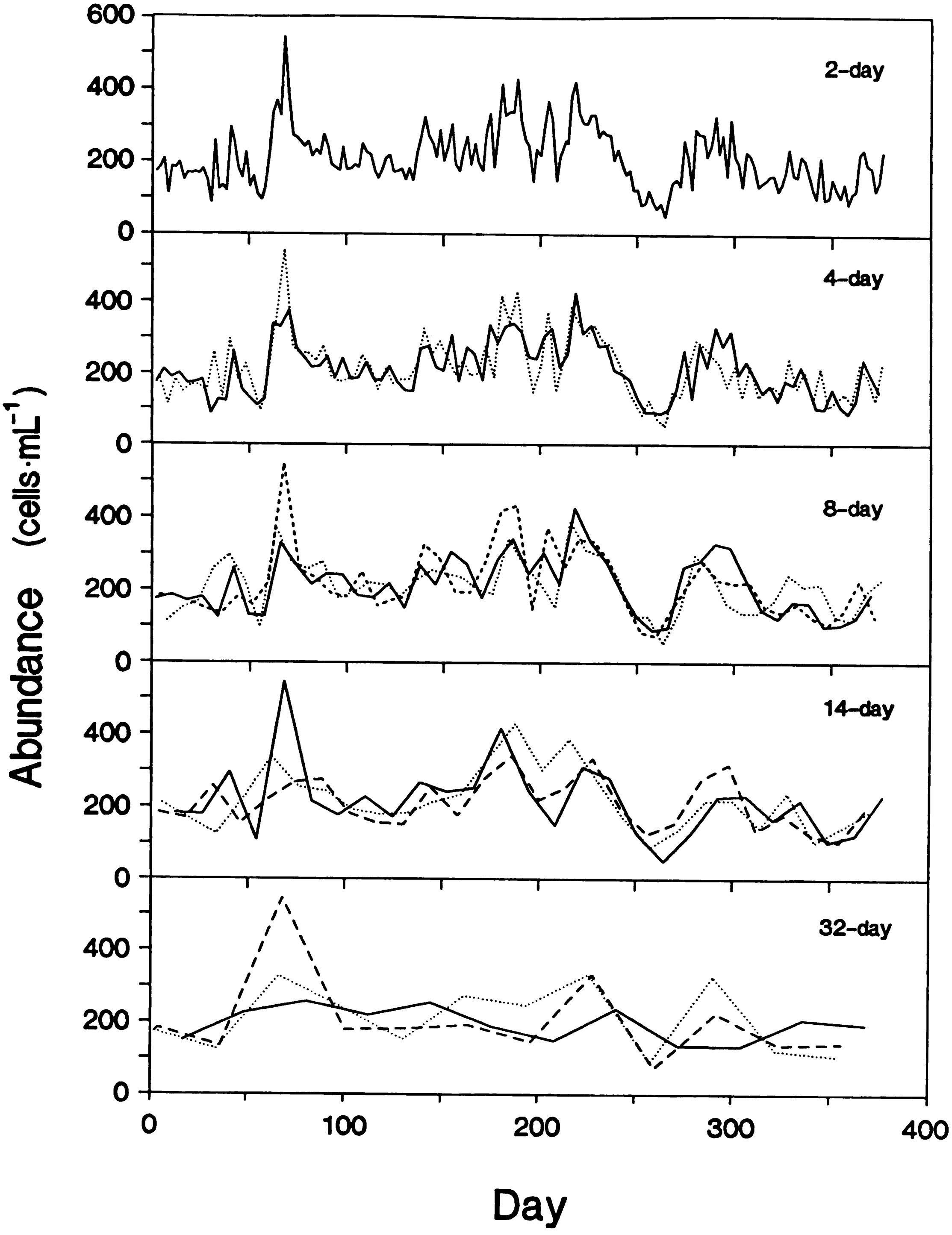
600
400
200
0
2-day
400
200
0
4-day
400
200
0
8-day
400
200
0
14-day
400
200
0
32-day
0
100
200
300
400
Abundance (cells·mL⁻¹)
Day

Figure 2.6

interval are shown in the remaining panels to illustrate the effect of starting date, an element of pure chance, on the patterns. There were 16 possible patterns at 32-day intervals, seven patterns at 14-day, four at eight-day and two at four-day intervals. Details of population dynamics rapidly decreased with increasing sampling interval, e.g., at four days there was a 50 percent chance (depending upon starting day) of missing the annual maximum (near day 70). The importance of the day 70 population pulse could easily have been missed at eight-day sampling intervals. The extended population depression near day 250 was apparent at all sampling intervals illustrated in the figure except for one at 32 days where nearly all seasonal events were reduced to a flattened line. The risk of missing important population fluctuations greatly increased in Rhodomonas as sampling intervals extended beyond seven days. Greater sampling flexibility existed with Cryptomonas. A similar analysis showed that two-week intervals were adequate to characterize important Cryptomonas fluctuations because of the more extended growth periods in the species (Figure 2.3).

Effects of sampling interval on growth rate

Phytoplankton species have been characterized as fast (r-selected) or slow (K-selected) growing forms (Kilham and Kilham 1980, Sommer 1981). Calculation of the exponential growth constant for a species is one method of quantifying this variable. Under optimal laboratory conditions maximum growth rates can be determined. Reynolds (1984) compiled a table of growth rates for a wide variety of algal species from the literature. Growth at these maximal rates is rarely measured _in situ_ where cells are constantly lost by cell lysis, sedimentation, grazing, vertical and horizontal transport and through wash-out, and where optimal conditions are rare or ephemeral. The true growth rate constant is controlled by ambient conditions prevalent at any given time. Observed or net growth rate will usually be less than the true growth rate for a given species. Estimates of true growth rate constants during specified periods have been made by variously accounting for loss factors (e.g. Crumpton and Wetzel 1982, Lund and Reynolds 1982) or by using special techniques that are not affected by losses (Braunwarth and Sommer 1985, Campbell and Carpenter 1986).

Growth rate is affected by temporal and spatial processes. Grazing impacts, for example, vary seasonally within lakes, and vertically within the water column on a diel basis. Growth rate has been inversely correlated with cell size (Fogg 1975, Banse 1976, Reynolds 1984) so that sampling intervals suitable to characterize large cells may be too broad for smaller cells. Sommer (1981), however, refutes the inverse relationship for all but the largest microflagellates. Errors in growth rate estimates will result when wind mixing or lateral transport of cells within water masses occurs at time scales close to or less than the sampling interval. Harris (1986) places environmental fluctuations at scales of 50 to 200 h, a range of time intervals leading to interaction with growth rates and therefore population dynamics.

In this study 187 paired data points, at two-day intervals, were used for calculating the net growth rate constant (k_n). In order to examine the apparent affects of sampling interval on observed Rhodomonas growth rates, k_n was calculated for all combinations of 2-, 4-, 8-, 14- and 30-day intervals (Figure 2.7). The greatest range of k_n values occurred at 2-day intervals and it progressively decreased with increasing sampling intervals. The assumption of exponential growth necessarily becomes invalid as sampling interval increases, i.e. the longer the interval between observations the more likely there will be a shift in the trend of population change (Tilzer 1984). This does not imply that exponential growth was always occurring at 2-day intervals. Similar results are presented for Cryptomonas 'erosa' in Figure 2.8. The maximal k_n values for Cryptomonas occurred in winter and spring during the annual population minimum and are misleading because, at that time, relatively small counting errors greatly affected the calculation of k_n.

Figure 2.7. Seasonal Rhodomonas cell abundance (upper) and observed growth rate constants (k_n) calculated at sampling intervals from 2 to 30 days in the 0-4-m stratum (remaining panels).

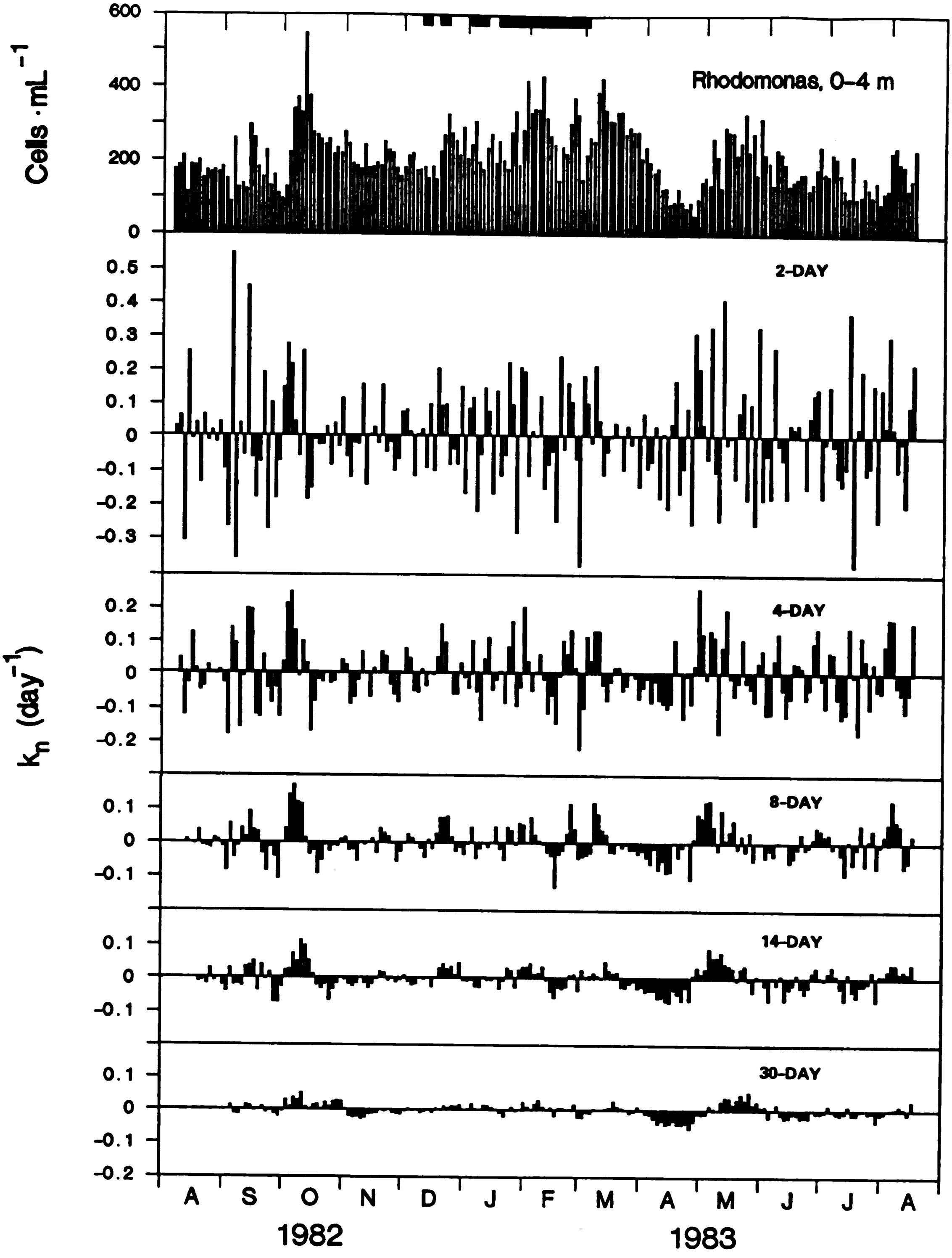
Cells · mL^{-1}
600
400
200
0
Rhodomonas, 0–4 m
k_n (day^{-1})
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
2-DAY
4-DAY
8-DAY
14-DAY
30-DAY
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 2.7

Figure 2.8. Seasonal <u>Cryptomonas</u> cell abundance (upper) and observed growth rate constants (k_n) calculated at sampling intervals from 2 to 30 days in the 0-4-m stratum (remaining panels).

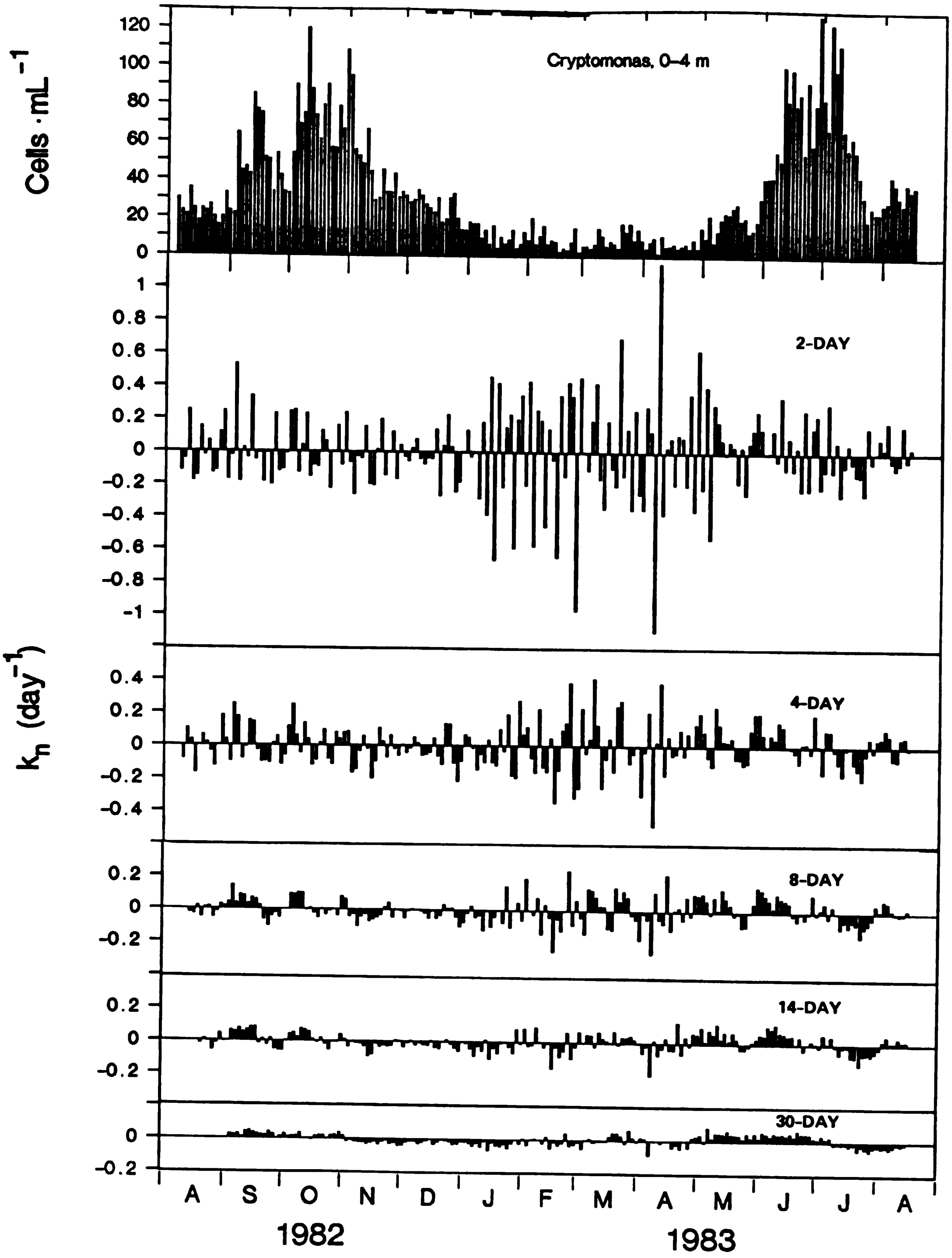
Cells · mL⁻¹
120
100
80
60
40
20
0
Cryptomonas, 0–4 m
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
2-DAY
kn (day⁻¹)
0.4
0.2
0
-0.2
-0.4
4-DAY
0.2
0
-0.2
8-DAY
0.2
0
-0.2
14-DAY
0
-0.2
30-DAY
A
S
O
N
D
J
F
M
A
M
J
J
A
1982
1983

Figure 2.8

Decreases in k_n with increasing sampling interval were presented as annual means in Figure 2.9 for both taxa. Apparent in this figure is the possibility that optimal sampling interval for maximizing k_n may be less than two days. The smallest usable sampling interval for the calculation of k_n is dependent upon the growth estimator, in this case numerical abundance. If, as was shown for *Rhodomonas* in culture (this study, Table 2.1), cell division occurs once each day, the optimal sampling interval would be one day. Light-synchronized *Rhodomonas* populations, both in culture and at times *in situ* (Lawrence Lake, June 1984), undergo cell division during the dark period (W. D. Taylor, unpublished data). In this case, calculation of k_n based on multiple daylight samplings during one daylight period would be meaningless.

Frequency distributions of k_n for *Rhodomonas* and *Cryptomonas* '*erosa*', are presented in Figures 2.10 & 2.11, respectively. Values of k_n near zero resulted from small changes in population abundance between sampling intervals. The significance of these low values is difficult to interpret because at one extreme they derive from the lack of growth and losses through a time period, while at the other extreme they derive from a realistic balance between growth and loss rates. The latter is a dynamic and active situation while the former is static. Positive k_n values less than 0.1 represent doubling times greater than seven

Figure 2.9. Annual mean k_n of Rhodomonas and Cryptomonas calculated at sampling intervals of 2 to 30 days in the 0-4-m stratum. Values for positive growth (k_n) and negative growth ($-k_n$) were meaned separately.

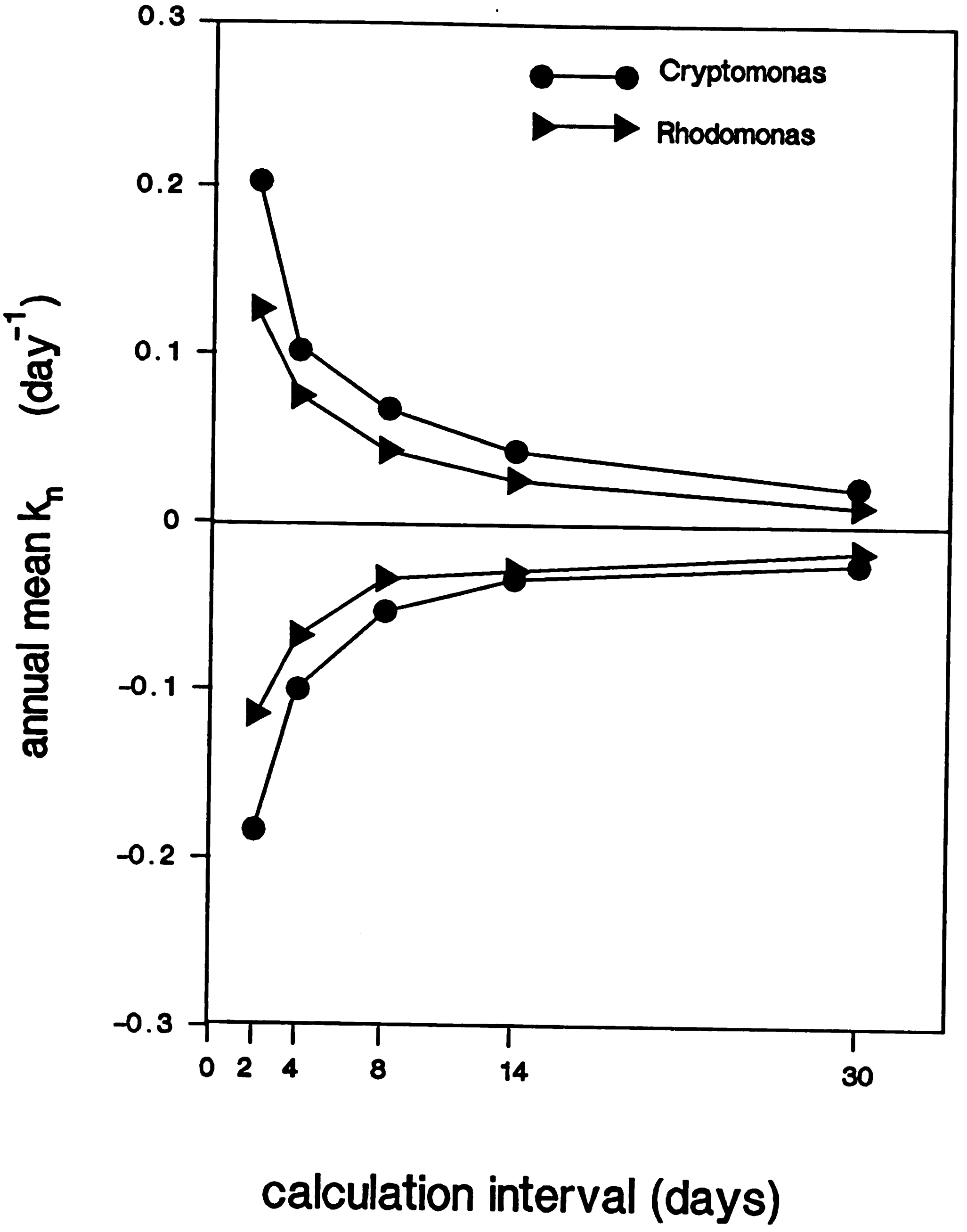
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
Cryptomonas
Rhodomonas
annual mean k_n (day^{-1})
0
2
4
8
14
30
calculation interval (days)

Figure 2.9

Table 2.1. Specific growth rates (k) in ln units and doubling times (G) reported in the literature for field and laboratory studies of Cryptomonas and Rhodomonas.

Species	k_n (day^{-1})	G (days)	Location	Source
R. minuta	0.16	4.4	in situ	1
R. minuta	0.46-0.62	1.5-1.1	in situ	2
R. minuta	0.11	6.3	enclosure	3
R. lacustris	0.27	2.6	in situ	4
R. minuta	0.23	3.0	in situ	5
R. minuta	0.20-0.34	2.0-3.5	in situ	6
R. minuta	0.17	4.1	enclosure (spring)	7
R. minuta	0.71	1.0	enclosure (ES)	7
R. minuta	0.29	2.3	enclosure	8
R. minuta	0.24	2.9	in situ	9
R. minuta	0.44	1.6	in situ	13
R. minuta	0.69	1.0	batch culture	10
R. lacustris	1.13	0.6	batch culture	4
C. ovata	0.5	1.4	batch culture	11
C. erosa	0.85	0.8	batch culture	12
C. (4 spp.)	0.19	3.4	in situ	1
C. sp.	0.6	1.2	enclosure	8
C. sp.	0.15	4.6	Enclosure (spring)	7
C. sp.	0.49	1.4	enclosure (ES, MS)	7
C. ovata	0.48-0.89	0.8-1.4	in situ	2
C. ovata	0.24-0.25	2.8-2.9	in situ	6

[1] Wright 1964; under snow-free ice and low grazing pressure.

[2] Sommer 1981; R. minuta in spring, C. ovata in spring and summer.

[3] Reynolds et al. 1983; high grazing pressure.

[4] Gavrieli 1984; in situ at Greifensee, 1978, in culture at 22°C and 214.5 μEinst$\cdot$m$^{-2}\cdot$s^{-1}.

[5] Taylor & Wetzel 1984; seven days of log growth in autumn.

[6] Braunwarth & Sommer 1985; mitotic index used to calculate potential growth rate.

[7] Reynolds et al. 1982; ES and MS are early and mid-stratification, respectively.

[8] Reynolds et al. 1985; depressed zooplankton biomass (July).

[9] Elser et al. 1987.

[10] This study; 12L/12D cycle, 150 μEinst$\cdot$m$^{-2}\cdot$s^{-1}, 20°C.

[11] Cloern 1977; 15L/9D cycle, 150 μEinst$\cdot$m$^{-2}\cdot$s^{-1}, 20°C.

[12] Morgan and Kalff 1979; 138 μEinst$\cdot$m$^{-2}\cdot$s^{-1} continuous light, 23.5°C.

[13] Calculated from data given in Willén et al. 1982.

Figure 2.10. Frequency distribution of observed k_n for *Rhodomonas* in the 0-4-m stratum.

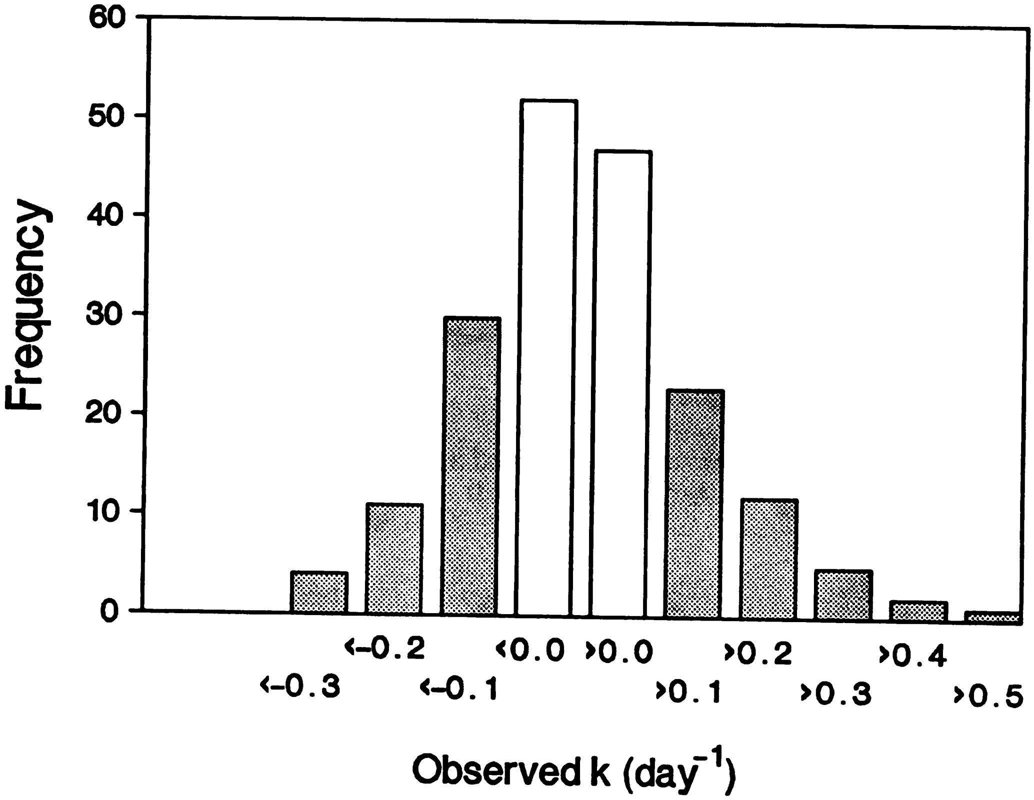
Frequency
60
50
40
30
20
10
0
<-0.3
<-0.2
<-0.1
<0.0
>0.0
>0.1
>0.2
>0.3
>0.4
>0.5
Observed k (day^{-1})

Figure 2.10

Figure 2.11. Frequency distribution of observed k_n for *Cryptomonas* in the 0-4-m stratum.

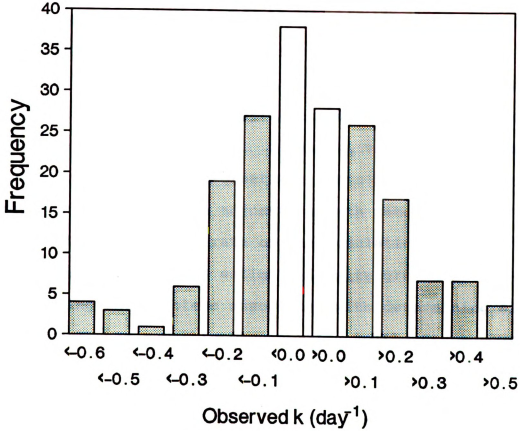
40
35
30
25
20
15
10
5
0
Frequency
<-0.6
<-0.5
<-0.4
<-0.3
<-0.2
<-0.1
<0.0
>0.0
>0.1
>0.2
>0.3
>0.4
>0.5
Observed k (day^{-1})

Figure 2.11

days while negative k_n values larger than -0.1 represent halving times greater than seven days. A large number of cases fell within this narrow range (open bars in Figures 2.10 and 2.11), 52 and 34 percent for *Rhodomonas* and *Cryptomonas*, respectively, indicating that during much of the year observable growth or loss was negligible. When k_n approaches the laboratory-derived potential maximum growth rate ambient conditions are optimal and losses of any kind can be assumed to be minimal. Larger k_n values contain more directly interpretable information. When losses can be measured or estimated the adjusted growth rate should be close to the true growth rate of the population. Use of the mitotic index to directly estimate *in situ* growth rates, thus avoiding the problems associated with determining all loss factors, has recently been applied to the cryptophytes (Braunwarth and Sommer 1985). Very low negative values of k_n represent observed cell losses in great excess of gains.

Culture studies provide the means to determine growth characteristics of algal isolates under optimal nutrient, light and temperature conditions without the confounding factors of species interactions and environmental variability. There has been much critical discussion, however, on the transfer of laboratory-derived growth parameters to field situations where growth controlling factors (light, temperature, nutrients) are variable and, in the case of nutrients, with *in situ* concentrations often orders of magnitude lower than in the culture situation. Still, laboratory estimates of growth rate constants establishes potential maxima for various species and provide standards against which *in situ* estimates can be compared. Maximum growth rates observed for *Rhodomonas* and *Cryptomonas* from culture and *in situ* studies are summarized in Table 2.1. Laboratory-derived doubling times of less than one day were reported for both taxa in cultures grown in continuous light (Gavrieli 1984, for *Rhodomonas*, and Morgan and Kalff 1979, for *Cryptomonas erosa*). We found light-synchronized *Rhodomonas* cultures to double at daily intervals under a 12L/12D cycle with cell division occurring in the dark phase. The minimum doubling time was greater for *C. ovata* (G = 1.4 days) within a 15L/9D cycle (Cloern 1977). Minimum doubling times reported in studies of natural populations of cryptophytes varied widely from 0.8 days for *C. ovata* (Sommer 1981) to 6.3 days for *Rhodomonas* (Reynolds et al. 1983); this range encompassed extremes in grazing pressure and growth conditions found in a variety of lake types. In Lawrence Lake, near maximal growth rates (i.e. $G \leq 1$ day) were not observed for *Rhodomonas* and only rarely and in winter for *Cryptomonas* (occurring less than two percent of the time). Observed doubling times were nearly always greater than three days for both species.

Distributions of k_n values occurring during an annual period are useful for evaluating population dynamics relative to known maximum growth rates. However, an evaluation of the frequency of switching between positive and negative growth provides insight into how well growth or loss was sustained during consecutive sampling intervals. Switching frequencies (the percentage of pairs of adjacent k_n values with opposite signs) at several sampling intervals are presented in Figure 2.12. At two-day sampling intervals more than 60 percent of the pairs of adjacent values (for both taxa) switched signs, indicating apparent frequent reversals during growth and loss phases. High frequency switching at the closest intervals resulted largely from minor variability in cell abundances. Increasing sampling interval reduced switching frequency by spanning relatively minor close-interval variations in cell abundance, thereby focusing on longer-term population phenomena. However, rapid changes in the magnitude of kn may be associated with the ability of these species to respond quickly to changing conditions (Stewart and Wetzel 1986). On the contrary, reductions in k_n may indicate high mortality associated with intense zooplankton grazing or cell lysis. The reduction in switching frequency with increasing sampling interval is also apparent in the lower panels of Figures 2.7 and 2.8.

There were few periods of sustained exponential growth by Rhodomonas or Cryptomonas during this study. The assumption of exponential growth in the calculation of k_n was frequently invalidated when intervals exceeded several days. With these data, minimizing day to day variations in k_n by increasing sampling interval automatically resulted in a reduction in calculated k_n. This change was so because the denominator in the equation for calculating k_n increased with longer sampling intervals while the difference between the population maximum and minimum remained constant for any given data base.

Figure 2.12. Switching frequency as the percentage of pairs of adjacent k_n values with opposite signs at sampling intervals of 2 to 30 days in the 0-4-m stratum.

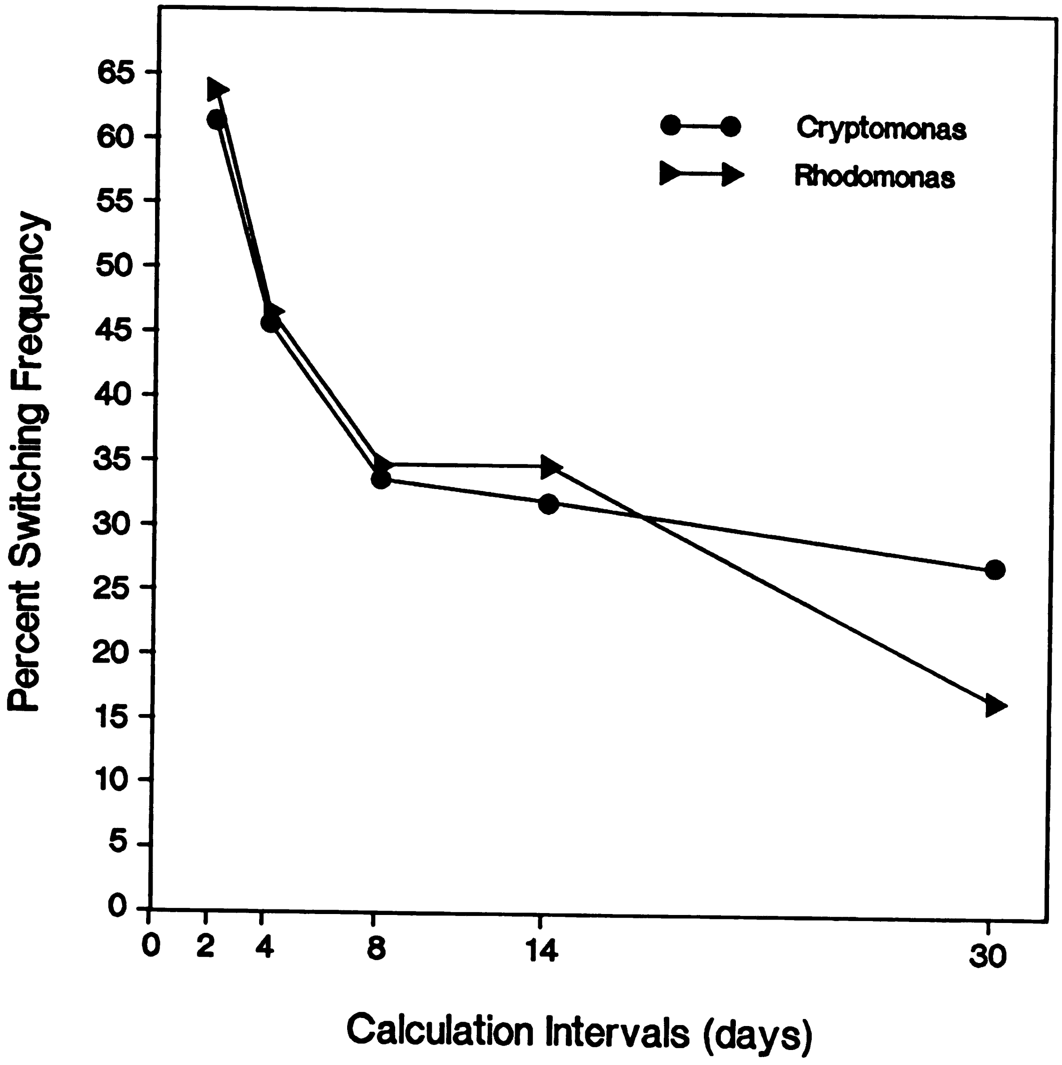
Percent Switching Frequency
65
60
55
50
45
40
35
30
25
20
15
10
5
0
0
2
4
8
14
30
Calculation Intervals (days)
Cryptomonas
Rhodomonas

Figure 2.12

Summary

1. The cryptophytes, *Rhodomonas minuta* and *Cryptomonas 'erosa'*, dominated the phytoplankton community during autumn, and accounted for a maximum of 50 percent of the total cell volume.

2. Annual seasonal cryptophyte dynamics varied between species. *Rhodomonas* had unusually stable population dynamics throughout the study while *C. 'erosa'* developed broad maxima in summer and autumn with a much reduced population during winter and spring.

3. Differences in abundance with depth of *Rhodomonas* and *Cryptomonas* were generally small and restricted to periods of thermal stratification. Metalimnetic maxima occurred during parts of March, April, July and August with *Rhodomonas* and during July and August with *Cryptomonas*.

4. The risk of missing important population fluctuations substantially increased as sampling intervals extended beyond one week for *Rhodomonas* and two weeks for *Cryptomonas*.

5. The greatest observed growth rates occurred at the closest sampling intervals and often when cell abundance was lowest. Calculations of k_n at these times were most susceptible to small variations in abundance estimates. Dynamic population trends were better reflected in larger sampling intervals but exponential growth, an assumption for

calculating k_n, was frequently invalidated at intervals exceeding three or four days.

6. During much of the year observable growth and loss was negligible (±G > 7 days), for 52 and 34 percent of the time for Rhodomonas and Cryptomonas, respectively.

7. Rhodomonas was never observed to change in situ at maximum laboratory measured growth rates while Cryptomonas was observed at maximum rates in less than two percent of the cases.

8. High frequency switching, between positive and negative k_n, at the closest intervals was thought to be largely due to minor variability in cell abundances. Increasing sampling interval reduced switching frequency by spanning relatively minor close-interval variations in cell abundance, thereby focusing on longer-term population phenomena.

9. Few periods of sustained growth occurred by either species during this study even though both were present continuously. Rhodomonas was always present in great enough abundance to take advantage of periodic optimal growth conditions. That such rapid responses did not occur is an indication of either continuous limitation by an essential nutrient (e.g. phosphorus), strong competition by other phytoplankton for limited nutrients, or finely adjusted population control by grazers.

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CHAPTER 3

PRODUCTIVITY OF THE CRYPTOPHYCEAE VERSUS GRAZING IMPACTS DURING EPILIMNETIC DEEPENING IN AUTUMN

Introduction

Periods occur during the year when increasing rates of change in weather cause rapid alterations in the physical and chemical structure of most north temperate lakes. After several months of relatively high thermal stability and maximal algal biomass, decreasing solar radiation in autumn causes rapid cooling of the surface waters. With cooling, thermal stability is eroded, mixed depth is increased and available light is reduced. These events lead to the decline of the summer phytoplankton community and its replacement by species better adapted to a less stable environment. Stewart and Wetzel (1986) proposed a modified model of phytoplankton community dynamics in which microflagellates and the Cryptophyceae can function as couplers to maintain productivity between the waxing and waning of major algal community components. Characteristics of these organisms cited in support of their model included intermittent numerical dominance, high nutritional quality, short turnover times, ability to grow and reproduce at low light intensities, and pulse timing (i.e., growth coinciding with periods of decomposition of dominant populations. Many of these factors are operating in Lawrence Lake, Michigan, where dominance by cryptophytes during the autumnal epilimnetic deepening period has been consistently observed (Taylor and Wetzel 1984, Stewart and Wetzel 1986).

Worldwide, cryptophytes have been reported as dominants in the phytoplankton community in all seasons (reviewed by Stewart and Wetzel 1986). Cryptophytes dominate in large lakes (Munawar and Munawar 1975) and in small ponds (Kalff 1967), and under a wide range of lake trophic states, e.g., oligotrophic (Findenegg 1971), mesotrophic (Moss 1972), eutrophic (Willén 1976) and dystrophic (Ramberg 1979). Distribution is cosmopolitan, ranging from the tropics (Lewis 1978) to tundra ponds in the high northern latitudes (Kalff 1967). Their widespread occurrence in freshwater plankton communities is unquestioned and yet very little is known about their ecology (Oakley and Santore 1982).

Taxonomically the Cryptophyceae, at the light microscope level, are an exceptionally difficult group with less than 100 described freshwater species (Huber-Pestalozzi 1968). Taxonomic difficulties arise from the simplicity of their external morphology and the reliance of classical taxonomists on characteristics such as color, cell shape and orientation of trichocysts. Cells of cryptophytes are unsymmetrical and the shape of even slightly rotated cells may vary considerably from published illustrations and descriptions. Taxonomic problems have hindered study of cryptophyte ecology. Ultrastructural investigations are revealing distinctive features unavailable to the light microscopist that should allow a more natural separation of species and genera (Oakley and Santore 1982). Recently, expanded interest in the Cryptophyceae has extended our knowledge of their ecology (Morgan and Kalff 1975, Cloern 1977, 1978, Sommer 1982, Gavrieli 1984, Pedrós-Alió 1987).

The purpose of this study was to verify the timing of transitional population shifts, make direct measurements of cryptophyte productivity for comparison with the rest of the autotrophic community, and evaluate the potential impact of the grazer community on cryptophyte populations in Lawrence Lake.

Materials and Methods

Site description

Lawrence Lake is a small, dimictic, hardwater lake with low pelagic productivity in southwestern Michigan, U.S.A. The lake has been well described morphometrically, chemically, and biologically (e.g. Rich et al. 1971, Wetzel et al. 1972, Wetzel 1983). Details of annual phytoplankton dynamics and community structure are presented in Chapter 1 of this dissertation.

Sampling schedule

Studies for general limnology, zooplankton grazing, zooplankton density and cryptophyte productivity were staggered because the work load precluded their simultaneous execution. General limnology and zooplankton grazing studies were conducted biweekly. Samples for zooplankton densities were collected at 3 to 5-day intervals; those nearest to the sampling dates for zooplankton grazing were used in this analysis. Cryptophyte productivity studies were conducted at intervals varying from 5 to 16 days between August 7 and November 30. However, intervals were from 5 to 9 days during the very active period of cryptophyte growth, September 18 to November 16. Phytoplankton samples were collected at 1 to 7-day intervals.

Physical and chemical

Light and temperature measurements were made at 1-m intervals with a LiCOR model LI-185 quantum photometer and a YSI 43JD thermistor, respectively. Samples for determination of conductivity, alkalinity, pH, alkaline phosphatase activity (APA), and chlorophyll a (Chla) were collected with an opaque 3-L Van Dorn bottle at 0, 1, 2, 3, 4, 5, 6, 7, and 10-m depths.

APA of whole lake water samples was measured by the enzymatic hydrolysis of non-fluorescent 3-0-methyl fluorescein phosphate mono-cyclohexylammonium to the fluorescent product, 3-O-,ethyl fluorescein as slightly modified from Hill et al. (1968) and Perry (1972) by Wetzel (1981).

Chla was measured using the trichromatic method of Strickland and Parsons (1968) as presented by Wetzel and Likens (1979). Samples of 500 to 750 mL were filtered onto AA Millipore filters (0.8-μm pore size) at a vacuum differential of less than 0.5 atm.

Alkalinity was determined by titration with H_2SO_4 using a mixed indicator. A Coleman 38A pH meter was used to measure pH in the laboratory with samples at room temperature. Total available inorganic carbon was calculated from pH, temperature, and alkalinity measurements (Wetzel and Likens 1979).

Because phytoplankton samples were integrated over 4-m intervals (see below), equivalent integrated values were determined for some of the parameters that were measured at discrete depths. Integral mean values, i.e. adjusted for differences in volume with depth, were calculated for APA and Chla for the 0-4-m and 4-8-m strata.

Phytoplankton

Crumpton and Wetzel (1982) evaluated phytoplankton patchiness in Lawrence Lake and consistently found no greater variance among five stations than between replicates at a single station. Further periodic testing in this study at four stations supported their findings (Table 3.1).

Vertically integrated phytoplankton samples (130 mL) were collected over the central basin with a 4-m long 5-L capacity Van Dorn type sampler and immediately preserved with 1 mL of acid Lugol's solution (Vollenweider 1974). Utermöhl's (1958) sedimentation method was used to prepare the samples for identification and enumeration. The recommendations of Lund et al. (1958) were followed for counting precision. In all cases, between 600 and 2000 total algal units were counted giving a counting error of less than ten percent for each sample. Complete transects of the chamber diameter were counted at several magnifications (360x, 180x, 90x); the magnification was dependent upon the size and abundance of the cells being evaluated. The entire chamber was used to enumerate large forms such as Ceratium. Species identification under oil immersion (900x) was routine. Counting and cell measurements were made with a Wild M40 inverted microscope. Twenty-five mL samples were settled for at least 15 h within a styrofoam insulated box to minimize convective currents caused by temperature fluctuations throughout the day.

Cell volumes were calculated for each species using formulae for solid geometric shapes most closely matching the cell shape. Mean cell volumes were based on individual

Table 3.1. Results of one-way ANOVA to examine horizontal patchiness of phytoplankton in Lawrence Lake, Michigan, using *Rhodomonas minuta* as a test organism[1]. (means as cells·mL^{-1})

Date	Range of Means from 4 Stations	Grand Mean (n=12)	F	Significance Level
30-Oct-82	210-224	215.1	0.5249	0.677
02-May-83	156-169	163.2	0.2133	0.884
21-Jun-83	157-173	167.6	0.5843	0.642
23-Jul-83	130-159	138.8	1.2212	0.363

[1] Three replicate integrated 0-4 meter samples were collected from each of four stations 50 to 100 meters apart in the open water. Cells were counted according to the methods described in the text.

cell volume calculations. Cell volumes were determined seasonally when changes in cell size were apparent.

Given the difficulty of directly measuring cell carbon for individual algal species in a mixed population, workers generally rely on conversions from measurable attributes such as cell volume (Nauwerk 1963, Beers et al. 1975, Banse 1976, Smayda 1978, Reynolds 1984). Cell volumes are commonly calculated from measurements of cell dimensions. Significant differences occur between conversion factors in accordance with whether or not the cells are preserved prior to measurement. For example, Borsheim and Bratbak (1987), using three measuring techniques, reported a 55-percent mean reduction in microflagellate cell volume after fixation with acid Lugol's solution. The latter authors determined a cell volume to cell carbon conversion of 0.10 pg $C \cdot \mu m^{-3}$ for living flagellates and 0.22 pg $C \cdot \mu m^{-3}$ for preserved flagellates. The latter conversion factor is very close to that calculated from Strathmann's (1967) empirically derived formula for non-diatom species when applied to fixed cryptophytes of similar cell volume (this study). A conversion factor for <u>Rhodomonas</u> of 0.28, based on direct measurements of cultured cells, was provided by Yngvar Olsen (personal communication). He stressed the importance of using this factor only with fixed cells. The formulae of Strathmann were used throughout this study because they accounted for differences between diatom and non-diatom species, reflected changes in relative carbon content with increasing cell size and they provided a consistent method for estimating cell carbon in a mixed community. Cell volumes varied by a factor of 5×10^4 during this study.

The phytoplankton community was subdivided into particle size classes (<10 μm, 10-30 μm, 30-50 μm, >50 μm) based on microscopic determination of their greatest linear dimension. Rhodomonas and Cryptomonas were in the <10 and 10-30 μm size classes, respectively. The grazing studies directly measured loss rates for the Rhodomonas and Cryptomonas size classes of particles.

Calculation of specific growth rates (k) for the phytoplankton community and for selected cryptophyte species was as follows:

$$k = P/C \qquad (1)$$

where P is ^{14}C productivity per day and C is algal carbon (Redalje and Laws 1981). Methods for ^{14}C productivity estimates are given below.

Zooplankton Sampling

Zooplankton population estimates were based on aggregate samples collected from four stations in the main basin (data provided by M. Leibold). The stations were at least 20 m apart. Samples were collected with a 10.5 L

Schindler trap, equipped with a 75-μm mesh net, at one meter intervals at each station, beginning at 0.5 m. The trap was 0.5 m high. The samples were combined across stations and by depths, i.e., depths 0.5 plus 1.5 m and 2.5 plus 3.5 m. Final aggregate samples were thus the result of eight Schindler trap samples with a total sample volume of 84 L. Samples were collected at night and during the day on each sampling date. Nighttime samples were collected at least one hour after sunset (total darkness) although some were collected later, up to three hours after sunset. Although zooplankton samples were collected twice weekly throughout much of the study period, only the samples closest to grazing rate study dates were used in this analysis.

Zooplankton were preserved in 4% sucrose formalin solution (Haney and Hall 1973). Samples were counted under a dissecting microscope at 250x using an ocular micrometer for measurements. Subsamples for counting were taken with a calibrated 'dipper' from a well-stirred sample. Enough subsamples were counted to ensure that at least 100 individuals (Daphnia species) were counted for each vertical profile. Individuals were sorted by size class on the basis of length between the eye and origin of the tail spine.

Zooplankton grazing

The grazing rate studies were conducted to estimate the impact of zooplankton on cryptophytes in the epilimnion of

Lawrence Lake. The general approach was to measure in situ grazing rates for species and size classes of zooplankton on a per individual basis. Independent zooplankton population estimates were used in conjunction with measured grazing rates to calculate total grazing impact.

All grazing rate estimates were made in situ using a 5.9-L Haney chamber (Haney 1971). Grazing rates for two algal size classes were obtained with a dual label. Selenastrum capricornutum was used for the <10 μm size class. It varied in cell volume from 40-70 μm^3 with a greatest linear dimension of about 9 μm. Chlamydomonas sp. was used to represent the 10 to 30 μm size class. The cell volume of Chlamydomonas varied from 700 to 1800 μm^3 with a greatest linear dimension of about 16 μm. Cell concentrations amended in feeding experiments were kept as low as possible to minimize the direct effect of particle number on grazing rate. Addition of the final labeled algal suspension to the incubation chamber increased cell abundances by less than 20 percent for each size class.

Labeling procedure

Stock algal cultures were maintained in freshwater medium (Guillard and Lorentzen 1972) with phosphorus and nitrogen at half strength on a 12:12 L:D cycle at 140 $\mu Einst \cdot m^{-2} \cdot s^{-1}$ and 20°C. Selenastrum was kept axenic to eliminate the possibility of bacterial uptake of ^{32}P during the labeling period. Pre-labeling cultures were prepared about one week prior to each grazing analysis. A 1-2-mL inoculation was made into 25 mL of fresh media producing rapidly growing populations of cells for labeling.

The process of labeling cultures was started 48 to 72 h prior to each grazing determination. The entire pre-labeling culture of *Chlamydomonas* was concentrated by centrifugation to about 5 mL. The cells were added to 35 mL of standard media with about 200 $\mu Ci^{14}C$ (7.4×10^6 Bq). About 4 to 6 mL of the pre-labeling *Selenastrum* culture was added to 35 mL fresh media at 1/4-strength phosphorus. Sufficient stock ^{32}P, as $NaPO_4$, was added to the *Selenastrum* inoculum to insure an activity of about 1 mCi (3.7×10^4 Bq) one week after the run. The labeling cultures were buffered to pH 7.5 with tricine/HCO_3 and were kept at 20°C in constant light. Final preparation included concentration and washing by centrifugation and resuspension to final density for the experiments.

The stocks of labeled algae were kept on ice in the dark after the field experiments began. Calibration samples were taken immediately before and after laboratory preparations for the first and last field experiments. This calibration activity was interpolated for each experimental run during the 24-h day. The inoculation cylinders were kept on ice in a cooler until used in the field. A one-mL sample from each culture was preserved with acid Lugol's solution for microscopic cell counts.

Field methods

Large diel variations in zooplankton grazing rates have been well documented in several lakes (e.g. Haney and Hall 1975, Crumpton and Wetzel 1982). Lakes dominated by daphnids have greater nighttime grazing rates; experiments were therefore conducted three times during the day on each sampling date over the central depression of the lake. Two experiments, predawn and 1-2 h after dusk, were made in total darkness and the third was made at noon. Two replicate incubations of less than ten minutes each were made at two depths, 2 and 9 m. Grazing rate estimates from the 2-m depth were assumed to be representative for the epilimnion (0-4 m).

After the incubations the grazing chamber was evacuated into a pair of nested Nitex screens mounted on Plexiglas cylinders. The inner screen (140-μm mesh) trapped the larger zooplankton while the outer screen (70-μm mesh) trapped the smaller rotifers and nauplii. Separation of the two groups in the field greatly enhanced the efficiency of sorting in the laboratory which was done between field trips. The screens with zooplankton were immediately placed in wide mouth glass jars half full of ice-chilled filtered lake water. The water was filtered through a 30-μm mesh size screen and a 0.5 mgP$\cdot$L^{-1} inoculum was added to exchange with any ^{32}P adsorbed to the zooplankton. An equal volume of chilled carbonated soda water was added to the container before it was sealed. No further preservation was used other than to keep the samples chilled with ice until they were processed. These measures were taken to lessen leakage of label resulting from chemical or heat killing of the animals (cf. Holtby and Knoechel 1981).

Sample processing

Between field experiments the samples were processed in the laboratory. The large zooplankton were separated and counted by species and size class directly into scintillation vials. When available at least twenty individuals from each category were sorted. In most cases rotifers and nauplii were segregated into groups of 100 individuals each. Rotifer and nauplii grazing activity was always inconsequential relative to total grazing activity. Therefore their contributions were not considered further in the analysis.

The samples were dried in a forced air oven at 80°C for 3-6 h and then digested for liquid scintillation radioassay in 0.75 mL per vial of Packard Soluene 350 at 55°C. After a 20-h digestion 10 mL of a compatible liquid scintillation cocktail was added to each vial. The samples were mixed twice, one hour apart, and then were undisturbed for 8 h at room temperature to reduce chemiluminescence. Radioassay was done in two channels to separate ^{14}C and ^{32}P activities in a Beckman 8000 liquid scintillation counter. Samples with either ^{14}C or ^{32}P internal standards were used to determine counting efficiency for each isotope. Blanks (filtered lake water) and calibration samples were processed with the zooplankton samples.

Quantification of zooplankton grazing rates

Zooplankton grazing rates were determined for individual species and size classes during one light and two dark periods on each date. Zooplankton population estimates were made for each species and size class at noon and 1 to 2 hours after sunset within 2 days of the grazing rate determinations. This information was reduced, using the following formula, to provide an estimate of daily grazing rate:

$$G = h_d[\Sigma((F_{id1} + F_{id2})/2)*A_{id}] + h_l[\Sigma(F_{il}*A_{il})] \qquad (2)$$

where G is the integrated 24-h grazing rate ($mL \cdot L^{-1} \cdot day^{-1}$), h_d and h_l are the length of the dark and light periods (hours), respectively, F_{id1} and F_{id2} are replicate means of the first and second dark period instantaneous grazing rates for the ith species ($mL \cdot animal^{-1} \cdot h^{-1}$), respectively, F_{il} is the replicate mean light period instantaneous grazing rate for the ith species, and A_{id} and A_{il} are the abundance estimates for the ith species in the dark and light periods (animals$\cdot$L^{-1}), respectively.

Nuclear track microautoradiography (NTM)

Field methods

In situ ^{14}C incubations were used to estimate community primary productivity (Steemann Nielsen 1951, 1952) and for estimating the productivity of selected cryptophyte species using nuclear track microautoradiography (Knoechel and Kalff 1976). Replicate 500-mL glass-stoppered reagent bottles and a 130-mL bottle for phytoplankton enumeration were filled with vertically integrated lake water (0-4 m) collected over the central basin with a 4-m long Van Dorn type sampler. The sampler, made of opaque PVC, had an inside diameter of 5 cm with a total volume of about 5 L. Possible algal toxicity from PVC was minimized since the sampler had been used daily for more than a year prior to this study.

Optimal recommended radioactivity for NTM prepared material should be 0.1-1.0 disintegrations$\cdot$cell$^{-1}\cdot$day^{-1} with a usable range of 0.01-10 disintegrations$\cdot$cell$^{-1}\cdot$day^{-1} (Knoechel and Kalff 1976). Preliminary testing indicated that this criterion could be met in Lawrence Lake with 3-mL injections of 20-26 μCi ^{14}C (7.4-9.6 x 10^{5} Bq). This activity was also suitable for total productivity determinations.

Three replicate light bottles and one dark bottle were incubated at a depth of two meters for about two hours. All incubations were made between 10:00 and 14:00, with most occurring between 10:30 and 12:30. After incubation with ^{14}C the bottles were placed in the dark, chilled with ice and returned immediately to the laboratory (usually within 30 minutes) for processing.

The leakage problem

There has been considerable recent discussion about the problem of label leakage from cells after chemical fixation in microautoradiography studies. Silver and Davoll (1978) and Paerl (1984) used unacidified Lugol's solution in their experiments and found losses near 50% within minutes of adding the fixative. Their reason for using unacidified Lugol's in their experiments was not stated, but acidified Lugol's solution has been a preferred general algal fixative for many years. Davenport and Maguire (1984) used acidified Lugol's and found the samples to be within <5% of the control. Carney and Fahnenstiel (1987) reported ^{14}C losses on preservation with acid Lugol's solution lower and more consistent than previously reported (0-21%). Watt (1971) and later Paerl (1984) used a combination of filtration, quick freezing, and lyophilization to minimize leakage problems. Both workers mounted and cleared the filters for grain density autoradiography. Smith and Kalff (1983) used a combination of very brief fixation with acid Lugol's solution followed within seconds by filtration to minimize

^{33}P losses. The filters were air dried and mounted on slides for clearing.

Cryptophytes are especially susceptible to cell lysis during mechanical manipulations (e.g. filtration, centrifugation) and must be fixed prior to processing to ensure cell integrity. The methods mentioned above were modified to minimize the time that cells were suspended in water after fixation thereby reducing their susceptibility to leakage. Hewes and Holm-Hansen's (1983) filter-transfer-freeze (FTF) method was combined with the basic approach of Watt (1971) and Paerl (1984). The FTF technique was developed to concentrate and recover intact nanoplankton cells for light microscopy and eliminate the filter from the final slide mount thus improving resolution of the microflagellates. The general procedure was as follows: after filtration the filter was frozen face down on a microscope slide and then peeled off leaving the cells transferred in a frozen state to the slide. Hewes et al. (1984) found the FTF technique equal or superior to other methods for estimating nanoplankton populations.

NTM laboratory procedure

Two replicate 50-mL aliquots from each of the four incubation bottles (three light, one dark), one replicate fixed with acid Lugol's solution (at a ratio of 0.1:50) and the other untreated, were filtered onto HA Millipore filters

(0.45-μm pore size) and analyzed by Geiger-Muller radioassay (Nuclear-Chicago D-47 of known counting efficiency) for total primary productivity estimates. The acid Lugol fixed samples were used to estimate loss of label due to fixation for the total autotrophic community.

Six 50-mL replicate aliquots from each incubation bottle were processed as follows for NTA: each aliquot was fixed with acid Lugol's (at a ratio of 0.1:50) and immediately filtered onto a polycarbonate filter (1.0-μm pore size) at a vacuum less than 0.3 atm. Vacuum was released just as the meniscus reached the surface of the filter leaving a thin film of water on the filter. The filter was removed while the surface was still wet, placed face down on a drop of filtered (0.22-μm pore size) lake water on a glass slide and frozen on a liquid-N_2 cooled aluminum plate (Paerl 1984). The glass slides had previously been cleaned and coated with a five percent gelatin-chrom-alum solution (5 g gelatin plus 0.5 g chromium aluminum sulfate$\cdot L^{-1}$; Rogers 1979). These procedures reduced the critical processing time (i.e., from the addition of fixative through freezing) to less than one minute. Slides with frozen filters were temporarily stored at -70°C in an ultrafreezer until all filtrations were completed. The filters were peeled off, transferring the frozen cells to the slide as described by Hewes and Holm-Hansen (1983), the sample remaining frozen at all times. The complete slide-set was placed directly into a lyophilizer with a shelf temperature pre-cooled to -30°C. After lyophilization, all slides were fumed over HCl for four minutes to drive off inorganic ^{14}C (Davenport and Maguire, 1984). Slides were stored at room temperature under desiccation until prepared for autoradiography. Loss of label from lyophilized cell preparations was assumed to be negligible. Slide preparations for the dark bottle incubations served as controls for dark fixation, chemography, and background.

The NTM procedure was modified from Knoechel and Kalff (1976). Lyophilized slides were dipped in liquid (33 - 34°C) Kodak NTB3 nuclear track emulsion (Eastman Kodak Company, Rochester, New York), chilled on inverted ice-cooled pans and dried at room temperature in a desiccator for at least 1 h. Coated slides were stored in light-tight boxes at 4°C with desiccant for 1-3 d. These procedures were carried out in total darkness except for filling the dipping jar with emulsion which was done at least 1 m from a Kodak No. 2 safe light with a 15-Watt bulb.

Slides were developed in complete darkness using Kodak D-19 developer (7 min), followed by a 1% acetic acid stop bath (5 min), rinses in 30% and then 10% Kodak Fixer (30 min each), and two final rinses in deionized water (15 min each). Gentle mixing was maintained for each step during development. The slides were dried in a laminar flow hood and stored at room temperature in a desiccator.

The emulsion was rehydrated with 1-2 drops of 30% glycerin solution. A cover slip sealed with clear nail enamel reduced desiccation and produced a semipermanent mount for viewing with a light microscope. Emulsion on the bottom of the slide was removed with a razor blade. Slides with emulsion >25 μm thick were used for counting tracks on an Olympus BH microscope with dark field phase contrast optics at 800x magnification.

A strict track counting protocol was used. *Cryptomonas 'erosa'* and *Rhodomonas minuta* cells selected for track evaluation had cell membranes intact and were isolated from neighbors to avoid interference from track overlap. Otherwise the cells were evaluated as they were encountered in random transects of the preparation. A track consisted of a trace with at least 4 grains in a definite sequence, arising within 5 μm of the cell (Knoechel and Kalff 1976). A range of 30 to 150 cells per species were evaluated for tracks on each slide.

A factor of 1.14x was used to correct track counts for losses from sample fixation with acid Lugol's solution. The factor was derived from a time series batch culture experiment using *Rhodomonas* as the test organism. A unialgal culture in late exponential growth (20°C, 140 $\mu\text{Einst}\cdot m^{-2}\cdot s^{-1}$, 12L/12D light cycle, defined medium of

Guillard and Lorentzen 1972) was split between the three 500-mL glass-stoppered light bottles used during the routine *in situ* productivity studies. After a two-hour incubation with ^{14}C at an activity similar to that used in field studies, 25-mL samples were filtered onto polycarbonate filters (1.0-μm pore size) at a vacuum less than 0.3 atm. Samples were taken just prior to fixation, immediately after fixation, and thereafter at 1, 2, 4, 8, 20 and 45-minute intervals. Activity dropped immediately to 93.8% (std = ± 5.2%) after addition of fixative and to 85.9% (std ±3.3%) after 1 min. Activity was reduced to about 30 percent of initial activity after 45 minutes. Additional less rigorous batch culture experiments showed similar results with immediate post-fixation losses of label ranging from 9.6 to 12.7 percent of non-fixed sample. Finally, pre- and post-fixed samples from all *in situ* productivity studies were filtered and counted to evaluate label loss for the entire phytoplankton community. Results of these tests showed mean losses of 13.7 percent (std = ±11.4%, n=18) 13 to 29 minutes after fixation. Since elapsed time from fixation to stabilization (freezing) of microautoradiography samples took slightly less than one minute, the correction was based on one minute using results from the time series experiment.

Comparison of phytoplankton community productivity with microautoradiography derived productivity for selected cryptophyte species required common units. The ^{14}C

productivity equations given by Wetzel and Likens (1979) were used in both cases. No adaptations were required for calculation of phytoplankton community productivity. It was necessary to convert track counts to $dps \cdot species^{-1} \cdot mL^{-1}$ of lake water before they could be used in the equations. Mean track counts per cell were corrected for cell size, cell-emulsion geometry, length of exposure to the emulsion, beta particle energy and latent image erasure according to Pip and Robinson (1982). Independent estimates were made of species cell abundances which were multiplied by the corrected track count to give the required units.

Results and Discussion

This study was conducted during the annual cooling period from August, a time of maximum surface water temperatures, until December, with minimum water temperatures (Figure 3.1). Maximum cryptophyte development occurred during this period of epilimnetic deepening as the mixed zone approached a depth of eight meters (Chapters 1 and 2). Wide fluctuations in solar radiation from frequent passage of weather fronts characterized the light climate at the lake surface during much of this period (September through December). The declining surface water temperature closely followed the seasonal decline in solar radiation. The lake mixed during the first week in November at a water column temperature of about 11.5°C.

Figure 3.1. Daily solar radiation (photosynthetically active radiation, 400-700 nm) (upper) and Secchi disk transparency, temperature at the two-meter depth and depth of the mixed layer (lower) in Lawrence Lake, Michigan during 1984.

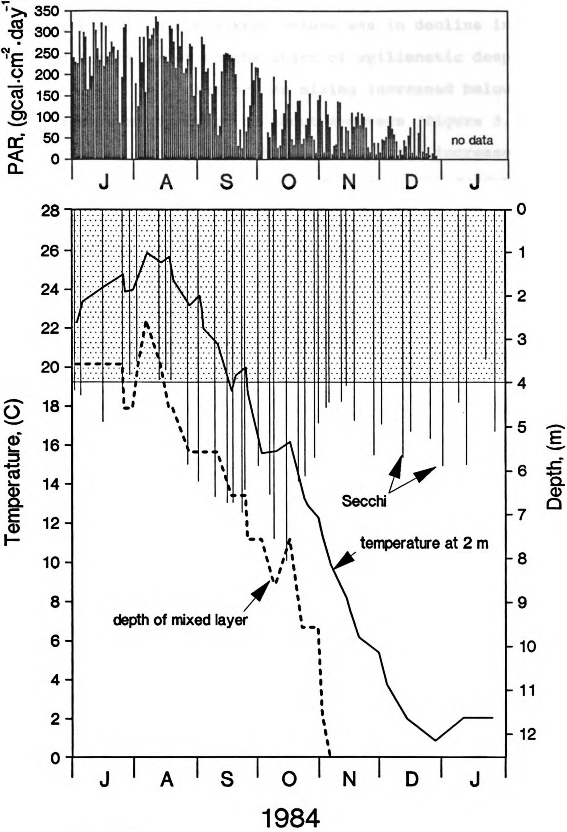
PAR, (gcal·cm⁻²·day⁻¹)
350
300
250
200
150
100
50
0
no data
J
A
S
O
N
D
J
Temperature, (C)
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
Depth, (m)
0
1
2
3
4
5
6
7
8
9
10
11
12
Secchi
temperature at 2 m
depth of mixed layer
J
A
S
O
N
D
J
1984

Figure 3.1

The summer phytoplankton volume was in decline in late July and August prior to the start of epilimnetic deepening (Figure 3.2). In September, as mixing increased below the normal summer mixed depth of about 4-meters (Figure 3.1) biomass (as chlorophyll) in the 0-4-m stratum increased, probably because of upward mixing from the more densely populated metalimnion (Figure 3.3). Water clarity (as Secchi depth transparency, Figure 3.1) increased throughout the deepening period until the development of an exceptionally large *Chrysosphaerella longispina* population in late October (Figure 3.2). Several sources of independent evidence indicate that the epilimnetic *Chrysosphaerella* population represented new biomass rather than a mixing of a deeper population into the surface water: chlorophyll (Chla) concentrations increased simultaneously throughout the 0-8-m stratum in October (Figure 3.3), total water-column particulate organic carbon increased (carbon data from a concurrent study by M. F. Coveney and R. G. Wetzel, in preparation), and microscopic examination of the water column showed clearly the absence of a large *Chrysosphaerella* population prior to late October.

Alkaline phosphatase activity (APA), used as a relative indicator of phosphorus stress (see Chapter 1 for more details), was greatest in the metalimnion (4-8 m) until September (Figure 3.3). A precipitous decline occurred in August followed by increased activity in September.

Figure 3.2. Percentage volume of major phytoplankton groups in the 0-4-m stratum (upper) and phytoplankton volume (lower) in that stratum in Lawrence Lake, Michigan in 1984. The large increase in late October (lower) was nearly entirely from *Chrysosphaerella*.

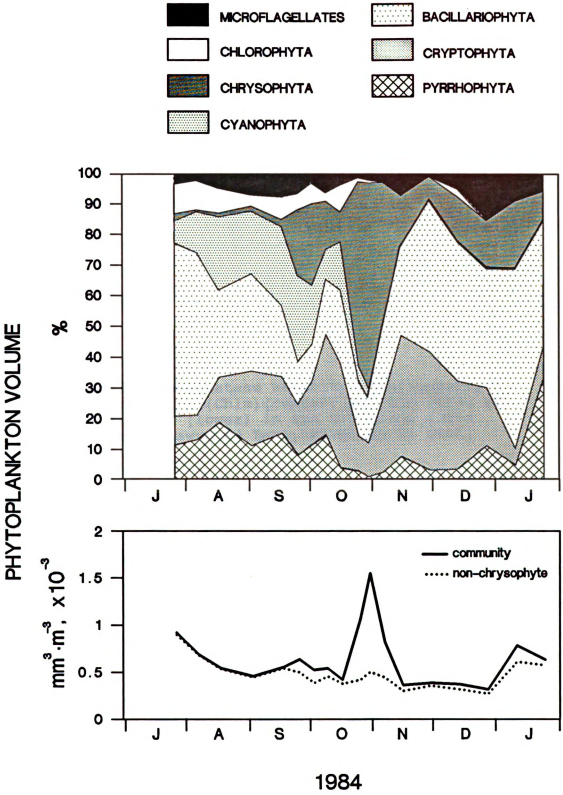
MICROFLAGELLATES
CHLOROPHYTA
CHRYSOPHYTA
CYANOPHYTA
BACILLARIOPHYTA
CRYPTOPHYTA
PYRRHOPHYTA
PHYTOPLANKTON VOLUME
%
100
90
80
70
60
50
40
30
20
10
0
J
A
S
O
N
D
J
mm³·m⁻³, x10⁻³
2
1.5
1
0.5
0
community
non-chrysophyte
J
A
S
O
N
D
J
1984

Figure 3.2

Figure 3.3. Alkaline phosphatase activity (APA)(upper), chlorophyll a (Chla)(center) and the ratio of APA to Chla (lower) in the 0-4-m and 4-8-m strata in Lawrence Lake, Michigan in 1984.

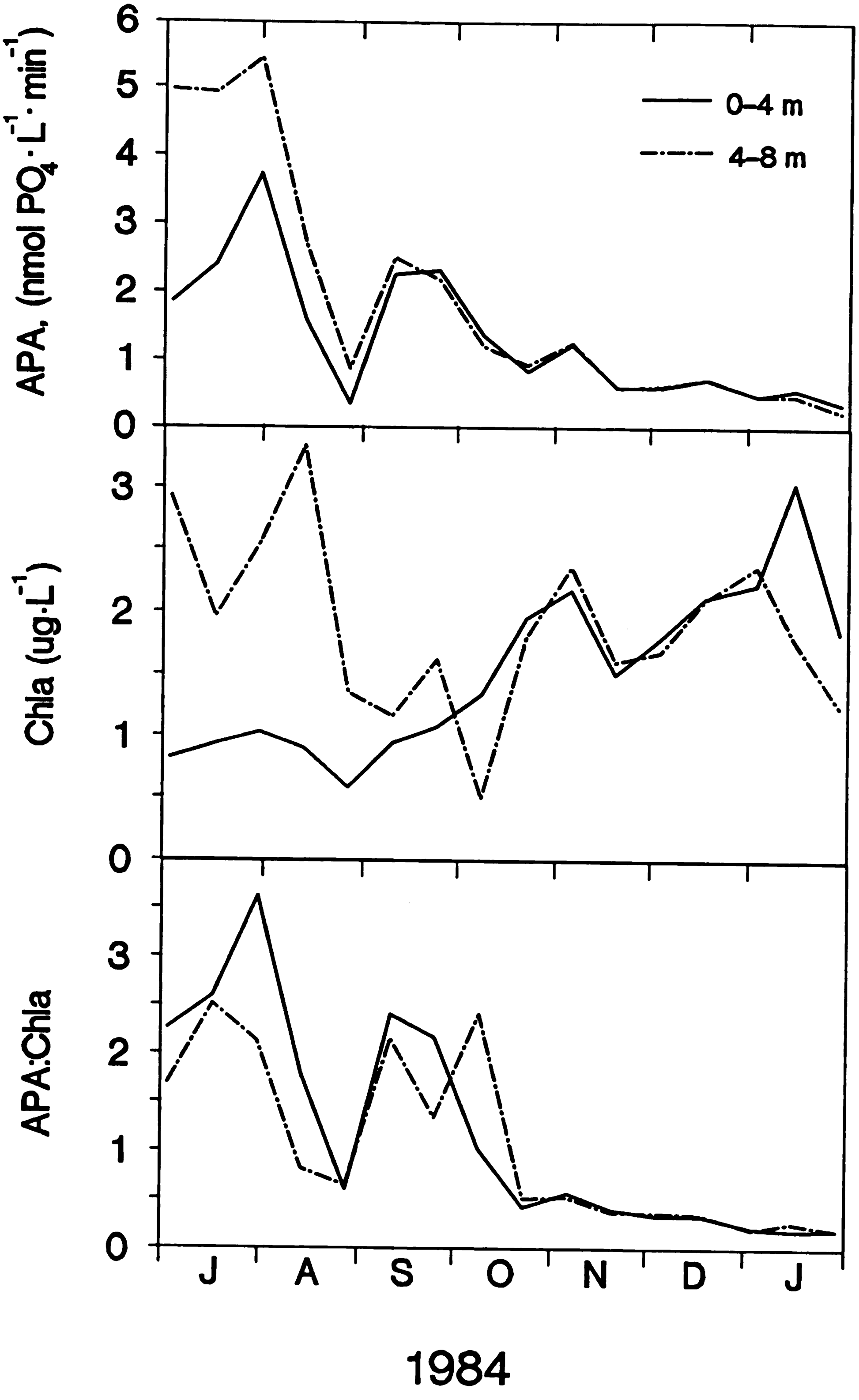
APA, (nmol $PO_4 \cdot L^{-1} \cdot min^{-1}$)
0
1
2
3
4
5
6
0–4 m
4–8 m
Chla ($ug \cdot L^{-1}$)
0
1
2
3
APA:Chla
0
1
2
3
J
A
S
O
N
D
J
1984

Figure 3.3

Thereafter APA declined steadily to annual low levels. Chla was similarly more concentrated in the metalimnion through initial stages of the epilimnetic deepening process until October. After an initial decrease with deepening, Chla concentrations in the 0-4-m stratum increased into January 1985 when the lake was ice-covered. The high January Chla values were consistent with increased diatom and dinoflagellate volume (Figure 3.2). Phytoplankton phosphorus stress during the study is apparent with an examination of the ratio of APA to Chla. Seasonal patterns were similar within the 0-8-m stratum (Figure 3.3); high summer values, indicating greater relative phosphorus limitation, were followed by a marked decline in August. Increased phosphorus limitation developed in September and then declined to annual low values by the end of October as the hypolimnion was gradually eroded. September APA/Chla maxima coincided with maximum zooplankton filtration rates (details below) which indicates that grazing activities may have increased the pool of organic phosphorus compounds. The phytoplankton of the 0-4-m stratum exhibited greater phosphorus limitations during most of July, early August and September than those of the 4-8-m stratum. The specific growth rates of <u>Rhodomonas</u> and <u>Cryptomonas</u> (details below) were greatest toward the end of August and during October when APA:Chla ratios were declining to low levels, a time of minimal phosphorus stress.

Phytoplankton dynamics

The emphasis of this study was on the period of maximal development of cryptophytes which occurs during the time of temperature decline and epilimnetic deepening, August through January (Taylor and Wetzel 1984, Stewart and Wetzel 1986; Chapters 1 and 2 of this dissertation). With the exception of the chrysophytes, the seasonal dynamics of the community structure and total phytoplankton volume were quite similar during the autumn period in 1982 and 1984 (Figures 1.11 and 3.2). The dominant phytoplankton species (≥5% of total biovolume) are given in Table 3.2 for the period June 23, 1984 to January 11, 1985. A mid-October bloom of *Chrysosphaerella*, a colonial chrysophyte, tripled the phytoplankton volume in the open water (Figure 3.2). This increase markedly altered the relative pattern of phytoplankton dominance from earlier years and added an unexpected degree of complexity to the study of cryptophyte productivity. The *Chrysosphaerella* bloom of 1984 was about ten times that observed in 1982 and it occurred three weeks earlier than previously. This population maximum greatly shifted the relative biovolume in the lake and returned phytoplankton volume to maximal summer levels. The pattern of cryptophyte growth and volume was not appreciably altered from 1982 but its relative importance within the phytoplankton community was much reduced.

Table 3.2 Dominant phytoplankton species (≥ 5% of total biovolume) listed from most to least important (left to right, respectively) in Lawrence Lake, Michigan.

DATE	SPECIES
23-JUN-84	Sd, Cb, Ce
27-JUL-84	Cb, Pp, Ce, col b-g, Pl
07-AUG-84	Cb, col b-g, Pp, Cr
18-AUG-84	Cb, col b-g, Pp, Ce
03-SEP-84	Cb, col b-g, Ce, Pp, Fc
18-SEP-84	col b-g, Ce, Fc, Cb, Ch
26-SEP-84	Cl, col b-g, Ce, Cb, Lb, Ch, Fc
03-OCT-84	Cl, Ce, col b-g, Ch, Cb, Lb
10-OCT-84	Ce, Cl, Ch, Fc, Cb
17-OCT-84	Ce, Fc, col b-g, Cb, Rm, Cr
26-OCT-84	Cl, Fc, Cb, Ce
31-OCT-84	Cl, Fc, Ce, Cb
07-NOV-84	Cl, Fc, Ce, Rm
16-NOV-84	Ce, Fc, Cl, Rm, mf
30-NOV-84	Fc, Ce, Cb, Rm, Ap, Mt
14-DEC-84	Fc, Ce, Mt, Cb, Dd
28-DEC-84	Fc, mf, Pw, Cb, Ce, Dd
11-JAN-85	Fc, Cb, mf, Dd

KEY:

Sd	Stichoglea doederleinii (Schmidle) Wille
Cb	Cyclotella bodanica var. affines Grunow
Ce	Cryptomonas erosa Ehrenberg and C. ovata Ehrenberg
Pp	Peridinium polonicum Wolosz.
col b-g	colonial blue-greens
Cr	Crucigenia rectangularis (A. Braun) Gay
Fc	Fragilaria crotonensis Kitton
Cl	Chrysosphaerella longispina Lauterborn
Ch	Ceratium hirundinella fa. austriacum (Zedb.) Bachmann
Rm	Rhodomonas minuta var. nannoplanctica Skuja
Dd	Dinobryon divergens Imhof
Pw	Peridinium willei Huitfeldt-Kass
Pl	Planktonema lauterborni Schmidle
Lb	Lyngbya bergei
mf	microflagellates
Ap	Aphanocapsa sp.
Mt	Mallomonas tonsurata Teiling em. Krieger

Chrysosphaerella is common in hardwater lakes in Michigan. Its colonial organization and cells with long, stout siliceous spines extending outwardly give it an effective diameter of about 200 µm, thus rendering it virtually immune from predation by zooplankton until the colonies degrade and fragment. It is possible that its presence in sufficient numbers would act as a physical barrier thus interfering with the grazing process on smaller food items or perhaps cause some daphnids to modify their filtration apparatus and thus reduce their filtering efficiency (Gliwicz and Siedlar 1980).

Cryptophyte volume followed the same general pattern in 1982 and 1984 (Figure 3.4) and continued to be dominated by Rhodomonas minuta Skuja and Cryptomonas 'erosa' Ehr. From a low point in August, biovolume reached a maximum level in October, after which it fluctuated into November before declining to low levels in January. The primary difference between years was a more persistent 1984 maximum of lesser magnitude than was observed in 1982. Competition for nutrients with the rapidly developing Chrysosphaerella population may have interfered with full cryptophyte development.

The seasonal distribution of phytoplankton particles and biovolume may influence the grazing activities of zooplankton (Gliwicz 1977). In Lawrence Lake, the pattern and magnitude of seasonal changes in the total number of

Figure 3.4. Seasonal variations in the total volume of the Cryptophyceae during 1982 and 1984 in Lawrence Lake, Michigan.

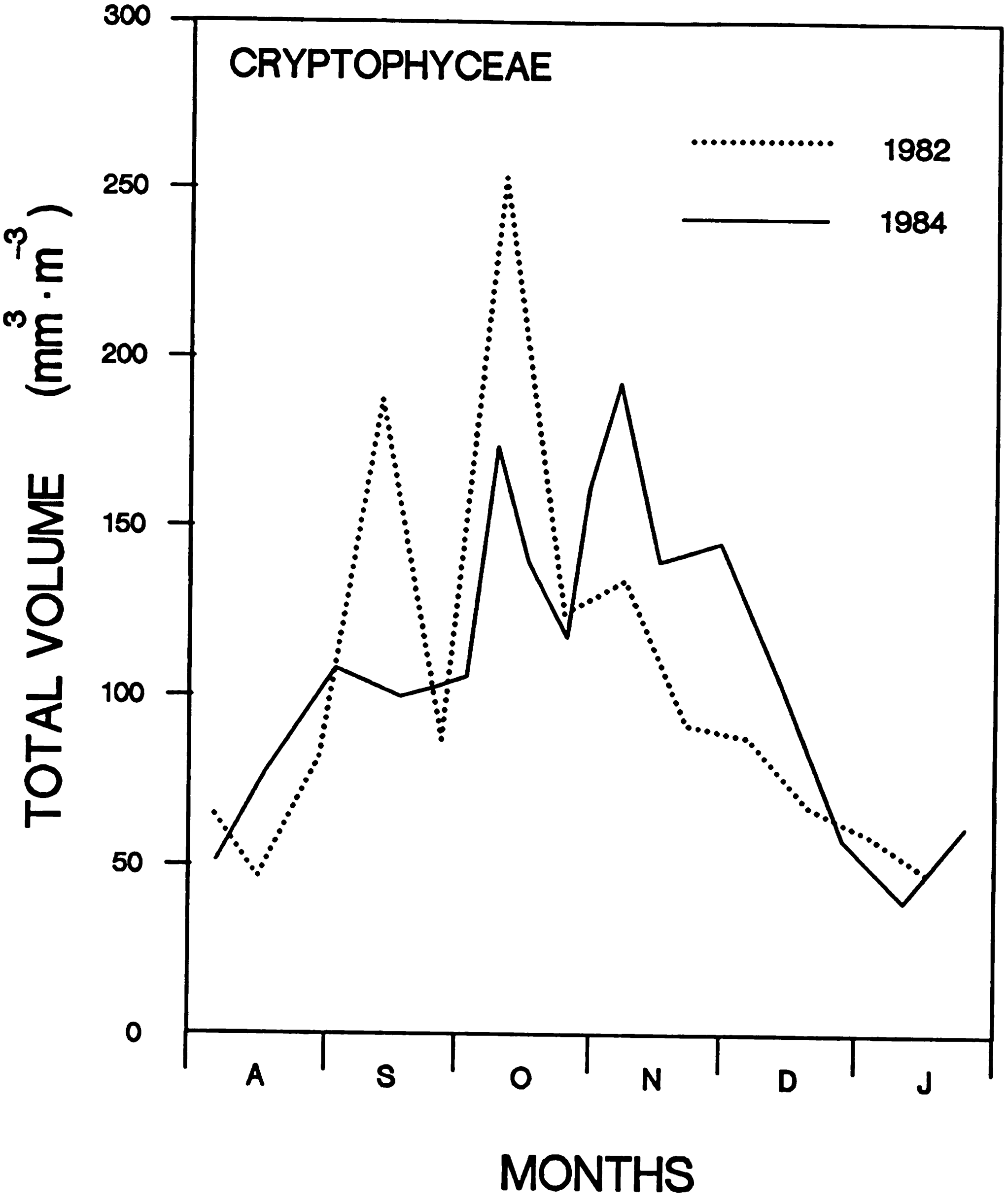
CRYPTOPHYCEAE
1982
1984
TOTAL VOLUME $(mm^3 \cdot m^{-3})$
300
250
200
150
100
50
0
A
S
O
N
D
J
MONTHS

Figure 3.4

algal units was very similar to that encountered in 1982 (Chapter 1). About 90 percent of the algal particles were in the readily grazable fraction (i.e. <30 μm maximum linear dimension), and most of those cells were in the <10 μm fraction (Figure 3.5). The <10 μm size class was essentially composed of microflagellates. Burns (1968) set an upper limit of 30 μm for maximum particle size ingestible by the cladocerans. Gliwicz (1977) demonstrated that the most efficient grazers need particles <10 μm in diameter. In comparison to particle abundance, phytoplankton volume categorized by size class showed a change in the pattern of dominance by the <10 μm size class which accounted for a much smaller portion of the total algal volume (6-19%). Much of the biovolume dominance was in the 10 to 30-μm size class (15-70%). The less grazable particles (>30 μm) accounted for a variable but large portion of the phytoplankton volume (20-80%), particularly in October-November during the <u>Chrysosphaerella</u> bloom.

<u>Rhodomonas</u> and <u>Cryptomonas</u> were important components of the <10 μm and 10-30 μm particle size classes, respectively. The relative magnitude of their abundances and volume differed, giving each a unique role in trophic interactions of the upper stratum (Figure 3.6). Both populations developed during the autumn cooling period as they did in 1982, and together accounted for more than 90 percent of the cryptophyte volume. <u>Rhodomonas</u> developed a

Figure 3.5. Percent algal units and algal volume by size classes (upper) and total algal units and total phytoplankton volume (lower).

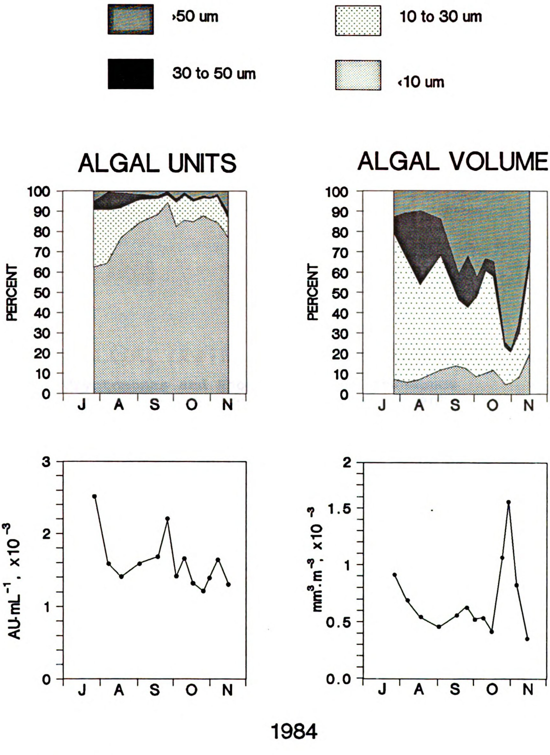
›50 um
10 to 30 um
30 to 50 um
‹10 um
ALGAL UNITS
ALGAL VOLUME
PERCENT
100
90
80
70
60
50
40
30
20
10
0
J
A
S
O
N
AU·mL^{-1}, x10^{-3}
3
2
1
0
mm^3.m^{-3}, x10^{-3}
2
1.5
1
0.5
0.0
1984

Figure 3.5

Figure 3.6. *Cryptomonas* and *Rhodomonas* cell abundance (upper), volume (center) and the percent species volume of the total volume (lower).

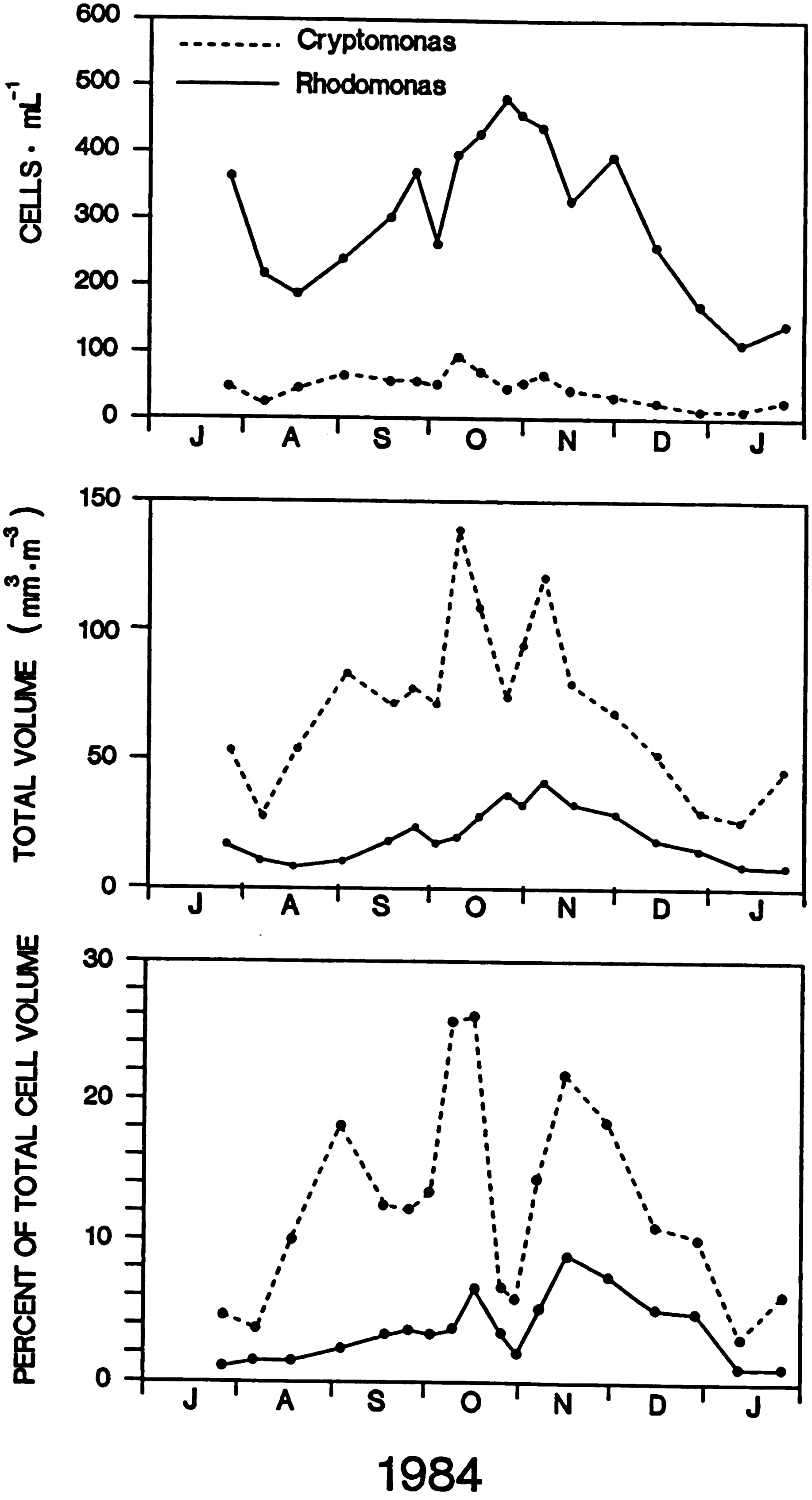
600
500
400
300
200
100
0
CELLS · mL^{-1}
Cryptomonas
Rhodomonas
J
A
S
O
N
D
J
150
100
50
0
TOTAL VOLUME ($mm^3 \cdot m^{-3}$)
J
A
S
O
N
D
J
30
20
10
0
PERCENT OF TOTAL CELL VOLUME
J
A
S
O
N
D
J
1984

Figure 3.6

relatively large population with a maximum in the third week of October, and the *Cryptomonas* maximum occurred two weeks earlier. The larger *Cryptomonas* cells, nearly 20 times the volume of *Rhodomonas*, were sufficient to offset the numerical advantage of *Rhodomonas*. As a result, *Cryptomonas* made a much larger contribution to total phytoplankton volume (Figure 3.6).

The October *Chrysosphaerella* bloom markedly altered the relative importance of both *Cryptomonas* and *Rhodomonas* (Figure 3.6, bottom) to total phytoplankton volume. *Cryptomonas* was reduced from 26 to about 6 percent of the total biovolume during the bloom. *Rhodomonas*, with a maximum contribution of nine percent during the study period, was reduced to about two percent during the bloom period. Competitive interactions between *Chrysosphaerella* and cryptophytes for resources are unknown, but the pattern and magnitude of cryptophyte development was similar to that in 1982, suggesting a minor influence by *Chrysosphaerella*.

Both cryptophyte species showed a significant seasonal variation in mean cell volume during the study (Figure 3.7). Cells were smallest during the summer, they increased in volume during autumn, and were reduced in cell volume during December and January. These seasonal variations had a direct affect on estimates of cell carbon. Culture studies with *Rhodomonas* showed diel variations in cell volume on the same scale as those found in the lake

Figure 3.7. The seasonal variation in cell volume of *Rhodomonas* (upper) and *Cryptomonas* (lower) in Lawrence Lake, Michigan in 1984. (±S.E., n=25-30)

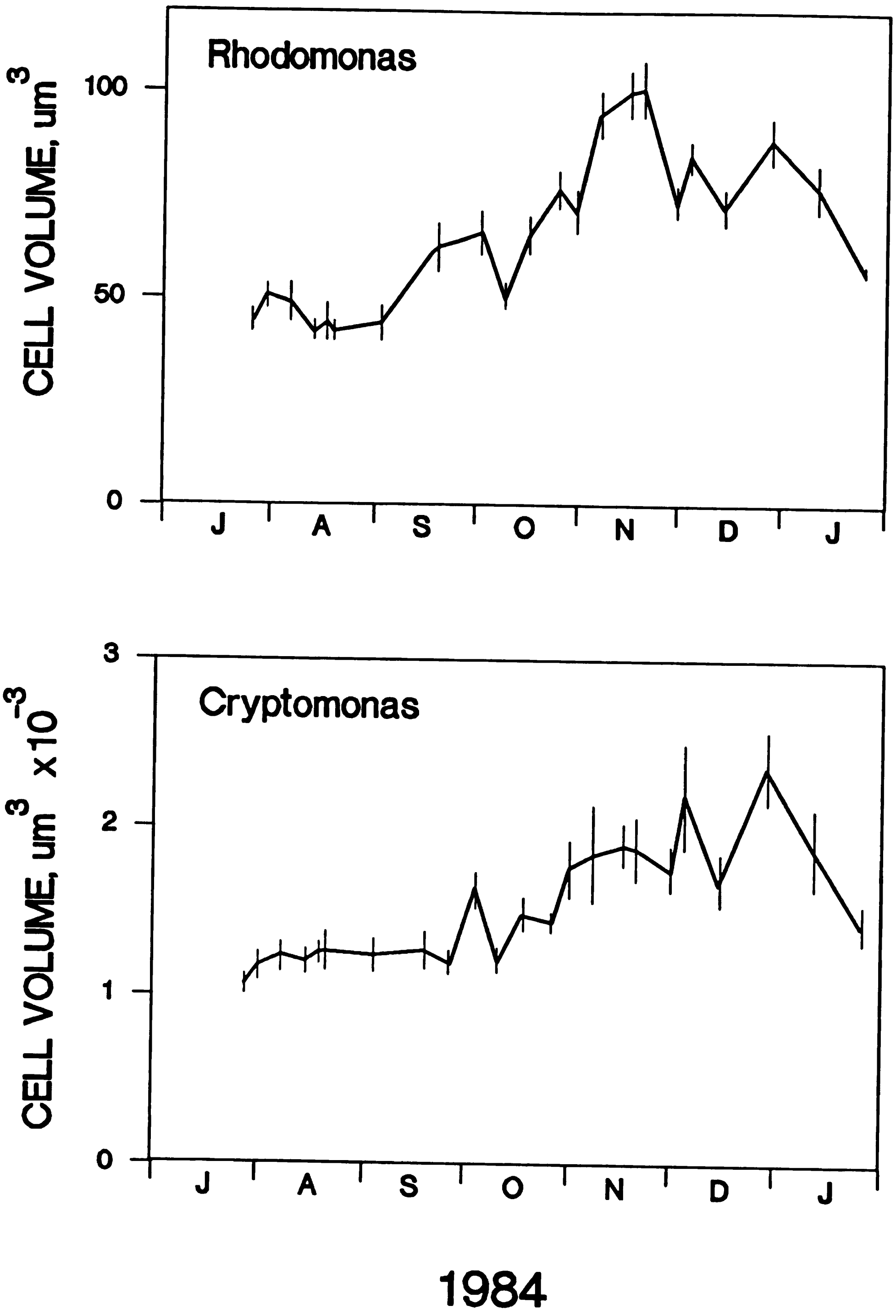
Rhodomonas
CELL VOLUME, um^3
100
50
0
J
A
S
O
N
D
J
Cryptomonas
CELL VOLUME, um^3 x10^{-3}
3
2
1
0
J
A
S
O
N
D
J
1984

Figure 3.7

seasonally (W. D. Taylor, unpublished data). The diel changes resulted from synchronized cell division during the dark period which halved pre-dark period cell volume. The same phenomenon was observed in Lawrence Lake during late September, 1983. Interruptions in synchronized cell division should be expected if conditions during the daylight period are not suitable for cell growth leading to a critical size necessary for cell division during the dark period. Under these conditions larger cells would be expected in samples collected before noon, and the average cell volume of the population would increase. If this were the case, a critical overestimate of the fixed particulate carbon required for cell division was used in calculations of specific growth rates (see below). The consistent times of sampling, however, would result in consistency in the daily estimates.

Zooplankton dynamics and grazing

Diel vertical migration occurred in *Daphnia* and *Diaptomus*. Day-night differences in abundance are presented as light period abundance of animals expressed as a percentage of dark period abundance in various depth-strata (Figure 3.8). Migration was strongest in *Daphnia*. Surface water (0-4 m) abundances of *Daphnia* were reduced 30 to 80 percent during the light period, while the reductions ranged from 3 to 60 percent for *Diaptomus*. When the surface water

Figure 3.8. Abundance of *Daphnia* spp. and *Diaptomus* spp. in the light period presented as the percent of dark period abundance in various depth-strata. (data provided by M. Leibold)

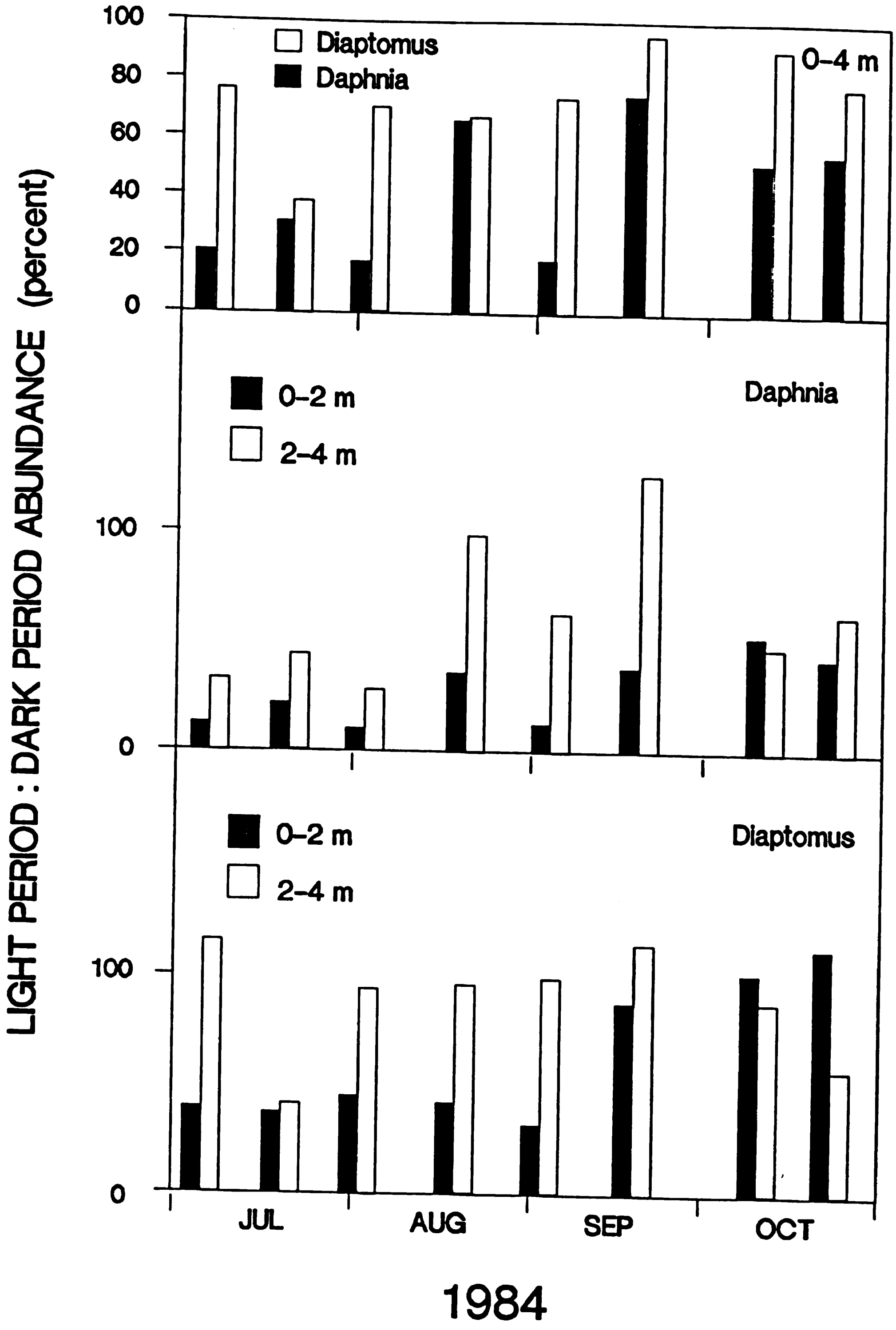
LIGHT PERIOD : DARK PERIOD ABUNDANCE (percent)
100
80
60
40
20
0
Diaptomus
Daphnia
0-4 m
0-2 m
2-4 m
Daphnia
100
0
0-2 m
2-4 m
Diaptomus
100
0
JUL
AUG
SEP
OCT
1984

Figure 3.8

was similarly examined as two strata (0-2 and 2-4 m) different patterns appeared (Figure 3.8). There was a greater relative decrease in abundance in the 0-2-m stratum for both genera, much less so for *Diaptomus* in the later part of the study. In the 2-4-m stratum, however, a small relative increase in animal abundance was observed on several dates. This increase was a one-time event for *Daphnia* but it occurred on several dates with *Diaptomus*. It seems clear that near-surface populations descended but on some occasions only small ± net changes in abundance were observed in the 2-4-m stratum.

Details of day-night *Daphnia galeata mendotae* abundance by depth-strata are presented in Figure 3.9. This species was responsible for most of the grazing pressure during this study (details below). With one exception in September, *D. galeata* abundance was always greater at night in the upper four meters of the water column than it was during the daylight period. At night when grazing rates were highest there was a variable and inconsistent distribution of *D. galeata* with depth. These data show that *D. galeata* was not always uniformly dispersed within the upper water column during the dark or the light periods. As a result, the assumption that grazing was uniform throughout the mixed layer must be used with caution.

Important differences in surface water (0-4 m) grazing rates existed between the dark and light periods of the day

Figure 3.9. Day-night *Daphnia galeata mendotae* abundance by depth-strata from July through October, 1984. Eight samples from four stations were combined to form one 84-L composite sample for abundance estimates at each depth stratum. (data provided by M. Leibold.)

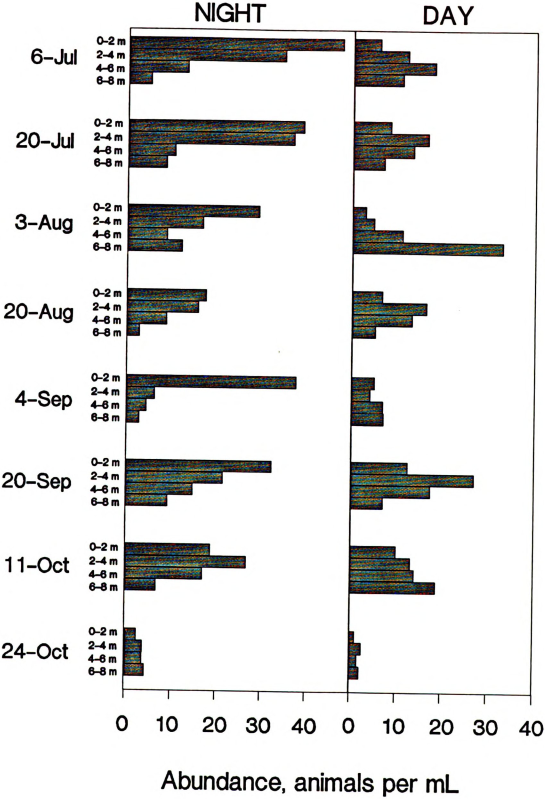
NIGHT
DAY
6-Jul
20-Jul
3-Aug
20-Aug
4-Sep
20-Sep
11-Oct
24-Oct
0-2 m
2-4 m
4-6 m
6-8 m
0
10
20
30
40
0
10
20
30
40
Abundance, animals per mL

Figure 3.9

(Figure 3.10, lower). Daytime grazing rates ranged from 6 to 31 percent of those found at night. Differences like these have been attributed to vertical migration by zooplankton to greater depths and a reduction in filtration rate per individual during daylight hours (Haney and Hall 1975, Crumpton and Wetzel 1982). The light-period abundance of zooplankton in the surface water (0-4-m) was reduced to between 22 and 80 percent of dark period levels.

Grazing was dominated throughout the 24-h day by *Daphnia galeata mendotae* for both size classes of labeled algal cells (Figure 3.10). *Daphnia pulicaria* accounted for only 3 to 4 percent of the total grazing rate. However, important day-night differences in grazing impact emerged. *Diaptomus* grazing became progressively more important at night for the larger particle size class (10-30 μm) than it did for the smaller particle size class (<10 μm) (Figure 3.10, upper). The relative importance of cyclopoids increased at night late in October after *Daphnia* abundance declined. The total grazing pressure progressively decreased to very low levels towards the end of October. During daylight hours (Figure 3.10, middle) *Diaptomus* and cyclopoids (on larger cells), contributed considerably more to the grazing impact than they did at night.

Figure 3.10. Distribution of grazing by *Daphnia*, *Diaptomus* and cyclopoids during dark (upper) and light (middle) periods and by particle size class (<10 µm, left and 10-30 µm, right) as a percentage of the total 0-4-m stratum grazing rate for the dark and light periods. Zooplankton grazing rates during dark and light periods in the 0-4-m stratum for <10 µm and 10-30 µm size classes (lower).

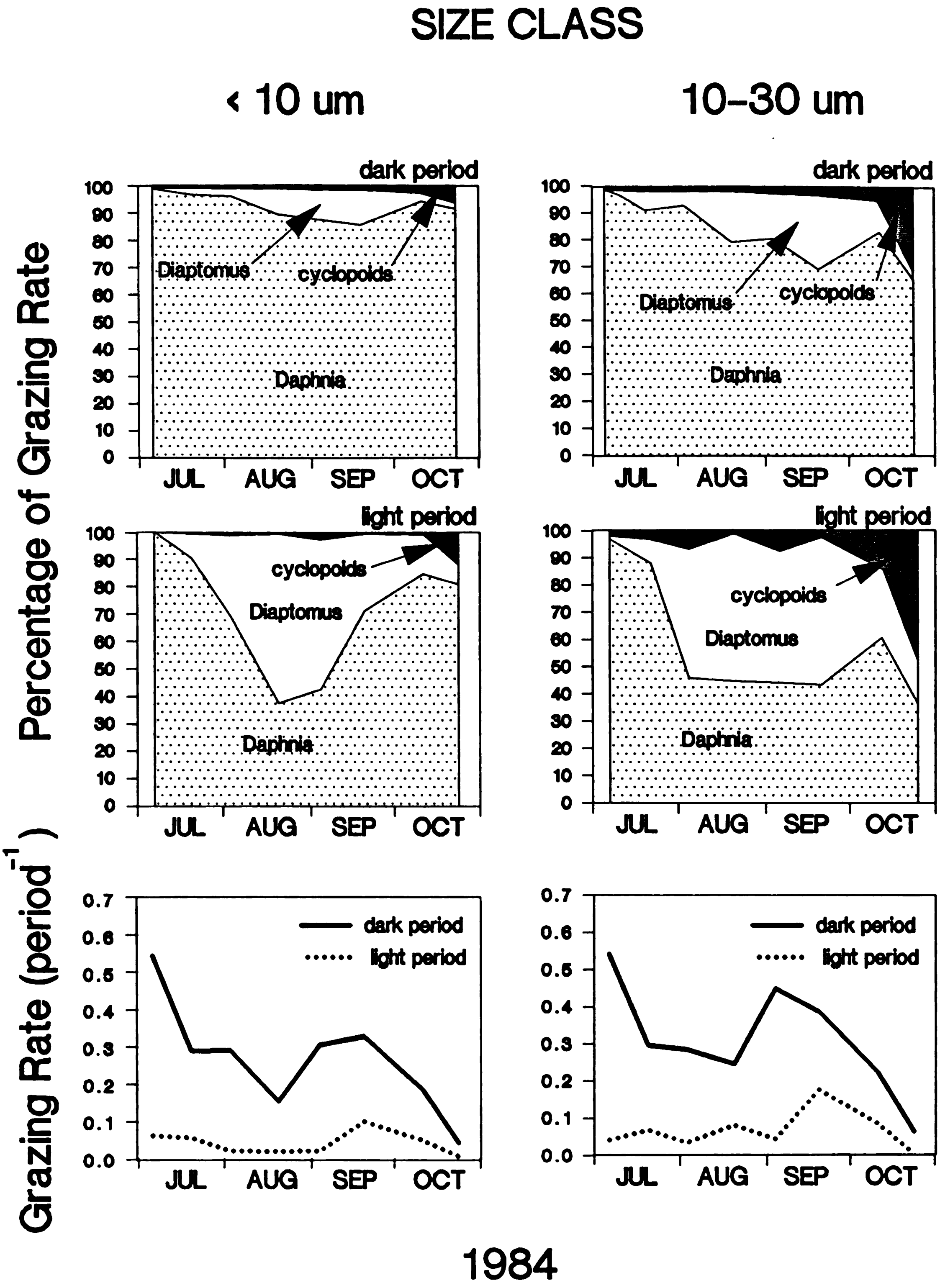
SIZE CLASS
< 10 um
10–30 um
Percentage of Grazing Rate
dark period
light period
Daphnia
Diaptomus
cyclopoids
100
90
80
70
60
50
40
30
20
10
0
JUL
AUG
SEP
OCT
Grazing Rate (period^{-1})
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
dark period
light period
1984

Figure 3.10

Cryptophyte productivity

The productivity rates of both *Cryptomonas* and *Rhodomonas* populations were low and variable, ranging from about 0.3 to 2.8 $mgC \cdot m^{-3} \cdot day^{-1}$ in the 0-4-m stratum (Figure 3.11), as compared to the entire phytoplankton community which varied from 12.7 to 58.4 $mgC \cdot m^{-3} \cdot day^{-1}$ in the same period. Populations of both species fixed carbon at the highest rates in early October followed by rapid declines by turnover in early November. The *Cryptomonas* population also had higher rates in September than at other times. Such similar productivity between the two species was not expected because of the great disparity between their cell volumes and abundance (Figure 3.6). The similarity in productivity resulted partly from the combination of small cells-high abundance for *Rhodomonas* and large cells-low abundance for *Cryptomonas*, but it resulted also from the low productivity per unit cell carbon (equivalent to specific growth rate, k) for *Cryptomonas* (Table 3.3).

A number of studies have demonstrated an inverse relationship between cell size and growth rate (e.g. Banse 1976, Schlesinger et al. 1981, Munawar and Munawar 1982, Rai 1982, Reynolds 1984). This relationship suggests that smaller algae can be expected to have productivity rates that are proportionally greater than their contribution to the total phytoplankton volume. In this study the opposite was observed, i.e., productivity rates for *Rhodomonas* and

Figure 3.11. *In situ* productivity of *Cryptomonas* and *Rhodomonas* populations determined by nuclear track microautoradiography in Lawrence Lake, Michigan, 1984 (±S.E., n=3-8).

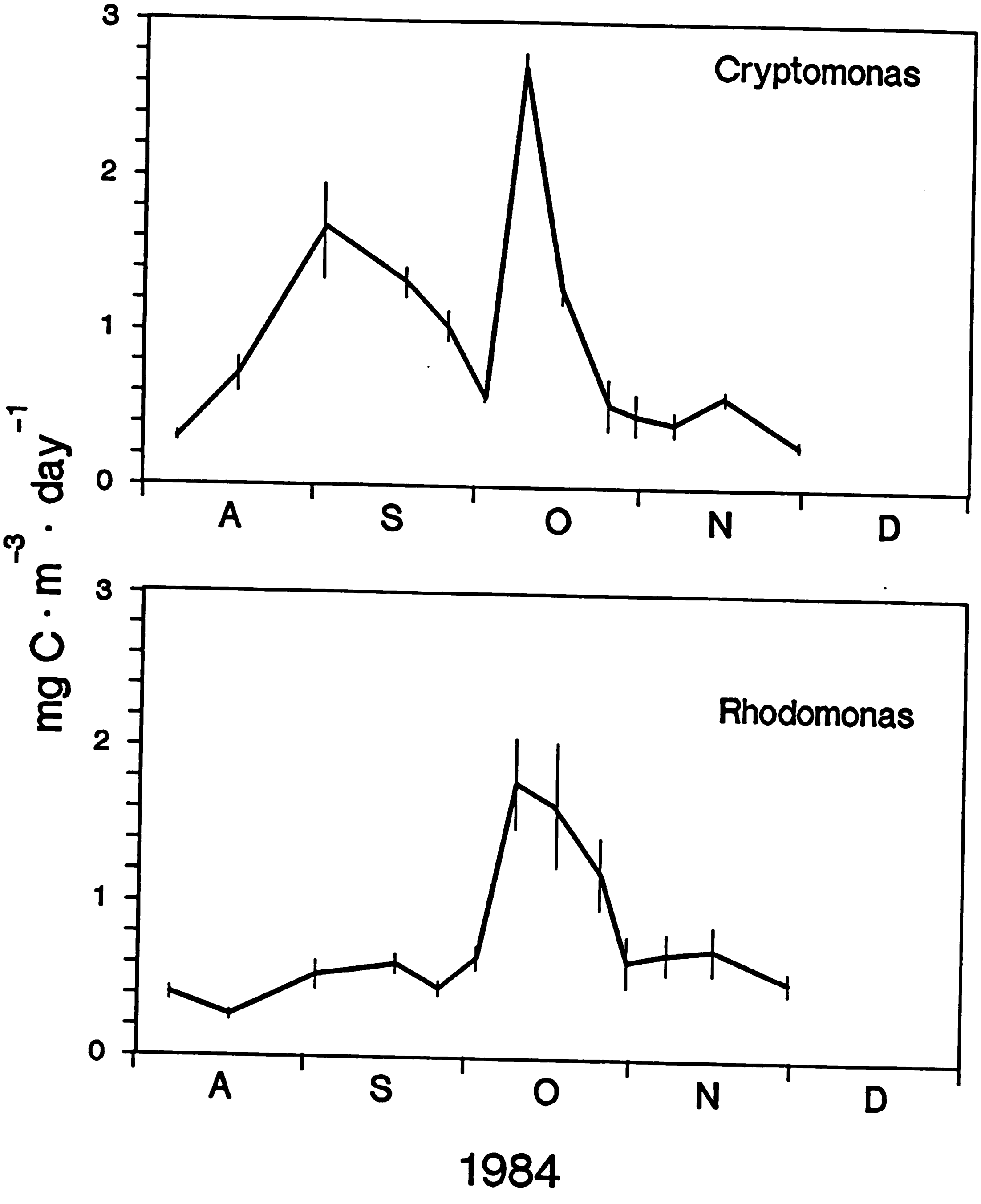

Figure 3.11

Table 3.3. Specific growth rate (k) and doubling time (G) for *Cryptomonas* '*erosa*' (Ce), *Rhodomonas minuta* (Rm) and the phytoplankton community (pc) based on the ratio of carbon fixed per day to cell carbon.

DATE	k (day^{-1})			G (days)		
	Ce	Rm	pc	Ce	Rm	pc
07-AUG-84	0.07	0.16	0.46	9.4	4.3	1.5
18-AUG-84	0.08	0.13	0.58	8.4	5.1	1.2
03-SEP-84	0.13	0.21	0.44	5.4	3.3	1.6
18-SEP-84	0.12	0.14	0.44	5.8	4.9	1.6
26-SEP-84	0.09	0.08	0.35	8.0	8.4	2.0
03-OCT-84	0.05	0.16	0.55	13.1	4.2	1.3
10-OCT-84	0.13	0.38	0.73	5.4	1.8	0.9
17-OCT-84	0.08	0.26	0.60	8.8	2.7	1.2
26-OCT-84	0.05	0.14	0.36	14.2	4.8	2.0
31-OCT-84	0.03	0.09	0.18	20.9	8.0	3.8
07-NOV-84	0.02	0.08	0.29	29.6	9.2	2.4
16-NOV-84	0.05	0.10	0.52	13.7	6.9	1.3
30-NOV-84	0.03	0.08	0.28	24.1	8.9	2.5

Cryptomonas were proportionally smaller than their contributions to total phytoplankton volume (Figure 3.12). The discrepancy was generally larger with Cryptomonas. The differences between the two species, as reflected in these ratios, are apparent in the specific growth rate constants which were nearly always lower for Cryptomonas (Figure 3.13). The range of doubling times based on these growth rates was 2-9 days for Rhodomonas and about 5 to 30 days for Cryptomonas (Table 3.3).

One method of evaluating the productivity of Cryptomonas and Rhodomonas is to compare their carbon based specific growth rates (k) with those of the autotrophic community (Figure 3.13). Carbon was derived from cell volumes according to the equations of Strathmann (1967). Most evidence from comparative studies indicates that the ^{14}C method measures photosynthetic rates closer to net than to gross photosynthesis (Wetzel and Likens 1979). It was assumed that net ^{14}C fixation reflects algal particulate carbon formation (Ryther and Menzel 1965).

Great differences were found between the specific growth rates of the three taxonomic entities examined. Without exception, total autotrophic community growth rates were greater than growth rates for either of the cryptophyte species alone. Growth rates generally tended to decline from August to November but in all three cases maxima developed during October. The sharp decline in growth rates

Figure 3.12. Ratio of *Cryptomonas* and *Rhodomonas* cell volume to total phytoplankton volume and the ratio of *Cryptomonas* and *Rhodomonas* primary productivity to total phytoplankton productivity.

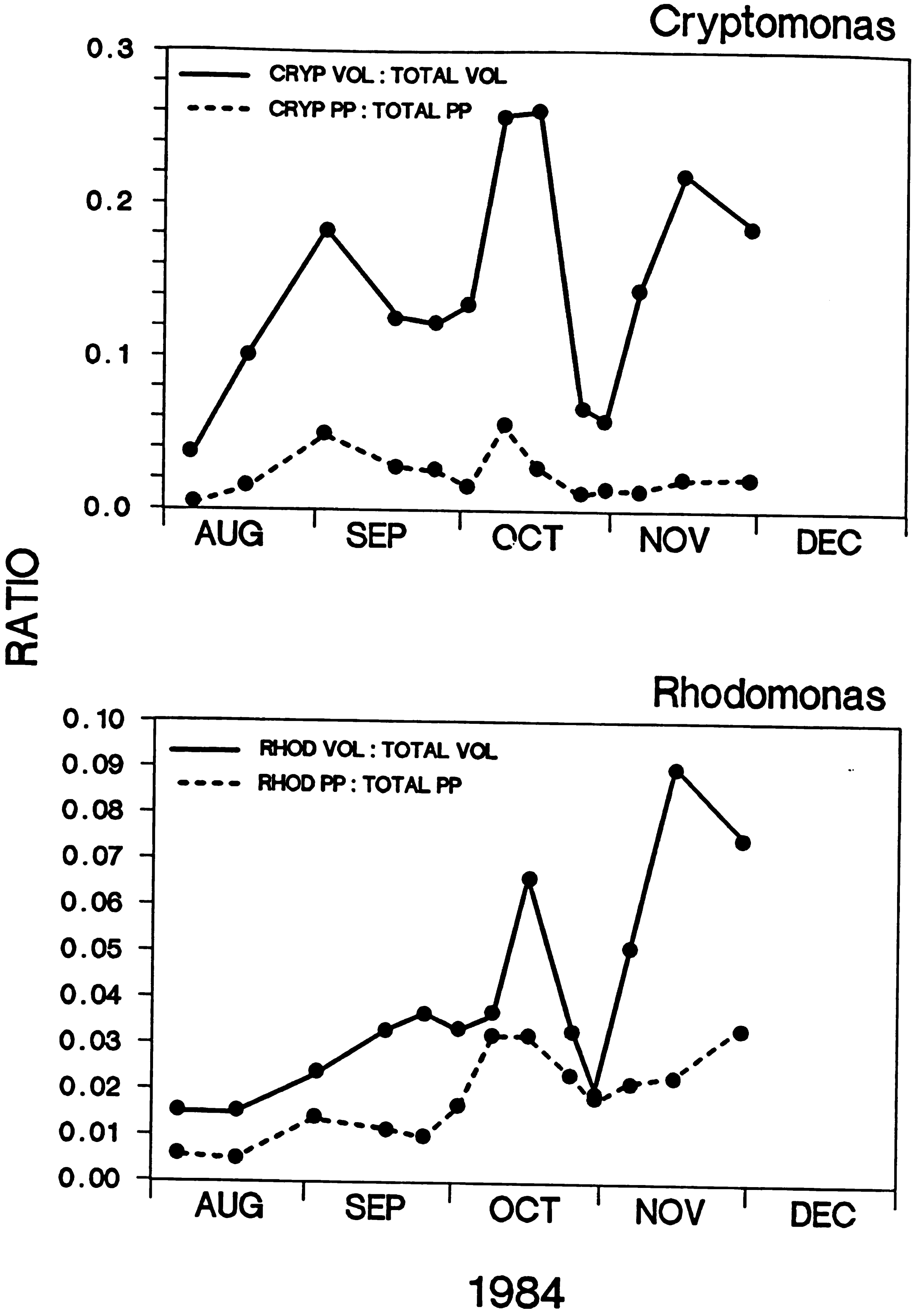
Cryptomonas
0.3
0.2
0.1
0.0
CRYP VOL : TOTAL VOL
CRYP PP : TOTAL PP
AUG
SEP
OCT
NOV
DEC
RATIO
Rhodomonas
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
RHOD VOL : TOTAL VOL
RHOD PP : TOTAL PP
AUG
SEP
OCT
NOV
DEC
1984

Figure 3.12

Figure 3.13. Growth rate constants (k) of Rhodomonas, Cryptomonas and the total phytoplankton community based on the ratio of carbon fixed per day to total cell carbon. Carbon was derived from cell volumes according to the equations of Strathmann (1967). There were no corrections for dark respiration.

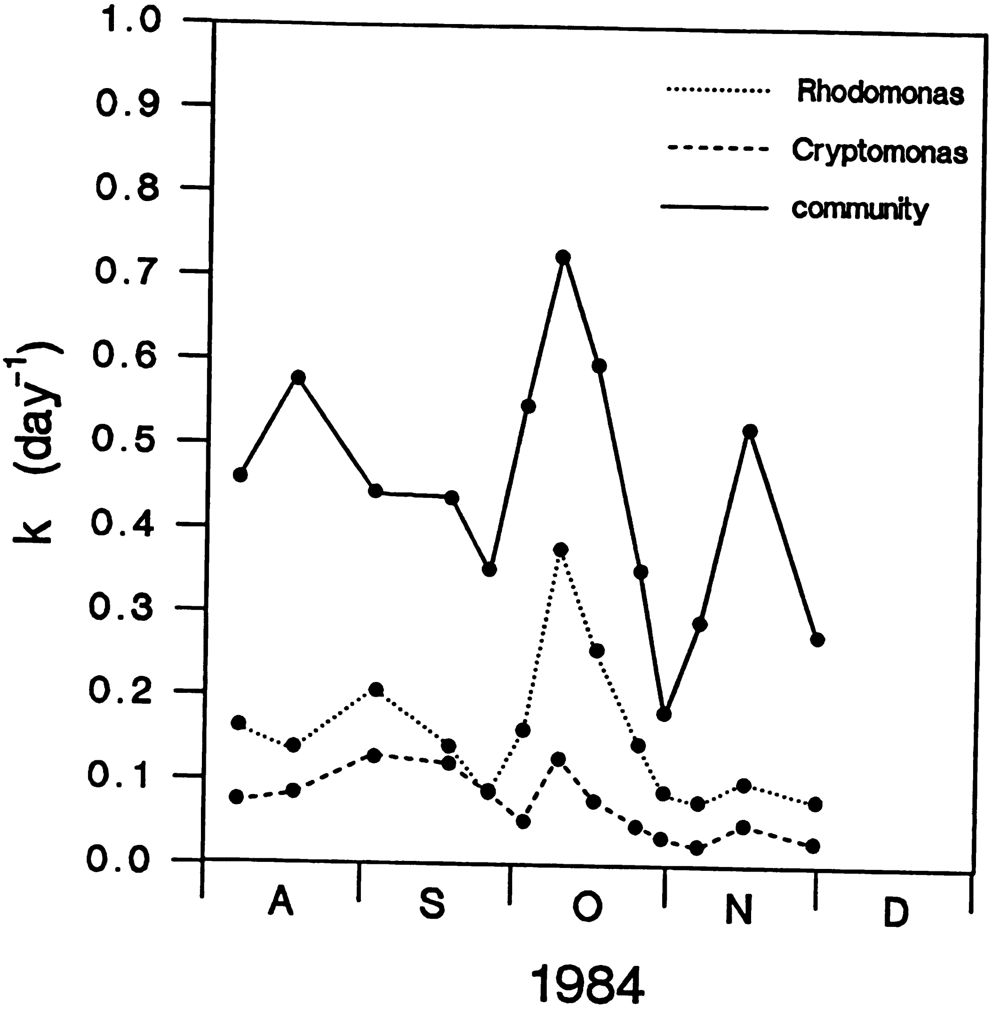
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
k (day^{-1})
Rhodomonas
Cryptomonas
community
A
S
O
N
D
1984

Figure 3.13

after mid-October coincided with the rapid deepening of the mixed zone leading to turnover in early November. Community and Rhodomonas growth rates fluctuated broadly, reaching a maximum two weeks prior to the Chrysosphaerella maximum. Cryptomonas growth rates were quite low, averaging only 16 percent of the community growth rates, and they were less variable through time. Rhodomonas growth rates were more similar to those of the community growth rates, but still averaged only 34 percent of those values.

Theoretically, the specific growth rate of a species must equal or exceed the sum of all loss rates (e.g., grazing, flushing, sedimentation, cell lysis) if the population is to be maintained or to expand (Crumpton and Wetzel 1982). Loss processes have recently been emphasized for their importance in influencing algal species succession (Jassby and Goldman 1974, Kalff and Knoechel 1978, Smayda 1980, Reynolds 1984). In this study only losses resulting from grazing activities were critically investigated.

The importance of sedimentation as a loss factor varies depending largely on thermal stratification, turbulence, the physiological state of the population and the species under consideration (Livingston and Reynolds 1981, Sommer 1984). In several studies, using non-poisoned sedimentation traps, cells of cryptophytes were seldom found even though they were abundant in the water column (Reynolds 1976, Livingston and Reynolds 1981, Reynolds and Wiseman 1982, Sommer 1984).

Sommer (1984) concluded that cryptomonads were unaffected by sedimentary losses. As pointed out by Reynolds (1976), however, the lack of cryptophytes in traps may result from avoidance (motility), consumption by zooplankton, or death and decomposition in the immediate water column. That Rhodomonas and Cryptomonas migrate diurnally in response to light and that their direct contribution to sedimenting particulate carbon was small, was clearly demonstrated by Burns and Rosa (1980). Pedrós-Alió et al. (1987), however, successfully collected Cryptomonas with non-poisoned traps set in anoxic water below extremely dense metalimnetic populations. Cryptophytes lack structures resistant to decay and should not be expected to persist in an unpreserved state. In this study, living Rhodomonas cells were observed bursting upon lysis to form nondescript bubbles which would certainly be unidentifiable if present in traps. It appears that cryptophyte motility and their demonstrated tendency for vertical migration minimizes their losses due to sedimentation except in unusual situations (e.g. Pedrós-Alió et al. 1987).

Flushing losses were not measured in this study but a calculation of epilimnetic flushing losses by Crumpton and Wetzel (1982), assuming that all precipitation impinging on the drainage basin went through the epilimnion, at no time indicated that losses were greater than a few percent.

Potential loss of cells from zooplankton grazing was evaluated for two size classes; <10 µm, representative of Rhodomonas and comprised almost exclusively of microflagellates (Figure 3.14) and 10-30 µm, representative of Cryptomonas (Figure 3.15). In each figure, carbon based growth rates (k) for Rhodomonas or Cryptomonas and the entire autotrophic community are plotted along with loss rates from all grazing activity. In the lower panel of each figure are total cell volumes of the size class and the cryptophyte species of interest.

Biovolume in the <10-µm particle size class fluctuated with the grazing rate (Figure 3.14) until the end of October when zooplankton abundance and grazing were minimal, then the <10 µm algae rapidly increased in abundance. Rhodomonas biovolume followed the same pattern but was reduced in magnitude. It accounted for most of the biovolume in its size class only during the declining period of zooplankton grazing. By November the non-Rhodomonas microflagellates had recovered while Rhodomonas was in decline. The continuous decline in the total volume of Rhodomonas during November and December coincided with decreased growth rates.

The autumnal transition period of rapid environmental changes provided conditions for opportunistic species to flourish. With decreasing surface water temperatures and increasing mixed depth, summer phytoplankton were in decline. Nutrient (phosphorus) availability improved,

Figure 3.14. _Rhodomonas_ specific growth rate as the ratio of carbon fixed per day (NTM) to cell carbon (volume conversion), total phytoplankton community specific growth rate as the ratio of carbon fixed per day (^{14}C productivity) to total phytoplankton carbon (cell volume conversion), and the daily loss rate constant by zooplankton grazing on the <10μm size class (as the fraction of the water filtered per day) (upper). Seasonal dynamics of _Rhodomonas_ and particles in the <10 μm size class as total volume (lower).

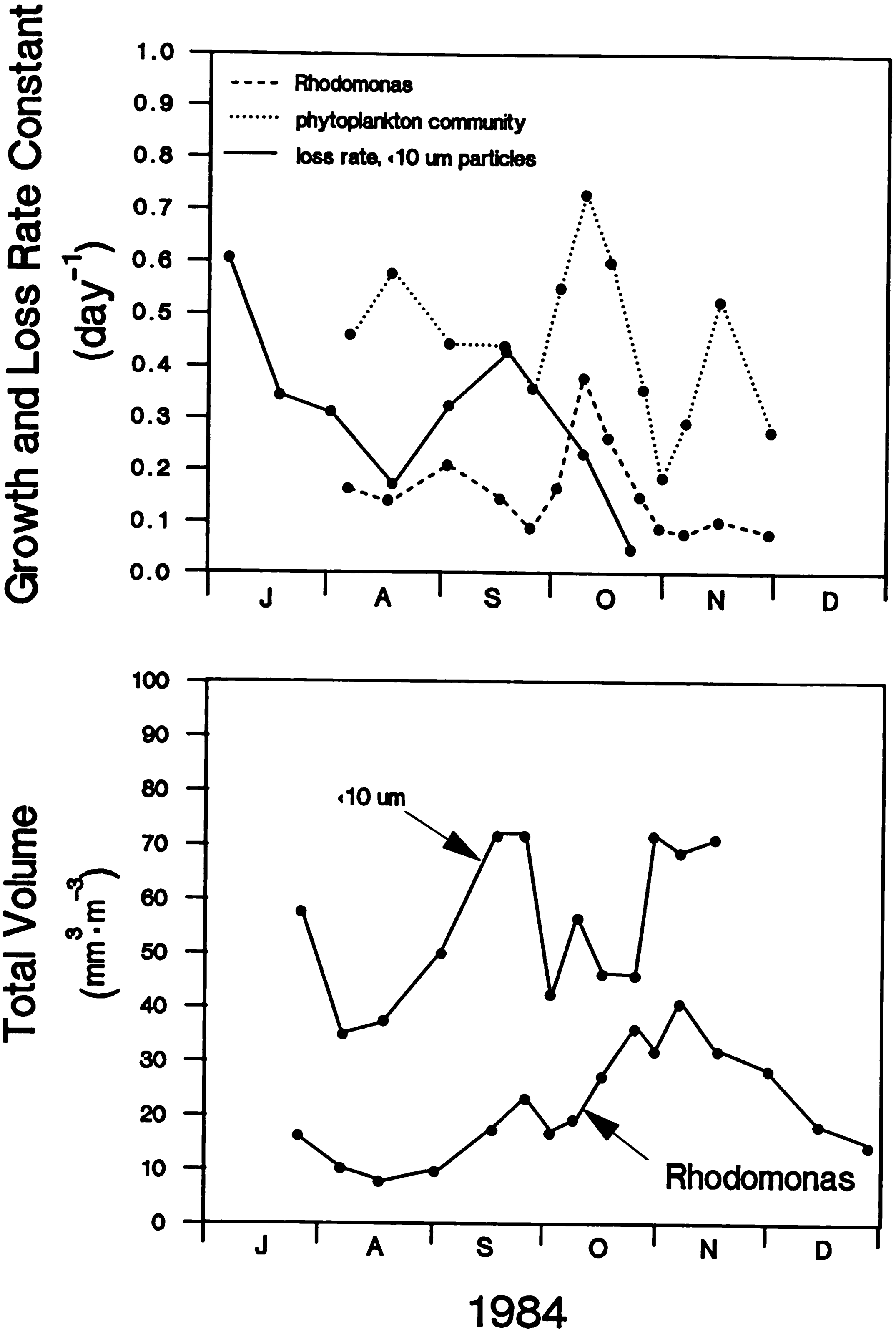
Growth and Loss Rate Constant (day^{-1})
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Rhodomonas
phytoplankton community
loss rate, <10 um particles
J
A
S
O
N
D
Total Volume (mm^3·m^{-3})
100
90
80
70
60
50
40
30
20
10
0
<10 um
Rhodomonas
J
A
S
O
N
D
1984

Figure 3.14

Figure 3.15. Cryptomonas specific growth rate as the ratio of carbon fixed per day (NTM) to cell carbon (volume conversion), total phytoplankton community specific growth rate as the ratio of carbon fixed per day (^{14}C productivity) to total phytoplankton carbon (cell volume conversion), and the daily loss rate constant by zooplankton grazing on the 10-30 μm particle size class (as the fraction of the water filtered per day) (upper). Seasonal dynamics of Cryptomonas and particles in the 10-30 μm size class as total volume (lower).

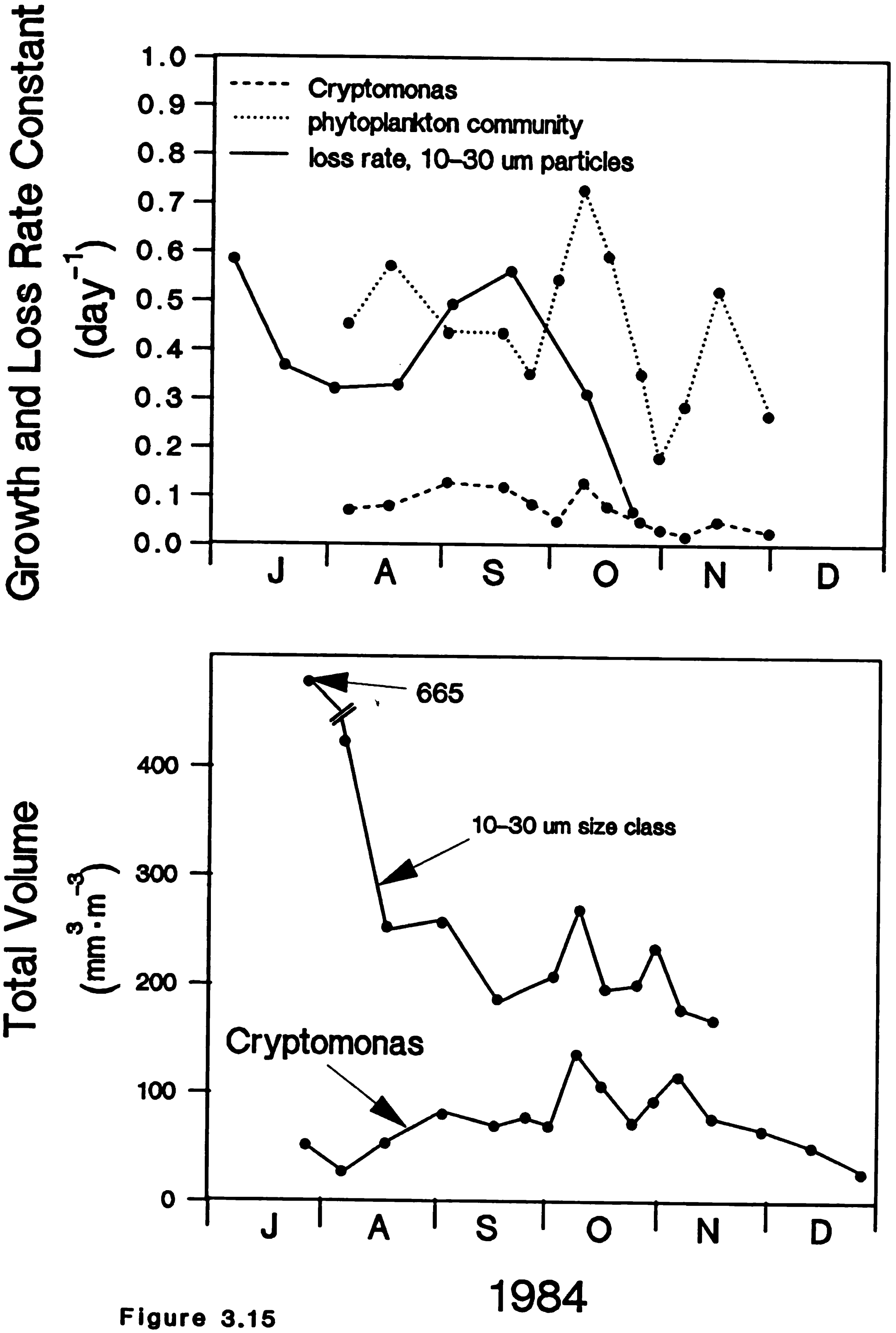
Growth and Loss Rate Constant
(day^{-1})
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Cryptomonas
phytoplankton community
loss rate, 10–30 um particles
J
A
S
O
N
D
Total Volume
(mm^3·m^{-3})
400
300
200
100
0
665
10–30 um size class
Cryptomonas
J
A
S
O
N
D
1984

Figure 3.15

probably from phytoplankton cell decomposition and increased mixing of deeper hypolimnetic water. Microflagellate growth was obviously stimulated during this period. The increased zooplankton abundance and grazing may have been in response to more than the microflagellates. Non-algal particulates (bacterial and non-living organic particles) may also have been in concentrations sufficiently large to stimulate zooplankton growth and subsequently add to increased autumnal grazing rates. Preliminary estimates indicated that total pelagic bacterial cell volume was nearly constant and at levels equal to maximal cryptophyte contributions throughout the study period (M. F. Coveney, personal communication). The rapid decline in the <10 μm size class during late September appears to be more directly related to grazing pressure as it coincides with maximal grazing rates (Figure 3.14). Competitive interactions between microflagellates and Chrysosphaerella in late October were obscured since both developed rapidly together as grazing pressure and phosphorus limitation decreased.

Grazing rates were generally higher on particles in the 10-30 μm size class than they were on <10 μm size class particles. Reduction of particles in the 10-30 μm size class appears to have followed increased grazing pressure during August and September (Figure 3.15). But Cryptomonas, after growth in August, maintained a nearly constant volume during September which suggests some kind of refuge from the grazing pressure.

Specific growth rates were much lower than apparent grazing loss rates for Rhodomonas until mid-October and for Cryptomonas until the zooplankton population was reduced to very low levels in November (Figures 3.14 & 3.15). In the most extreme case for Cryptomonas in September, assuming uniform distribution and no algal growth, zooplankton would reduce the 10-30 μm size-class population by one half in 1.3 days, while it would take eight days for the Cryptomonas population to double assuming no losses (Figure 3.15). The phytoplankton community as a whole had specific growth rates at levels greater than or equal to grazing losses for all dates except two in September (Figure 3.15). The obvious discrepancy between the high grazing loss rates and low cryptophyte growth rates requires some explanation since cryptophytes annually form a significant portion of the phytoplankton community during the autumn. Their continued presence and growth requires growth rates sufficiently high to overcome losses of all kinds or a mechanism to avoid cell death. Potential methodological errors which may contribute to the discrepancy are discussed below.

Calculation of a specific growth rate is dependent upon accurate estimates of cell carbon and ^{14}C productivity for the species. Strathmann's (1967) equations for estimating cell carbon from cell volume account for decreasing relative cell carbon with increasing cell size and for differences between diatoms and other algae. Strathmann's formula has not been specifically tested for cryptophytes but it results in carbon estimates similar to independent determinations for the class (discussed in methods section). These equations are probably most applicable to cells in exponential growth phase (Smayda 1978), an event of questionable frequency in Lawrence Lake because of continual phosphorus limitation. Strathmann's equations may overestimate cryptophyte cell carbon which would lead to underestimated specific growth rates.

Cryptophyte productivity was determined via nuclear track microautoradiography where several sources of potential error were possible. Microscopic observations showed more cell damage associated with sample preparation to Cryptomonas than to Rhodomonas. The larger cells may have been more susceptible to lysis if the acid Lugol's solution did not fix them quickly enough. Cryptophytes lack a rigid cell wall but the smaller more compact geometry of Rhodomonas may give it a mechanical advantage over the larger Cryptomonas and therefore make it less susceptible to lysis under the same physical stresses.

Optimally, preparations for track counting should provide cells with no more than ten tracks per cell (Knoechel and Kalff 1976). Cryptomonas cells with 10-20 tracks were encountered in some preparations. The difficulties associated with accurately sorting overlying tracks from one another could lead to a significant underestimate of track abundance and therefore an underestimate of ^{14}C productivity for that species. Track number per cell can be controlled, within limits, by varying any of numerous factors during field and laboratory stages of sample preparation that would effectively alter the activity associated with the cells. A common method for controlling track number is to adjust the length of time the photographic emulsion is exposed to decay events prior to development. In order to ensure proper track to cell ratios for cells of all sizes, many replicate slide preparations are required. In this study only six slides per incubation bottle could be prepared, reducing the opportunity for multiple exposure periods. The methods were optimized for Rhodomonas cells which may have resulted in underestimates for Cryptomonas productivity.

A recent comparison between light microscopy and scanning electron microscopy indicated that the latter enabled resolution of tracks formed by grains sufficiently small to be overlooked under light microscopy (Burkholder 1986). This comparison showed a mean of 2.8-fold more tracks per unit algal volume were counted with SEM- than with LM-autoradiography, a potential source for significant underestimates of algal productivity. Corrections for the difference were not applied in this study since Burkholder (1986) was testing material labeled with ^{32}P.

The zooplankton grazing rates given here were within ranges reported in the literature, but they were frequently greater than rates reported by Crumpton and Wetzel (1982) for Lawrence Lake. They found a maximum grazing rate of about $0.41 \cdot day^{-1}$ while in this study rates were generally higher and greater than $0.5 \cdot day^{-1}$ on several occasions (Figure 3.15). The grazing rates of Crumpton and Wetzel (1982) were based on direct counts of the combined zooplankton community while in this study grazing rates were determined separately for individual species and size classes of zooplankton and then combined with independent abundance estimates to arrive at a zooplankton community grazing rate. The former approach provides a more direct estimate of total grazing impact without the uncertainty associated with numerous independent estimates of subcomponents. The advantage of the latter approach is in providing information on the distribution of grazing pressure within the zooplankton community. The trade-off is precision (Crumpton and Wetzel 1982) for detail (this study). Therefore, it is possible that grazing rates reported here are overestimates, thereby exaggerating the discrepancy between grazing rates and growth rates.

Rates of algal mortality inflicted by zooplankton have been demonstrated to be species-specific (Lehman and

Sandgren 1985). Therefore, extrapolation of grazing rates based on labeled non-cryptophyte species to Cryptomonas and Rhodomonas may be erroneous. That cryptophytes were grazed at a lower rate than the labeled cells seems implausible given much evidence to the contrary, i.e., high nutritional value (Pejler 1977, Stemberger 1981), readily digested and assimilated (Porter 1973, Schindler 1971), apparent selective removal by Daphnia of cryptomonads from the water column (Lehman and Sandgren 1985, Vaga 1985) and the decided preference for Cryptomonas over Chlamydomonas in laboratory studies by the rotifer Polyarthra (Gilbert and Bogdan 1984).

Productivity rates for the cryptophytes were probably underestimated but they indicate that these algae were not major contributors to total phytoplankton productivity as their continual presence and contributions to the phytoplankton volume would suggest. The timing of their growth and maximal biovolume with rapid transition periods in the lake is still consistent with their suggested role as couplers (Stewart and Wetzel 1986) maintaining productivity during those times. It appears that cryptophyte populations are tightly coupled to zooplankton grazing activities in Lawrence Lake. Even so, the cryptophytes, especially Rhodomonas, maintained a significant numerical presence at all times in the lake. The continuous Rhodomonas population suggests a lower limit to cell abundance below which the grazers are not efficient at harvesting the cells regardless of their measured grazing rate.

There are other possible explanations for the discrepancies between grazing loss rates and cryptophyte growth rates. Cryptophytes have been shown to be auxotrophic as a result of requirements for certain vitamins. Problems associated with growing them in defined culture media were overcome only after this discovery. In addition, recent conceptual developments and expansion of theory which recognizes the importance of the microbial food loop has led to a renewal of interest in mixotrophy in pigmented flagellates (reviewed by Sanders and Porter 1988). Phagotrophy by pigmented cryptophytes has been demonstrated in several studies using a variety of particles: bacteria (Porter et al. 1985), small flagellates (Pratt and Cairns 1985) and polystyrene beads (Porter 1988). That cryptophytes are capable of using particles as a source of organic carbon has been established but its importance in the nutrition of the group is uncertain. Sanders and Porter (1988) suggest that extreme environmental conditions may be necessary to induce feeding by autotrophic cryptomonads. During this study a large bacterial biomass (equal to that of the cryptophytes) was observed (M. F. Coveney, personal communication) providing a large pool of particulate organic carbon. The relatively large autumnal cryptophyte community in Lawrence Lake had the potential for satisfying its nutritional requirements phagotrophically. If this were the case, underestimates of total cryptophyte productivity using the ^{14}C method offers a partial explanation for the results reported here.

Another possible explanation for the discrepancy between grazing loss rates and cryptophyte growth rates emerges from a closer examination of the primary operational assumption of this study, i.e., uniform processes within the mixed layer of the lake. It was shown that the vertical distribution of *Daphnia galeata*, the primary grazer, varied inconsistently with depth at any given time as well as on a diel basis (Figure 3.9). The implication is that epilimnetic grazing impacts varied with depth at intervals of less than four meters during the day. Additionally, diel vertical migration by cryptophytes has been well documented (Sommer 1982, Salonen et al. 1984). Simultaneous differential diel migration by zooplankton and cryptophytes may result in dynamic vertical patchiness forming refuges within the epilimnion that were not apparent with the integrated sampling approach used in this study.

Summary

The cryptophytes increased in numbers and volume during the autumn transition period in Lawrence Lake. Their contribution to total algal volume was masked by the exceptional bloom of *Chrysosphaerella* even though cryptophyte volume was similar to that observed in other years. The ability of *Chrysosphaerella* to attain maximum summer biovolume levels during the autumn indicated adequate nutrient availability at that time.

Daphnia galeata mendotae was responsible for most of the grazing pressure in the lake. Summer grazing rates remained large until the zooplankton populations declined in October. Grazing had a negative effect on the 10-30-μm size class but was positively correlated with density of the <10-μm particle size class. The latter was suggestive of nutrient recycling by the grazers.

The productivity rates of *Cryptomonas* and *Rhodomonas* populations were low compared to the entire phytoplankton community, but similar to each other even though great differences occurred between their cell volumes and abundances. The productivity of cryptophytes relative to total phytoplankton productivity was proportionally smaller than their contribution to total phytoplankton volume. In addition, the specific carbon based growth rates of the cryptophytes were lower than the total phytoplankton community growth rates. These findings likely reflect an underestimate of cryptophyte productivity resulting from methodological problems, but, the conclusion to be drawn from these data is that cryptophyte contributions to total phytoplankton productivity during the autumn are not as great as expected from their volume contributions to the total phytoplankton community.

The continued presence of cryptophytes in the lake under high grazing pressure and with low primary productivity and growth rates may have resulted from a combination of processes. Simultaneous differential diel migration by zooplankton and the cryptophytes may have created spatial patches of refuge from predation thus reducing apparent grazing losses. Mixotrophy may have provided cryptophytes with alternative modes of nutrition and result in an underestimate of their total productivity when productivity was based only on autotrophy.

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APPENDICES

Appendix A. Phytoplankton Species List
(N = number measured)

TAXON	N	Mean cell Volume (μm^{-3})
PYRRHOPHYTA		
Ceratium hirundinella fa. *austriacum* (Zedb.) Bachmann	40	56800
Gymnodinium helveticum Penard	15	30900
Gymnodinium ordinatum Skuja	13	322
Gymnodinium sp.	8	14300
Peridinium cinctum (Muell.) Ehrenberg		
Peridinium inconspicuum Lemmermann	8	2290
Peridinium polonicum Woloszynska	60	25200
Peridinium gatunense Nygaard	18	50000
Peridinium willei Huitfeldt-Kass	56	84600
Peridinium willei fa. *lineatum* Lindemann		
Peridinium sp. 1	9	2600
Peridinium sp. 2	1	37000
CRYPTOPHYTA		
Cryptomonas caudata Schiller	14	470
Cryptomonas (erosa-ovata size class)	720	1666
Cryptomonas erosa Ehrenberg		
Cryptomonas marssonii Skuja	29	700
Cryptomonas ovata Ehrenberg		
Cryptomonas phaseolus Skuja	22	340
Cryptomonas rostratiformis Skuja	6	5300
Ketablepharis ovalis Skuja	22	66
Rhodomonas minuta var. *nannoplanctica* Skuja	938	67.4
CYANOPHYTA		
Anabaena planktonica Brunnthaler	19	340
Anabaena flos-aquae (Lyngb.) De Brébisson	30	150
Anabaena inaequalis (Kuetz.) Bornet & Flahault		
Anabaena sp.	8	67
Anabaenopsis elenkinii Miller	1	220
Aphanizomenon flos-aquae (L.) Ralfs	1	85
'*Aphanocapsa*-*Aphanothece*'	47	4.2
Aphanocapsa elachista West & West		
Aphanothece nidulans P. Richter		
Coelosphaerium palidum Lemm.	25	4.9

Appendix A, cont'd,

TAXON	N	Mean cell Volume (μm^{-3})
Coelosphaerium naegelianum Unger	1	31
Chroococcus limneticus Lemmermann	71	69
Chroococcus prescottii Drouet & Daily		
Chroococcus sp.	4	261
Dactylococcopsis smithii Chodat & Chodat	1	43
Gomphosphaeria aponina Kuetzing	25	41
Lyngbya bergei G. M. Smith		
Lyngbya limnetica Lemmermann		
Merismopedia tenuissima Lemmermann	4	1.8
Microcystis aeruginosa Kuetzing	50	63
Oscillatoria limnetica Lemmermann	12	15
Oscillatoria sp.		
Radiocystis geminata Skuja		
Spirulina sp.		
CHRYSOPHYTA		
Bitrichia chodatii (Reverdin) Chodat	10	155
Chromulina magna? Doflein	3	1255
Chrysochromulina parva Lackey	10	24
Chrysococcus sp.	1	1440
Chrysosphaerella brevispina Korshikov		
Chrysosphaerella longispina Lauterborn	36	890
Chrysoikos skujai (Nauwerck) Willen	3	58
Dinobryon accuminatum Ruttner	3	121
Dinobryon bavaricum Imhof	5	121
Dinobryon crenulatum W. & G. S. West	2	83
Dinobryon divergens Imhof	53	221
Dinobryon social var. *americanum* (Brun.) Bachmann	1	84
Mallomonas spp. (combined mean volume)	38	1570
Mallomonas acaroides Perty em. Iwanoff		
Mallomonas caudata Iwanoff em. Krieger		
Mallomonas crassisquama (Asmund) Fott		
Mallomonas heterospina Lund		
Mallomonas mangofera Harris & Bradley		
Mallomonas tonsurata Teiling em. Krieger		
Mallomonas tonsurata var. *alpina* (Pascher & Ruttner) Krieger		
Mallomonas pseudocoronata Prescott	5	1600
Ochromonas sp.	2	65
Psuedokephyrian attenuatum Hilliard	2	390
Spiniferomonas trioralis Takahashi		
Stichogloea doederleinii (Schmidle) Wille	25	210

Appendix A, cont'd,

TAXON	N	Mean cell Volume (μm^{-3})
Synura curtispina (Petersen & Hansen) Asmund		
Synura petersenii Korshikov		
Uroglenopsis americana (Calkins) Lemmermann		
BACILLARIOPHYCEAE		
Achnanthes minutissima Kuetzing	4	94
Amphiprora sp.		
Amphora sp.		
Asterionella formosa Hassall	50	645
Cyclotella bodanica var. affines Grunow	405	4986
Cyclotella comta (Ehren.) Kuetzing		
Cyclotella meneghiniana Kuetzing		
Cyclotella michiganiana Skvortzow	86	1546
Cyclotella comensis Grunow		
Cymbella sp.	5	7000
Eunotia sp.		
Fragilaria crotonensis Kitton	50	750
Melosira sp.	1	690
Meridian circulare (Grev.) C. A. Agardh		
Navicula spp.		
Nitzschia sp.		
Pinnularia sp.		
Stephanodiscus sp.	1	13700
Stephanodiscus astrea (Ehren.) Grunow	6	33300
Synedra acus Kuetzing		
Synedra delicatissima W. Smith		
Synedra ulna (Nitzsch) Ehrenberg		
Synedra (large)	8	18300
Synedra (medium)	24	4760
Synedra (small)	4	1240
Synedra (very small)	26	360
Tabellaria fenestrata (Lyng.) Kuetzing		
CHLOROPHYTA		
Ankistrodesmus falcatus (Corda) ralfs	9	112
Ankistrodesmus falcatus var. acicularis (A. Braun) G. S. West		
Botryococcus braunii Kuetzing	10	56
Carteria sp.	1	394
Chlamydomonas sp.	3	154
Closterium gracile De Brébisson	2	9380
Cosmarium sp.	5	9530

Appendix A, cont'd,

TAXON	N	Mean cell Volume (μm^{-3})
Crucigenia rectangularis (A. Braun) Gay	30	226
Desmidium sp.	1	16689
Elakatothrix gelatinosa Wille		
Nephrocytium agardhianum Naegeli	10	212
Nephrocytiom limneticum G. M. Smith		
Mougeotia sp.	7	2103
Oocystis submarina Lagerheim	6	120
Oocystis sp. 1	12	600
Oocystis sp. 2	5	3820
Pediastrum boryanum (Turp.) Meneghini	1	493
Pediastrum duplex Meyen		
Planktonema lauterborni Schmidle	25	33
Quadrigula lacustris (Chod.) G. M. Smith	10	56
Schroederia setigera (Schroeder) Lemmermann	6	76
Scenedesmus abundans (Kirch.) Chodat	1	38
Sphaerocystis schroeteri Chodat	26	69
Staurastrum sp.		
Tetraëdron minimum (A. Braun) Hansgirg	1	44
Tetraëdron pentaedricum West & West	1	109
EUGLENPHYTA		
Euglena sp.	14	34200
Phacus pyrum (Ehrenberg) Stein		
Trachelomonas sp.	12	600
MISCELLANEOUS		
microflagellates		
size class no. 1 (<3 µm dia)		
size class no. 2 (3-6 µm dia)		
size class no. 3 (6-10 µm dia)		

Appendix B. Abundance of *Rhodomonas minuta* and *Cryptomonas* '*erosa*' in Lawrence Lake from August 1982 until August 1983.

	$\text{Cells}\cdot\text{mL}^{-1}$ by stratum (m)					
	Rhodomonas			*Cryptomonas*		
Date	0-4	4-8	8-12	0-4	4-8	8-12
08/06/82	102	139	63	17	74	51
08/07/82	173	204	52	30	51	34
08/09/82	184	234	141	23	62	49
08/11/82	209	186	33	21	54	31
08/13/82	112	196	58	35	68	35
08/15/82	186	149	53	24	81	34
08/17/82	183	117		18	59	
08/19/82	198	145	71	25	47	37
08/21/82	150	249	37	23	63	26
08/23/82	170	221	48	27	33	29
08/25/82	166	162	124	20	48	29
08/27/82	171	146	55	16	36	36
08/29/82	165	146	109	20	28	19
08/31/82	180	86		33	43	
09/02/82	148	142	104	23	34	50
09/04/82	86	87	40	22	43	30
09/06/82	257	146	93	65	34	46
09/08/82	125	173	70	45	49	20
09/10/82	135	123	132	47	63	51
09/12/82	120	124	83	43	48	46
09/14/82	295	161		85	73	
09/16/82	260	170	76	77	75	55
09/18/82	180	137	134	75	71	47
09/20/82	154	145	145	52	65	54
09/22/82	225	143	121	51	60	33
09/24/82	130	122	103	34	39	31
09/26/82	159	102	144	54	47	51
09/28/82	110	115		43	33	
09/30/82	95	140	105	34	27	41
10/01/82	108	155	154	39	66	42
10/02/82	127	151	157	33	63	53
10/03/82	153	196	145	40	59	33
10/04/82	219	222	200	54	58	55
10/05/82	232	265	226	50	60	28
10/06/82	337	326	236	90	63	63
10/07/82	373	377	379	45	91	45
10/08/82	368	377	359	70	64	62
10/09/82	486	357	350	78	79	99
10/10/82	328	490	322	75	47	53

Appendix B, cont'd,

	Cells·mL^{-1} by stratum (m)					
	Rhodomonas			Cryptomonas		
Date	0-4	4-8	8-12	0-4	4-8	8-12
10/11/82	439	344	462	68	68	68
10/12/82	544	348	345	120	100	
10/13/82	331	424	290	81	55	89
10/14/82	373	488	279	88	88	51
10/15/82	341	392	322	78	77	89
10/16/82	273	317	377	74	72	83
10/17/82	286	283	206	64	53	58
10/18/82	268	255	233	62	63	66
10/19/82	258	301	293	80	72	88
10/20/82	254	307	218	80	71	61
10/21/82	319	300	278	73	65	69
10/22/82	242	332	284	91	56	74
10/23/82	255	281	334	72	50	63
10/24/82	256	273	261	58	75	55
10/25/82	259	223	229	83	121	55
10/26/82	215	247		57	56	
10/27/82	278	222	230	58	32	26
10/28/82	233	218	210	79	77	68
10/29/82	239	208	252	69	80	58
10/30/82	219	239	210	67	58	82
10/31/82	285	284	230	98	58	59
11/01/82	275	214	253	109	47	42
11/03/82	243	271	257	95	55	42
11/05/82	191	230	187	56	66	56
11/06/82	207	223	198	50	53	67
11/07/82	184	242	208	53	41	57
11/09/82	176	175		49	39	
11/11/82	240	273	282	67	65	
11/12/82	222	228	231	63	52	50
11/13/82	179	215	207	45	55	44
11/15/82	181	182	157	30	38	48
11/17/82	191	194	187	31	46	46
11/19/82	184	181	209	46	47	39
11/21/82	249	265	205	34	31	19
11/22/82	222	239	210	35	33	26
11/23/82	227	230		34	24	
11/25/82	219	200	207	43	35	21
11/27/82	178	173	187	31	21	36
11/29/82	155	211	204	34	30	36
12/01/82	180	152	174	32	20	28
12/03/82	211	181	154	28	27	26

Appendix B, cont'd,

	Cells·mL^{-1} by stratum (m)					
	Rhodomonas			Cryptomonas		
Date	0-4	4-8	8-12	0-4	4-8	8-12
12/05/82	217	181	186	30	27	34
12/07/82	172	160		35	43	
12/09/82	174	183	140	32	24	30
12/11/82	181	232	176	27	28	27
12/13/82	151	185	170	25	24	26
12/15/82	182	261	223	23	31	31
12/16/82	214			23		
12/17/82	148	172	203	31	18	31
12/18/82	241				30	
12/19/82	223	186	169	18	19	15
12/21/82	267	239		20	22	
12/22/82	317				20	
12/23/82	324	185	272	31	19	28
12/24/82	225				20	
12/25/82	273	273	230	33	18	15
12/27/82	253	220	234	20	24	16
12/29/82	214	199	243	14	14	26
12/31/82	288	286	251	14	19	27
01/02/83	205	198	184	18	20	15
01/04/83	242	218		17	11	
01/06/83	305	278	234	17	12	23
01/08/83	196	165	171	10	15	17
01/10/83	175	145	111	14	15	16
01/12/83	234	237	160	6	7	12
01/14/83	271	254	223	16	11	9
01/16/83	193	214	145	4	12	10
01/18/83	252	202		10	20	
01/20/83	199	240	199	6	11	6
01/22/83	178	204	222	9	12	10
01/24/83	276	197	155	14	13	7
01/26/83	334	284	267	4	15	15
01/28/83	188	231	278	6	8	10
01/30/83	283	227	268	13	5	4
02/01/83	417	437		9	20	
02/03/83	329	308	308	20	17	9
02/05/83	340	456	389	6	11	4
02/07/83	339	232	278	11	11	11
02/09/83	430	332	305	16	11	6
02/11/83	316	241	192	6	7	4
02/13/83	267	253	215	8	12	13
02/15/83	244	221		8	7	

Appendix B, cont'd,

	Cells·mL^{-1} by stratum (m)					
	Rhodomonas			Cryptomonas		
Date	0-4	4-8	8-12	0-4	4-8	8-12
02/17/83	147	186	171	2	9	5
02/19/83	237	216	213	4	5	6
02/21/83	219	191	181	3	2	11
02/23/83	302	291	303	7	0	8
02/25/83	371	288	333	15	7	12
02/27/83	324	228	261	2	12	13
03/01/83	150	233		5	10	
03/03/83	216	283	275	5	3	4
03/04/83	332	265	289	9	13	6
03/06/83	263	261	285	4	3	13
03/07/83	253	339	278	6	14	10
03/09/83	386	456	395	15	16	24
03/11/83	424	438	478	11	17	6
03/13/83	338	386	364	5	5	9
03/15/83	309	370		8	17	
03/17/83	307	375	395	6	7	12
03/19/83	333	455	360	4	7	3
03/21/83	333	340	431	17	13	15
03/23/83	273	322	305	13	17	9
03/25/83	291	290	195	11	13	6
03/27/83	278	317	338	8	2	6
03/29/83	279	195		14	6	
03/31/83	207	228	261	9	10	7
04/02/83	237	232	205	4	7	6
04/04/83	196	228	187	7	6	4
04/06/83	169	213	224	10	6	5
04/08/83	180	84	149	1	5	4
04/10/83	125	149	174	11	7	6
04/12/83	127	181		5	7	
04/14/83	83	108	102	5	3	
04/16/83	89	126	131	6	3	4
04/18/83	125	89	120	4		7
04/20/83	89	91	88	5	1	4
04/22/83	74	115	122	6	2	5
04/24/83	87	142	118	4	6	10
04/26/83	52	97		9	2	
04/28/83	96	147	171	4	3	9
04/30/83	145	151	178	15	7	11
05/02/83	155	122	120	10	4	13
05/04/83	136	175	118	21	13	11
05/06/83	262	184	157	7	6	7

Appendix B, cont'd,

	Cells·mL^{-1} by stratum (m)					
	Rhodomonas			Cryptomonas		
Date	0-4	4-8	8-12	0-4	4-8	8-12
05/08/83	212	248	184	13	18	14
05/10/83	129	220		19	10	
05/12/83	292	272	219	23	16	9
05/14/83	279	223	168	22	5	6
05/16/83	277	250	189	26	20	12
05/18/83	216	188	216	28	17	21
05/20/83	250	176	219	19	12	17
05/22/83	327	222	155	20	9	18
05/24/83	226	245		12	28	
05/26/83	275	246	179	14	27	13
05/28/83	164	158	152	18	20	13
05/30/83	316	152	181	31	17	13
06/01/83	218	169	112	41	13	17
06/03/83	195	71	49	41	13	11
06/05/83	135	176	170	42	37	41
06/07/83	231	151		55	62	
06/09/83	220	157	140	51	45	68
06/11/83	192	154	142	100	58	50
06/13/83	133	76	93	82	58	57
06/15/83	144	123	115	99	116	58
06/17/83	152	144	123	80	75	79
06/19/83	164	186	107	86	83	71
06/21/83	165	121		54	67	
06/23/83	122	116	72	92	74	38
06/25/83	138	141	112	59	64	39
06/27/83	178	167	136	80	98	60
06/29/83	238	178	88	128	85	44
07/01/83	167	171	91	83	97	41
07/03/83	161	195	118	67	92	50
07/05/83	218	218		123	119	
07/07/83	207	231	81	98	141	43
07/09/83	164	171	112	112	113	54
07/11/83	123	232	156	66	125	73
07/13/83	102	157	121	57	149	68
07/14/83	97	179	96	53	109	67
07/15/83	214	208	170	63	93	78
07/17/83	99	161	129	56	102	64
07/19/83	105	187		42	54	
07/21/83	156	150	87	32	58	39
07/23/83	125	105	77	19	40	24
07/25/83	105	143	89	26	26	22
07/27/83	143	115	119	23	19	23

Appendix B, cont'd,

	Cells·mL^{-1} by stratum (m)					
	Rhodomonas			*Cryptomonas*		
Date	0-4	4-8	8-12	0-4	4-8	8-12
07/29/83	87	91	77	23	33	28
07/31/83	115	124	74	28	37	19
08/02/83	123	140		29	38	
08/04/83	224	218	155	43	58	30
08/06/83	237	322	236	38	74	34
08/08/83	194	310	188	32	75	30
08/10/83	188	356	298	28	80	59
08/12/83	124	264	387	39	51	28
08/14/83	149	210	154	35	58	22
08/16/83	231	268		37	51	