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Segregation in natural phytoplankton communities.

by

Duncan Wall

A Thesis
presented to the University of Ottawa
in partial fulfillment of the
requirements for the degree of
Master of Science
in
Department of Biology

Ottawa, Ontario, 1980

April 4, 1980.

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ABSTRACT

The role of depth segregation in phytoplankton was investigated in two years of field experiments at Heney Lake, Quebec. The seasonal succession and temporal species associations are described in the lake and in six polyethylene-enclosed communities. Blue-green algae dominated in midsummer with diatoms becoming the major group in autumn. Diatoms had more positive associations than blue-greens.

When associated species were analyzed along the depth gradient during the stable, stratified period, they were found to be separated irrespective of taxonomic division.

Two possible factors responsible for depth separation, nutrients and light, were investigated by direct manipulation of the communities. With weekly nitrate and phosphate enrichment, most species decreased their niche overlap compared with the control, indicating increased competition. Only two species, the diatoms, Fragilaria crotonensis and Synedra delicatissima, did increase their overlap. They are viewed as superior exploitative competitors.

Phytoplankton preferences for light intensity and colour were then determined by enclosing plankton communities in coloured plexiglass cubes suspended at different depths. Diatoms and green algal cell volume were favoured

by intensities greater than 5% surface irradiance, contrary to dinoflagellates and other flagellates which preferred lower intensities. The response of blue-green algae was inconclusive. Colour preferences were less distinct, as less than 25% of the species showed a definite preference. Therefore, light appears to be less important than nutrients in influencing species separation but seems to play a role in overall succession at the group level. Possible strategies adopted by phytoplankton species with respect to these resources are discussed.

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Chapter I

GENERAL INTRODUCTION

Species diversity is a central and unifying theme in ecology. Its variation between communities has been attributed to many potential factors, in particular spatial heterogeneity, time, competition, predation, climatic stability, and productivity. It is the influence of spatial heterogeneity that will be addressed here, specifically with regard to the high diversity observed in lake phytoplankton communities.

High spatial heterogeneity is considered one of the major prerequisites for a large number of species to coexist, as it provides a variety of habitat types with different resource characteristics. The open water of lakes appears extremely homogeneous and yet it supports a large number of phytoplankton species, all of which utilize the same types of resources (e.g. light and inorganic nutrients). As pointed by Hutchinson (1961) this appears to contradict the competitive exclusion principle (Hardin, 1960), which predicts that at equilibrium one species alone should outcompete all of the others in planktonic communities. Numerous hypotheses have been proposed ever since to account for this "paradox". They fall into two categories.

In the first, one assumes that contrary to one of the prerequisites of the competitive exclusion theory, competitive equilibrium is not fulfilled. In other words, environmental changes would occur before competitive exclusion is achieved. Therefore a species in the process of eliminating the other members of the community would not retain its advantage long enough to complete the process (Hutchinson, 1961). This can also provide a temporal means of ecological differentiation (Connell, 1978). Grenney et al. (1973) demonstrated mathematically that a large number of species with different growth characteristics could coexist, given random variations in the supply of limiting nutrients. Although competitive equilibrium may not be achieved on a yearly scale, during successional stages such as summer or winter stagnation, equilibrium may be assumed given the short (ca. 1 day) generation time of the algae (Hulburt, 1977). In this case, other explanations must be invoked. These are the equilibrium hypotheses.

Predation has been shown to foster coexistence among competing species in a variety of communities. The precise mechanisms depend on the characteristics of the interaction. Selective predation on dominant competitors can reduce their monopoly on resources, and thus prevent exclusion of poor competitors (Paine, 1966; Lubchenko, 1978). In some cases non-selective and switching predation may also enhance species richness (Roughgarden and Feldman, 1975; Yodzis, 1976).

The effects of varying grazing pressures of herbivorous zooplankton on phytoplankton species composition (Porter, 1973) and species richness (McCauley and Briand, 1979) have demonstrated the role of predation in alleviating competition. In phytoplankton, nutrient uptake rate is linked to the surface: volume ratio of the cell (Eppley et al., 1969; Lewis, 1976) and the smaller species grow more rapidly. However, they are also the preferred prey (Porter, 1973; Briand and McCauley, 1978) which allows larger species to persist in the community. In a similar fashion, parasitism of superior competitors may also mediate phytoplankton coexistence. Several cases of parasitism are reported to cause severe reduction of some populations. They include fungal attacks on diatoms (Canter and Lund, 1951; Canter, 1970; Reynolds, 1973) and on desmids (Canter and Lund, 1969) and viral infections of blue-green algae (Safferman and Morris, 1964; Shilo, 1971). The extent of these occurrences is not known, so the importance of parasitism in limiting phytoplankton abundance in nature is open to speculation.

Symbiosis and allelopathy were among other phenomena proposed by Hutchinson (1961) to potentially increase coexistence in phytoplankton. Allelopathy is quite widespread in lake algae, especially among blue-greens, and plays a role in observed successional patterns (Keating, 1977; 1978). In marine systems, dinoflagellates are known to secrete substances responsible for the inhibition of diatoms,

(Uchida, 1977). According to theory (Case and Gilpin, 1974), this form of interference competition can result in a higher number of species. Symbiosis may also enhance species diversity, and it has been reported in culture experiments (Tassigny and Lefevre, 1971; Harris, 1971). However, recent theoretical work has shown that this relation is largely unstable (May, 1976).

Resource partitioning may also account for phytoplankton diversity. According to MacArthur and Levins (1964) as many species can be supported as there are distinct resources. This was demonstrated experimentally by Titman (1976) who maintained two diatom species at equilibrium by varying silicon:phosphate ratios. Moreover, stable equilibrium between two species may be possible on a single resource if one species is favored at low concentrations and the other at high concentrations (Stewart and Levins, 1973). Preferences for different nutrient concentrations are known for many freshwater species (for reviews see Fodne, 1948; Lund, 1965), mainly from culture studies. More recently, Levins (1980) even proposed that high environmental variability in a resource level may itself act as a resource, further promoting species diversity.

While most of the above-mentioned mechanisms assume relative homogeneity in lakes, there is evidence for spatial heterogeneity in both environmental conditions and phytoplankton populations, despite what some (Hutchinson, 1961;

Lewis, 1976) consider the overriding effects of water movement and the poor motility of the organisms. Habitat separation has been shown to play a major role in segregating the niches of sympatric rotifers (Miracle, 1977). The hypothesis of habitat separation in phytoplankton was proposed by Richerson et al. (1970). They demonstrated that much patchiness exists in phytoplankton, which is determined by a balance between reproduction and dispersal due to turbulence. These patches can vary greatly in species composition and persist for varying lengths of time depending on the stability of the water column and weather conditions (Reynolds, 1976a). Patchiness occurs on both a horizontal and vertical scale, and is generally more pronounced with depth (Richerson et al., 1975). The present study investigates the degree of segregation in depth occurring between sympatric species in lake phytoplankton communities. Then it examines some of the environmental and biotic variables responsible for the segregation.

The work is divided into four parts. First I describe the succession and species associations occurring in Heney Lake, Quebec and in a series of water columns enclosed in polyethylene bags suspended in the lake. The associations are determined by a Chi-squared analysis based on presence-absence data which allows identification of strongly linked pairs of species. These pairs, are then further analyzed for their degree of association at differ-

ent depths. Next, the degree of niche overlap between the major species is determined, based on two dimensions, time and depth.

Then, by perturbing communities and observing the responses of the various species, I investigate some of the mechanisms employed by phytoplankton species to reduce potential competition. One set of manipulations involves fertilization of communities with inorganic nutrients, and comparison of niche overlap with that of unenriched communites. The other series of experiments tests the effects of varying light intensity and colour on phytoplankton communities incubated at various depths in plexiglass cubes of different colours.

Chapter II

SUCCESSION AND SPECIES ASSOCIATIONS

The phytoplankton composition and succession of freshwater lakes vary according to a variety of factors including latitude, size, morphology, edaphic characteristics of the surrounding land mass and biological interactions. Heney Lake, Quebec, is a dimictic, temperate (46°02' N, 75°55' W) hard water lake. Lakes such as this are characterized by four successional periods throughout the year marked by the onset and breakdown of thermal stratification. The major phytoplankton groups of hard water lakes are blue-green algae and diatoms (Prescott, 1962). In some instances green algae and chrysophytes also become important members of the community. Depending on the indicator used, abundance maxima are usually registered at the spring and fall circulation periods (Rodhe et al., 1958) and are dominated by diatoms or chrysophytes and diatoms (Hutchinson, 1967). The summer phytoplankton community is commonly dominated by blue-green algae. Among the factors responsible for the shifts in group and species are chemical (Hutchinson, 1944;1967; Lund, 1965) and biological (Shilo, 1971; Reynolds, 1976a; Keating, 1977) variations.

Within and between successional stages, the recognition of discrete groupings of species depends largely on the method of evaluation and purpose of the investigator. The community can be characterized either as the product of a continuous gradient of independent species requirements or as a series of distinct species groups which are identifiable in different communities and are distinct enough to warrant their classification (MacIntosh, 1967). One can reconcile the association and continuum concepts by allowing that species associations do have extensive intergradations (Becking, 1957). Depending upon which view of community organization one takes then, the stress of the analysis is either on similarity of communities or species, or distance between these units. An example of the latter approach in comparing communities of phytoplankton is the study of Levandowsky (1972a) who used an ordination procedure to compare pond phytoplankton along a salinity gradient. Among methods used to determine similarity of phytoplankton species are multivariate analysis (Allen and Koonce, 1975; Bartell, et al., 1978), comparison of net growth rates (Lewis, 1977a), or comparison of the shapes of species frequency-abundance curves (Lewis, 1977b).

For the purpose of this study, one must recognize species that may have strong competitive interactions. While similar species are expected to be more severe competitors than dissimilar species (Jaeger, 1974), similarity al-

one is not an indicator of potential competition, since selection will be strong to render them more different (Pianka, 1974). The indices mentioned are thus not suitable for this study since a means of assessing temporal cooccurrence is required.

One of the most widely used methods of detecting associated species is the Chi-squared analysis, which is based on presence and absence data. This measure compares the number of simultaneous presences and absences of each possible pair of species in a number of communities with the number of times each member of the pair is present without the other. Pairs of species will be found to be either unassociated or positively or negatively associated at a particular probability level. A review of different manipulations of the Chi-squared technique is presented in Kershaw (1973).

This purely qualitative technique of detecting species associations avoids some of the pitfalls associated with others. When one uses quantitative indices one must choose the best indicator of abundance, either standing stock, volume or biomass. Since the species are very divergent in size, the choice can markedly affect the result. Moreover, with such indices, two cooccurring species can yield either a positive or negative correlation coefficient, while they should indeed be associated (Hurlbert, 1969). With a large number of samples, the interrelationships become more complete (Kershaw, 1973) and with the use

of a computer a large number of species and samples can be analyzed. Thus a very thorough picture of community structure can be seen. The validity of the method also increases if the sample size is large in relation to the organisms (MacIntosh, 1967) which is certainly the case for phytoplankton.

The Chi-squared analysis also becomes more representative with greater numbers of different types of communities, as the associations of a particular species can be averaged over conditions in which the ecological pressures are different. This gives greater generality to conclusions made about the species and more predictive ability. The heterogeneity of communities can be achieved by sampling at different times or in a variety of habitat types. Since sampling in a large number of lakes is logistically difficult, this is simulated by various manipulations of communities from one lake, in enclosed water columns. The use of in situ enclosures has recently become popular in investigating the effects of some physico-chemical or biological parameters on phytoplankton communities (Lund, 1975; Parsons et al., 1978). Here it is used to provide a broad data base from which to evaluate species associations.

This chapter describes the seasonal succession of the dominant phytoplankton divisions and species in Heney Lake from June to November 1976, and examines the species associations found in the lake and in six polyethylene tubes sub-

jected to various manipulations (nutrient enrichment, crustacean zooplankton removal and isolation from- or connection with the bottom sediment).

2.1 MATERIALS AND METHODS

The sampling program was undertaken in a bay 10 m deep in Heney Lake from 23 June to 2 November, 1976. The lake is characterized by extremely low PO_4^{3-} and NO_3^- levels in midsummer and high hardness (see Briand et al., 1978). Seven water columns were sampled weekly throughout the season, that is, in the lake proper and in six polyethylene enclosures. The containers were each 1 m in diameter and 10 m in length. The polyethelene sheets were impermeable to gases and dissolved material.

Variations in species composition were generated by several treatments. Two tubes were connected freely with the sediment while the other four were sealed at the bottom. In two of the sealed containers adult crustaceans were removed weekly with a 135 µm zooplankton net of 0.75 m diameter passed through the enclosures once. The last sealed pair of enclosures was left unmanipulated. Finally, 3 enclosures, one from each treatment, were enriched weekly with NO_3^- and PO_4^{3-} to concentrations of 100 µg N/l and 10 µg P/l respectively while the others were left unfertilized.

Phytoplankton samples were taken with a 2 l Van Dorn bottle at depths of 0, 3, 6, and 9 m in each water column. The 2-liter sample was filtered in the field through a plankton bucket of mesh size 35 µm down to 100 ml. In each sample 5 ml aliquots were enumerated for phytoplankton density and species composition using the Utermohl (see Lund et

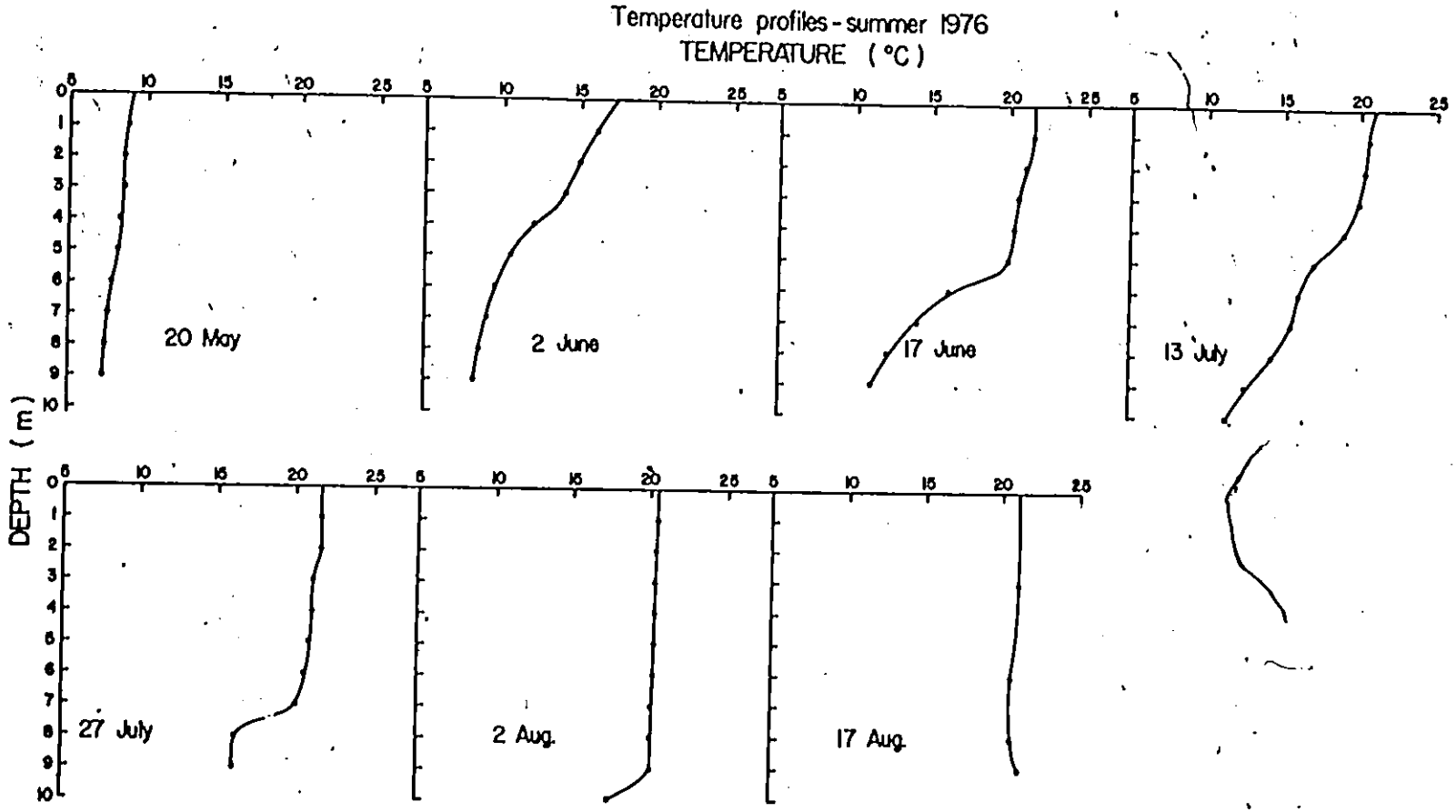
al., 1958) sedimentation technique. In all cases at least 100 individuals were counted at 320X magnification on a Zeiss inverted phase contrast microscope. This counting technique detects all species present at densities higher than 5000/l. Weekly temperature profiles were taken to determine the degree of thermal stratification present. Representative profiles are presented in Fig. 1.

For the successional analysis, changes in both species and group abundance, expressed as density or volume, were followed throughout the sampling season. First the four depth-samples for a particular date were averaged to provide an estimate of each population density (standing stock) in the lake. The volume of each species was either calculated from direct measurements using the formulae of Kovala and Larrance (1966) or taken from the published record, when available (Wetzel, 1975).

For the Chi-squared association analysis, data taken from each of the four depths were combined into a water column sample for each date and enclosure. The abundance data were then converted to binary presence-absence data. While 52 species were recorded throughout the season, only those species present in at least 25% of the water columns were included in the analysis. A Chi-squared value was computed for each pair of species using a FORTRAN Crosstabs program using the raw frequencies. The sign of the association was determined by the association coefficient $\sqrt{\frac{\chi^2}{n}}$ as suggested by Williams and Lambert (1960).

Figure 1: Temperature profile and thermal stratification in Heney Lake, Quebec.

Selected temperature profiles indicating the onset (23 June and deterioration (27 July) of thermal stratification in Heney Lake, Quebec in 1976.


Temperature profiles - summer 1976
TEMPERATURE (°C)
DEPTH (m)
20 May
2 June
17 June
13 July
27 July
2 Aug.
17 Aug.

2.2 RESULTS

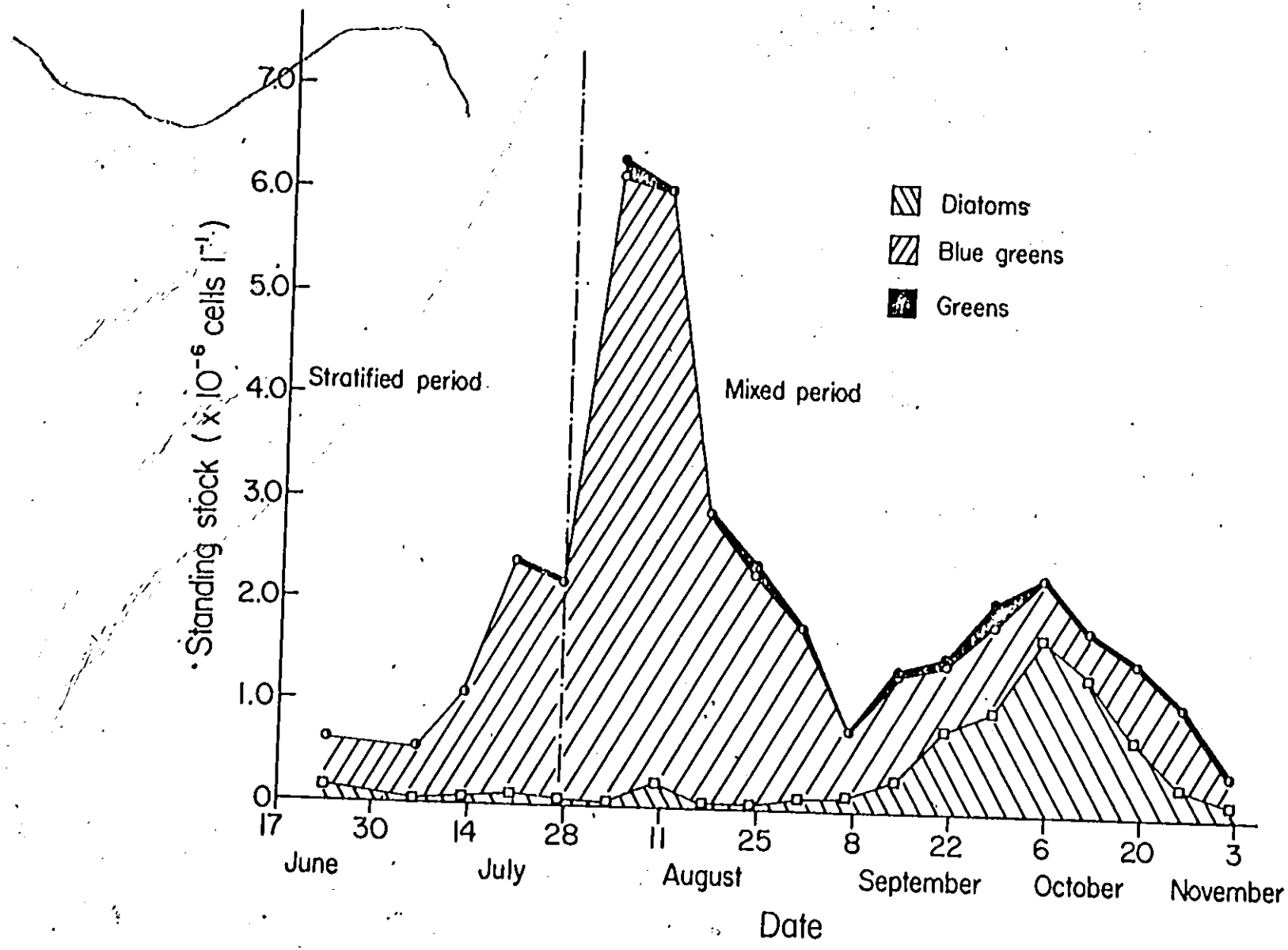
2.2.1 Seasonal succession

The succession in the lake will be described first at the level of the taxonomic division and then at the species level. Patterns in abundance of standing stock and cell volume are illustrated in Figures 2 and 3. The abundances represent the average of the four depths sampled on each date. There are six groups present: blue-greens, diatoms, greens, chrysophytes, cryptophytes and dinoflagellates. Of these, only the blue-greens and diatoms are dominant members of the community in the sampling period, both in standing stock and volume. As seen in Fig. 2, the total standing stock of the community rises from less than 1,000,000 cells/l in late June to a maximum of 6.25 million cells/l on 3 August. This pulse is attributable mainly to an increase in blue-greens, particularly Aphanizomenon and Anabaena spp. Following this maximum, algal numbers decline rapidly until 7 September. An increase in diatom abundance, due mostly to Asterionella formosa, then raises the density levels to approximately 2.5 million cells/l on 5 October. During this period of growth in the population levels, green algae also become dominant members of the community. After 5 October, the community standing stock gradually subsides until the end of the sampling period.

The total cell volume of the community (Fig. 3) registers variations of less amplitude, but greater frequency

Figure 2: Weekly variations in phytoplankton standing stock.

Weekly variations in phytoplankton standing stock of the major taxonomic groups in the lake during the period studied. Abundances are the average taken from the four depths sampled on each date.


Standing stock (x 10⁻⁶ cells l⁻¹)
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
Stratified period
Mixed period
Diatoms
Blue greens
Greens
17
30
14
28
11
25
8
22
6
20
3
June
July
August
September
October
November
Date

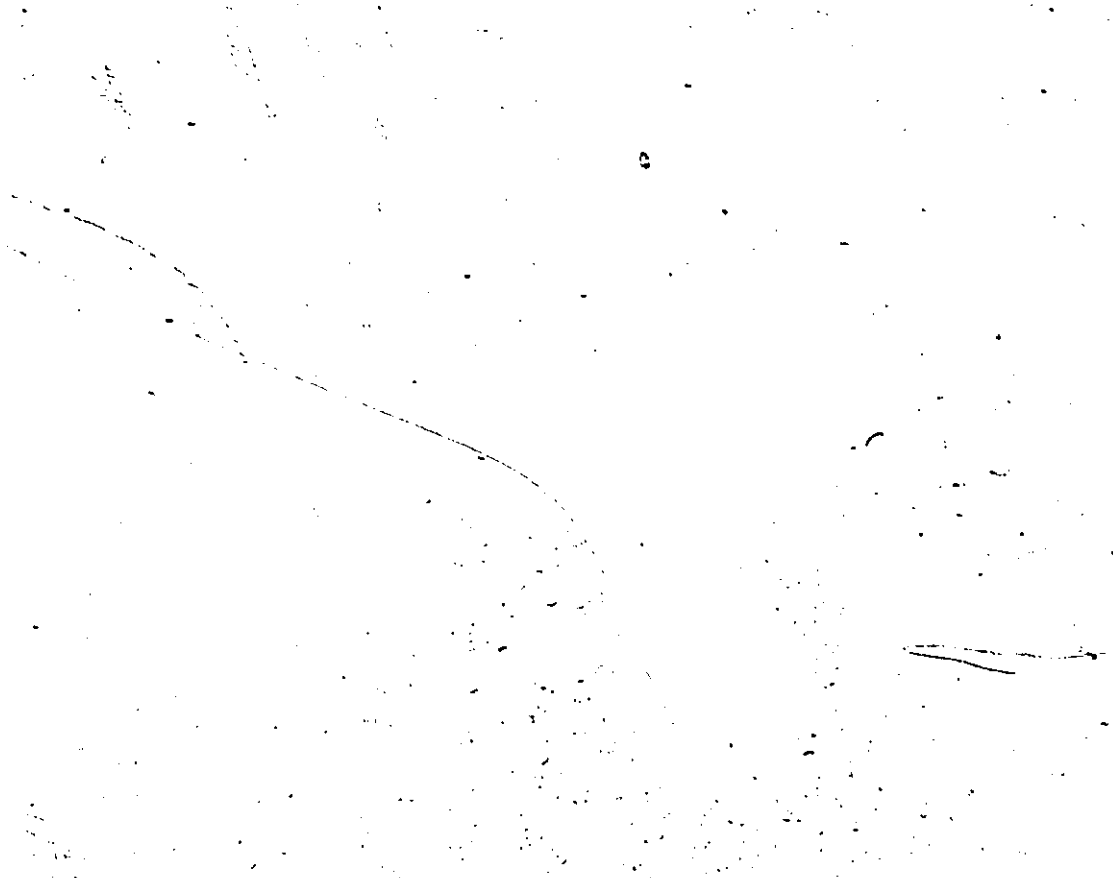
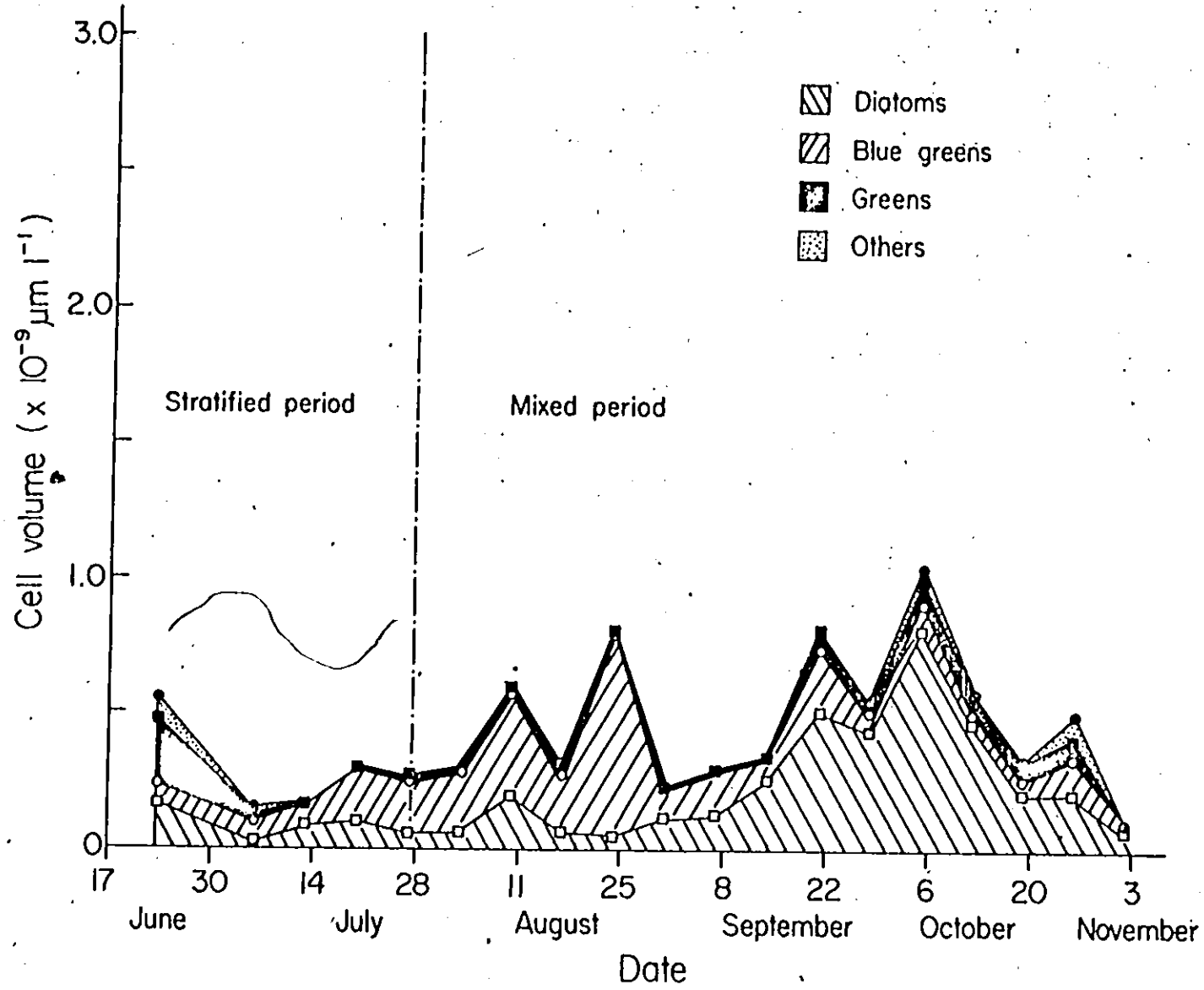


Figure 3: Weekly variations in phytoplankton volume.

Weekly variations in lake phytoplankton volume during the period studied.


3.0
2.0
1.0
0
Cell volume (x 10^{-9} µm l^{-1})
Stratified period
Mixed period
Diatoms
Blue greens
Greens
Others
17
30
14
28
11
25
8
22
6
20
3
June
July
August
September
October
November
Date

than those observed in standing stock. While a nearly ten-fold range exists in cell numbers, only a four-fold difference applies to cell volume. Peaks in cell volume, such as those on 23 June, 24 August, 21 September and 26 October, often do not correspond to pulses in standing stock.

Figures 4,5 and 6 show the changes in percent contribution of each group to the total standing stock and cell volume throughout the season. While the two indices of abundance do not closely parallel each other, some general trends are similar.

2.2.1.1 Blue-greens

This group dominated the phytoplankton from 2 July to 31 August. Peak levels were registered on 3 August in terms of relative abundance (96.6%) and on 24 August in terms of relative volume (92.6%). A steep decline in both indices was observed from this date forward until 5 October when blue-greens constituted only 25.9% and 8.2% of standing stock and algal volume, respectively. Finally, this group increased its relative abundance until 26 October when they contributed 69.4% to the standing stock and 24.7% to the cell volume.

Figure 4: Blue-green algal contribution to phytoplankton abundance.

Weekly variations in relative contribution of blue-green algae to total phytoplankton abundance (●——● standing stock O- - - - - - O cell volume).

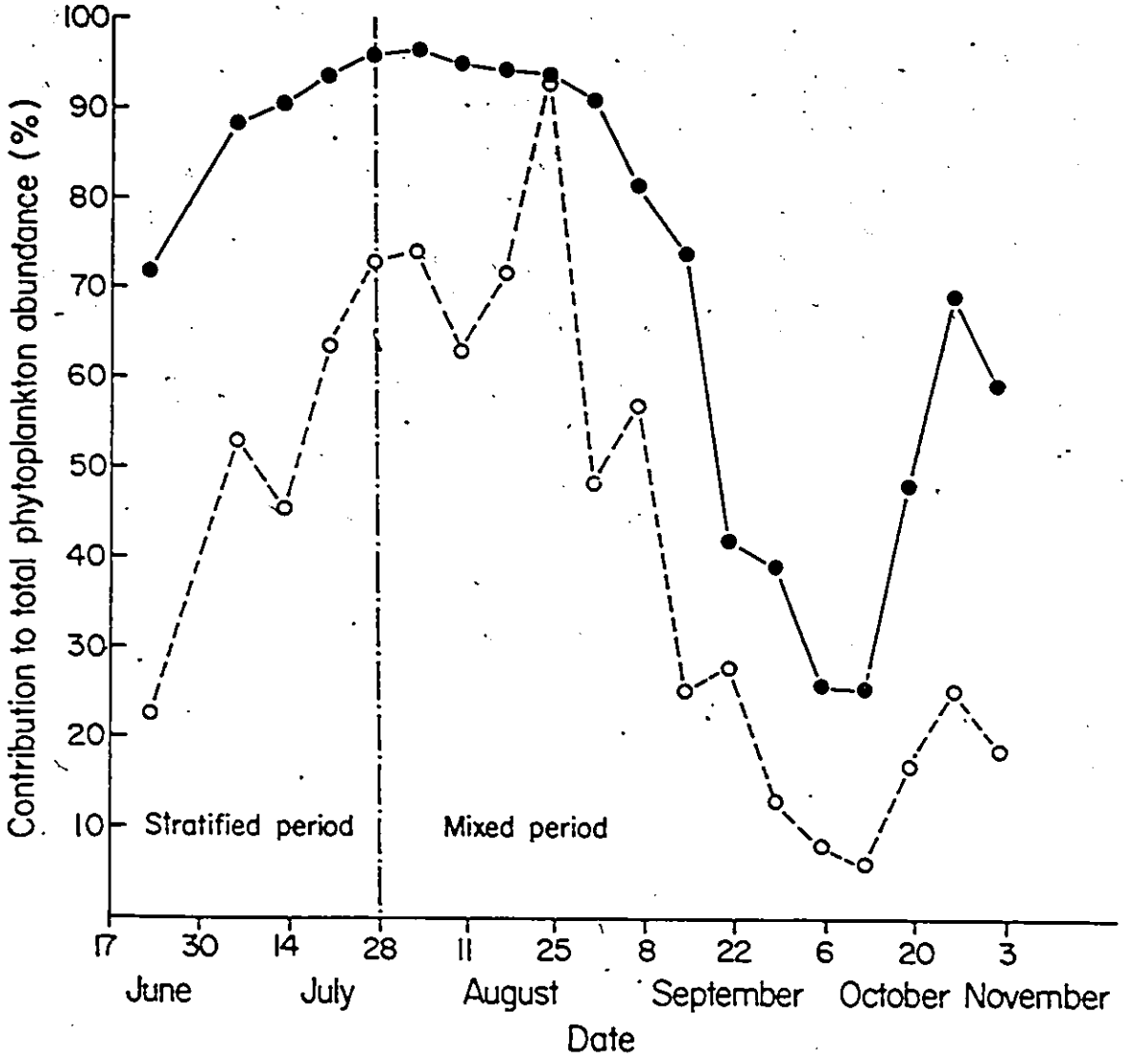

Contribution to total phytoplankton abundance (%)
100
90
80
70
60
50
40
30
20
10
Stratified period
Mixed period
17
30
14
28
11
25
8
22
6
20
3
June
July
August
September
October
November
Date

Figure 5: Diatom contribution to phytoplankton abundance.

Weekly variations in relative contribution of diatoms to total phytoplankton abundance. (Symbols as in Fig. 4).

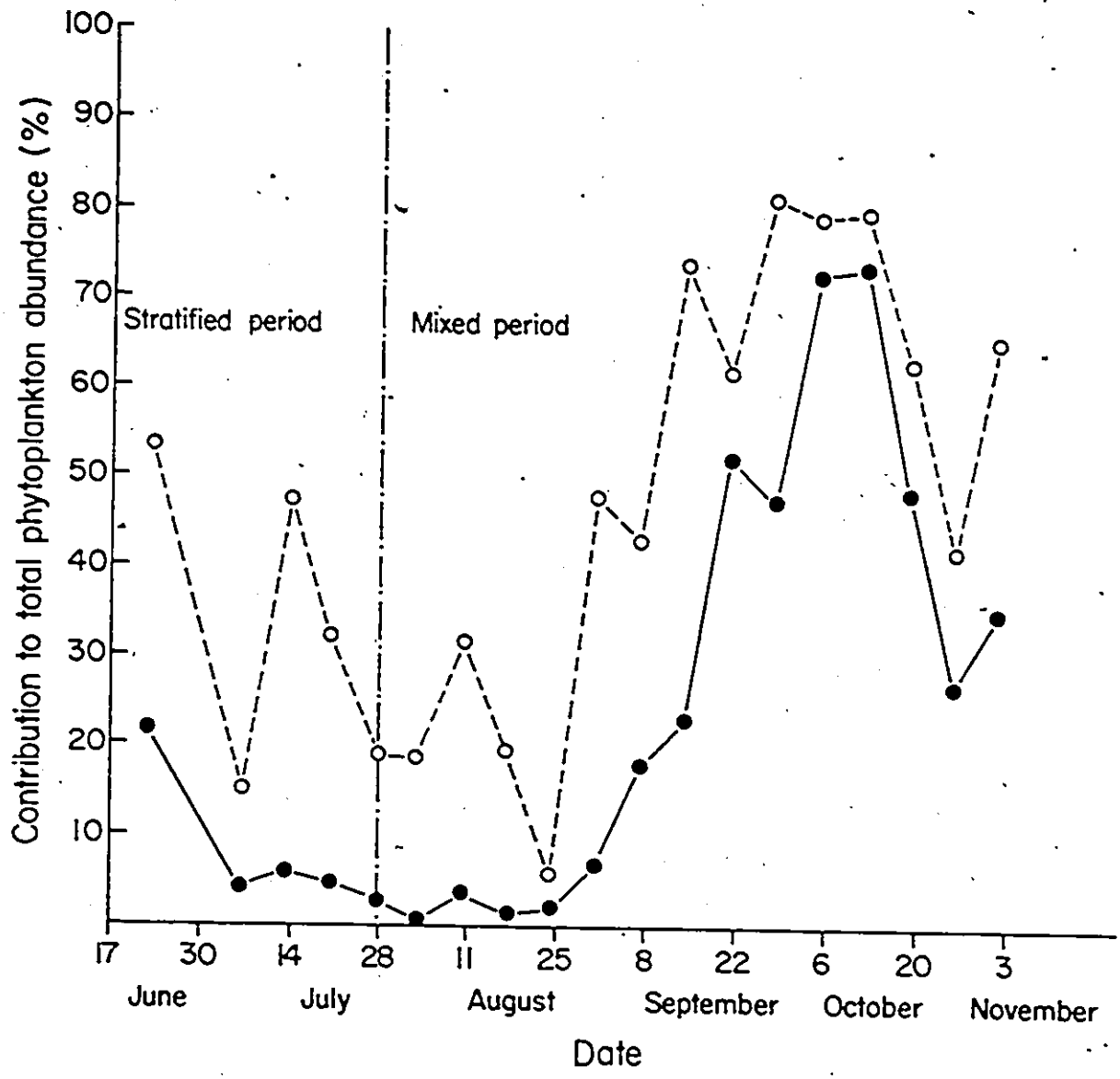
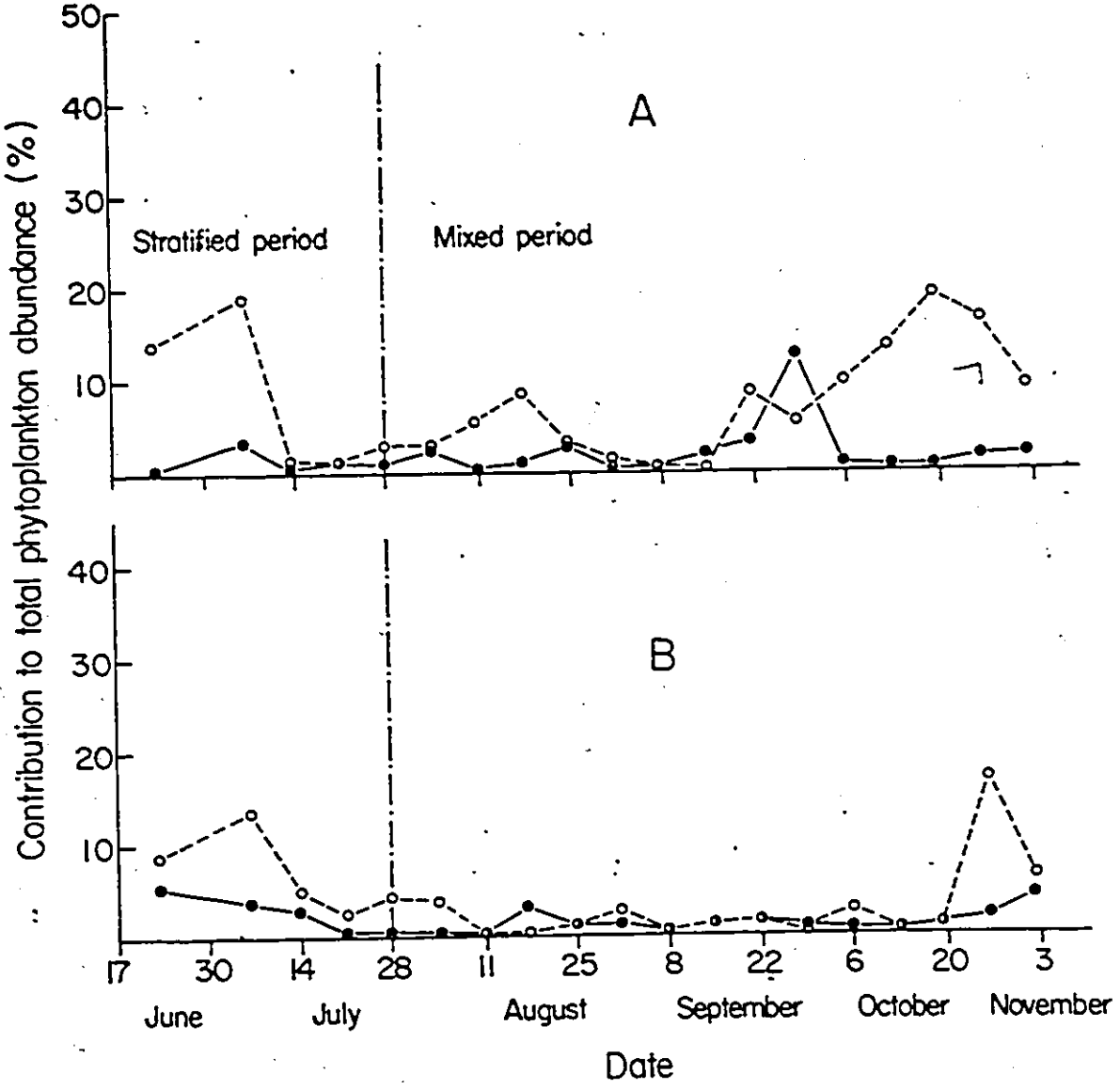

Contribution to total phytoplankton abundance (%)
100
90
80
70
60
50
40
30
20
10
Stratified period
Mixed period
17
30
14
28
11
25
8
22
6
20
3
June
July
August
September
October
November
Date

Figure 6: Contribution of Green algae and other groups to phytoplankton abundance.

a) Weekly variations in relative contribution of green algae to total phytoplankton abundance.

b) Weekly variations in relative contribution of other groups to total phytoplankton abundance. (Symbols as in Fig. 4).


Contribution to total phytoplankton abundance (%)
50
40
30
20
10
A
Stratified period
Mixed period
40
30
20
10
B
17
30
14
28
11
25
8
22
6
20
3
June
July
August
September
October
November
Date

2.2.1.2 Diatoms

The diatom levels (see Fig. 5) show a greater variability than those of blue-greens. They tend to dominate later in the year. Since diatom cell volumes are often higher than those of blue-greens, their contribution to the community is larger when using this parameter. The contribution of diatoms to standing stock fluctuates from 1.3% on 17 August to 73.6% on 12 October, while the relative volume varies from 6.0% on 24 August to 80.0% on 12 October.

2.2.1.3 Greens

While green algae (Fig. 6a) are never as large a component of the phytoplankton as the preceeding groups, there are periods when they constitute nearly 20% of the total cell volume and over 10% of the cell numbers. The peaks in cell volume occurred on 6 July (18.5%) and 19 October (19.2%). The standing stock maximum was recorded on 26 September when they reached 12.3%. At all other times greens contributed less than 4% to the standing stock of phytoplankton.

2.2.1.4 Others

The chrysophytes, cryptophytes and dinoflagellates, taken collectively, are similar to the greens in their abundance patterns, exhibiting peaks at the beginning and end of the sampling season (Fig. 6b). Again their abundance is

higher when cell volume is taken as the indicator. Their proportion of total cell volume peaks at 13.5% on 6 July and 16.8% on 26 October. The highest percentage of total standing stock was achieved at the beginning of the sampling period (5.7%), and remained below 4% for the duration of the season.

2.2.2 Species succession patterns

Seasonal changes in the densities of the major phytoplankton species are given in Fig. 7,8 and 9 (blue-greens), 10 and 11 (diatoms), 12 and 13 (greens), and 14 (others). Most of the blue-greens showed maxima in July and August. The order of species population peaks is approximately Anabaena spiroides, Anabaena sp., Aphanizomenon flos-aquae, Phormidium sp. and Microcystis aeruginosa. Other species, however, such as Anabaena flos-aquae, Dactylococcopsis acicularis, and Oscillatoria limnetica, had less obvious seasonal preference, fluctuating erratically throughout the sampling period.

Among the diatom species, Tabellaria fenestrata, Fragilaria capucina, Asterionella formosa, Fragilaria crotonensis and Melosira granulata succeed each other during the fall pulse. Only a few diatom species, such as Rhizosolenia longiseta, Cyclotella sp. and Synedra delicatissima, registered their greatest abundance earlier in the year.

Figure 7: Changes in density of blue-green algal species (i).

Weekly variations in the density of the major blue-green algal species, Aphanizomenon flos-aquae.

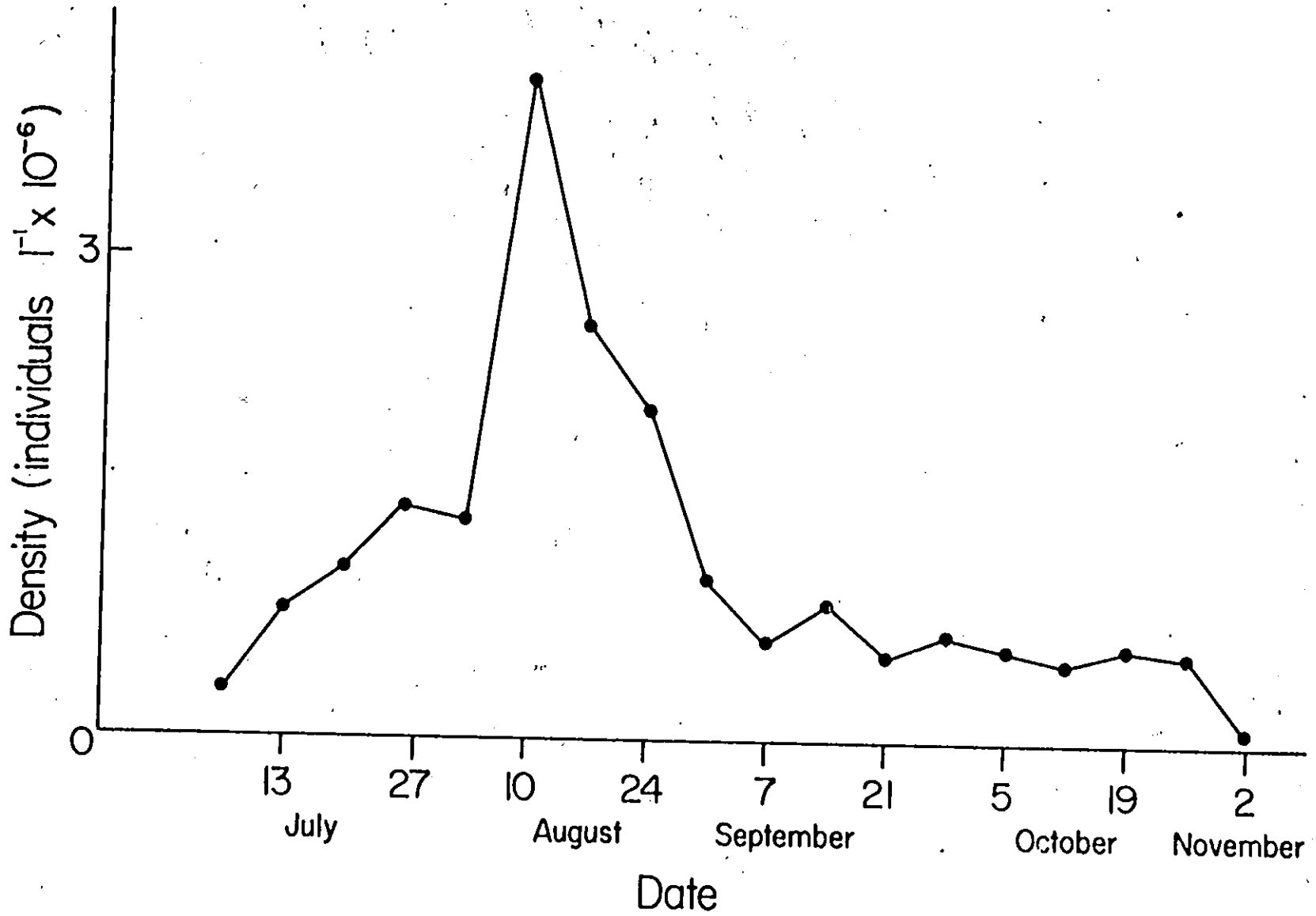
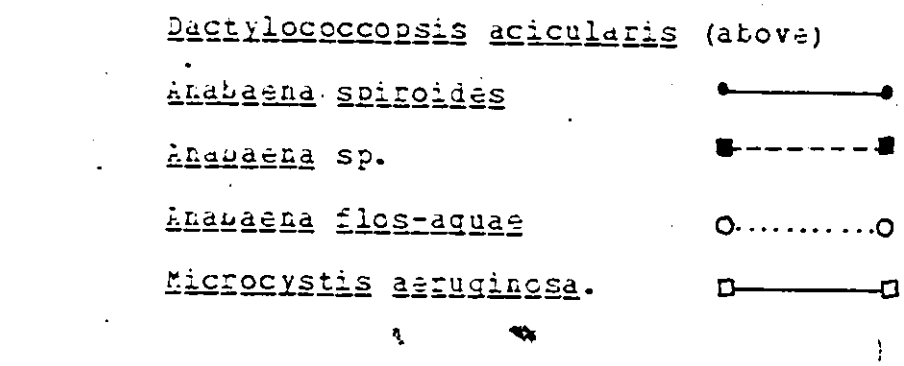

Density (individuals l^{-1} x 10^{-6})
3
0
13
27
10
24
7
21
5
19
2
July
August
September
October
November
Date

Figure 8: Changes in density of blue-green algal species (ii).

Weekly variations in the density of the major blue-green algal species.



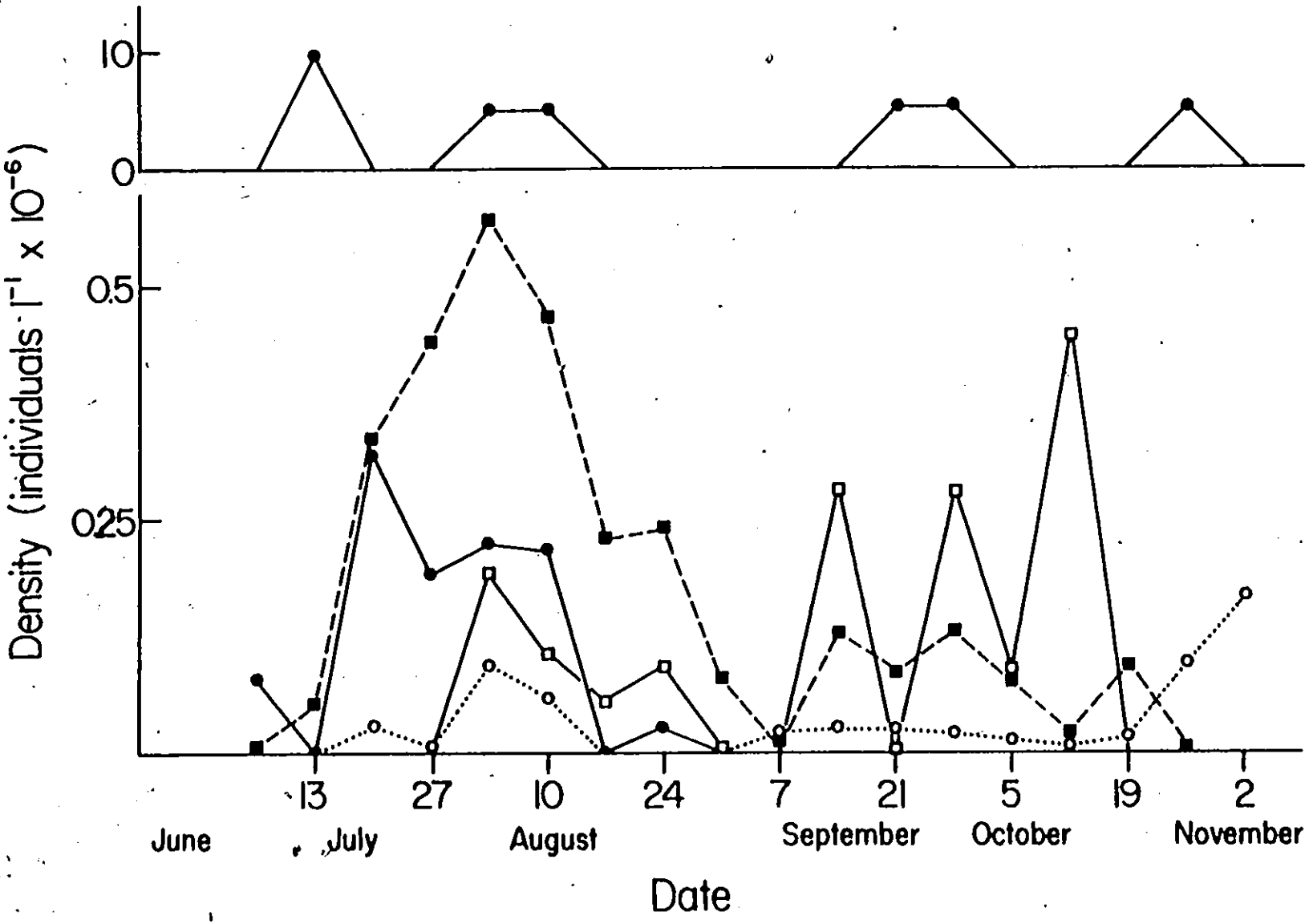
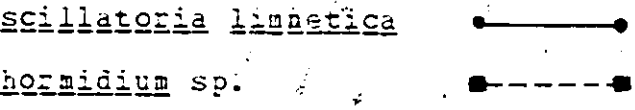

10
0
0.5
0.25
Density (individuals·l⁻¹ x 10⁻⁶)
13
27
10
24
7
21
5
19
2
June
July
August
September
October
November
Date

Figure 9: Changes in density of blue-green algal species (iii).

Weekly variations in the density of the major blue-green algal species.



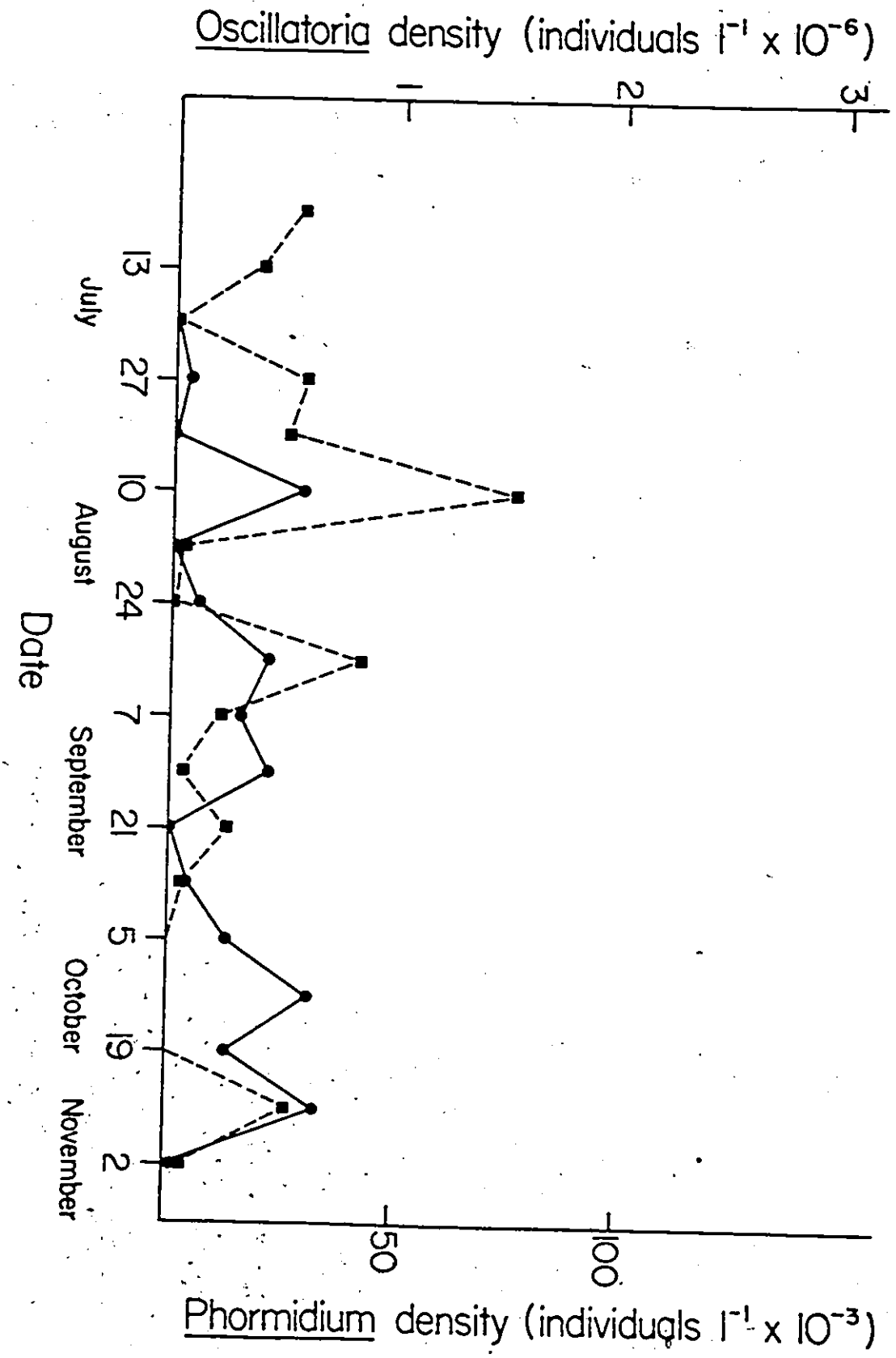
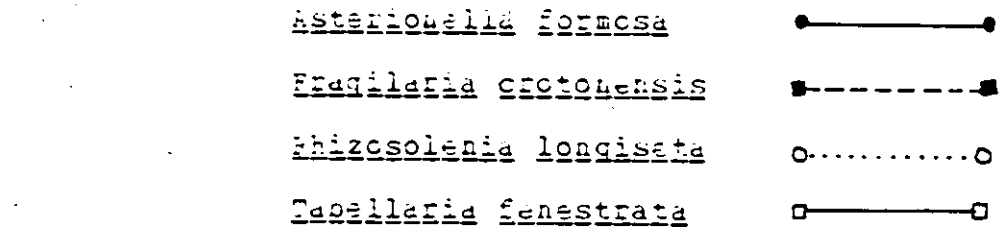

Oscillatoria density (individuals l⁻¹ x 10⁻⁶)
1
2
3
Date
July
13
27
August
10
24
September
7
21
October
5
19
November
2
50
100
Phormidium density (individuals l⁻¹ x 10⁻³)

Figure 10: Changes in density of diatom species (1).

Weekly variations in the density of the major diatom species.



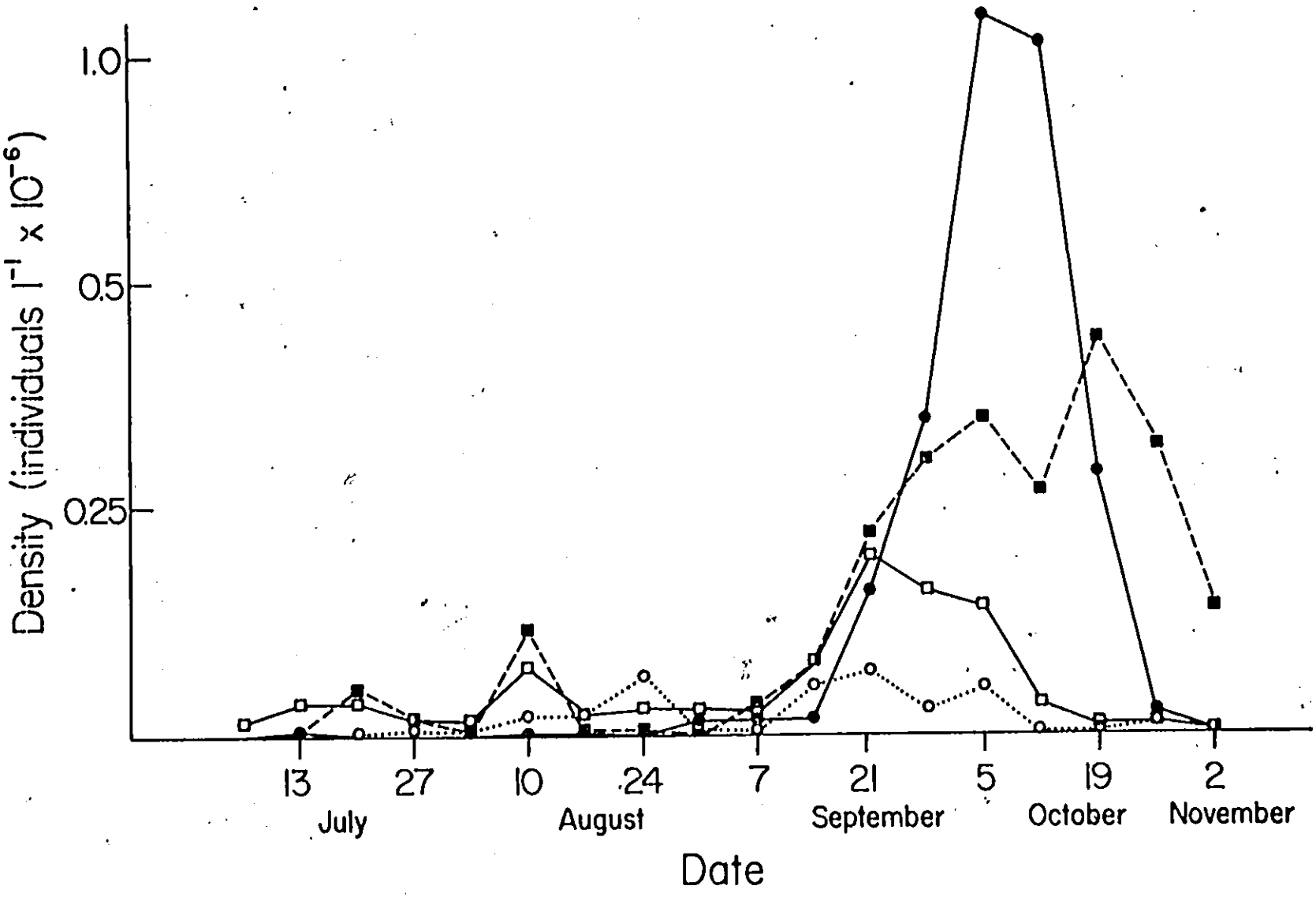
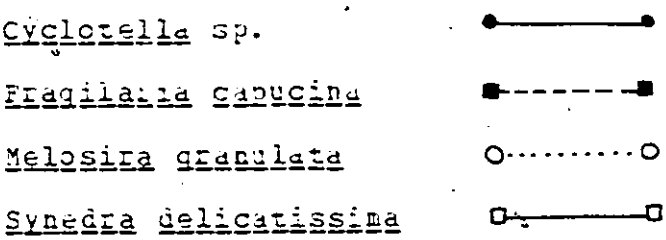

1.0
0.5
0.25
Density (individuals l⁻¹ x 10⁻⁶)
13
27
10
24
7
21
5
19
2
July
August
September
October
November
Date

Figure 11: Changes in density of diatom species (ii).

Weekly variations in the density of the major diatom species.



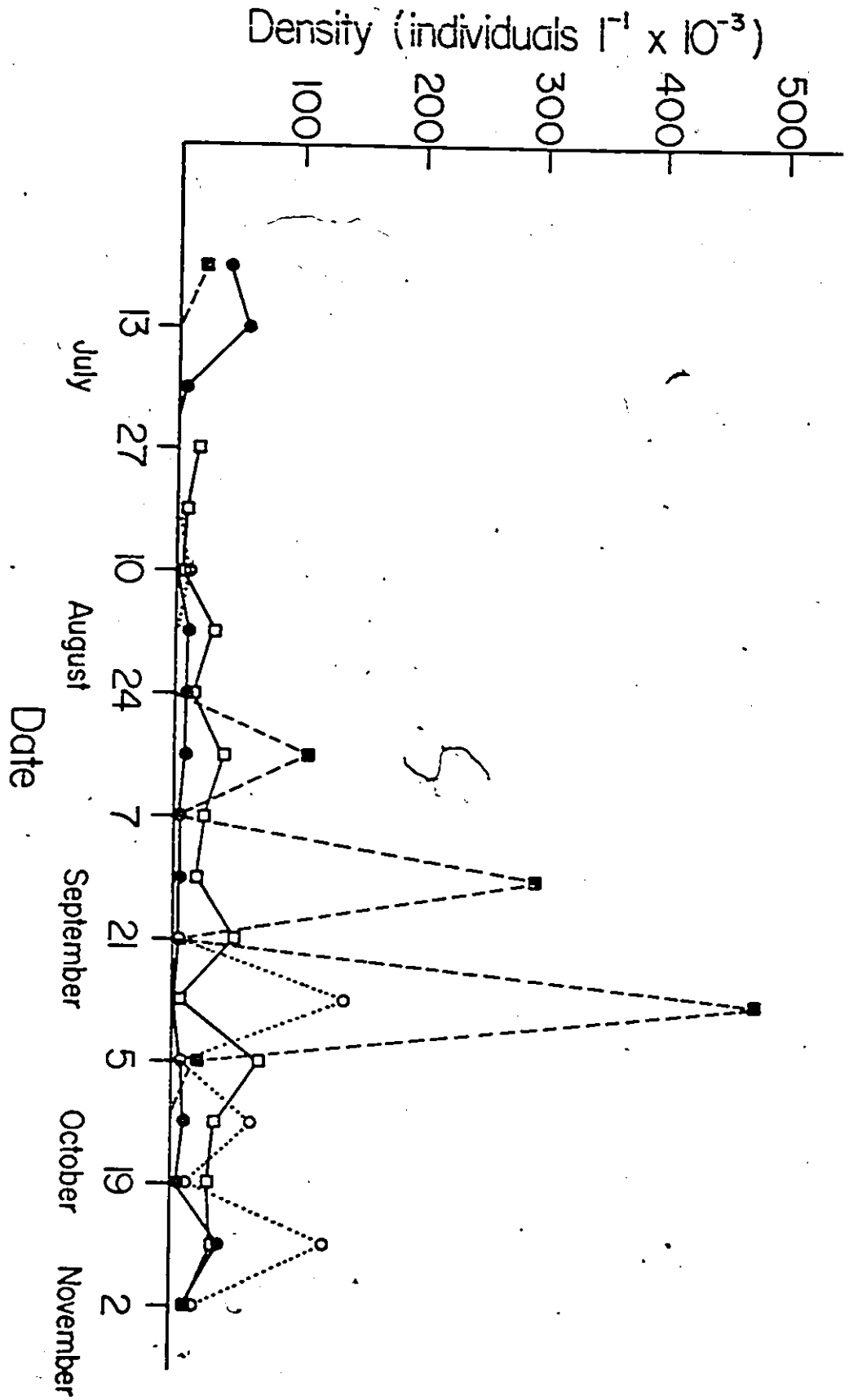
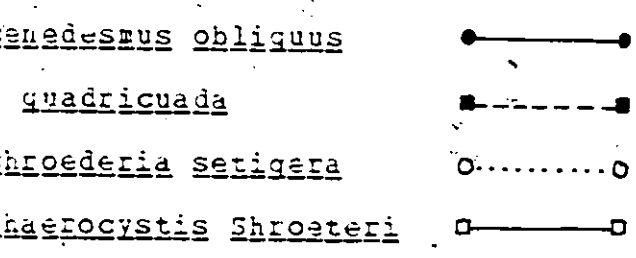

Density (individuals l⁻¹ x 10⁻³)
100
200
300
400
500
Date
July
13
27
August
10
24
September
7
21
October
5
19
November
2

Figure 12: Changes in density of green algal species (i).

Weekly variations in the density of the major green algal species.



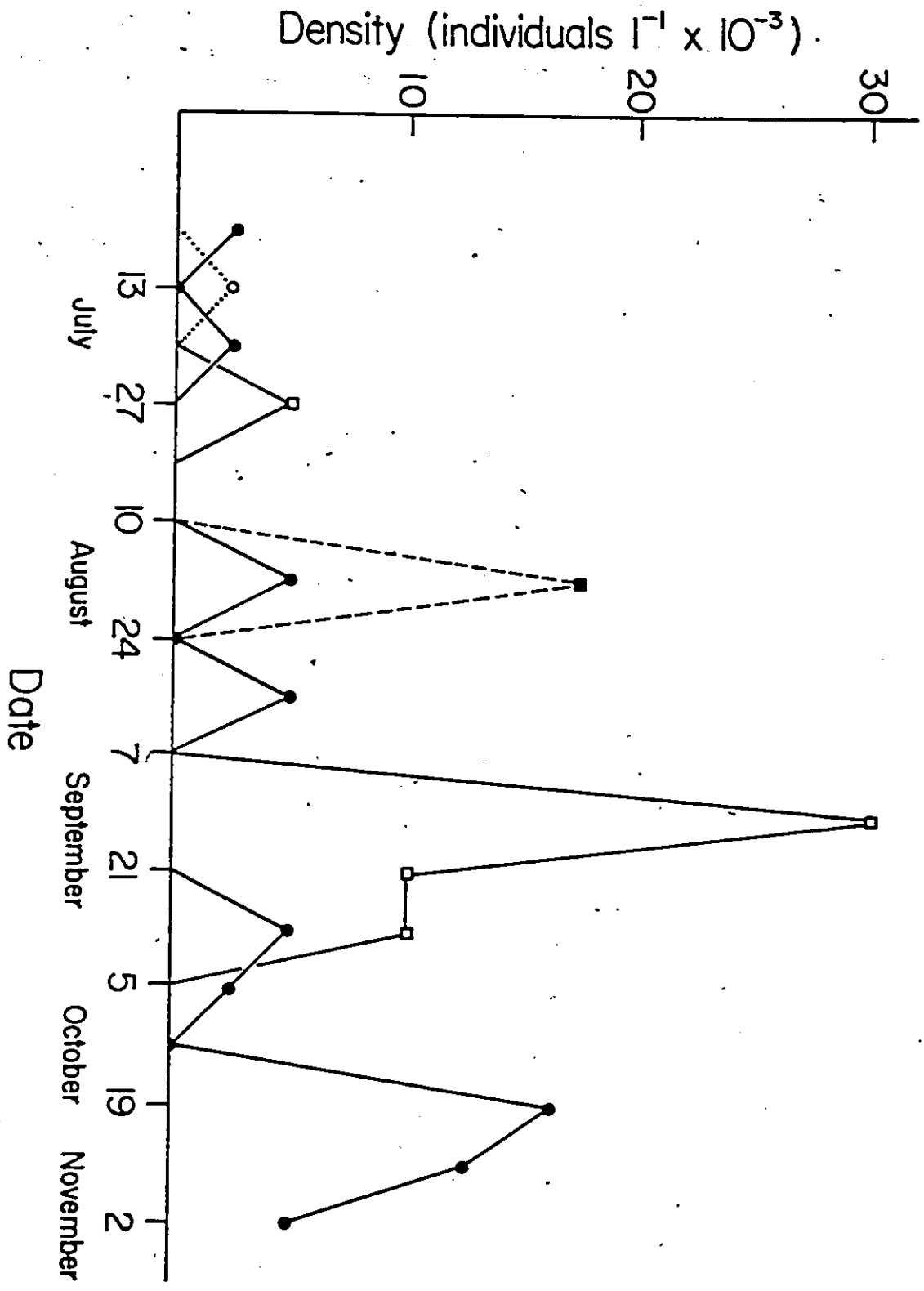
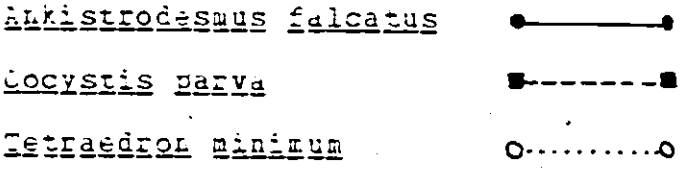

Density (individuals l⁻¹ x 10⁻³)
10
20
30
Date
July
13
27
August
10
24
September
7
21
October
5
19
November
2

Figure 13: Changes in density of green algal species (ii).

Weekly variations in the density of the major green algal species.



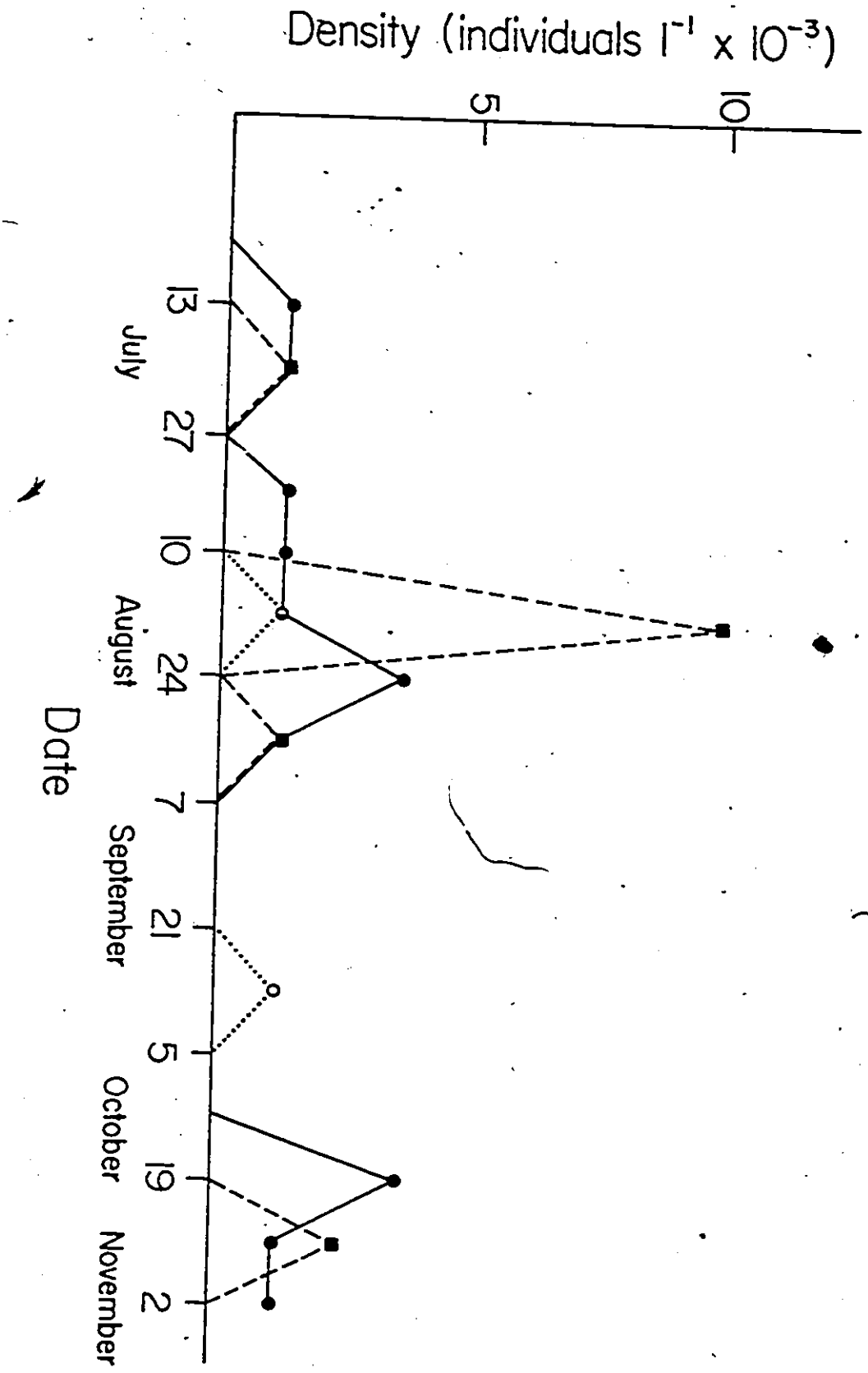
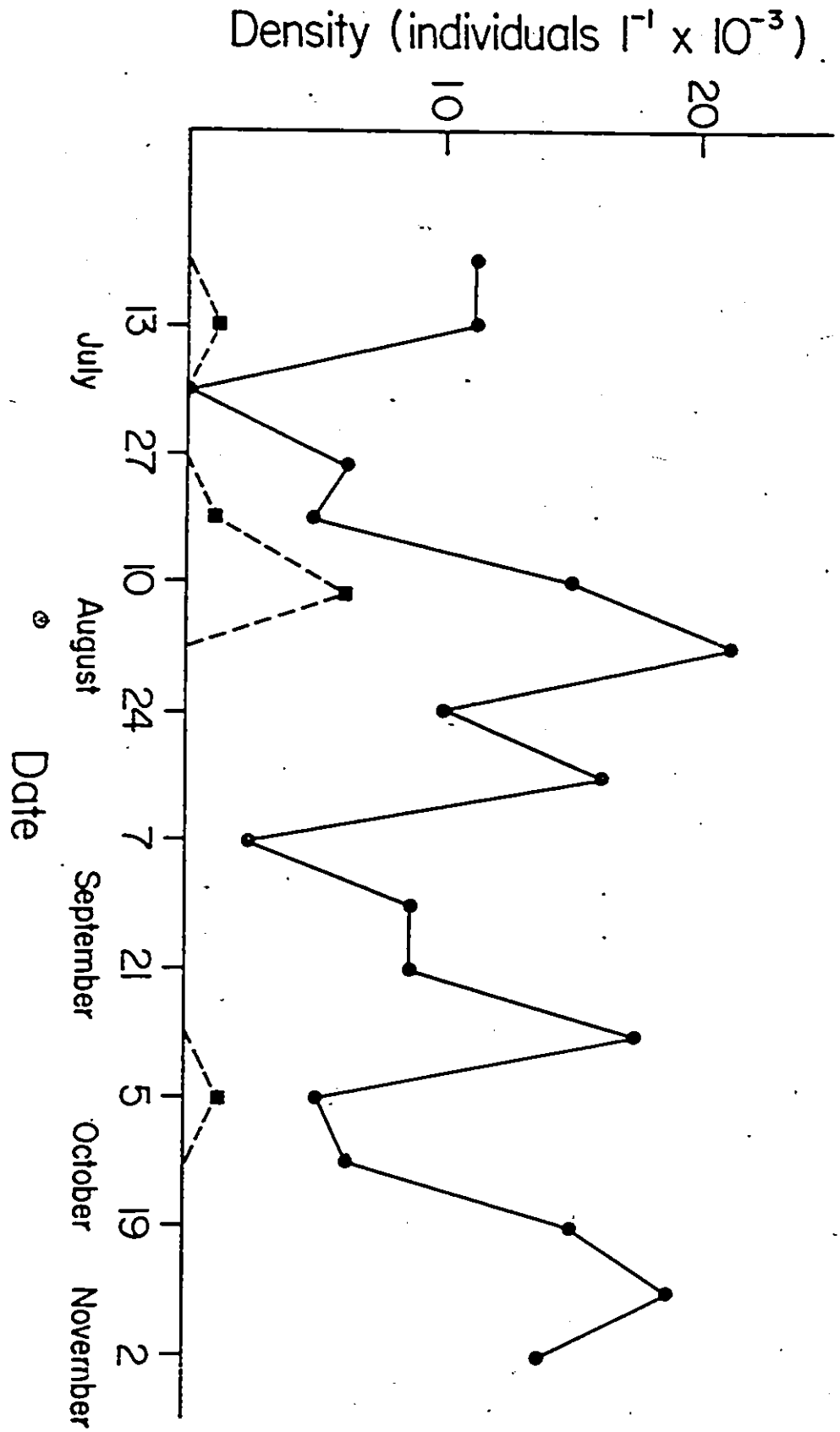

Density (individuals l⁻¹ x 10⁻³)
5
10
Date
July
13
27
August
10
24
September
7
21
October
5
19
November
2

Figure 14: Changes in density of the major flagellates.

Weekly variations in the density of the other major flagellates.

Chlorochromonas minuta ●——●

Cryptomonas erosa ■- - - -■


Density (individuals l⁻¹ x 10⁻³)
10
20
13
27
10
24
7
21
5
19
2
July
August
September
October
November
Date

The green algae were much more sporadic in their population levels than the above groups and no species ever exceeded densities of 40,000 cells/l. Most species showed summer population maxima except for Sphaerocystis Schroeteri (September) and Scenedesmus obliquus (October).

The two major species belonging to other divisions, Chlorochromonas minuta and Cryptomonas erosa, registered peaks in August and otherwise showed irregular fluctuations throughout the sampling period.

2.2.3 Species richness

Species richness, that is, the number of species recorded in counts, varied from a maximum of 28 species on 10 August to a minimum of 15 on 7 September (see Table 1). In terms of averages it was slightly higher in the "mixed" period than in the preceeding stratified period (s=22.1 compared with 19.2). In addition, the three major divisions all had slightly higher numbers of species present in the mixed period. Diatoms (s=7.4) and blue-greens (s=6.1) contribute the most to total species richness. Both reached a peak of 9 and 10 species respectively on 10 August. Both groups had a minimum of four species which the blue-green algae reached on 20 July and 19 October and the diatoms on 6 July. The number of green algal species varied from 1 on 7-14 September to 8 on 19 October.

TABLE 1

Total and group species richness in Heney Lake, 1976.

Species richness represents the cumulative number of species found in counts at the four depths sampled in the lake.

Date	Algal Group			
	Blue-greens	Diatoms	Greens	Total
Stratified Period				
23 June	6	9	0	19
6 July	6	4	3	18
13 July	5	6	2	19
20 July	4	7	5	19
27 July	7	6	3	21
Mixed Period				
3 August	7	6	6	24
10 August	10	9	5	28
17 August	6	6	5	23
24 August	7	6	5	21
31 August	7	8	4	22
7 September	5	7	2	15
14 September	7	8	3	19
21 September	6	8	3	22
28 September	7	8	3	23
5 October	5	7	3	19
12 October	6	8	3	20
19 October	4	9	5	26
26 October	6	9	5	27
2 November	5	9	3	20
Mean	6.1	7.4	3.7	21.3
Mean-Stratified Period	5.6	6.4	2.6	19.2
Mean-Mixed Period	6.3	7.7	4.1	22.1

2.2.4 Enclosure treatments

A total of 99 species were recorded throughout the year in the lake and in the enclosures. Among these 26 were counted in at least 25% of the water columns. The major species are listed in Table 2 along with their frequencies. The blue-greens, diatoms and green algae were each represented by eight species while chrysophytes and cryptophytes had one species each. In the lake proper, blue-greens and diatoms generally had higher frequencies than in the enclosures. Most notable were Aphanizomenon and Tabellaria which were recorded in the lake throughout the entire season. Eleven of the species had higher frequencies in the enclosures than in the lake. This applied particularly to six of the eight green algae that were enhanced by the enclosure treatments.

2.2.5 Species associations

The association matrix of the 26 species is shown in Fig. 15. Among the 325 pairs analyzed, 59 significant associations were found, over three times the number (17) that would be expected due to chance alone. Forty-two of the associations were positive, of which 18 were at the 0.1% significance level, six at the 0.5% level, two at the 1% level and 16 at the 5% level. Of the 17 negative associations three each were at the 0.1% and 0.5% significance levels,

TABLE 2

Phytoplankton frequencies in lake and enclosures.

Frequencies (expressed as percent) of the 26 major phytoplankton species in the lake and enclosures.

Species	Frequency in lake	Frequency in enclosures	Overall Frequency
BLUE-GREEN ALGAE			
Anabaena flos-aquae	73.7%	73.0%	73.1 %
A. spiroides	42.1	23.7	26.5
Anabaena sp.	84.2	85.1	85.0
Aphanizomenon flos-aquae	100.0	97.1	97.5
Dactylococcopsis acicularis	26.3	28.2	27.9
Microcystis aeruginosa	63.2	33.4	37.9
Oscillatoria limnetica	79.0	81.5	81.1
Phormidium sp.	63.2	79.7	77.2
Diatoms			
Asterionella formosa	63.4	50.0	52.8
Cyclotella sp.	79.0	41.5	47.2
Fragilaria capucina	26.3	27.1	27.0
F. crotonensis	94.7	82.7	84.5
Melosira granulata	42.1	36.4	37.3
Rhizosolenia longiseta	84.2	42.7	49.0
Synedra delicatissima	79.0	77.7	77.9
Tabellaria fenestrata	100.0	77.6	81.0

Table 2 (cont'd)

Species	Frequency in lake	Frequency in enclosures	Overall Frequency
Green Algae			
Ankistrodesmus falcatus	42.1	37.4	38.1
Chlamydamonas sp.	63.2	43.0	46.1
Cocystis parva	26.3	39.5	37.5
Scenedesmus obliquus	42.1	60.5	57.7
S. quadricauda	5.3	29.7	26.0
Schroederia setigera	10.5	28.7	25.9
Sphaerocystis Shroeteri	21.1	34.3	32.3
Tetraedron minimum	10.5	30.4	27.4
OTHERS			
Chlorochromonas minuta	89.5	55.4	60.6
Cryptomonas erosa	63.2	26.1	31.7

Figure 15: Chi-squared species association matrix.

Chi-squared association matrix showing the positive (+) and negative (-) associations among the 26 most common phytoplankton species. Levels of significance are indicated as follows:

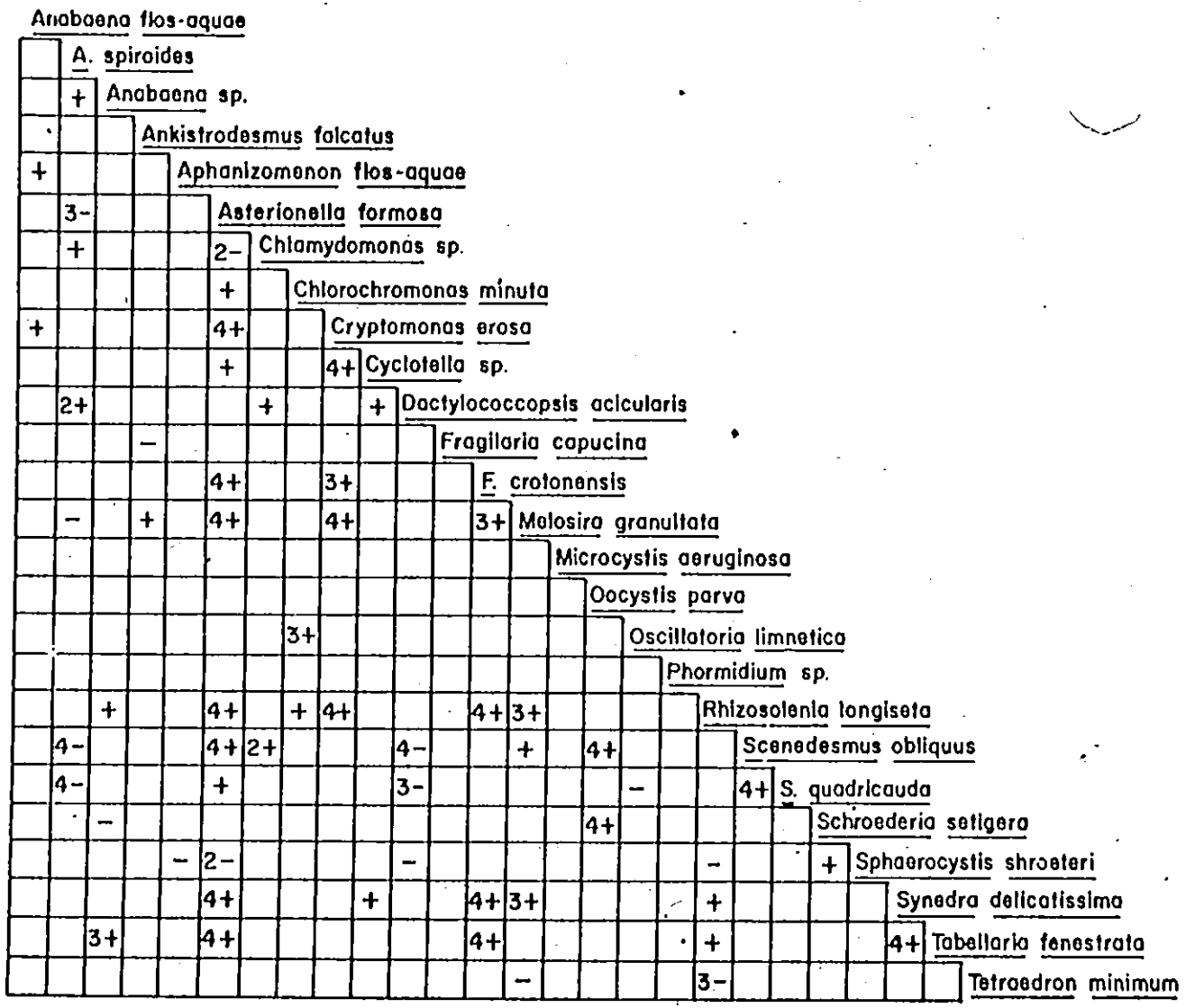
4+ or 4- for $P < 0.001$

3+ or 3- for $P < 0.005$

2+ or 2- for $P < 0.01$

\+ or - for $P < 0.05$

Vacant squares indicate no association.


Anabaena flos-aquae
A. spiroides
Anabaena sp.
Ankistrodesmus falcatus
Aphanizomenon flos-aquae
Asterionella formosa
Chlamydomonas sp.
Chlorochromonas minuta
Cryptomonas erosa
Cyclotella sp.
Dactylococcopsis acicularis
Fragilaria capucina
F. crotonensis
Melosira granulata
Microcystis aeruginosa
Oocystis parva
Oscillatoria limnetica
Phormidium sp.
Rhizosolenia longiseta
Scenedesmus obliquus
S. quadricauda
Schroederia setigera
Sphaerocystis shroeteri
Synedra delicatissima
Tabellaria fenestrata
Tetraedron minimum

two at the 1% level and nine at the 5% level. In general, diatoms were part of more associations than the other groups. As shown in Table 3, diatoms averaged 5.8 associations/species while blue-greens and greens averaged 1.8 and 2 respectively. Asterionella, Rhizosolenia and Melosira were associated with more species than any others. Two species, Anabaena spiroides and Aphanocystis Shroeteri each had four negative associations.

Species tend to be associated more often with members of their own taxonomic division than with members of other divisions. Conversely, all 17 negative associations involved two species from different divisions. This trend is reflected in Table 4 where 29.8% of all possible pairs involving members of the same division are positively associated while only 6% of the interdivisional pairs are associated. Again diatoms exhibited this trend more markedly, with 60.7% of all diatom pairs positively associated. This is much greater than blue-greens and greens which were associated with only 10.7% and 17.9% of their members, respectively.

TABLE 3

Number of association for each species.

Number of positive and negative Chi-squared associations for each species.

Species	Positive	Negative
Asterionella formosa	10	3
Rhizosolenia longiseta	8	2
Melosira granulata	7	2
Synedra delicatissima	6	0
Cryptomonas erosa	6	1
Fragilaria crotonensis	6	0
Scenedesmus obliquus	5	2
Cyclotella sp.	5	1
Tabellaria fenestrata	5	0
Anabaena spiroides	3	4
Anabaena sp.	3	1
Chlamydamonas sp.	3	1
Chlorochromonas minuta	3	0
Dactylococcopsis acicularis	3	3
Anabaena flos-aquae	2	0
Oocystis parva	2	0
Scenedesmus quadricauda	2	3
Schroederia setigera	2	1
Ankistrodesmus falcatus	1	1
Oscillatoria limnetica	1	2
Sphaerocystis Shroeteri	1	4
Fragilaria capucina	0	1
Microcystis aeruginosa	0	0
Phormidium sp.	0	0
Tetraedron minimum	0	2
Diatom Average	5.8	1.1
Blue-green Average	1.8	1.4
Green Average	2.0	1.8
Overall Average	3.3	1.3

TABLE 4

Intra- and interdivisional associations.

Comparisons of the number of Chi-squared associations between members of the same division and members of different divisions.

	Within Divisions	Between Divisions
Total Number of Pairs	84	241
Positive Associations	25	17
Percentage of Pairs Positively Associated	29.8	7.1
Percentage of Blue-greens Positively Associated	10.7	
Percentage of Diatoms Positively Associated	60.7	
Percentage of Greens Positively Associated	17.9	
Negative Associations	0	17
Percentage of Pairs Negatively Associated	0	7.1

2.3 DISCUSSION

2.3.1 Seasonal succession

The major portion of the phytoplankton standing stock and volume in Heney Lake is made up of blue-green algae and diatoms. This is characteristic of most temperate, hard-water lakes, especially during the time period sampled (Rodhe et al., 1958; Prescott, 1962; Hammer, 1964). Among the other groups present at this time, green algae are more predominantly found in small fertile lakes or ponds (Hutchinson, 1967) while chrysophytes become important in some lakes immediately before the onset of summer stratification (Moss, 1972). Dinoflagellates often become dominant during the fall mixing period but did not reach high densities in this lake.

The total phytoplankton abundance showed two peaks in standing stock (August and October) and at least three maxima in cell volume (June, August, and October). Generally, lakes of this type register two main peaks in abundance (usually measured as biomass or productivity) corresponding to the vernal and autumnal isothermal mixing periods (Rodhe et al., 1958; Round, 1971). These maxima are due to the distribution throughout the water column of nutrients from the sediments. In this study, one peak in abundance corresponds to the initial breakdown of stratification at the end of July (see Fig.1) while there is no apparent explanation for the others. One possible reason for the other fall

peaks in abundance may be that, despite isothermal conditions in August, mixing was not as complete or constant as it was later in the year. It has been reported that in summer, periods of calm weather, lasting up to several days can result in small-scale stratification of otherwise isothermal water columns (Reynolds and Walsby, 1975; Reynolds, 1976a), which would reduce the input of nutrients from the sediment.

The seasonal shift in dominance from blue-greens in summer to diatoms in autumn is standard for lakes of this type (Fodhe et al., 1958; Hammer, 1964; Moss, 1972; Reynolds, 1976a; Jones, 1977a) although timing and species composition of course vary greatly. The explanations for the shift place emphasis either on changes in nutrient levels (Hutchinson, 1944; Lund, 1965), different temperature preferences between groups (Patrick, 1969; Jones, 1977b), and changes in the physical stability of the water column (Reynolds, 1973a; 1976a; Knoechel and Kalff, 1975).

With respect to preferences for different nutrient conditions, blue-greens are known to predominate when nutrient levels are at their lowest during summer stagnation (Reynolds and Walsby, 1975) while diatoms reach their peak when input of nutrients from the sediments is high (Lund, 1954). The ability of blue-greens to tolerate very low nutrient levels has been ascribed to luxury consumption during transient high concentrations. (Reynolds and Walsby, 1975) and to growth at depths where nutrients are in greater sup-

ply followed by ascension into the better-illuminated levels of the water column to photosynthesize (Reynolds, 1976a). The latter option is not open to diatoms as they can not control their vertical position in the water column. Also, the unique diatom requirement for silicon may be met only during the fall mixing period.

The preference of blue-greens for warmer temperatures than diatoms is well known (Patrick, 1969) and this agrees with the seasonal occurrence of these groups in Heney Lake. The influence of temperature is probably tied to that of thermal stratification which will be discussed at greater length later.

Explaining the sequence of species within a group is difficult as it varies greatly from lake to lake. Among the blue-greens one trend which may be explained is that of the filamentous forms, such as Aphanizomenon, Anabaena spp. and Phormidium sp., which preceeded the non-filamentous algae such as Dactylococcopsis and Microcystis. It has been postulated that filamentous forms require greater water column stability than colonial ones such as Microcystis because they can not regulate buoyancy as efficiently due to their smaller size. Thus, Microcystis would tolerate greater turbulence and occurs later in the year (Reynolds and Walsby, 1975). Conversely, the unicellular Dactylococcopsis is not known to regulate buoyancy, probably owing to its small size, and would thus be limited to turbulent water columns for a different reason.

The peaks of diatom species appear closer together than the blue-green peaks, and are limited to the period from September to November. These diatom species are commonly reported to take part in either the spring or fall diatom pulse, or both, in different lakes (Podhe et al., 1958; Davis, 1964; Moss, 1969) although some species may dominate the phytoplankton of larger temperate lakes throughout the year (Holland, 1969). It is therefore difficult to put forth a unifying hypothesis for this group.

Although green algal species showed more erratic population fluctuations than the other groups, most of them peaked in midsummer as is usual for similar lakes (Hickman, 1974).

Species richness reaches its maximum following the onset of isothermal conditions in August. This is contrary to the trend in many lakes and also to what would be expected if the stratified water column provided a more heterogeneous environment, and thus separation of specific populations (Margalef, 1958; Richerson et al., 1970). A possible explanation for this increase in the number of species under mixed conditions is an influx of species from the sediments, littoral zone or hypolimnion upon circulation of water from these regions. These border effects would be more prevalent in the bay than in the lake proper. Such a dispersal of latent populations has been reported for the diatom Melosira from bottom sediments (Lund, 1954), for the

diatoms Cyclotella and Tabellaria and desmids from the littoral zone (Round, 1971), and for Fragilaria from the hypolimnion (Moss, 1972). In more open waters, only influx from the hypolimnion would be a significant source of new species. The increase in species richness under isothermal conditions applies to all taxonomic groups, and this seeding of populations apparently overrides the influence of increased habitat heterogeneity in the stratified period.

2.3.2 The enclosure treatments and species associations

The manipulations performed on the enclosures had the desired effect of varying community composition. Overall, they created conditions more favourable for the growth of green algae, and reduced the dominance of blue-greens and diatoms.

The Chi-squared association analysis indicates that, despite the distinct succesion of individual species, more associations were present than would be expected due to chance alone. The low number of negative associations may be explained by the relatively low frequencies of some species which precludes any significant negative relationship between their distributions (Agnew, 1961).

Several patterns emerge from the association analysis. The first is that species tend to be associated more often with other species in the same taxonomic division. This is not surprising since physiological and ecological

adaptations are related to taxonomic similarity among algae. Previous phytoplankton studies also found closer similarity in preferences and distribution within taxa than between taxa (Allen and Koonce, 1973; Margalef, 1974; Briand, 1976; Lewis, 1977a,b).

Diatoms showed by far the greatest degree of intra-divisional association. This together with the sudden peak of most diatoms in the circulating water column of late September would suggest that most diatoms exhibit a relatively opportunistic strategy. Their success appears linked to a particular set of environmental conditions when overall competition may be low in the community as nutrient levels are high.

Conversely, blue-greens and greens were less closely associated than diatoms. The greater number of morphological types and sizes within these groups (e.g. single-celled, filamentous and colonial blue-greens; single celled and colonial greens) indicates a more varied ecology than that exhibited by the diatoms.

The Chi-squared analysis isolated pairs of species which are associated temporally and are thus potential competitors. These species may require means to avoid competition. In the next chapter the degree of association in space, as well as time, will be investigated in order to determine whether potential competition is alleviated by spatial segregation of phytoplankton.

Chapter III

SPATIAL SEGREGATION IN PHYTOPLANKTON SPECIES

3.1 INTRODUCTION

In the previous chapter, the phytoplankton succession and species associations of Heney Lake in the summer of 1976 were described. If the two major groups, the blue-greens and diatoms, have distinctly different seasonal abundance patterns, they also exhibit broad overlap in time. A large number of temporal associations between species within and between the groups was also observed. This chapter will explore the means used by these strongly sympatric species to alleviate potential competition. This will be investigated by determining the degree of association between species at different depths in the water column and by calculating the amount of niche overlap along time and depth.

Niche theory has not been rigourously applied to field studies of phytoplankton. Although phytoplankton utilize largely the same nutrients, species preferences for nutrient concentrations vary widely (Rodhe, 1948; Lund, 1965). These differences must be expressed in the niche dimensions of time and space (habitat). Although habitat is the most important factor separating the niches of animal taxa (Schoener, 1974) it is considered by some to be unimportant

in separating phytoplankton species (Hutchinson, 1961; Lewis, 1977a). Because the niche of a species at a point becomes incompressible along any one dimension, Levins (1968) predicted that as more species are packed into a community, competitive pressure will dictate that they separate along more dimensions. For this reason, habitat, in this case depth and horizontal distance, may have to be partitioned to allow coexistence in phytoplankton, despite the apparently poor control of spatial position by phytoplankton.

The effects of habitat heterogeneity on competitive interactions are known mainly from theoretical studies. The question has been approached from the standpoint of island biogeography based on either different (Horn and Hutchinson, 1972) or similar patches within a habitat (Levins and Culver, 1971). The latter authors argue that since the balance of local extinction and colonization of patches would leave some areas unoccupied even in the absence of competitors, species may coexist even if the patches are the same. This reasoning applies when a patch contains a small fraction of the species able to live in it or when a species occupies a small fraction of the habitable patches. These assumptions are reasonable for phytoplankton since some communities have been shown to be highly patchy (Richerson et al., 1970). In a more highly saturated environment coexistence or exclusion depends on colonization and extinction rates, even if each species has a competitive advantage on a different type of patch (Horn and MacArthur, 1972).

Richerson et al. (1970) view much of the phytoplankton diversity in lakes as due to between- rather than within-habitat diversity. The heterogeneity in phytoplankton community structure can be generated by either non-biological means, such as Langmuir circulations or other water movements, or through biological agents. Among these are zooplankton grazing, which is commonly known to be non-uniform (Richerson et al., 1970; Levin and Segal, 1976) or modification of patches of water caused by founder effects which can be important given the short doubling time of some species.

Spatial heterogeneity is known to be greater on the vertical scale than on the horizontal (Margalef, 1958; Richerson et al., 1975), and phytoplankton associations are organized more strongly with depth (Richerson et al., 1975). The reason for this lies undoubtedly in the greater magnitude of physical and chemical differences which exist along this dimension, especially when the lake is thermally stratified. Among the factors which vary most drastically with depth are light, temperature, and nutrient concentrations.

Vertical density profiles of phytoplankton are known also to vary with depth and from species to species (Moss, 1969; Baker, 1970; Hickman, 1974; Happey-Wood, 1976; Reynolds, 1976 a,b). In comparing species distributions taken during calm weather, diatoms are often found below the euphotic zone while blue-greens can be concentrated either

deep in the water column or closer to the surface, depending on the stage in seasonal successional and nutrient status of the cells (Reynolds, 1976a; Konopka et al., 1978). Flagellates can also maintain to some degree their vertical position, with greens in the upper regions and cryptomonads deeper in the euphotic zone (Happey-Wood, 1976; Hickman, 1974).

The question is to what degree these different preferences allow for actual habitat separation among potentially competing phytoplankton species. This will be investigated in two ways. First, those species found to be positively associated in time will be analyzed for their degree of association in depth.

Three outcomes are possible for each pair of species. First, a positive association may be retained with depth. This would indicate either potential competition, enhancement of one species by the other, or occupation of the same habitat without competition. The second outcome is a weakening of the association, which occurs when species are randomly distributed throughout the water column. This would not rule out strong competition but mean that competitive exclusion is not occurring between the two species because of their frequency or cooccurrence. The most conclusive result from this test would be a switch from an association that is positive in time to one that is negative with depth. This would indicate active avoidance of one species by another or competitive exclusion.

The Chi-squared depth association analysis is run here on two time periods: the entire sampling season from June to November and the stratified period from June to July. Only during the stratified period should one expect significant segregation to take place. At other times the effects of water movement should overcome the ability of algae for maintenance of vertical position, and disperse populations (Reynolds, 1976a).

In the second analysis, the degree of niche overlap is determined. Niche overlap is a measure of how the abundance of species a varies with the abundance of species b and vice versa along a resource gradient (MacArthur and Levins, 1967; Pianka, 1972). Here the gradients are time and depth. If species are segregating along one or both of these axes to avoid competition, niche overlap values will be low.

3.2 MATERIALS AND METHODS

3.2.1 Chi-squared Association Analysis with Depth

The enclosures and sampling methods are described in Chapter 2. The analysis was applied to the 36 pairs of species found to have positive temporal associations (see Fig. 16 in Chapter 2). Only those water columns containing both members of a pair were considered and the presence-absence data from the four component depths retrieved. Using these data, two separate analyses were performed on the time periods of 23 June to 27 July (the stratified period) and 23 June to 2 November (the entire sampling season).

3.2.2 Niche Overlap in Time and Depth

For this quantitative method several modifications were performed on the species abundance data. First, only samples taken from two of the unenriched enclosures were used. One enclosure was sealed at the bottom and the other was connected with the sediment.

As for the Chi-squared analysis, only species present in 25% of the water columns were used, but this time for a species to be considered present, four of its individuals were required in a count. This higher cutoff point was dictated by counting error: only with four or more individuals is the lower limit of the counting confidence interval greater than one (see Lund et al., 1958). Conversely, this was not required in the association analysis because of the

purely qualitative nature of the technique and the larger number of samples. This reduced the number of species analyzed to nine and the number of pairs to 36.

Overlap in time for the five-month period was determined using presence and absence data within each integrated four-sample water column. The choice of a strictly qualitative technique was dictated by the lack of knowledge of the density distributions to each species between the four discrete depths sampled. In such conditions, any extrapolation of the four densities recorded would be inaccurate.

For each of the 36 pairs, the amount of overlap in time was calculated as follows:

$$\alpha_{ij} = \frac{n_{ij}}{\sqrt{n_i n_j}}$$

where n_i and n_j represent respectively the number of occurrences of species i and j in all samples and n_{ij} represents their number of occurrences.

Overlap in depth was measure using the species abundance data and the definition of Pianka (1973) adapted from Levins (1968).

$$\alpha_{ij} = \frac{\Sigma p_i p_j}{\sqrt{\Sigma p_i^2 p_j^2}}$$

where p_i and p_j represent respectively the relative proportion in volume of species i and j in each sample. Here the analysis was restricted to the period when the lake was stratified. As in the Chi-squared depth analysis, only those water columns containing both members of a pair were considered and the four component depths were treated separately.

3.3 RESULTS

3.3.1 Chi-squared Association with depth

The associations along depth for temporally associated pairs of species are presented in Table 5. Eleven pairs retained their positive association along depth over the entire sampling season while five pairs did so for the 5-week stratified period. There was only one negative association with depth (4-) for the period June to November, the pair Anabaena flos-aquae - Cryptomonas erosa. None was found over the stratified period.

Pairs of species belonging to the same division were more likely to retain their association along depth than pairs from different divisions. Of the positive intradivisional pairs 41% (9/22) were still associated at different depths, while only 14% (2/14) of the interdivisional pairs did so during the entire season. All five pairs which retained their association during the stratified period involved species from the same division.

3.3.2 Niche Overlap in Time and Depth

The distribution of the 36 pairs of species along time and depth is shown in Figures 16 and 17. The maximum overlap in either dimension is 100% and for convenience the graph is divided into four quadrants along the 50% overlap lines. Those pairs of species that are separated by either time or depth are located in quadrants 2 and 4 respectively.

TABLE 5

Chi-squared depth associations of phytoplankton species pairs.

Depth associations of temporally associated phytoplankton pairs (level of temporal association in brackets).

Species pair	Depth Association June-November	June-July
Asterionella formosa-Fragilaria crotonensis (4+)	4+	
A.f.-Melosira granulata (4+)	+	2+
A.f.-Synedra delicatissima (4+)	3+	
A.f.-Tabellaria fenestrata (4+)	4+	+
Cryptomonas erosa - Cyclotella sp. (4+)	+	
Fragilaria crotonensis - Synedra delicatissima (4+)	4+	+
Scenedesmus obliquus - S. quadricauda (4+)	4+	
Synedra delicatissima - Tabellaria fenestrata (4+)	4+	
Anabaena flos aquae - Cryptomonas erosa (+)	4-	
Anabaena spiroides - Cryptomonas erosa (+)	4+	
A. spiroides - Anabaena sp. (+)	2+	2+
Chlorochromonas minuta - Cryptomonas erosa (+)	4+	
Rhizosolenia longiseta - Tabellaria fenestrata (+)	+	2+

Figure 16: Niche overlap in time and depth of species pairs.

Niche overlap of species pairs along time and depth dimensions in two unenriched enclosures.

- pairs involving species from different divisions
+ species in same division

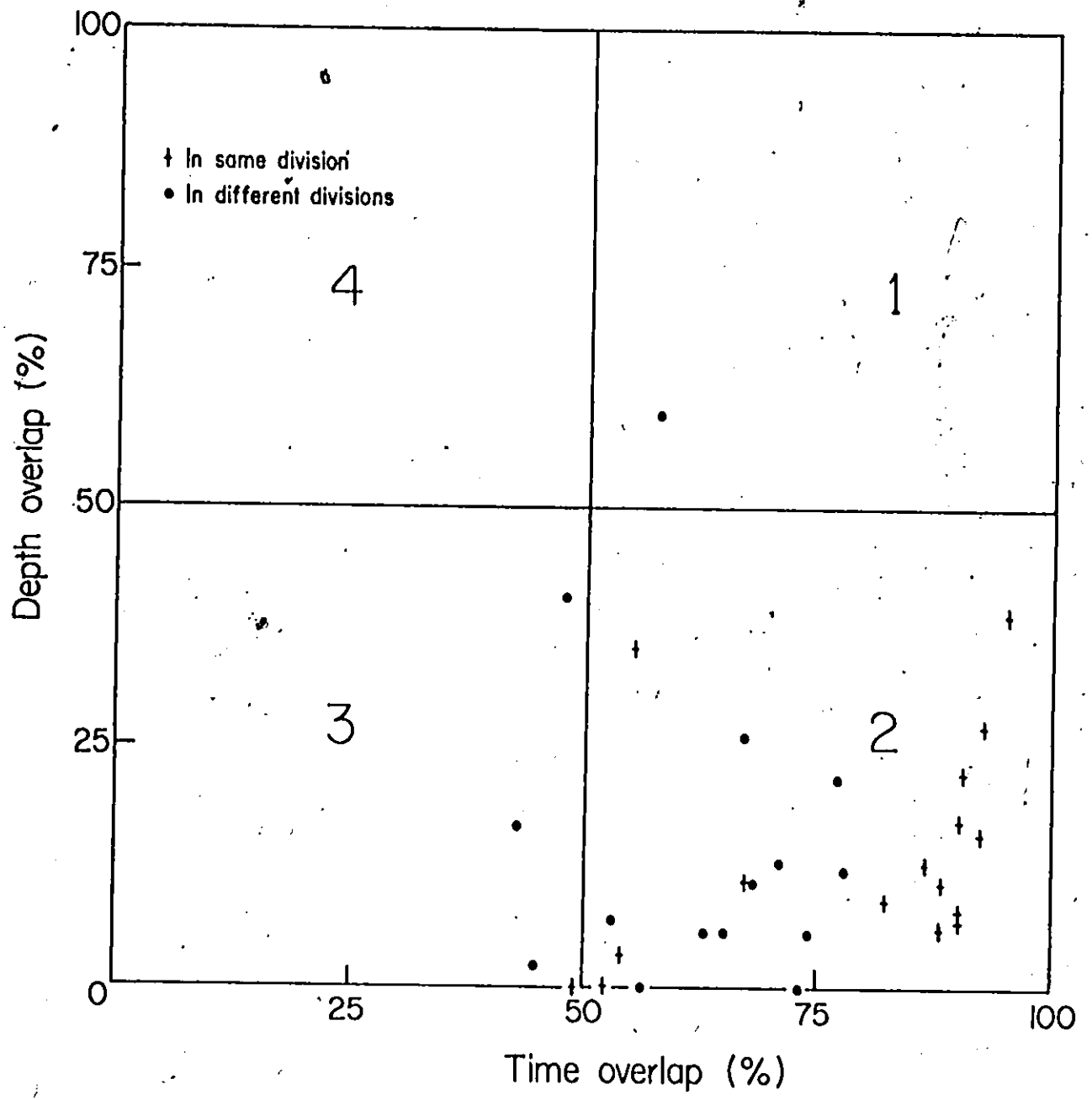

100
75
50
25
0
Depth overlap (%)
† In same division
• In different divisions
4
1
3
2
25
50
75
100
Time overlap (%)

Figure 17: Matrix of species overlap quadrants.

Matrix showing the location in overlap quadrants of each species pair (quadrant numbers 1 to 4 as indicated in Fig. 16).

Control

Anabaena flos-aquae							
2	Anabaena sp.						
2	2	Aphanizomenon flos-aquae					
2	1	1	Asterionella formosa				
2	2	2	2	Fragilaria crotonensis			
2	2	2	2	2	Oscillatoria limnetica		
2	2	2	1	2	2	Phormidium sp.	
3	2	2	2	2	3	3	Synedra delicatissima
2	2	2	2	2	2	2	3 Tabellaria fenestrata

Pairs that segregate along both axes are included in quadrant 3 while quadrant 1 represents those species that do not separate along either dimension. From Fig. 17, and Table 6 it is clear that depth is the major separating dimension. Most of the pairs exhibit less than 25% overlap along this axis. There is little temporal partitioning: all pairs registered at least 40% time overlap, and most at least 60%. No pair was found in quadrant 4. There are slight differences in segregating patterns between pairs of species belonging to the same division and those that do not. Intradivisional pairs are more likely (93%) to segregrate in quadrant 2 than are species from different divisions (70%), while interdivisional pairs are more likely to be found in quadrant 3, with low overlap in both dimensions, or quadrant 1 (high overlap in both axes).

The patterns of overlap exhibited by each species are summarized in Table 6. Two different modes of segregation are represented by the diatoms Fragilaria crotonensis and Synedra delicatissima. The former uses only depth to separate from the other species (quadrant 2) while the latter uses both time and depth (quadrant 3). The seven other species are closer to Fragilaria in their behaviour. Asterionella formosa is noticeable for exhibiting high overlap (>50%) in both dimensions with three other species.

TABLE 6

Species frequencies and niche overlap distributions.

Species frequencies (expressed as a decimal) and number of occurrences in each niche overlap quadrant.

Species	Frequency	Overlap Quadrant 1	2	3	4
Anabaena flos-aquae	0.91	0	7	1	0
Anabaena sp.	0.91	1	7	0	0
Aphanizomenon flos-aquae	1.00	1	7	0	0
Asterionella formosa	0.46	3	5	0	0
Fragilaria crotonensis	0.59	0	8	0	0
Oscillatoria limnetica	0.97	0	7	1	0
Phormidium sp.	0.84	1	6	1	0
Synedra delicatissima	0.28	0	4	4	0
Tabellaria fenestrata	0.53	0	7	1	0
Total		3	29	4	0

3.4 DISCUSSION

The Chi-squared analysis with depth reveals several responses of temporally associated species. By far the majority of the pairs are not associated along depth (67.5% in the season-long analysis). It is striking that twelve of the 36 pairs did retain their positive association considering that the majority of the water columns involved were isothermal. This points to a great similarity between these pairs of species. Indeed most pairs involved species from the same division, and most were diatoms. The general explanations of within-group similarity in successional trends and seasonal associations can also be invoked here.

The blue-green Anabaena flos-aquae and the cryptomonad Cryptomonas erosa are negatively associated along the depth gradient. This suggests active partitioning or strong inhibition since within the same water column the mere presence of one species at concentrations above 5000/l precludes the other species from occupying that habitat. Allelopathy may explain the relationship as secretions of blue-green algae are inhibitory to the growth of other species, particularly some greens (Bowowna et al., 1975) and diatoms (Keating, 1977). The susceptibility of cryptomonads to these compounds is not known. Blue-greens and cryptomonads are commonly found together in lakes and differential depth dis-

tributions have been reported in a number of studies (Moss, 1969; Reynolds, 1976a). Moss (1969) studied the depth distribution of algae in a 3 m deep pond, and found segregation of Cryptomonas and another blue-green Dactylococcopsis. Greater depths might allow an even larger degree of species segregation. While Moss (1969) found that Cryptomonas tended to aggregate near the surface, Reynolds (1976a) found that another species, Cryptomonas ovata, was concentrated in the lower regions of the euphotic zone of another pond. Anabaena circinalis began its growth phase in similar depths and ascended several weeks later. In order to determine the causes of these distributions, Reynolds (1976b) placed traps at different depths and found that Cryptomonas actively sought these lower depths while Anabaena maintained its population above.

While a negative depth association was found only once, the niche overlap determination indicate that segregation is common. This discrepancy is no doubt due to the greater sensitivity of the niche ovelap test which uses abundance rather than presence and absence. Most of the algal pairs that retained their association and were included in the overlap determination segregated along the depth gradient with overlaps normally less than 50%.

While species segregated greatly along depth, time was of minor importance in separating the phytoplankton populations. The rarity of temporal partitioning found in

this study exceeds that found by Schoener (1974) in animal communities. This would be expected for several reasons. In considering only the nine most common species, a bias is introduced in the estimation of time overlap as commonness means a niche extended along the time axis. For example, Aphanizomenon was found throughout the entire sampling season, and exhibited therefore maximal time overlap with the other species. Notwithstanding this, a severely limited time axis for the niche of a given species would pose the problem of random local extinction given the stochastic nature of the lake environment. Many of the negative associations found (see Chapter 2), may be due to the artificially separated and extremely varied conditions between the containers.

Given the low incidence of temporal separation, the need for other means of segregation becomes more acute. Similarity of species along one axis should imply dissimilarity aong another, hence the segregation along depth observed here.

Depth partitioning requires some control of vertical position or at least mechanisms such as differential sinking rates. Evidence for this ability exists for some members of this community. Oscillatoria has the ability to maintain populations in the metalimnion of some lakes (Klemer, 1976), while Aphanizomenon (Konopka et al., 1978) and Anabaena (Dinsdale and Walsby, 1972) are known to regulate their

buoyancy in order to stay at a particular depth. Although diatoms were seen to partition along depth in this study, they have no active means of vertical positioning. The mechanism allowing segregation may be due to differential sinking rates, or higher growth rates at some depths than at others. Segregation of diatoms from blue-greens has been observed elsewhere (Moss, 1972; Reynolds, 1976b) with diatoms sinking to the lower strata and blue-greens occupying upper layers.

Depth segregation appears quite widespread in this community. As noted in the comparison of depth distribution between two Cryptomonas species in the studies of Moss (1969) and Reynolds (1976b), the actual preferred depth may vary from lake to lake in closely related species. These differences may be due to local community factors acting on the development of the characteristics of a species in a particular lake. It is therefore of interest to know the environmental cues allowing segregation in different species. Two possible influences, nutrient concentrations and light conditions, will be investigated in the next chapter.

Chapter IV

MECHANISMS OF PHYTOPLANKTON SEGREGATION

4.1 INTRODUCTION

It was found earlier that species strongly associated in time appear to alleviate potential competition through the segregation of their populations along the depth gradient. Still, it is difficult to evaluate the actual extent and action of competition without perturbing the system and observing species responses. This will also reveal possible cues and mechanisms for spatial separation. This chapter investigates the effects of two perturbations: altering nutrient levels and light conditions.

4.1.1 Response of Niche Overlap to Nutrient Enrichment

Nitrate and phosphate are required by all members of the algal community and are the most common limiting nutrients in lakes (Schindler, 1971). Addition of these nutrients usually results in an immediate increase in standing stock, followed by nutrient depletion. The prediction, based on Pianka's niche overlap hypothesis (Pianka, 1972), is that with the increase in competition due to higher population densities, the tolerable niche overlap in the community should decrease since the potential for competitive ex-

clusion is higher. It is supported by the findings of two theoretical studies: Reibesell (1974) and Abrams (1977) independently showed that the enrichment of competitive systems may magnify the advantage of the superior competitor, which increases its niche breadth and reduces or eliminates the niches of its poorer competitors. According to the results of these studies one would expect two responses to the treatment, based on the ability of species to take up and utilize the added resources. While the response of niche overlap to enrichment has not been measured, some studies have shown varying effects of enrichment on phytoplankton abundance. Among the species included in the present study, Moss (1972) observed that addition of phosphate increased the density of Fragilaria crotonensis in mixed cultures which was further enhanced by the addition of nitrate. A species of Anabaena, also increased by phosphate, was not further enhanced by enrichment with nitrates. F. crotonensis and Synedra filiformis were enhanced by enrichment of Lake Michigan water with nitrate and phosphate while Asterionella flos-aquae and Anabaena flos-aquae were depressed (Schelske et al., 1974). One might expect a similar divergent reponse of niche overlap to enrichment in the present long term study.

4.1.2 Response of Communities to Light Manipulation

Besides nutrient concentrations, light also varies greatly both temporally and spatially. In temperate latitudes the intensity and quality of light reaching algal cells varies with time of year, due to changes in the sun's altitude, degree of cloud cover (Gates, 1965), amount and nature of particulate and dissolved material in the water (Podhe, 1965), and the density of phytoplankton cells above (Talling, 1960).

The greatest difference in illumination occurs with depth due to the absorbing properties of water. The depth of the euphotic zone, that is, the depth to which approximately 1% of surface visible pentetrates (Talling, 1962), varies from more than 30 m in clear mountain lakes to 1 m or less in highly eutrophic lakes. In addition, because the absorption is selective with respect to wavelength, the spectral characteristics of the light vary greatly with blue and green wavelengths predominating at greater depths (Clarke, 1939; Jerlov, 1951). While phytoplankton exhibit a substantial amount of physiological adaptation to different light conditions, there is variation in the mechanisms employed depending on the pigment system present (Halldal, 1970). There exist two types of intensity adaptation (Steemann Nielsen and Jorgenson, 1968). Green algae exhibit the "Chlorella-type" adaptation in which at lower intensities the amount of chlorophyll in the cell is increased, re-

sulting in a compensation in photosynthetic activity. Diatoms and dinoflagellates show the "Cyclotella-type" adaptation in which the chlorophyll content remains the same regardless of illumination, and lower illuminations decrease the photosynthetic rate. Blue-greens and to some extent cryptophytes appear less flexible in their intensity adaptation ability (Brown and Richardson, 1968) as they can become severely damaged at high light intensities but can grow well under low light conditions. Despite these known differences, the light intensity preferences of the major freshwater algal groups are not as clearly delineated as those proposed by Pyther and Menzel (1959) for marine phytoplankton. They recognized dinoflagellates as "sun" forms, green algae as "shade" forms and diatoms as intermediate. In contrast, freshwater diatoms have traditionally been treated as a high light group (Lund, 1949; 1965) with the exception of some species that can flourish under extremely turbid, low light conditions (Chandler, 1944). Further, many freshwater greens are known to thrive under high illumination levels (Whitford, 1960; Happey-Wood, 1976).

The interdependence of light and other factors such as temperature is also recognized. The different algal preferences for combinations of these two parameters have led to the development of a successional classification of winter spring, summer, and autumn phytoplankton representing species preferring low light and low temperature, high light

and low temperature, high light and high temperature, and low light and high temperature (Findenegg, 1943). Nutrient concentrations are also known to affect the light responses of some algae, most notably blue-greens (Konopka et al., 1978).

Effects of light quality on phytoplankton are known mainly from physiological studies and have been reviewed by Haxo (1960) and Halldal (1970). While certain responses, such as an enhancement of growth under blue light, are similar across taxonomic lines, the degree of enhancement is species specific (Wallen and Geen, 1971; Qasim et al., 1972). Also, between divisions, the photosynthetic activity minimum seen in greens under green and yellow light is absent in diatoms, dinoflagellates, and blue-greens (Halldal, 1970), due to the presence of fucoxanthin, peridinin and phycobilins in these three groups, respectively. The differing forms of chlorophyll and pigment interactions in the algal groups also result in dissimilar reactions to spectral quality. Variation in proportions of photosynthetic pigments has been observed in many lakes (Dutton and Juday, 1944; Talling, 1966) which may be linked to segregation of algae along the light gradient (Giamotti, 1966).

In this chapter, two separate experiments will be described, investigating the effects of manipulating nutrient levels and light conditions on the phytoplankton community of Heney Lake. The first test compares niche overlap

values in enriched enclosures with control, unenriched enclosures described in Chapter 3. The second experiment determines the response of phytoplankton populations to light of varying intensity and colour under thermally stratified and mixed conditions.

4.2 MATERIALS AND METHODS

4.2.1 Response of Niche Overlap to Nutrient Enrichment

The enclosures and sampling methods are described in Chapter 2. The pairwise overlap determinations were calculated for enclosures enriched weekly with NO_3^- and PO_4^{3-} to 100 µg/l and 10 µg/l respectively.

4.2.2 Response of Communities to Light Manipulation

The field experiments took place from 30 July to 1 September 1977 in the bay where the previous studies had been performed. The tests involved incubating phytoplankton communitites in coloured plexiglass cubes containing 8 l of lake water suspended at various depths.

Four different sets of cubes were used: red, blue, green and clear for control. Three experiments were conducted, lasting six days each. The duration of the experiment was chosen after a preliminary study had determined that a longer period would lead to the development or a periphyton community on the surface of the plexiglass.

Total irradiance in the visible spectrum (from 420 to 680 nm) was measured with a Kahlsico radiometer (Model 268 WA 300) in the boxes at the depth of incubation. Irradiance in the blue (420 to 480 nm), green (490 to 570 nm), and red (620 to 680 nm) spectral bands was also determined using accessory filters. The values expressed in percent of surface irradiance are given in Table 7 for each combination of colour and depth.

The three experiments were started at dusk on 30 July, 13 August and 26 August, 1977, respectively. Phytoplankton communities were collected from their intended depth of incubation using a 2 l Van Dorn bottle. Prior to their transfer into the cubes, the samples were filtered through 135 µm zooplankton netting to remove adult crustaceans. This reduced fouling and prevented extensive grazing effects. In addition, temperature and oxygen profiles were taken in the lake at the onset and at the end of each experiment.

A total of 36 cubes were used in each experiment, representing four sets - one per colour - of nine cubes. In each set, trays of three replicate cubes were incubated at the depths of 1, 5, and 9 m. The upper depth was set at one meter to avoid possible photoinhibition (see Talling, 1966). The sets of trays were suspended from four buoys anchored within a 20 m radius in the bay. Iron projections welded into the buoys and used for support prevented shading by the buoys of cubes incubated at 1 m. The plexiglass walls of the cubes were 0.32 cm thick. This reduced internal turbulence substantialy, yet there was enough horizontal movement of the trays to prevent any visible sedimentation from occurring in the containers.

TABLE 7

Irradiance levels in cubes during light experiment.

Percent surface irradiance per colour band in cubes at the three depths of incubation. (N.B. "0" indicates levels < 0.05% Io).

Depth	Colour Band	Colour of Container			
		Control	Red	Blue	Green
1M	Red	40.0	15.0	1.8	0
	Blue	36.0	0.1	7.7	1.1
	Green	49.0	0.2	3.2	18.5
	Total	62.0	6.3	5.8	10.6
.5M	Red	3.8	1.2	0	0
	Blue	3.3	0	1.0	0
	Green	9.0	0	0	2.3
	Total	9.5	0.4	0.4	1.3
0M	Red	0.3	0	0	0
	Blue	0.2	0	0	0
	Green	1.7	0	0	0.3
	Total	1.5	0	0	0.2

Phytoplankton counts were made from unfiltered samples taken from each container before and after incubation. These were preserved in Utermohl's iodine solution. The counts were done with a Wild M40 inverted microscope on 50 ml subsamples which had been sedimented for a period of 24 hrs. Species and algal cell volumes were calculated as previously (see Chapter 1).

Significant differences ($P < 0.05$) in algal densities and group volumes were determined by the non-parametric Mann-Whitney U test, or, when the number of samples in a treatment was less than three, from the confidence limits of a Poisson distribution (see Lund et al., 1958). Differences between incubated communities were discarded from the analysis when they were found to already exist between the initial communities.

To distinguish between taxa preferring "high" and "low" light intensities, comparisons were made between cubes receiving either more or less than 5% surface irradiance (I_o). This arbitrarily chosen cut off point corresponded to the relative intensity recorded at the depth of 6 m in the lake.

The effects of light quality were determined by comparing algal densities and volumes for each pairwise combination of the four treatments. Here, to reduce possible effects between colours due to intensity differences, algal abundance in a tray was evaluated as a fraction of the total

abundance to that taxon recorded in the four trays (one per colour) incubated at each depth. Despite this manipulation, some of the intensity differences remained, due to the dissimilar total intensities recorded in cubes at the same depth.

4.3 RESULTS

4.3.1 Response of Niche Overlap to Nutrient Enrichment

The overlap distribution of the 36 pairs of species in the enriched enclosures is shown in Figures 18 and 19. The frequencies of occurrence for most species were lower in these containers, as seen from the ratios of enriched to control frequencies in Table 8. This reduced the potential time-overlap to such a degree that several pairs no longer co-occurred in the short stratified period. As a result there are no overlap points for these cases. This applies particularly to Asterionella formosa.

As indicated in Table 9, the overall effect of nutrient enrichment on the distribution of the 36 pairs was to reduce the degree of overlap. The exceptions to this general trend were provided by the diatoms Fragilaria crotonensis and Synedra delicatissima, which registered a net increase in overlap, mainly along depth, with Fragilaria also increasing its frequency of occurrence. The blue-green Aphanizomenon flos-aquae remained largely unaffected by the treatment. Except for Fragilaria, those species that increased their frequency with enrichment, Phormidium and Tabellaria, still showed a higher number of overlap decreases than increases.

Figure 18: Time and depth overlap species pairs in enriched enclosures.

Niche overlap of species pairs along time and depth dimensions in two enriched enclosures.

- pairs involving species from different divisions
- \+ species in same division

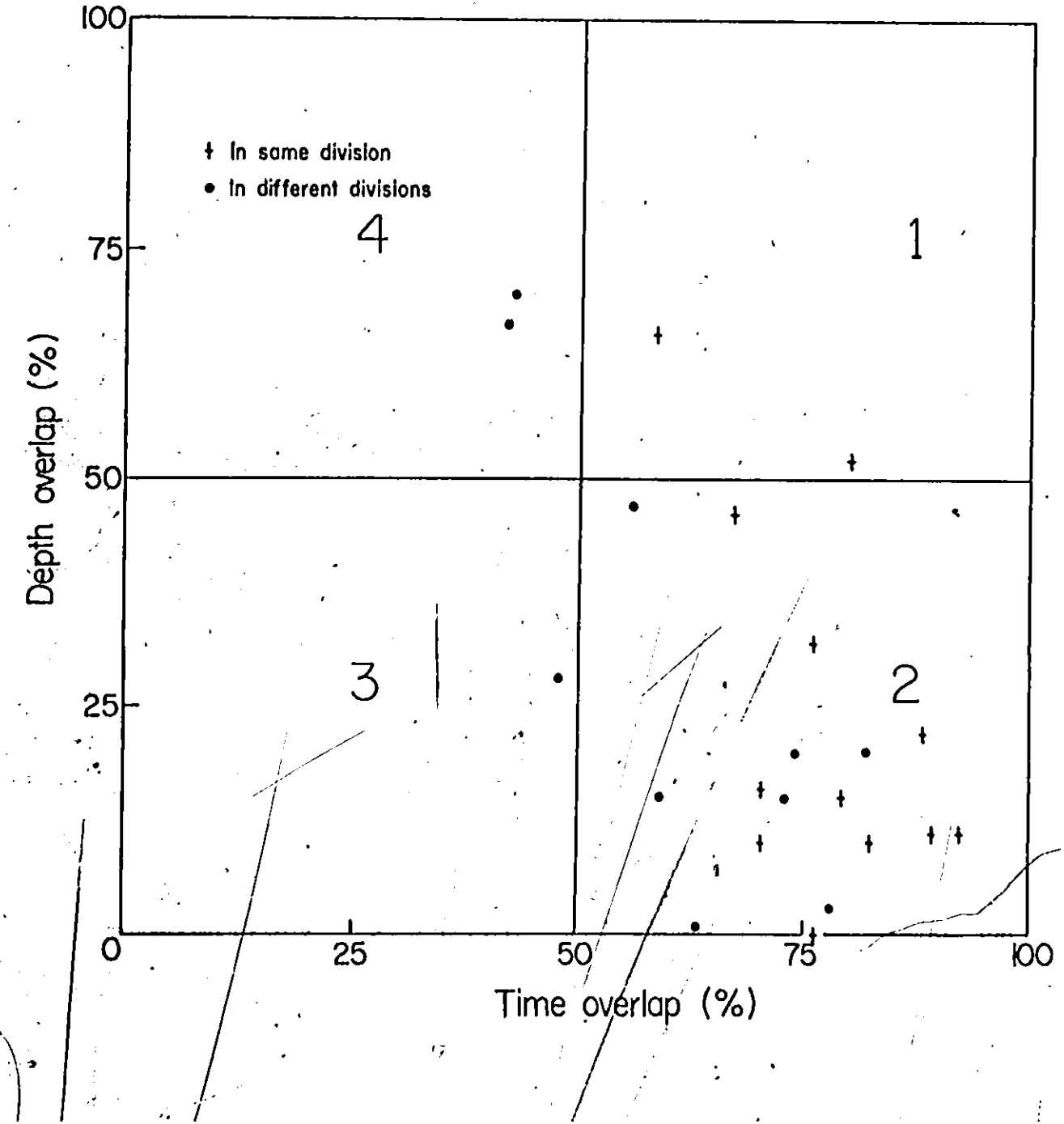

100
75
50
25
0
25
50
75
100
Depth overlap (%)
Time overlap (%)
In same division
In different divisions
4
1
3
2

Figure 19: Matrix of species overlap quadrants in enriched enclosures.

Matrix showing the location in overlap quadrants of each species pair in enriched enclosures (quadrant numbers 1 to 4 as indicated in Fig. 16).

Enriched

Anabaena flos-aquae							
2	Anabaena sp.						
2	1	Aphanizomenon flos-aquae					
–	–	–	Asterionella formosa				
2	2	2	–	Fragilaria crotonensis			
2	2	2	–	2	Oscillatoria limnetica		
2	2	2	–	2	2	Phormidium sp.	
4	–	3	–	1	4	4	Synedra delicatissima
–	–	2	–	2	2	2	– Tabellaria fenestrata

TABLE 8

Response of species frequency to enrichment.

Species frequencies (expressed as a decimal) in enriched enclosures and frequency ratios in enriched:control enclosures.

Species	Frequency in Enriched enclosures	Frequency Ratio (Enriched: control)
Anabaena flos-aquae	0.63	0.69
Anabaena sp.	0.69	0.75
Aphanizomenon flos-aquae	0.97	0.97
Asterionella formosa	0.38	0.82
Fragilaria crotonensis	0.66	1.12
Oscillatoria limnetica	0.81	0.83
Phormidium sp.	0.88	1.05
Synedra delicatissima	0.22	0.79
Tabellaria fenestrata	0.59	1.11

4.3.2 Response of Communities to Light Manipulation

While the first experiment was performed under thermal stratification, the second and third tests were done in isothermal water columns (Fig. 20). A greater number of preferences was found in the first experiment (Table 10) than in the following two.

Sixty two algal species were recorded in the counts. They are listed in Table 11 along with their frequency of occurrence. Two blue-greens, Aphanizomenon and Anabaena, had the highest frequencies, followed by the two dinoflagellates, Ceratium and Peridinium.

4.3.2.1 Species Preferences

Ten species belonging to various divisions exhibited a significant preference for the "high" intensity category (Table 12). In most cases the significant difference was observed in only one experiment. Two blue-greens, Anabaena and Aphanizomenon, were more consistent, as they recorded preferences in both the first and third experiments. Two species were favoured under "low" illumination: the blue-green Gomphosphaeria lacustris and the dinoflagellate Peridinium. These preferences were observed in the third and first experiments, respectively.

TABLE 9

Response of species niche overlap to enrichment.

Effect of enrichment on niche overlap quadrant distribution and on extent of overlap.

Species	Overlap Quadrant 1	2	3	4	Changes in Overlap Quadrant with enrichment: Decreases	Increases	Unaffected
Anabaena flos-aquae	0	5	0	1	5	1	2
Anabaena sp.	1	4	0	0	4	1	3
Aphanizomenon flos-aquae	1	5	1	0	0	1	7
Asterionella formosa	0	0	0	0	6	1	1
Fragilaria crotonensis	1	6	0	0	2	3	3
Oscillatoria limnetica	0	6	0	1	5	0	3
Phormidium sp.	0	6	0	1	2	2	4
Synedra delicatissima	1	0	1	3	1	3	4
Tabellaria fenestrata	0	4	0	0	4	1	3
					Total : 29	13	30

Figure 20: Temperature profiles at start of light experiments.

Temperature profiles at the beginning of the three light experiments:

Experiment 1 (30 July)

Experiment 2 (13 August)

Experiment 3 (26 August)

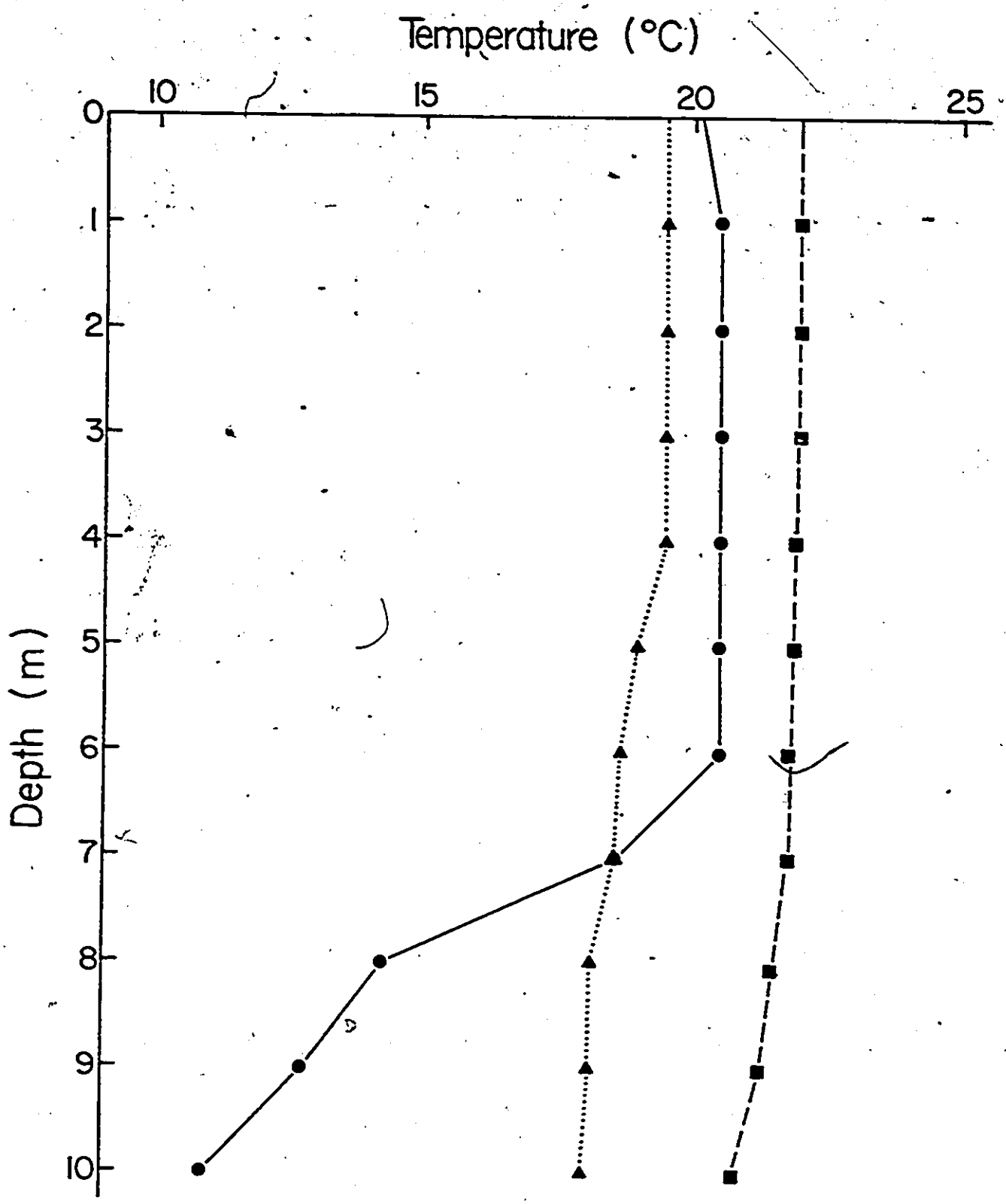

Temperature (°C)
10
15
20
25
0
1
2
3
4
5
6
7
8
9
10
Depth (m)

TABLE 10

Number of light intensity preferences.

Number of significant preferences for light intensity (greater or less than 5% I_o) found in the three experiments.

	Experiment		
Level of Comparison	1	2	3
Taxonomic Group	4	3	0
Ratio of Taxonomic Groups	9	5	2
Species	6	4	4
Total	19	12	6

Only four species, three blue-greens and one chrysophyte, showed preference for colour (Table 13). All were influenced by either red or blue light.

4.3.2.2 Group Preferences

As shown in Fig. 21, the total phytoplankton volume was not significantly affected by differences in light intensity. The responses of the groups were quite different: diatoms and green algae were favoured by high intensity compared to dinoflagellates and flagellates which increased their volume significantly under reduced illumination. The group ratios confirmed this dichotomy. As for specific preferences, most group differences were found in the first experiment (Table 10).

Red light was the only colour treatment that significantly altered community structure (Fig. 22). This manipulation generally increased the relative proportion of blue-greens, diatoms and green algae against that of dinoflagellates. The small group of chrysophytes and cryptophytes tended to be relatively enhanced by blue light.

TABLE 11

Species in cubes - frequency of occurrence.

List of species recorded in the cubes during the experiments with frequency of occurrence.

Species	Frequency
BLUE-GREENS	
Anabaena flos-aquae	0.980
Anabaena spiroides	0.007
Anabaena sp. 1	0.837
Anabaena sp. 2	0.204
Aphanizomenon flos-aquae	0.986
Aphanothece saxicola	0.007
Chroococcus limneticus	0.143
Coelosphaerium Naegelianum	0.014
Dactylococcopsis acicularis	0.415
D. Smithii	0.156
Gloeotrichia echinulata	0.102
Gomphosphaeria lacustris	0.218
Lyngbia birgei	0.014
Merismopedia punctata	0.020
Microcystis aeruginosa	0.279
Oscillatoria limnetica	0.837
O. limosa	0.041
Phormidium sp.	0.612
Rhabdoderma sigmoidea	0.238
CHRYSOPHYTES	
Chlorochromonas minuta	0.531
Chrysocapsa sp.	0.034
Dynobryon divergens	0.014
Mallomonas producta	0.007
CHRYPTOPHYTES	
Chroomona Nordstedtii	0.027
Cryptomonas erosa	0.224
C. ovata	0.034
DIATOMS	
Asterionella formosa	0.224
Cymbella ventricosa	0.388
Cyclotella sp.	0.653
Fragilaria crotonensis	0.102
Melosira granulata	0.068
Navicula sp.	0.068
Nitzschia sp.	0.068
Stephanodiscus niagarae	0.014
Synedra sp.	0.129
Tabellaria fenestrata	0.088

(Table 11 cont'd)

Species	Frequency
DINOFLAGELLATES	
Ceratium hirundinella	0.898
Peridinium spp.	0.898
GREENS	
Ankistrodesmus Braunii	0.075
A. falcatus	0.102
A. gelifactus	0.048
Botryococcus sp.	0.007
Chlamydomonas sp.	0.129
Closterium gracile	0.129
Coelastrum microporum	0.007
Cosmarium circulare	0.143
Elakatothrix gelitanosa	0.034
E. viridis	0.041
Golenkinia radiata	0.014
Kirchneriella lunaris	0.068
Oocystis parva	0.701
O. pusilla	0.014
Planktosphaeria sp.	0.102
Quadrigula closteroides	0.061
Scenedesmus bijuga	0.007
S. dimorphus	0.014
S. obliquus	0.435
Spaerocystis Shroeteri	0.048
Staurastrum paradoxum	0.503
Tetraedron minimum	0.381
OTHERS	
Microflagellates	0.980

TABLE 12

List of species affected by light intensity.

Symbols are used as follows: ! indicates a significant preference for intensity > 5% I_o; * indicates a significant preference for intensity < 5% I_o.

Species	Experiment		
	1	2	3
"High" light species			
Anabaena flos-aquae	!		!
Aphanizomenon flos-aquae	!		!
Cyclotella sp.		!	
Dactylococcopsis acicularis		!	
Gloeotrichia echinulata		!	
Microcystis aeruginosa	!		
Phormidium sp.			!
Planktosphaeria sp.	!		
Staurastrum paradoxum		!	
Tetraedron minimum	!		
"Low" light species			
Gomphosphaeria lacustris			*
Peridinium sp.	*		

TABLE 13

List of species affected by colour manipulations.

List of species significantly affected by the manipulations of colour relative to control.

Species	Response
Chrysocapsa sp.	enhanced under blue light
Dactylococcopsis Smithii	reduced under blue light
Gloeotrichia echinulata	reduced under red light
Rhabdoderma sigmoidea	reduced under blue light

Figure 21: Light intensity and algal group interactions.

Effect of light intensity on pairwise interactions between algal groups. Significant differences are indicated as follows: L denotes relative advantage under "low" intensity (< 5% I_o); H denotes relative advantage under "high" intensity (> 5% I_o). Superscripts indicate the experiment(s) where the effect was observed and apply to both halves of the box. Notation in brackets refers to the significant response - if any - of each single group.

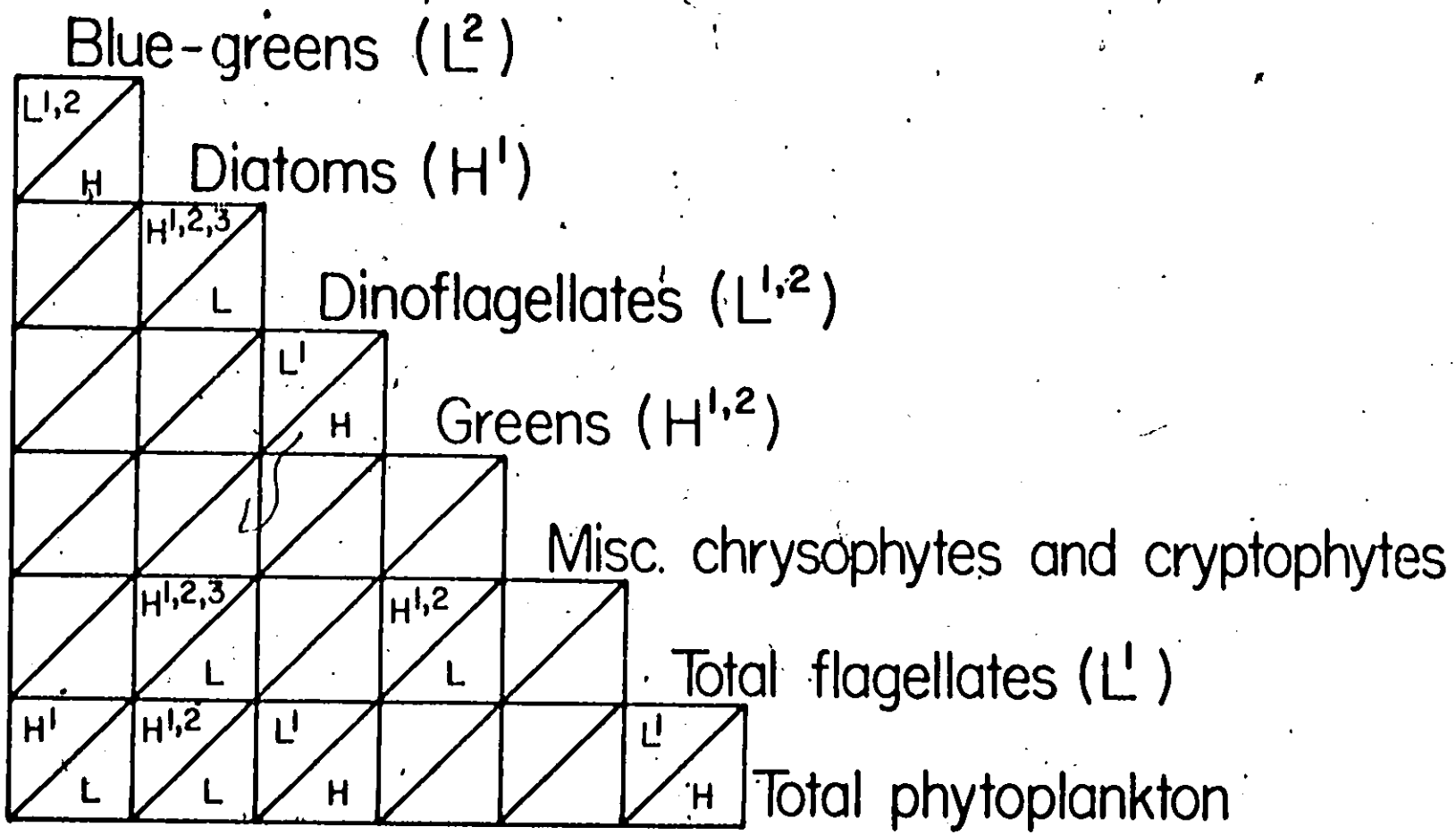
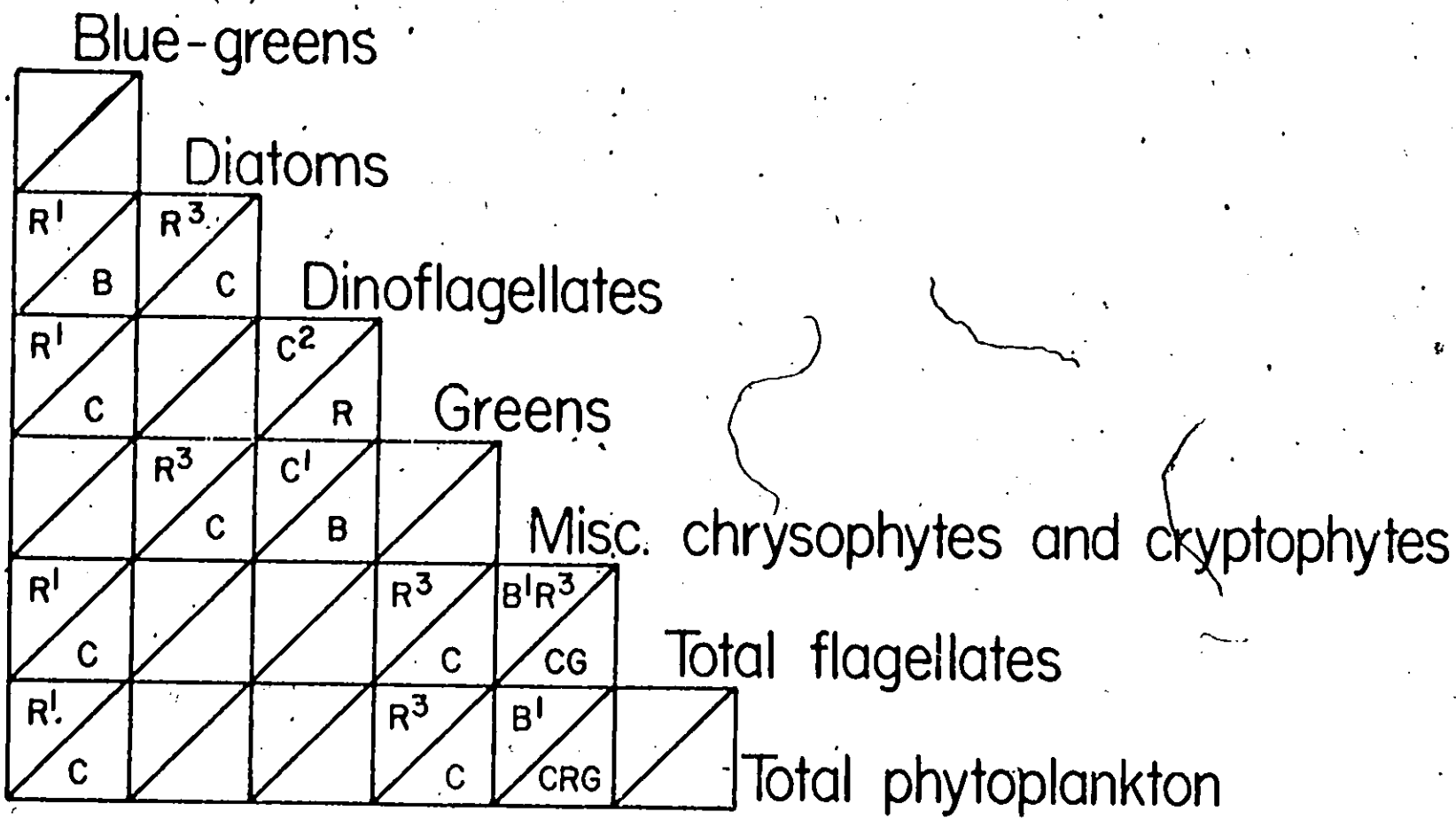

Blue-greens (L^2)
$L^{1,2}$
H
Diatoms (H^1)
$H^{1,2,3}$
L
Dinoflagellates ($L^{1,2}$)
L^1
H
Greens ($H^{1,2}$)
Misc. chrysophytes and cryptophytes
$H^{1,2,3}$
L
$H^{1,2}$
L
Total flagellates (L^1)
H^1
L
$H^{1,2}$
L
L^1
H
L^1
H
Total phytoplankton

Figure 22: Colour and algal group interactions.

Effect of colour on pairwise interactions between algal groups. Significant differences are indicated as follows: B denotes relative advantage in blue light, G in green light, R in red light, and C in control. Superscripts indicate the experiment where the effect was observed.


Blue-greens
Diatoms
Dinoflagellates
Greens
Misc. chrysophytes and cryptophytes
Total flagellates
Total phytoplankton
R1
B
R3
C
R1
C
C2
R
R3
C
C1
B
R1
C
R3
C
B1R3
CG
R1
C
R3
C
B1
CRG

4.4 DISCUSSION-

4.4.1 Response of Niche Overlap to Nutrient Enrichment

The overall decrease in niche overlap observed after nutrient enrichment and subsequent increased competition supports the niche overlap hypothesis of Pianka (1972). Moreover, it provides experimental support to the theoretical studies of Rapoport (1974) and Abrams (1977), as it demonstrates that increased competition magnifies the advantage of some species at the expense of poorer competitors.

This phenomenon can be seen in extremely eutrophic lakes which have dense algal blooms of low diversity (Levandowsky, 1972). Another, purely physical explanation for reduced diversity under bloom conditions is that the euphotic zone is shallower, and this presents less opportunity for depth partitioning.

The algae that increased their niche overlap with enrichment (Fragilaria and Synedra) can be viewed as superior exploiters of the nutrient resources provided. The other species which decreased their overlap are then poorer competitors for these resources. Asterionella, which was the most adversely affected by the treatment, is known to require high nutrient (especially silica) concentrations, which occur during the spring and autumn circulation (Lund et al., 1963). It is sometimes succeeded by Fragilaria crotonensis when nutrient levels fall (Gardiner, 1941).

Aphanizomenon remains largely unaffected by the increase in competition and some evidence suggests that some blue-greens can take up nutrients from deep in the euphotic zone as they diffuse from the sediment at high temperatures (Hutchinson, 1967, p. 459). This may allow for storage of these nutrients in the cells, followed by ascension into the nutrient-poor waters closer to the surface (Reynolds and Walsby, 1975). This ability for luxury consumption is probably responsible for this species' tolerance of a wide range of conditions, and hence for its ubiquity.

4.4.2 Response of Communities to Light Manipulation

While nutrient concentrations had substantial effects on algal species interactions, most of the phytoplankton analyzed for light intensity and colour preferences were not significantly favoured by a particular light condition. Also, no taxonomic consistency was observed in the species that did show preferences. In the context of the enrichment study this would imply that much of the depth segregation of species is controlled by factors other than the light gradient, for example, nutrients or grazing.

Ten species were, however, favoured under the "high" light condition. These will be at an obvious disadvantage in the deeper layers of lakes and will require mechanisms to maintain their position in the upper reaches of the euphotic zone. One does see adaptations which may allow reduction in

sinking. These include gas vacuoles in most of the blue-greens, plus a density-reducing mucilaginous sheath in Gloeotrichia, Microcystis and the green Planktosphaeria. Large surface:volume ratios would reduce sedimentation in small species such as the green alga Tetraedron. Cyclotella, which prefers high illumination has two adaptations which might result in reduced sedimentation from well-lit zones. Despite a relatively heavy silicon frustule it has a lower sinking speed than either Synedra delicatessima, Fragilaria crotonensis (Grim, 1939), Asterionella formosa, or Melosira agassiz (Tilman and Kilham, 1976). In addition, Cyclotella does not show higher sinking rates while in a stationary growth phase than when it is in an exponential phase, contrary to Asterionella and Melosira (Tilman and Kilham, 1976).

The two species significantly enhanced by lower light conditions should be found in the deeper strata in the water column, especially if they can tolerate the higher numbers of grazers at this level during day-time. This is probably true for Gomphosphaeria, which along with other blue-greens is allegedly distasteful to herbivores (Arnold, 1971) and Peridinium which may be too large to be ingested by grazers (Gliwicz, 1975). The ability to succeed at such low light levels may well have evolved in response to intense competition from the "high" light species in the upper euphotic zone.

The low number of specific colour preferences indicates that this is but a minor factor in determining species distributions. That two species, Dactylococcopsis acicularis and Gloeotrichia showed preferences for both intensity and quality suggests that wavelength may play a role as an added cue for vertical positioning in these algae.

The differential utilization of the light gradient among a few species indicates that the potential exists for partitioning this resource. This, along with the results of the enrichment experiments suggests several strategies for the major species. The two species competitively enhanced by enrichment were not favoured by a particular light condition. Therefore their cue for vertical segregation is probably nutrient levels as they are good competitors for this resource. This would place them at positions in the water column where nutrients are limiting to other species. The two species, Fragilaria and Synedra, are also known to be more resistant to blue-green algal allelopathic substances than are diatoms of other families such as Melosira and Tabellaria. This allows coexistence with blue-greens which, as stated earlier, also are favoured under low nutrient concentrations.

Conclusions can be drawn for several other species. Among the blue-greens, Anabaena and Phormidium, that are at a disadvantage in low-nutrient, high-competition communities, do not respond by displacement into the deeper reaches

of the water column where nutrients are more abundant. Instead they are enhanced by the higher intensities found in the upper strata and possess gas vacuoles for positioning within these regions. Aphanizomenon can tolerate high competition better than those two blue-greens. The competitive outcome between these three species may depend on nitrate and ammonium concentrations, as Aphanizomenon does not fix atmospheric nitrogen (Dugdale and Dugdale, 1962) while Anabaena does (Gorham et al., 1964).

Asterionella and Melosira are at a substantial disadvantage in high-competition communities. Asterionella requires high levels of both light and nutrients (Lund et al., 1963), which would limit its periods of increase to times when turbulence circulates nutrients from sediments and keeps it suspended in the water column. Its high light enhancement in midsummer is thus overridden by low nutrients and sinking. Melosira is especially well adapted to take advantage of periodic increases in turbulence as it can remain viable in the sediments for long periods of time (Lund, 1959).

Although there was no taxonomic consistency in the specific preferences for light conditions, the group preferences agree well with the published record. The reason for the lack of correspondence between group and species preferences may be that the component species within the groups are limited in most cases by other factors. A species pre-

ference, although not significant, may add with other non-significant preferences to produce a group effect. Fully 76% of the species analyzed showed no preference for intensity, indicating that while light plays a role in the gross characteristics of the seasonal succession, there are other factors which control species composition within a successional stage.

The preference of diatoms for high illumination is in accordance with the findings of Lund (1949), Javornicky (1966) and Reynolds (1973). Greens also favoured high light as proposed by Whitford (1960) and Happey-Wood (1976). Both groups should be found in the upper part of the water column and in periods of high light intensity - although exceptions do exist such as diatoms flourishing under ice (Lecewicz et al., 1973; and personal observation). The separation of these two groups appears to be temporal and may be based on differences in buoyancy or temperature preferences (Patrick, 1969). The result is that diatoms predominate in spring and greens in summer.

The low light enhancement of the dinoflagellate and total flagellates groups may account for the predominance of species from these groups at lower depths in many lakes (Giamotti, 1966; Rodhe et al., 1966). Success under these conditions is often attributed to the well known ability of some species to vertically migrate from dark to light regions of the water column (Berman and Rodhe, 1971; Tilzer,

1973; Reynolds, 1976b), that is, from light-limited to nutrient-limited regimes (Dugdale, 1967). In marine environments at least, Eppley et al. (1969) proposed that large dinoflagellates with high half-saturation constants for nitrate and ammonium depend on vertical migration between these strata to meet their nutrient and light requirements. This would, however, be extremely costly energetically. Since vertical migration was prevented in my experiments, I suggest that, instead of constituting a temporary refuge for dinoflagellates, the darker zone of lakes offers optimal conditions for their growth. Heterotrophy, which has been reported for a number of species of dinoflagellates and other flagellates (Droop, 1962; Morgan and Kalff, 1976), may be invoked to explain their growth at great depths. Its importance is probably a function of the intensity of competition with bacteria. Usually bacteria would be favoured because of their growth kinetics but in some cases, especially in high altitude ultraoligotrophic lakes, short wave radiation (300-400 nm) might contribute to the abnormally high production of species such as Peridinium at depths as great as 40 m (Rodhe et al., 1966).

The responses of blue-green algae were inconclusive. While they tended to favour higher intensities in the first experiment, they preferred the darker containers in the second. This may be due to a physiological adaptation which allows them to maintain their maximum rate of photosynthesis

while reducing the light intensity required for saturation (Jones, 1978). Blue-greens may have been responding to intermediate rather than high light levels in the first experiment as their accessory pigments are susceptible to bleaching by intense light (Brown and Richardson, 1968). This would cause them to lose their ability to maintain their cells at a particular depth and they would sink out of the euphotic zone (Reynolds, 1973b).

The response of blue-green:diatom ratio to differing light intensities is of special interest with respect to the succession of both groups in lakes. Jones (1977b) suggested that temperature may be the most important factor as diatoms are more severely penalized than blue-greens by respiratory losses at high temperatures. The present results show that even at the higher ambient temperatures of the upper euphotic zone, diatoms outcompeted blue-greens when illumination was high. This indicates that sinking out of the euphotic zone during stratified conditions, rather than high temperature, may be responsible for their midsummer decline. When kept suspended, as was the case in the present experiments, they can succeed, despite the high temperatures.

The degree of stratification also plays a role in the number of specific and group preferences observed. This is not surprising, considering that when the water column is isothermally mixing a preference would not be selected for as the algae could not remain in a preferred light regime

for any length of time. Talling (1966) found that the degree of physiological adaptation with depth in Asterionella was more pronounced during stratified conditions.

With regard to colour, the blue-greens, diatoms and greens were favoured over the other groups under red light, and not blue as reported in previous studies (Haxo, 1960; Wallen and Geen, 1971; Shimura and Ichimura, 1973). They may therefore be limited to the upper part of the water column, where red wavelengths are largely confined, which would agree with their preference for high intensity. Dinoflagellates, which were proportionately depressed by red light would be forced to occupy deeper regions during daytime. This is also consistent with their low light preference.

Chapter V

CONCLUSIONS

The algal community of Heney Lake is typical of temperate hardwater lakes in composition and in seasonal succession. Generally, the shifts in dominance from one group to another are due mainly to abrupt changes in the degree of water circulation, nutrient concentrations and light levels, which take place during the onset and breakdown of thermal stratification (Round, 1971).

In open lake habitats, the period of thermal stratification is expected to support a higher number of species than the mixed period because of increased spatial heterogeneity of the water column (Margalef, 1958; Richerson et al., 1970; 1975). In shallow or near-shore habitats, however, immigration of species from the sediments or shore area may increase the number of species during the mixed periods. Apparently the latter is the case in the bay where the present study was undertaken as species richness peaked in the unstratified months of August and September. Because of this immigration of new species and intermittent input of nutrients from sediments, competitive equilibrium is probably not achieved during this period of time. A lack of equilibrium may act to disrupt competitive interactions so

that dominant competitors are prevented from excluding other species (Hutchinson, 1961; Connell, 1978). During the stratified period, however, equilibrium conditions may be assumed (Hulburt, 1977).

In describing the competitive interactions of these communities, it was essential that a variety of different communities be sampled since the competitive tactics of a species may vary depending on the combination of other species present. The importance of this approach becomes more clear in light of phenomena such as alternative stable communities which can exist for a given species pool. The particular set of species present may depend on historical factors in the development of the community (Gilpin and Case, 1974) or from the often unpredictable results of diffuse competition (Diamond, 1975). The enclosure treatments clearly provided the opportunity to study a set of species in very different communities.

Despite the fairly distinct succession of phytoplankton species, a large number of algae were significantly associated in time. These species are similar in the general environmental conditions in which they occur, which have been termed the linking factors of the ecological niche (Lewandowsky, 1972b). The causes of these similarities may include general morphology, size, or taxonomic affinity. In the present study the latter criterion appears important as more associations occur between species of the same division

than between species from different divisions. Also, the number of associations within a particular division may reflect the general degree of competition present in the community at its peak period of abundance. Species which form communities in which a high number of associations are found may be able to afford strong co-occurrence without risking exclusion because of a low level of competition. Factors reducing the overall level of competition may include environmental instability, as discussed above, the cropping of populations by grazing, or habitat partitioning. Diatoms, which have the highest number of associations, predominate in unstable water columns and are also more susceptible to grazing than are blue-greens.

With depth many pairs of associated species became disassociated, and members of one pair even become negatively correlated. On this physical scale, the ecological differences between species became apparent. In general, depth appears to play a major role in segregating planktonic species. However, this time there is no apparent difference between blue-greens and diatoms with respect to spatial separation, even though blue-greens possess a greater ability to maintain vertical station in the water column.

Competitive abilities and species preference for light are not rigidly linked to taxonomic division. This suggests that similarities within groups account only for the large scale patterns of seasonal abundance. Within each

group, a variety of competitive strategies have developed, which reduce ecological similarity and allow coexistence of its members.

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