THE PHYTOPLANKTON COMMUNITIES OF NINE LAKES, WAIKATO, NEW ZEALAND: A COMPARATIVE STUDY OF FLORISTICS, SEASONAL DYNAMICS AND THE INFLUENCE OF HERBIVORY

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LIST OF ABBREVIATIONS

AODC	acridine orange direct count
C.V.	coefficient of variation
DHM	dissolved humic material
GALD	greatest axial linear dimension
I.D.	internal diameter
ISI	important species index
LC	limnocorral
n	sample size
ns	not significant
pu	plankton unit
r	value of the correlation coefficient
SD	standard deviation
SE	standard error
SGALD	second greatest axial linear dimension
SK	skewness statistic
yr BP	years before present
#	tentative identification due to lack of electron microscopical observations

CHAPTER SIX

PHYTOPLANKTON SEASONALITY

6.1 SEASONAL ANALYSES OF THE PHYTOPLANKTON COMMUNITIES OF THE NINE STUDY LAKES

Phycologists have advanced many explanations for the complex phenomenon of phytoplankton periodicity. The literature is extensive, and includes many reviews (e.g., Lund, 1965; Round, 1971; Fogg, 1975; Porter, 1977; Smayda, 1980). Much of the early material is descriptive, but recent work by Reynolds (1976, 1980, 1982, 1984a, b), Lewis (1978c, d; 1986), Sommer, 1985; Sommer *et al.*, 1986) and Stewart & Wetzel (1986) has demonstrated that, despite complex interactions between many regulators of periodicity, valid generalisations can be made upon which hypotheses may be formulated and experimentally tested.

'Phytoplankton succession' and 'seasonal periodicity' are frequently used synonomously (e.g., Guillard & Kilham, 1977; Smayda, 1980; Sommer *et al.*, 1986; Stewart & Wetzel, 1986). In its broadest sense, succession refers to a sequence of plant (or animal) communities in time. The term evolved in terrestrial ecology, with the floral studies of Clements (e.g., 1916, 1928, 1936) providing the basis for its acceptance. To Clements, successions were life histories of superorganisms, and consequently were both unidirectional and predictable. These early studies focused on species sequences, whereas more recent investigations have included analyses of changes in productivity, diversity, and niche breadth with time (see Odum, 1969). However, another interpretation of succession, which although generally attributed to Gleason (1926), has only recently been emphasised, views succession in the context of adaptations of individual species which are independent of any transcendant properties of the community as a whole (Connell, 1972; Colinvaux, 1973; Drury & Nisbet, 1973; Horn, 1974; Grime, 1977). In these terms, succession is a consequence of differential growth, reproductive and survival abilities, and therefore cannot necessarily be considered unidirectional.

The use of terrestrial succession as a model for phytoplankton periodicity has serious limitations (Smayda, 1980), and strong arguments have been advanced that succession is too narrow a term to

be appropriate for all types of periodicity (Reynolds 1980, 1982, 1984a, b). Instead, Reynolds considers temporal variations in phytoplankton composition and abundance to be of three sequential types: autogenic successions, which occur during periods of well-developed stratification and therefore are characterised by species-induced changes; reversions, which repeat earlier stages following brief, erratic disturbances of the water column; and shifts or allogenic changes, which result from long-term, sustained holomictic periods.

Phytoplankton periodicity is of fundamental importance to a lake's trophic organisation and thus, for a considerable period of time, seasonal dynamics have been the focus of numerous investigations. However, although phytoplankton seasonality can be examined with respect to either patterns of total biomass, taxonomic class, or individual species (Kalff & Knoechel, 1978), comprehensive investigations addressing all three areas are rare. Population dynamics and autecology of individual phytoplankters frequently receive the least attention, despite Gleason's views with regard to terrestrial ecology, and the conclusions of some phycologists (e.g., Lehman & Sandgren, 1985; p. 45) that 'understanding the dynamics of the plankton requires attention to the biological entities themselves'.

Furthermore, classical aspects of mixing, stratification and phytoplankton cyclic fluctuations described largely from dimictic Northern Hemisphere lakes, do not necessarily characterise either lakes in areas such as New Zealand which have oceanic climatic regimes (Chapter 3), or relatively shallow lakes.

In New Zealand, seasonal community dynamics are poorly understood because of the use of inappropriate sampling intervals and/or techniques, and the absence until recently of long-term sets of quantitative data (Chapter 1.1). However, from the small amount of data available, it appears that only a few genera (*Anabaena*, *Melosira* = *Aulacosira*, *Cyclotella*, *Synedra* = *Fragilaria* and *Dinobryon* seem to be of key importance (Viner & White, 1987). Also, none has been reported to show markedly pronounced seasonality.

Anabaena spp. may be found throughout most of the year, including winter (Pridmore & Etheredge, in press) (Appendix XI). *A. flos-aquae* increased in abundance during autumn in Lake Hayes (Burns & Mitchell, 1974) when the lake was holomictic (concentration approximately 560

cells ml^{-1}), and it bloomed in Lake Tarawera in winter (August 1983) (unpublished data). Also, *A. oscillarioides* has been dominant in Lake Rotongaio throughout the coldest months (April-September, 1975), comprising at least 90% of the total phytoplankton community (Forsyth *et al.*, 1983). *Melosira* spp. are also relatively unselective, although generally are more common in winter (Viner & White, 1987). Conversely, *Dinobryon* spp., *Cyclotella* spp., and *Synedra* spp., peak at various times of the year, but more frequently in winter.

This chapter details the seasonal periodicity of both total phytoplankton numbers and biomass, and the major species, for each study lake, and compares temporal patterns with varying mixing regimes and phytoplankton strategies.

6.1.1 LAKE KAINUI

6.1.1.1 Temporal Variations in Total Phytoplankton Density and Biomass

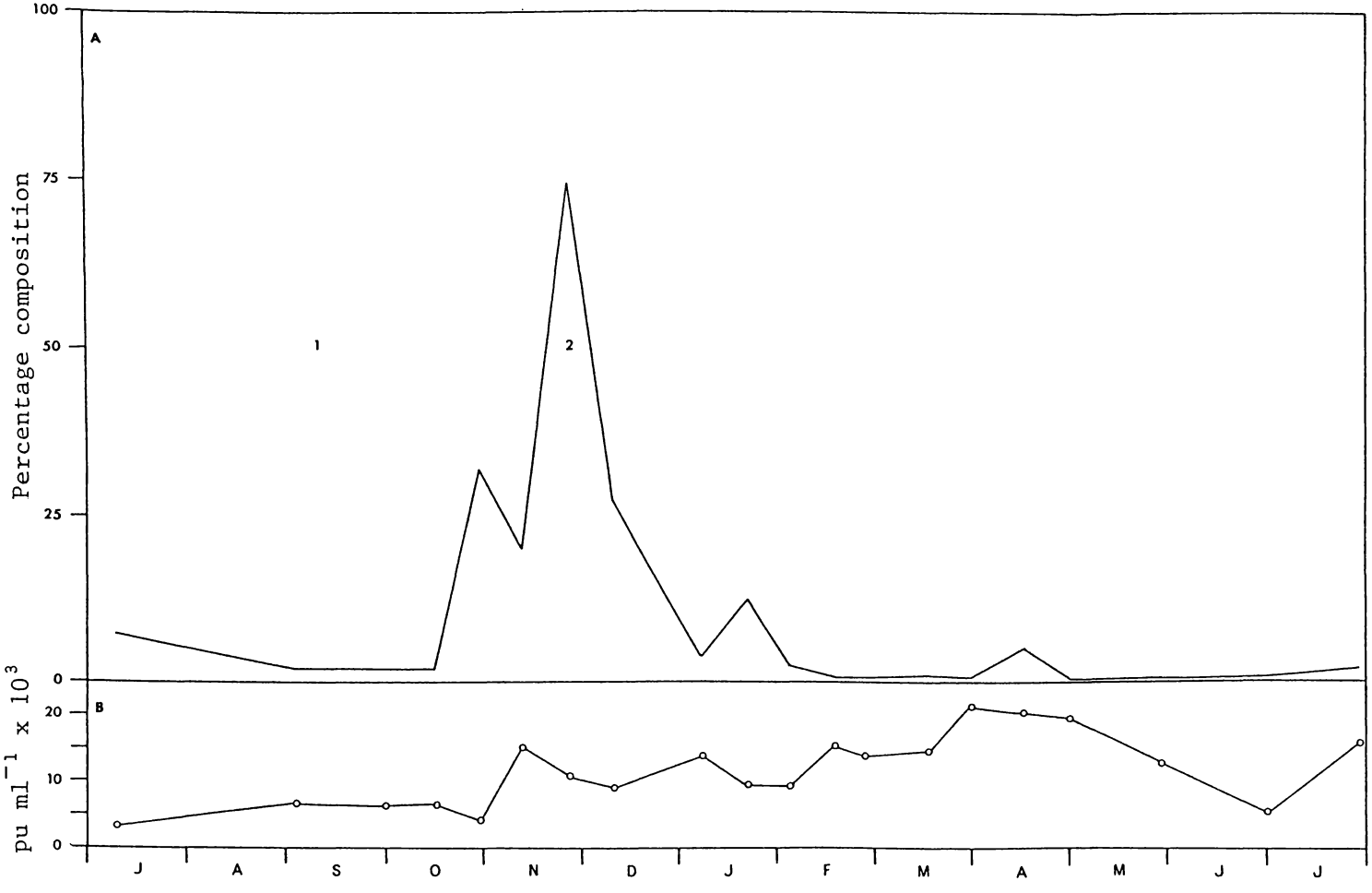
Total phytoplankton density varied considerably, ranging from 3234 to 21,141 pu ml^{-1}; the mean density, the highest of the nine study lakes (Table 7/0), was 11,640 pu ml^{-1} (n = 20). Densities were low during winter 1983, generally increased throughout spring and summer, and reached their maximum in autumn 1984 (Fig. 6/0).

Total biomass (Fig. 6/1) also fluctuated irregularly, ranging from 1.2 to 16.8 g m^3 (mean 7.9 g m^3 [n = 20]). It was relatively low during winter and spring, but increased rapidly throughout early summer (12.8 g m^3 [10.12.84]). After a decline in January, it increased again during late summer and autumn 1984. The maximum biomass (16.8 g m^3) was recorded in autumn (16.4.84), and levels then steadily declined before a further upsurge in mid-winter (12.7 g m^3 [28.7.84]).

6.1.1.2 Temporal Variations in the Composition of the Total Phytoplankton Standing Crop

Only two classes, the Zygophyceae and the Euchlorophyceae, were numerically important (Fig. 6/0). The Zygophyceae was dominant throughout the entire year, except for a brief period in early summer, when it was temporarily replaced by the Euchlorophyceae (74%). Excluding this early summer sample, the zygophycean proportion of the

Fig. 6/0 Temporal variations in: (a) phytoplankton class composition, in terms of abundance; (b) total number of pu ml^{-1}, in Lake Kainui, July 1983 to July 1984. Taxa with contributions <0.5% are not included in this figure.

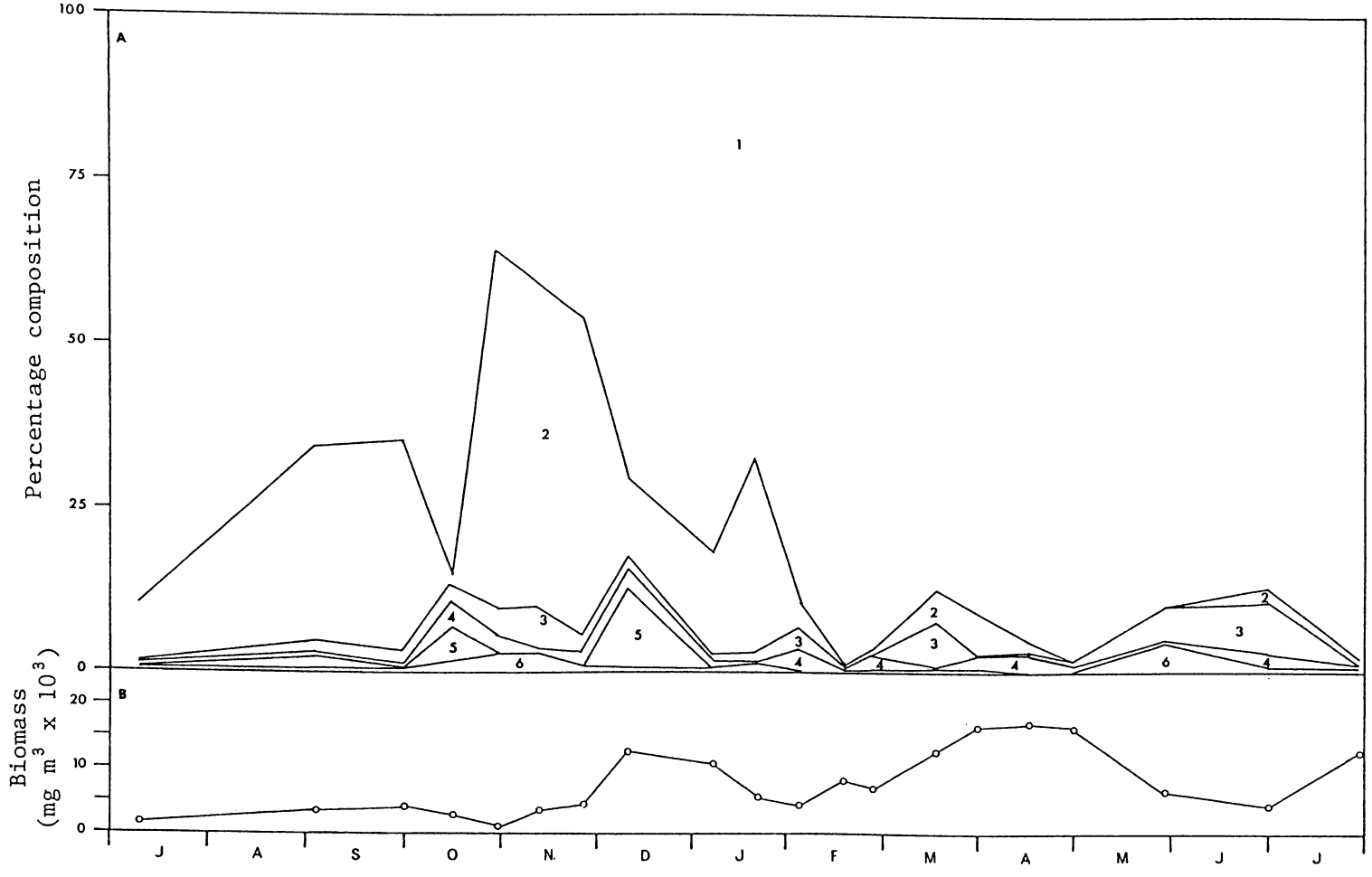


Key:

1. = Zygophyceae

2. = Euchlorophyceae

Fig. 6/1 Temporal variations in: (a) phytoplankton class composition, in terms of biomass; (b) total biomass (mg m^3 x 10^3) in Lake Kainui, July 1983 to July 1984. Taxa with mean contributions <0.5% are not included in this figure.



Key:

1. = Zygophyceae
2. = Euchlorophyceae
3. = Diatomophyceae
4. = Euglenophyceae
5. = Dinophyceae
6. = Cryptophyceae

mean total density ranged from 64 to 99% (mean 91% [n = 19]).

With three exceptions, the Zygophyceae also dominated the biomass throughout the entire sampling programme (Fig. 6/1). Its proportions ranged from 36 (29.10.83) to 99% (18.3.84), and it accounted for ⩾ 65% of the total biomass on 17 of the 20 sampling occasions (85%). Low zygophyte biomass coincided with euchlorophyte biomass peaks in late winter-early spring (3.8.83 and 1.10.83), early summer (29.10.83, 12.11.83, and 26.11.83), and mid-summer (7.1.84); at no other time did the Euchlorophyceae account for ⩾ 10% of the total biomass.

Despite the minor roles played by the other nine classes, two points are noteworthy. First, peaks of cryptophyte biomass followed periods of increased total biomass (29.10.83 and 12.11.83; 21.1.84; 28.5.84); secondly, diatom maxima occurred erratically throughout the sampling year (Fig. 6/1).

6.1.1.3 Temporal Variations in Phytoplankton Species Diversity

Species continuity was generally low (Table 6/0), with the number of species per sample ranging from 7 to 43 (mean 21 ± 11 [n = 20]). The Shannon-Wiener index ranged from 0.5 to 2.9 (mean 1.3 ± 0.6), and low indices coincided with both low species numbers and periods of peak phytoplankton abundance (Fig. 6/0).

The mean number of zygophyte species found per sample (7) (Table 6/1) was greater than that of the Euchlorophyceae (6), despite major differences in their total numbers (19 and 33 species, respectively). Although the numbers of diatoms (18), cyanophytes (17) and euglenophytes (18), were similar to the Zygophyceae, in each instance their mean frequency of occurrence was markedly lower.

6.1.1.4. Percentage Similarity of the Phytoplankton Communities

The percentage similarity of consecutive communities ranged from 18 to 97% (Table 6/2), the highest being recorded in mid-summer (18.2.84/27.2.84). It is noteworthy that the lowest number of species per sample was also recorded on 27.2.84, and futhermore, this trend was repeated on three further occasions: 17.3.84/31.3.84 (94%; 9 species in both communities); 16.4.84/1.5.84 (93%; 8 and 11 species, respectively); and to a lesser extent, 31.6.84/28.7.84 (92%; 17 and 11 species, respectively). The least similar consecutive communities occurred in early summer (26.11.83/10.12.83), coinciding with periods of high species richness (37 and 43 species, respectively [Table

TABLE 6/0 α diversity and Shannon-Wiener information index for each sampling date in Lake Kainui, July 1983 to July 1984.

Date	α Diversity		Shannon-Wiener Information Index
	s	d	
1983			
9.vii	34	9.69	1.52
3.ix	30	7.84	1.04
1.x	19	4.99	1.26
15.x	30	7.87	0.94
29.x	29	8.01	2.1
12.xi	31	7.42	1.18
26.xi	37	9.18	1.6
10.xii	43	10.87	2.93
1984			
7.i	31	7.48	1.84
21.i	26	6.53	2.28
4.ii	10	2.51	1.44
18.ii	15	3.59	0.98
27.ii	7	1.69	1.15
17.iii	9	2.16	1.12
31.iii	9	2.08	0.94
16.iv	8	1.85	0.66
1.v	11	2.56	0.71
28.v	11	2.68	1.28
31.vi	17	4.55	0.79
28.vii	11	2.62	0.47

TABLE 6/1 Variation in the number of species (plus varieties) per 1 ml aliquot in Lake Kainui, July 1983 to July 1984.

Taxon	Number of Species			
	Maximum	Minimum	Mean ± 1 SD (n = 20)	Total
CHLOROPHYTA				
Euchlorophyceae	15	1	6.5 ± 4.4	33
Ulothricophyceae	1	0	0.05 ± 0.2	1
Zygophyceae	14	3	7.3 ± 3.6	20
CHROMOPHYTA				
Chrysophyceae	2	0	0.4 ± 0.6	3
Diatomophyceae	8	0	2.4 ± 2.0	22
Xanthophyceae	1	0	0.05 ± 0.2	1
CYANOPHYTA				
Cyanophyeae	6	0	1.2 ± 1.6	17
EUGLENOPHYTA				
Euglenophyceae	3	0	1.3 ± 0.8	8
PYRRHOPHYTA				
Cryptophyceae	2	0	0.9 ± 0.4	3
Dinophyceae	2	0	0.5 ± 0.8	4
RAPHIDOPHYTA				
Raphidophyceae	1	0	0.1 ± 0.3	1
ALL SPECIES	43	7	20.7 ± 10.1	113

TABLE 6/2 Percentage similarity indices of consecutive and other specified phytoplankton communites in Lake Kainui, July 1983 to July 1984.

Dates	Community Type	Percentage Similarity Index
1983		
9.vii/3.ix	Consecutive	87
3.ix/1.x	"	91
1/x/15.x	"	89
15.x/29.x	"	25
29.x/12.xi	"	74
12.xi/26.xi	"	38
26.xi/10.xii	"	18
10.xii/7.i (1984)	"	58
1984		
7.i/21.i	"	77
21.i/4.ii	"	76
4.ii/18.ii	"	92
18.ii/27.ii	"	97
27.ii/17.iii	"	51
17.iii/31.iii	"	94
31.iii/16.iv	"	85
16.iv/1.v	"	93
1.v/28.v	"	40
28.v/31.vi	"	33
31.vi/28.vii	"	92
9.vii/15.x	winter-spring	81
15.x/7.i	spring-summer	6
7.i/16.iv	summer-autumn	15
16.iv/28.vii	autumn-winter	91
9.vii(1983)/28.vii(1984)	annual	4

6/1]). The mean index was 69 ± 27% (n = 19).

Spring/summer and summer/autumn communities showed marked dissimilarity, unlike those of the colder seasons which had relatively high indices.

6.1.1.5 Species Periodicity

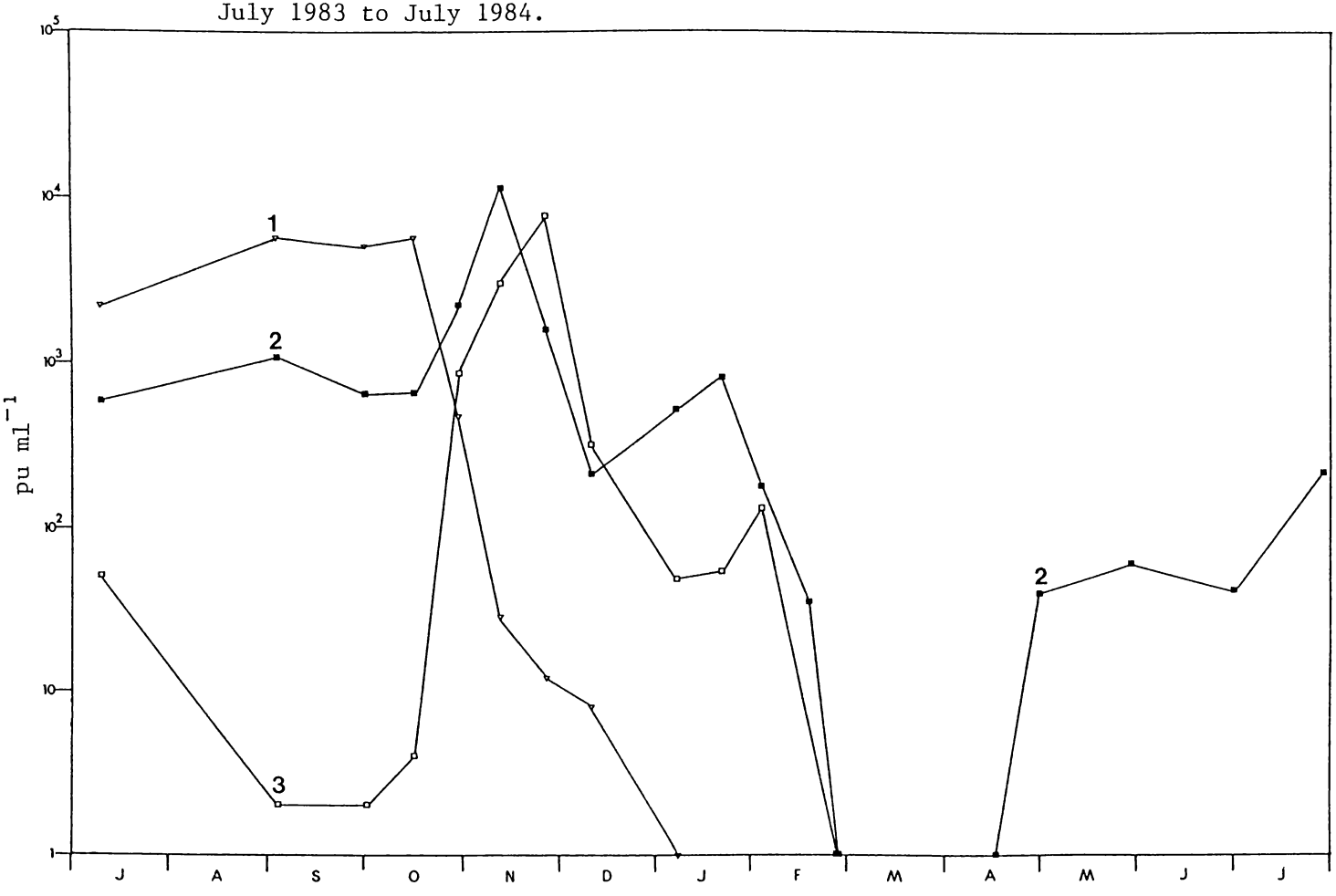
Annual patterns of abundance of the major phytoplankters were characterised by rapid increases followed by dramatic declines, and the absence of marked seasonality. Desmids dominated the plankton throughout the entire year, but no two species exhibited similar cycles.

Five taxa (*Staurastrum brachiatum*, *Closterium acutum* var. *variabile*, *Scenedesmus quadricauda* [the only dominant non-desmid species], *Staurastrum* sp. C and *Staurodesmus* spp. [*S. cuspidatus*, *S. dejectus* and *S. mammillatus*]) respectively occurred in six successive major peaks of abundance (Figs. 6/2 and 6/3).

Staurastrum brachiatum, the most temporally restricted species, was dominant throughout the first four months of the sampling programme. Its initial density was 2246 pu ml^{-1}, and its maximum (5424 pu ml^{-1}) was recorded on 15.10.83 (at which time 100% were parasitised with an unidentified chytrid and/or biflagellate fungus), but numbers then commenced to decrease rapidly, coinciding with a dramatic increase in numbers of both *Closterium acutum* var. *variabile* and *Scenedesmus quadricauda*. The density of *Closterium acutum* var. *variabile* fluctuated throughout early spring but increased dramatically after mid-October. The maximum density (11,096 pu ml^{-1} [12.11.83]) was followed, with the exception of a further peak in mid-summer (21.1.84), by an equally rapid decline. It reappeared in late autumn (40 pu ml^{-1}) (1.5.84), and was increasing once more when sampling ceased. Initially, *S. quadricauda* was present in minimal numbers but, like *C. a.* var. *variabile*, its density began to increase rapidly in early summer reaching 7536 pu ml^{-1} on 26.11.84. Its decline also was similar to *C. a.* var. *variabile*, but it was not found during winter 1984 (Fig. 6/3).

Staurastrum sp. C, like *Scenedesmus quadricauda*, was present in very low numbers throughout winter 1983. It was not found in October,

Fig. 6/2 Temporal variations in the densities (pu ml^{-1}) of *Staurastrum brachiatum*, *Closterium acutum* var. *variabile* and *Scenedesmus quadricauda* in Lake Kainui, July 1983 to July 1984.



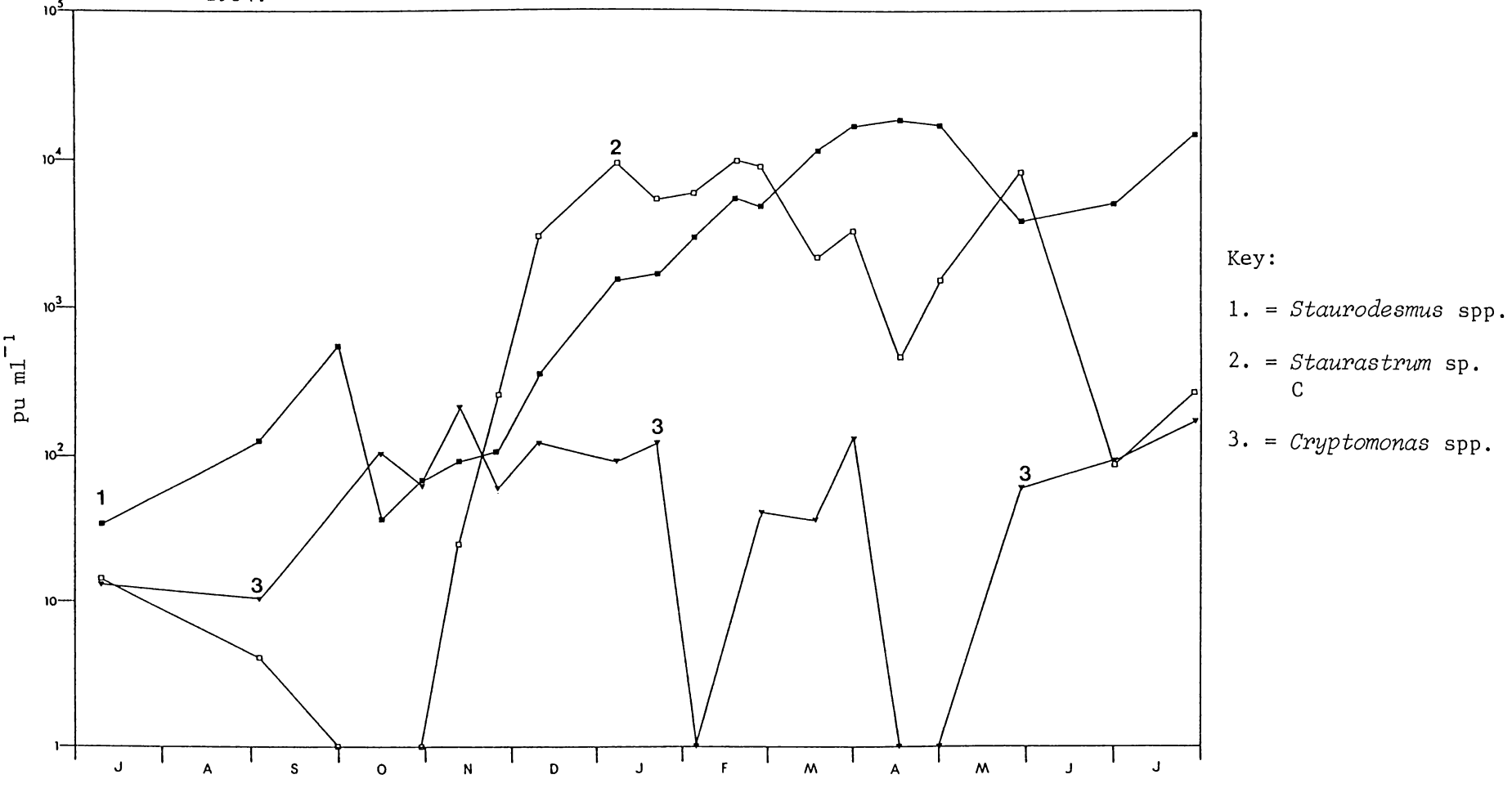
Key:

1. = *Staurastrum brachiatum*

2. = *Closterium acutum* var. *variabile*

3. = *Scenedesmus quadricauda*

Fig. 6/3 Temporal variations in the densities (pu ml^{-1}) of *Staurodesmus* spp., *Staurastrum* sp.C and *Cryptomonas* spp. in Lake Kainui, July 1983 to July 1984.



but between November and February showed a spectacular increase in abundance, reaching a maximum density [9600 pu ml^{-1}] in mid-summer (18.2.84).

Staurodesmus spp. (*S. cuspidatus*, *S. dejectus* and *S. mammillatus*) also were increasing in abundance throughout early summer, albeit at a slightly slower rate than *Staurastrum* sp. C. Their maximum density (18,040 pu ml^{-1}) was recorded on 16.4.84, and their subsequent decline coincided with a further upsurge in numbers of *Staurastrum* sp. C. From November 1983 onwards, dominance alternated between these two taxa.

Quantitatively, the cryptomonads (*Cryptomonas marssonii* and *C. ovata*) were unimportant (Table 4/0) (maximum density 204 pu ml^{-1} [12.11.83]). However, their periodicity is of special interest because, without exception, each cryptomonad peak followed high densities of another major taxon (Figs. 6/2 and 6/3).

6.1.2 Lake Mangahia

6.1.2.1. Temporal Variations in Total Phytoplankton Density and Biomass

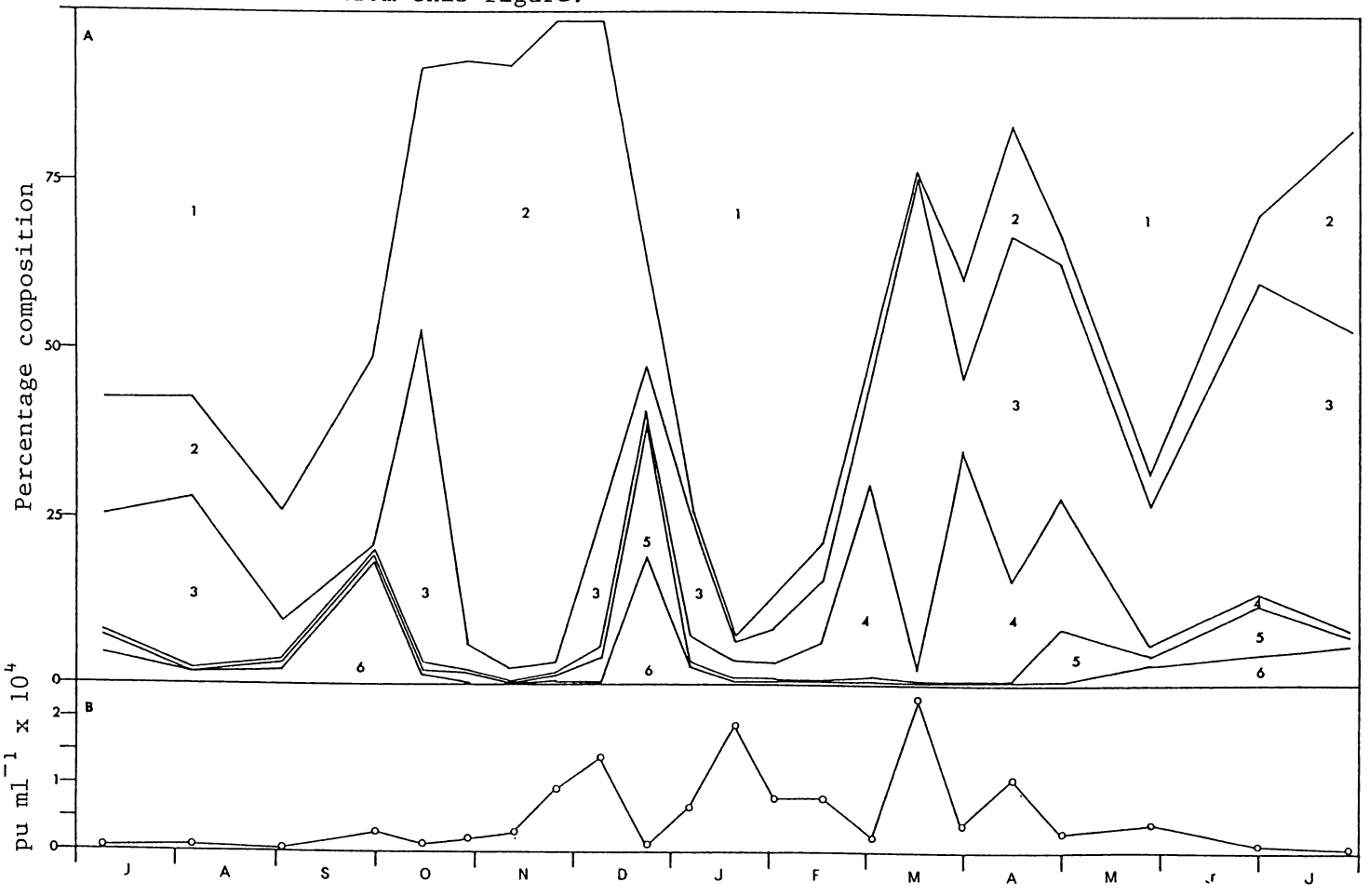
The community was characterised by a broad range of densities (400 to 23,542 pu ml^{-1}; mean 6320 pu ml^{-1} [n = 22]), and sudden, short-lived peaks of abundance (Fig. 6/4). Densities remained relatively low throughout winter 1983, but four major peaks (14,692, 19,122, 23,542 and 11,208 pu ml^{-1}) were recorded between November 1983 and April 1984.

Annual variations in biomass (Fig. 6/5) were similar to those of abundance, although the two maxima did not coincide because the biovolume of *Chlorella* sp. (28 μm^3), which comprised 72% of the mid-March density peak, was much smaller than that of either *Aulacosira distans* (350 μm^3) or *A. granulata* var. *angustissima* (1121 μm^3), which were co-dominants in the mid-January peak (Fig. 6/5). Total biomass ranged from 0.2 (27.7.84) to 10.1 g m^3 (21.1.84) (mean 2.5 g m^3 [n = 22]).

6.1.2.2 Temporal Variations in the Composition of the Total Phytoplankton Standing Crop

Numerically, diatoms and chlorophytes, which alternated their

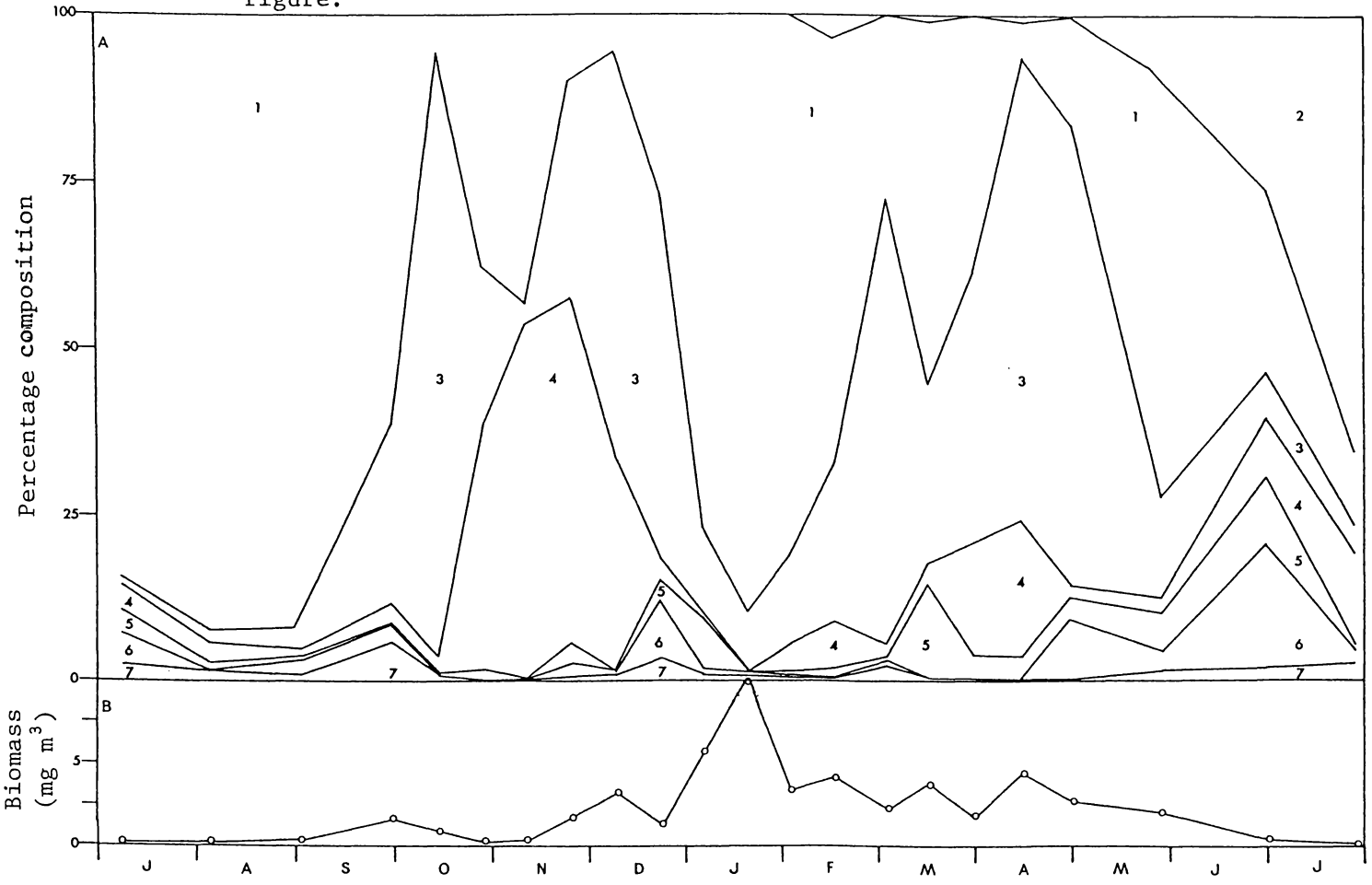
Fig. 6/4 Temporal variations in: (a) phytoplankton class composition, in terms of abundance; (b) total number of pu ml^{-1} x 10^4, in Lake Mangahia, July 1983 to July 1984. The Cyanophyceae, Dinophyceae and Xanthophyceae have been omitted from this figure.



Key:

1. = Diatomophyceae
2. = Zygophyceae
3. = Euchlorophyceae
4. = Euglenophyceae
5. = Chrysophyceae
6. = Cryptophyceae

Fig. 6/5 Temporal variations in: (a) phytoplankton class composition, in terms of biomass; (b) total biomass (mg m^3), in Lake Mangahia, July 1983 to July 1984. The Dinophyceae and the Xanthophyceae have been omitted from this figure.



Key:

1. = Diatomophyceae
2. = Cyanophyceae
3. = Euglenophyceae
4. = Zygophyceae
5. = Euchlorophyceae
6. = Chrysophyceae
7. = Cryptophyceae

periods of importance, were the dominant groups and, with one exception, all other classes were relatively insignificant (Fig. 6/4). From 8.7.83 to 30.9.83, diatoms were dominant (mean proportion 58% [n = 4], and zygophytes and euchlorophytes were sub-dominants. However, during spring and early summer 1984, chlorophytes (particularly zygophytes), increased in abundance and became the major group. From 28.10.83 to 9.12.83 the mean zygophyte proportion was 91% (n = 4). Dominance changed throughout January and February 1984, the mean diatom and chlorophyte proportions being 83 and 11%, respectively (n = 4). This pattern was repeated during the next five months, although the euchlorophyte proportion markedly exceeded that of the zygophytes. The Euglenophyceae, the only other significant class, increased in importance throughout late summer and autumn 1984.

With two exceptions, biomass dominance alternated between the Diatomophyceae and Euglenophyceae. From 8.7.83 to 30.9.83, diatoms were the most important group (mean proportion 83% [n = 4]. In early summer, however, dominance shifted to the euglenophytes (14.10.83 [91%] and 9.12.83 [(61%]). These pulses were short-lived, and diatoms were dominant again throughout January and February 1984 (mean proportion 78% [n = 4]). In autumn, euglenophytes became dominant once more (15.4.84 [70%] and 30.4.84 [69%]), but were replaced by diatoms in early winter (65% [29.5.84]).

This domination by only two taxa was briefly interrupted in early summer by an increase in the importance of the Zygophyceae (53% [11.11.83] and 52% [25.11.83).

The Cyanophyceae appeared in summer 1984, and although initially it was unimportant, by winter [30.6.84] it shared dominance with the diatoms (26 and 27%, respectively). Further increases continued, and by 27.7.84 cyanophytes had replaced diatoms as the dominant class (Fig. 6/5).

6.1.2.3 Temporal Variations in Phytoplankton Species Diversity

The number of species per sample ranged from 14 to 33 (mean 23 ± 6 [n = 22]), with high numbers being recorded in mid-summer 1984 (Table 6/3). However, not all classes showed an increase in species number throughout summer; for example, both the Euchlorophyceae and the Zygophyceae displayed continuous increases from July 1983 to April 1984, and the highest numbers of diatom and cyanophyte, and cryptophyte and dinoflagellate species were recorded in winter 1983

TABLE 6/3 α diversity and Shannon-Wiener information index for each sampling date in Lake Mangahia, July 1983 to July 1984.

Date	α Diversity		Shannon-Wiener Information Index
	s	d	
1983			
8.vii	22	8.11	2.74
5.viii	27	9.23	2.52
2.ix	14	5.08	1.93
30.ix	20	5.68	1.98
14.x	20	6.51	1.78
28.x	18	5.46	0.98
11.xi	16	4.59	0.83
25.xi	25	6.09	0.44
9.xii	19	4.56	0.38
23.xii	18	5.57	2.90
1984			
6.i	28	7.02	2.44
20.i	33	7.71	1.23
3.ii	25	6.34	1.04
17.ii	24	6.07	1.64
3.iii	30	8.71	2.28
16.iii	26	5.95	1.23
30.iii	32	8.82	2.22
15.iv	28	6.91	2.18
30.iv	26	7.43	4.21
27.v	25	6.76	2.23
30.vi	16	5.14	2.99
27.vii	15	5.76	2.96

and 1984, respectively (Appendix IV). Species continuity was generally low, as evidenced by a wide variation in the number of species occurring within each class (Table 6/4).

The Shannon-Wiener index ranged from 0.38 (9.12.83) to 4.21 (30.4.84) (mean 1.96 ± 0.94 [n = 22]) (Table 6/3). Low indices coincided with a period of overwhelming dominance by the Zygophyceae in early summer (28.10.83 to 9.12.83 [Fig. 6/4]), and in particular, *Closterium acutum* var. *variabile* (Fig. 6/2). Conversely, the highest index resulted from a more even distribution of abundance between chlorophytes, diatoms and euglenophytes (Fig. 6/4).

6.1.2.4 Percentage Similarity of the Phytoplankton Communities

Two periods of major community change resulted in a broad range of similarity indices (17 to 95%; mean 61 ± 23% [[n = 21]). The late winter indices (8.7.83/5.8.83 [66%] and 5.8.83/2.9.83 [74%]) were high, and diatoms dominated on both occasions (Fig. 6/4). However, a rapid shift to a chlorophyte community in mid-October, resulted in major alterations to community structure (38% [30.9.83/14.10.83]). The indices for the 28.10.83/11.11.83, 11.11.83/25.11.83, and 25.11.83/23.12.83 communities were also high (92, 91 and 95%, respectively), due to continued dominance by the Zygophyceae (Fig. 6/4); however, increased densities (particularly of chrysophytes and diatoms), caused a second period of dramatic change (17% [9.12.83/23.12.83]). The index fluctuated throughout the remainder of the sampling programme, but high values were generally associated with high diatom densities. In seasonal terms, spring/summer and summer/winter communities were markedly dissimilar (11 and 13%, respectively) (Table 6/5).

6.1.2.5 Species Periodicity

The major euchlorophyte species showed one of two distinct seasonal cycles (Fig. 6/6). *Scenedesmus quadricauda*, *Monoraphidium tortile* and *Tetrastrum triangulare* were usually present throughout the entire sampling period, each exhibiting one major peak of abundance; maximal densities were 652, 264 and 562 pu ml^{-1}, respectively. In contrast, both *Chlorella* sp. and *Raphidocelis contorta* were absent throughout winter and spring 1983. *Chlorella* sp. was first recorded in

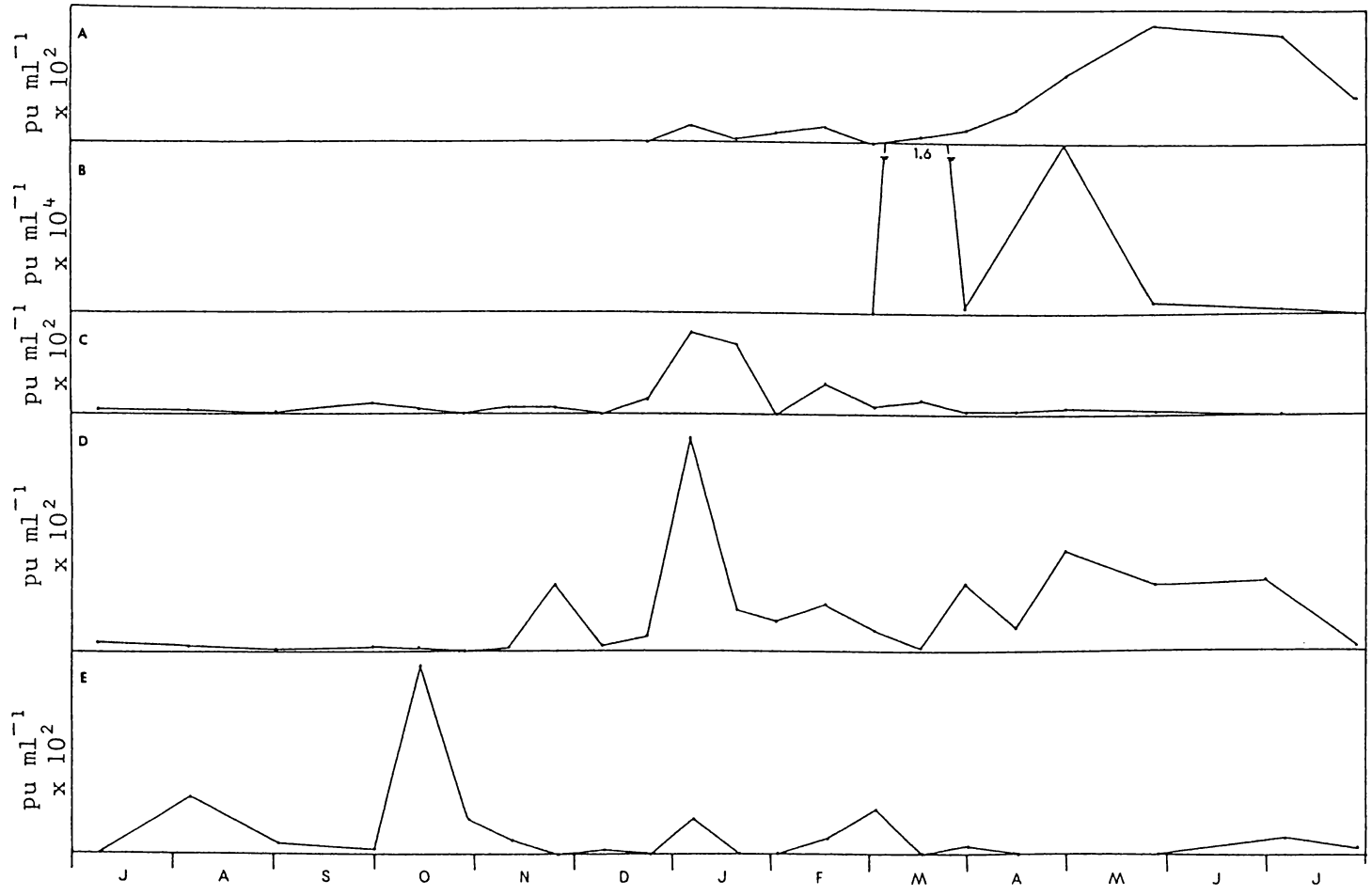
TABLE 6/4 Variation in the number of species (plus varieties) per 1 ml aliquot in Lake Mangahia, July 1983 to July 1984.

Taxon	Number of Species			
	Maximum	Minimum	Mean ± 1 SD (n = 22)	Total
CHLOROPHYTA				
Euchlorophyceae	15	1	8.3 ± 4.7	37
Ulothricophyceae	2	0	0.1 ± 0.4	2
Zygophyceae	5	2	3.4 ± 1.1	16
CHROMOPHYTA				
Chrysophyceae	6	0	1.4 ± 1.5	8
Diatomophyceae	9	2	5.0 ± 1.9	24
Xanthophyceae	2	0	0.3 ± 0.6	3
CYANOPHYTA				
Cyanophyceae	4	0	0.9 ± 1.2	12
EUGLENOPHYTA				
Euglenophyceae	10	1	2.6 ± 2.0	19
PYRRHOPHYTA				
Cryptophyceae	3	0	1.9 ± 0.7	3
Dinophyceae	2	0	0.3 ± 0.6	4
ALL SPECIES	33	14	23.0 ± 5.6	128

TABLE 6/5 Percentage similarity indices of consecutive and other specified phytoplankton communites in Lake Mangahia, July 1983 to July 1984.

Dates	Community Type	Percentage Similarity Index
1983		
8.vii/5.viii	Consecutive	66
5.viii/2.ix	"	74
2.ix/30.ix	"	70
30.ix/14.x	"	38
14.x/28.x	"	50
28.x/11.ix	"	92
11.ix/25.ix	"	91
25.ix/9.xii	"	95
9.xii/23.xii	"	17
23.xii/6.i	"	45
1984		
6.i/20.i	"	74
20.i/3.ii	"	80
3.ii/17.ii	"	86
17.ii/3.iii	"	83
3.iii/16.iii	"	27
16.iii/30.iii	"	29
30.iii/15.iv	"	50
15.iv/30.iv	"	49
30.iv/27.v	"	55
27.v/30.vi	"	48
30.vi/27.vii	"	59
8.vii/14.x	winter-spring	33
14.x/6.i	spring-summer	11
6.i/15.iv	summer-autumn	23
15.iv/27.vii	autumn-winter	13
8.vii (1983)/ 27.vii (1984)	annual	35

Fig. 6/6 Temporal variations in the densities (pu ml^{-1}) of the main euchlorophytes in Lake Mangahia, July 1983 to July 1984.



Key:

A. = *Raphidocelis contorta*

B. = *Chlorella* sp.

C. = *Tetrastrum triangulare*

D. = *Scenedesmus quadricauda*

E. = *Monoraphidium contortum*

late summer at its maximum density (16,984 pu ml^{-1} [16.3.84]), but this high density was short-lived, and rapidly dropped to 100 pu ml^{-1} (30.3.84). A further increase was recorded during late autumn (5256 pu ml^{-1} [15.4.84]), but it was not found throughout June and July 1984. *Raphidocelis contorta* was first found in mid-summer (6.1.84) and, with one exception (3.3.84), was present until the end of the sampling programme. Initially, its densities fluctuated irregularly, but then increased steadily throughout autumn, reaching a maximum (360 pu ml^{-1}) in early winter (27.5.84).

Both *Closterium acutum* var. *variabile* and *Aulacosira distans* (Fig. 6/7) were present throughout the entire year, had relatively minor peaks in early spring (926 pu ml^{-1} [30.9.83] and 1410 pu ml^{-1} [30.9.83], respectively), and substantial increases in summer; maximum densities were 13,944 (9.12.83) and 14,080 pu ml^{-1} (20.1.84), respectively. *A. granulata* var. *angustissima* showed a similar pattern, albeit on a smaller scale (maximum density 3480 pu ml^{-1} [20.1.84]). *Trachelomonas volvocina* also was present in all samples, but remained unimportant until mid-summer, after which time its density increased steadily (maximum density 1728 pu ml^{-1} [15.4.84]) (Fig. 6/7).

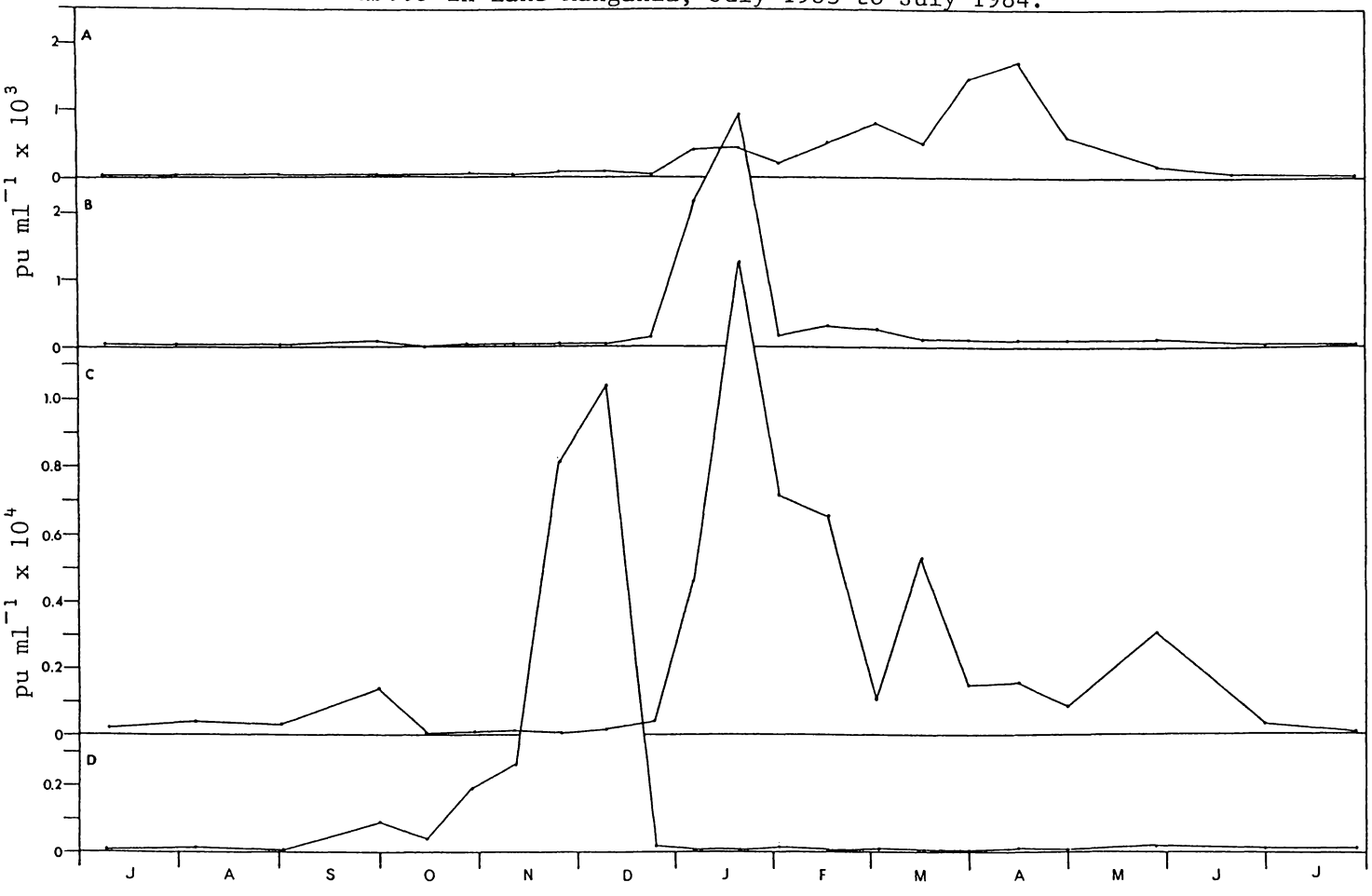
6.1.3. Lake Mangakaware

6.1.3.1 Temporal Variations in Total Phytoplankton Density and Biomass

In terms of abundance, the community was characterised by irregular fluctuations throughout the entire year. Total density ranged from 430 (27.7.84) to 29,362 pu ml^{-1} (27.5.84) (mean 5037 pu ml^{-1} [n = 21]). Densities increased throughout winter 1983, and a minor peak (10,134 pu ml^{-1}) was recorded on 2.9.83. However, these high densities were short-lived, and a rapid decline occurred throughout spring. With the exception of a second minor peak (11,736 pu ml^{-1}) in mid-summer [23.12.83]), densities fluctuated erratically throughout both the remainder of summer and autumn, increased dramatically at the commencement of winter (29,362 pu ml^{-1} [27.5.84]), but then declined equally rapidly (Fig. 6/8).

Total biomass ranged from 0.15 (27.7.84) to 17.9 g m^3 (23.12.83) (mean 3518 mg m^3 [n = 22]), and major peaks of biomass and density did

Fig. 6/7 Temporal variations in the densities (pu ml^{-1}) of *Trachelomonas volvocina*, *Aulacosira granulata* var. *angustissima*, *A. distans* and *Closterium acutum* var. *variabile* in Lake Mangahia, July 1983 to July 1984.



Key:

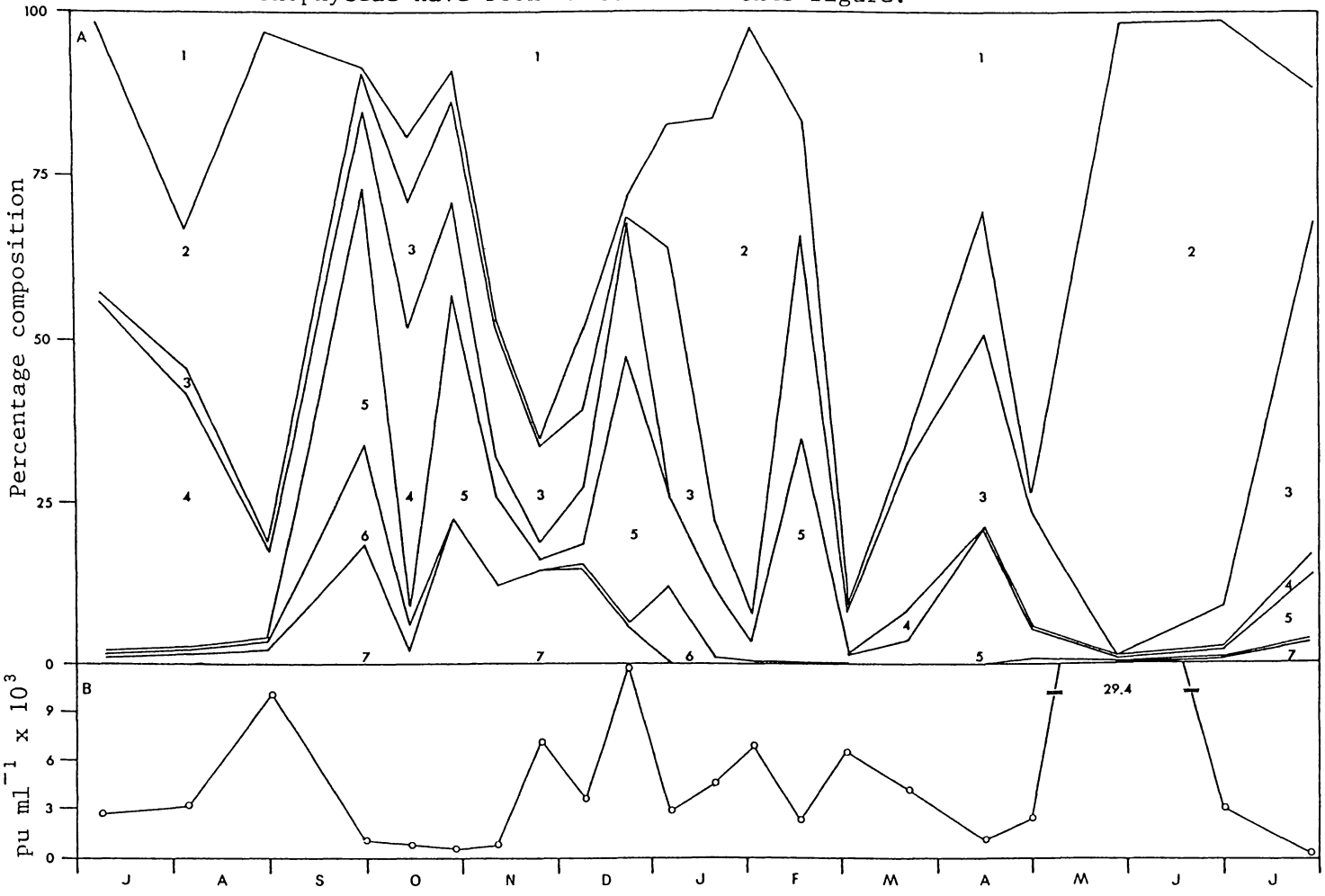
A. = *Trachelomonas volvocina*

B. = *Aulacosira granulata* var. *angustissima*

C. = *Aulacosira distans*

D. = *Closterium acutum* var. *variabile*

Fig. 6/8 Temporal variations in: (a) phytoplankton class composition, in terms of abundance; (b) total number of pu ml^{-1}, in Lake Mangakaware, July 1983 to July 1984. The Cyanophyceae, Raphidophyceae, Ulothricophyceae and Xanthophyceae have been omitted from this figure.



Key:

1. = Diatomophyceae
2. = Euchlorophyceae
3. = Zygophyceae
4. = Chrysophyceae
5. = Euglenophyceae
6. = Dinophyceae
7. = Cryptophyceae

not coincide. Biomass remained relatively low throughout winter 1983 (0.3 [8.7.83] and 0.5 g m^3 [5.8.83]), gradually increased (with some minor exceptions) during spring, and rose dramatically in summer (maximum 17.9 g m^3 [23.12.83]). It was high throughout early January 1984 but later fell rapidly. Minor increases were recorded in late summer and autumn (4.6 g m^3 [16.3.84] and 1.9 g m^3 [30.4.84], respectively), but values were markedly lower during winter 1984 (0.5 [29.6.84] and 0.1 g m^3 [26.7.84]) (Fig. 6/9).

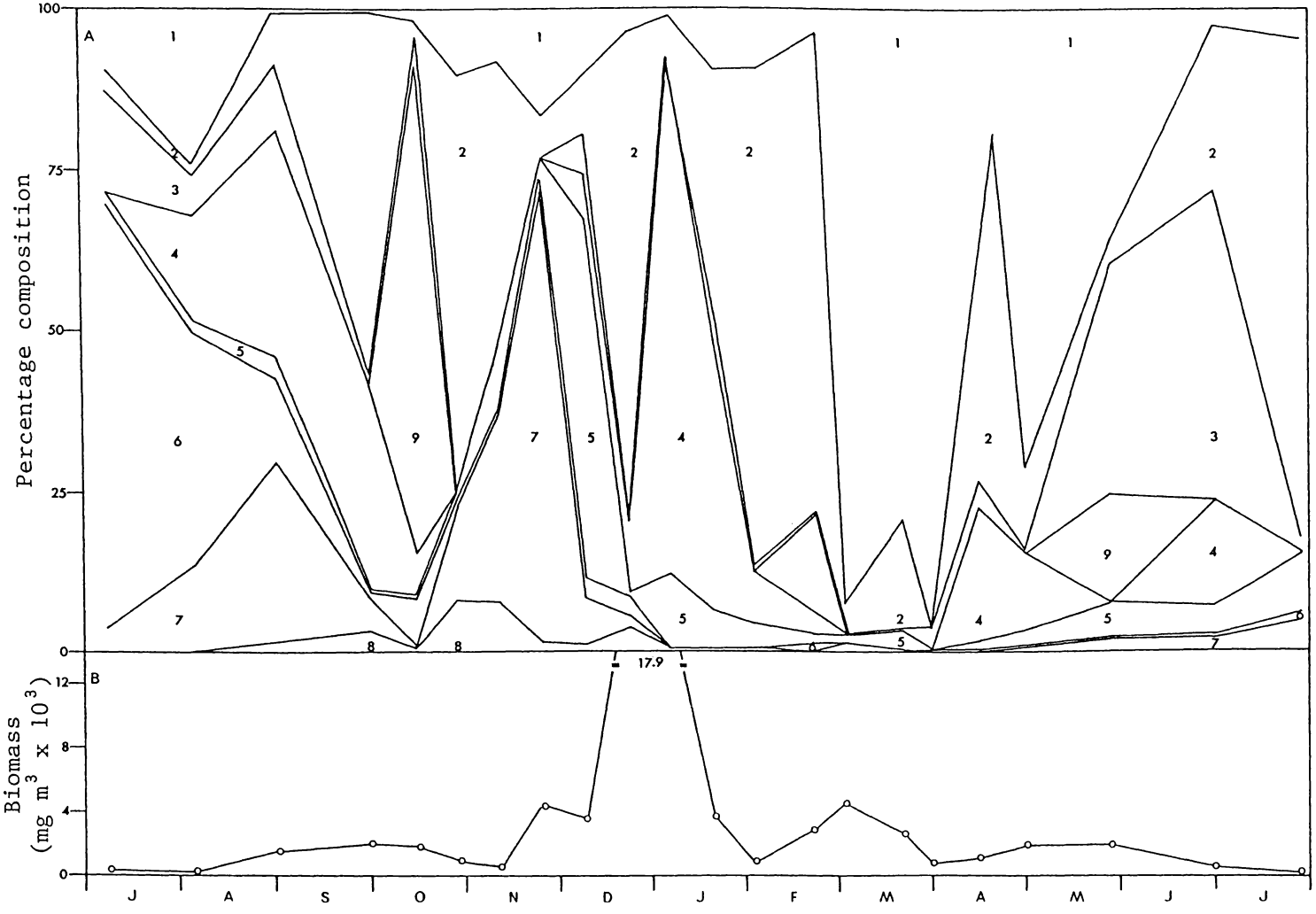
6.1.3.2. Temporal Variations in the Composition of the Total Phytoplankton Standing Crop

Initially, the dominant and sub-dominant classes, in terms of abundance, were the Chrysophyceae (55%) and the Euchlorophyceae (41%), respectively. However, as total densities increased throughout winter, the pattern was reversed; the Chrysophyceae, with the exception of an upsurge in early summer (42% [14.10.83]), was relatively unimportant throughout the remainder of the sampling year. Both the Euglenophyceae and the Cryptophyceae showed marked increases in importance (39 and 19%, respectively) immediately after a late winter period of euchlorophyte dominance (81% [30.9.83]). The Euglenophyceae showed a similar pattern with respect to peaks of total phytoplankton density, on three further occasions (17.2.84, 15.4.84, and 27.7.84, respectively). From November 1983 onwards, dominance alternated between the Diatomophyceae and the Euchlorophyceae, with the Zygophyceae increasing in importance at the end of the sampling programme (51% [27.7.84]) (Fig. 6/8).

In terms of biomass, the major temporal feature was that each class displayed at least one period of dominance, albeit brief in some instances (Fig. 6/9). Five classes (Chrysophyceae, Cyanophyceae, Cryptophyceae, Zygophyceae and Euchlorophyceae) were dominant only once. The Chrysophyceae was most important in winter (66% [8.7.83] and 36% [5.8.83]), its decline coinciding with an increase in the importance of the Cyanophyceae (76% [4.10.83]). The Cryptophyceae and Zygophyceae were co-dominants very briefly in early summer (70% [25.11.83] and 56% [9.12.83], respectively), while the Euchlorophyceae accounted for 48% of total biomass in winter (30.6.84).

The Dinophyceae and Diatomophyceae were both dominant twice. The former was most important on 2.9.83 (38%) and during January 1984 (80 and 42%). However, periods of diatom dominance were both more

Fig. 6/9 Temporal variations in: (a) phytoplankton class composition, in terms of biomass; (b) total biomass (mg m^3 x 10^3), in Lake Mangakaware, July 1983 to July 1984. The Xanthophyceae has been omitted from this figure.



Key:

1. = Diatomophyceae
2. = Euglenophyceae
3. = Euchlorophyceae
4. = Dinophyceae
5. = Zygophyceae
6. = Chrysophyceae
7. = Cryptophyceae
8. = Raphidophyceae
9. = Cyanophyceae

pronounced and longer-lived (92, 79 and 96% [March-April 1984] and 66 and 36% [May-June 1984]).

The Euglenophyceae, in marked contrast to other classes, was dominant for a brief period at least once during each season. It was the major class on eight sampling dates; the sequence of peaks (30.9.83 [57%], 28.10.83 and 11.11.83 [65 and 47%, respectively], 23.12.83 [76%], 17.2.84 and 3.3.84 [77 and 74%, respectively], 30.4.84 [53%] and 27.7.84 [78%]) indicates that, without exception, it became dominant immediately after a maximum contribution of another class.

6.1.3.3 Temporal Variations in Phytoplankton Species Diversity

α diversity fluctuated erratically (range 18 to 54; mean 29.5 ± 10.3 [n = 21]) (Table 6/6). Periods of high species richness generally coincided with maximal proportions (in terms of abundance) of the Euchlorophyceae (Fig. 6/8). Both the minimum (3) and maximum (24) number of euchlorophyte species occurred in early summer (11.11.83 and 9.12.83, respectively). The Zygophyceae, however, had both its minimum (1) and maximum number (10) in winter (30.6.84 and 27.7.84, and 8.7.83 respectively) (Appendix IV).

Despite relatively high species richness within both the Euchlorophyceae (46) and the Diatomophyceae (38) (Table 4/11), at no time did large numbers of species coexist; for example, on only one occasion were both classes represented by more than 50% of their species. With the exception of the pyrrhophytes, other classes exhibited a similar pattern (Table 6/7).

The Shannon-Wiener index also varied considerably (range 0.88 to 3.78; mean 2.23 ± 0.92 [n = 21]). The lowest value was recorded on 3.3.84 and reflected the importance of *Acanthoceras zachariasi* (5648 pu ml^{-1} [87% of total density]) at that time. Conversely, the highest index was recorded when species richness was relatively high (43 [6.1.84]), and the proportions of the major taxa were more evenly distributed than at any other time.

6.1.3.4 Percentage Similarity of the Phytoplankton Communities

With two exceptions (8.7.83/5.8.83 [62%]) and 3.3.84/16.3.84 [71%]), consecutive communities were not markedly similar. There was no evidence of seasonality (Table 6/8); for example, low indices were recorded in late winter-early spring (19% [5.8.83/2.9.83] and 17% [2.9.83/30.9.83]), mid-summer (12% [20.1.84/3.2.84] and 11%

[3.2.84/17.2.84]) and late autumn-winter (4% [30.4.84/27.5.84] and 6% [27.5.84/30.6.84]). High indices resulted from brief periods of dominance by one or two species (*Tetrastrum triangulare* and *Dinobryon cylindricum* [winter 1983] and *Acanthoceras zachariasi* [late summer 1984]). The ephemeral nature of the phytoplankton populations is reflected in the low mean (32 ± 20%), seasonal, and annual (July 1983/July 1984) indices.

6.1.3.5 Species Periodicity

Both *Tetrastrum triangulare* and *Dinobryon cylindricum* had maximal densities (1024 and 1407 pu ml^{-1}, respectively) in winter 1983, declined in abundance throughout spring, and exhibited minor peaks in summer (Fig. 6/10). However, their spring declines were not accompanied by concomitant increases and/or maxima of other major species, although minor peaks of *Cryptomonas* spp. (*C. marssonii* and *C. ovata*) and *Trachelomonas* spp. (*T. planctonica*, *T. playfairi* and *T. volvocina*) were apparent (Fig. 6/11).

Asterionella formosa was found only once prior to November 1983 (Fig. 6/12), but increased rapidly throughout early summer. Its maximum density (4424 pu ml^{-1}) was recorded on 25.11.83, and coincided with a major fungal infection (*Rhizophydium planktonicum* Canter emend. ?). Its decline (January 1984) coincided with the appearance of *Acanthoceras zachariasi* which, like the former species, also increased at a remarkably fast rate (maximum density 5648 pu ml^{-1} [3.3.84]).

It is noteworthy that the highest densities of both *Cryptomonas* spp. and *Trachelomonas* spp. were recorded after the maximum density of *Asterionella formosa*; and furthermore, the former reappeared in relatively high densities during the decline of *Acanthoceras zachariasi* (27.5.84). Generally both maximal and minimal densities of *Cryptomonas* spp. and *Trachelomonas* spp. coincided (Fig. 6/11). The densities of both *Closterium acutum* var. *variabile* and *Monoraphidium contortum* (Fig. 6/13) fluctuated, but the latter showed a major peak (27,374 pu ml^{-1}) in early winter (27.5.84).

Fig. 6/10 Temporal variations in the densities (pu ml^{-1}) of *Tetrastrum triangulare* and *Dinobryon cylindricum* in Lake Mangakaware, July 1983 to July 1984.

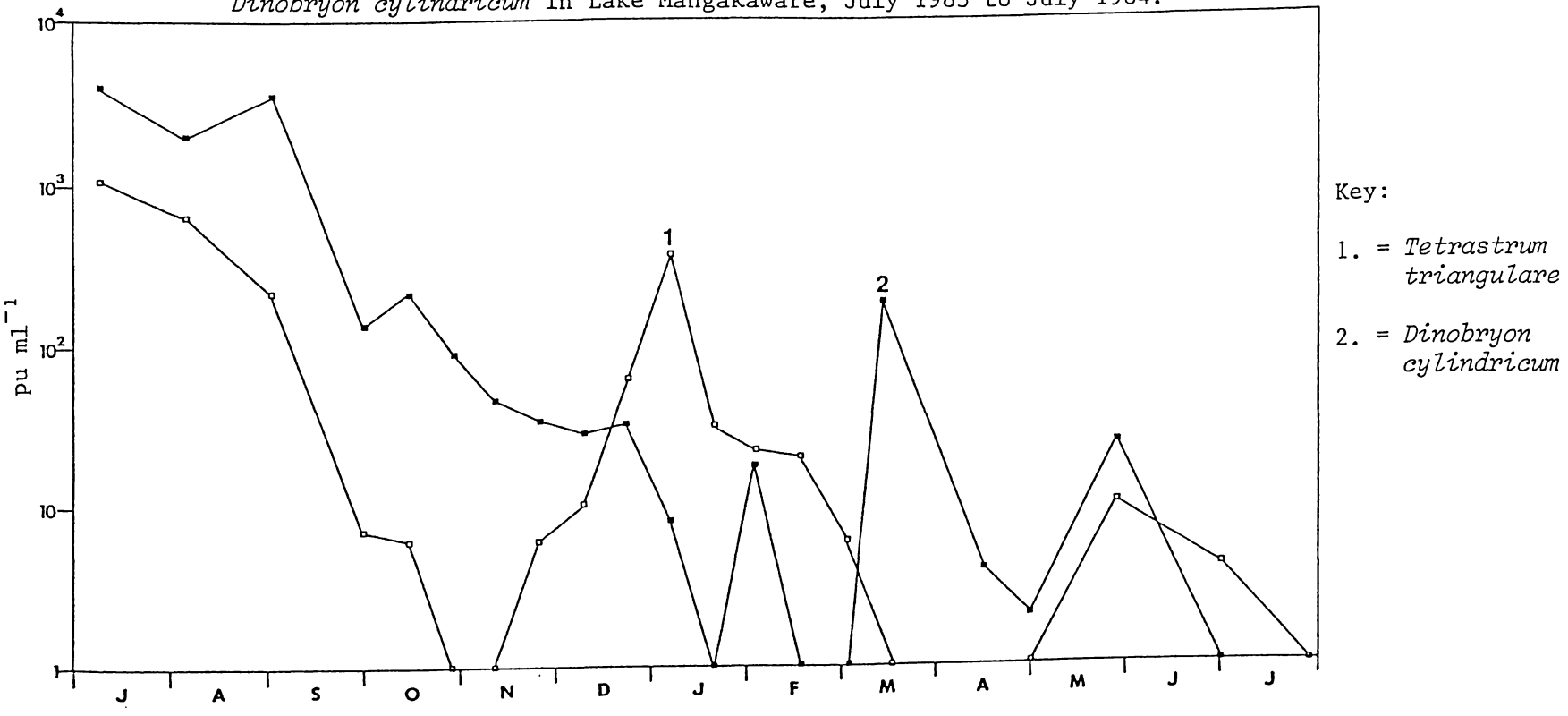


Fig. 6/11 Temporal variations in the densities (pu ml^{-1}) of *Cryptomonas erosa*, *C.* spp., and *Trachelomonas* spp. in Lake Mangakaware, July 1983 to July 1984.

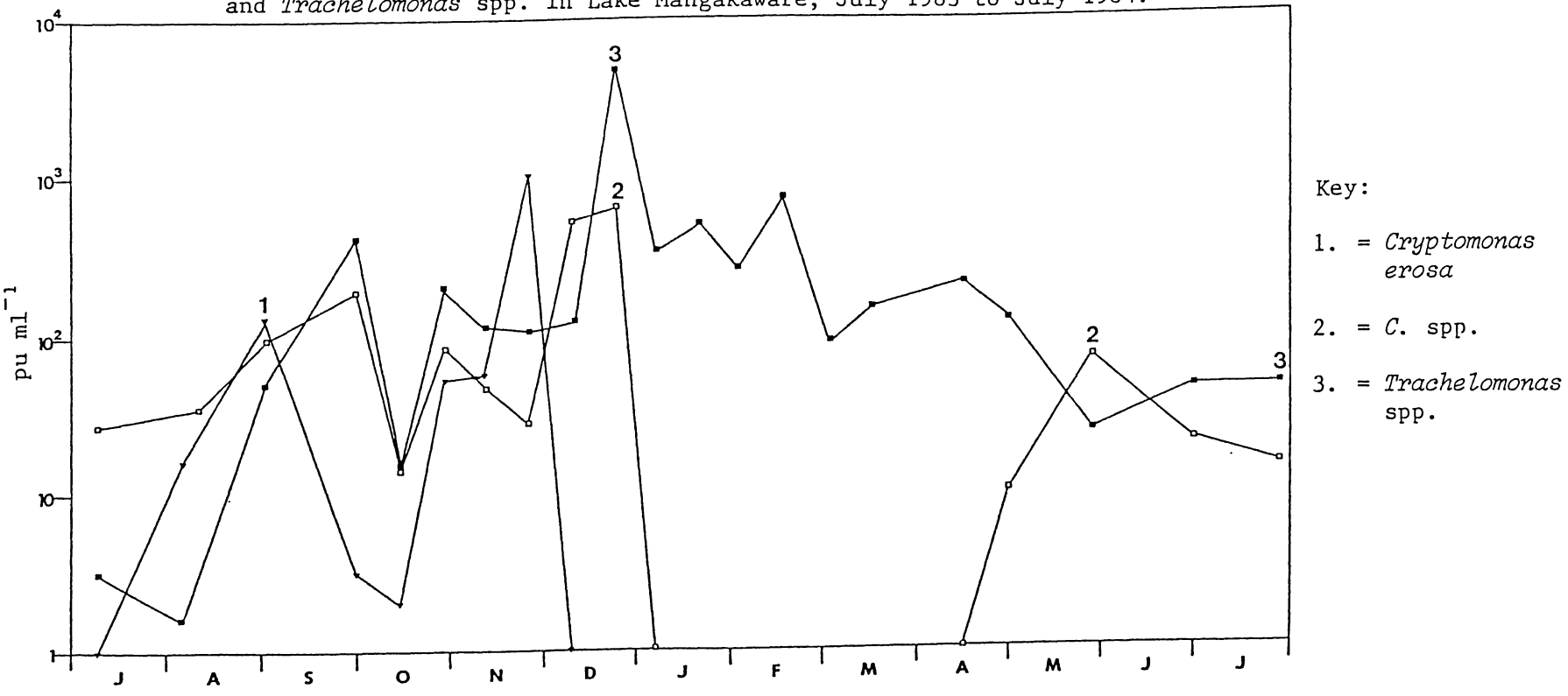
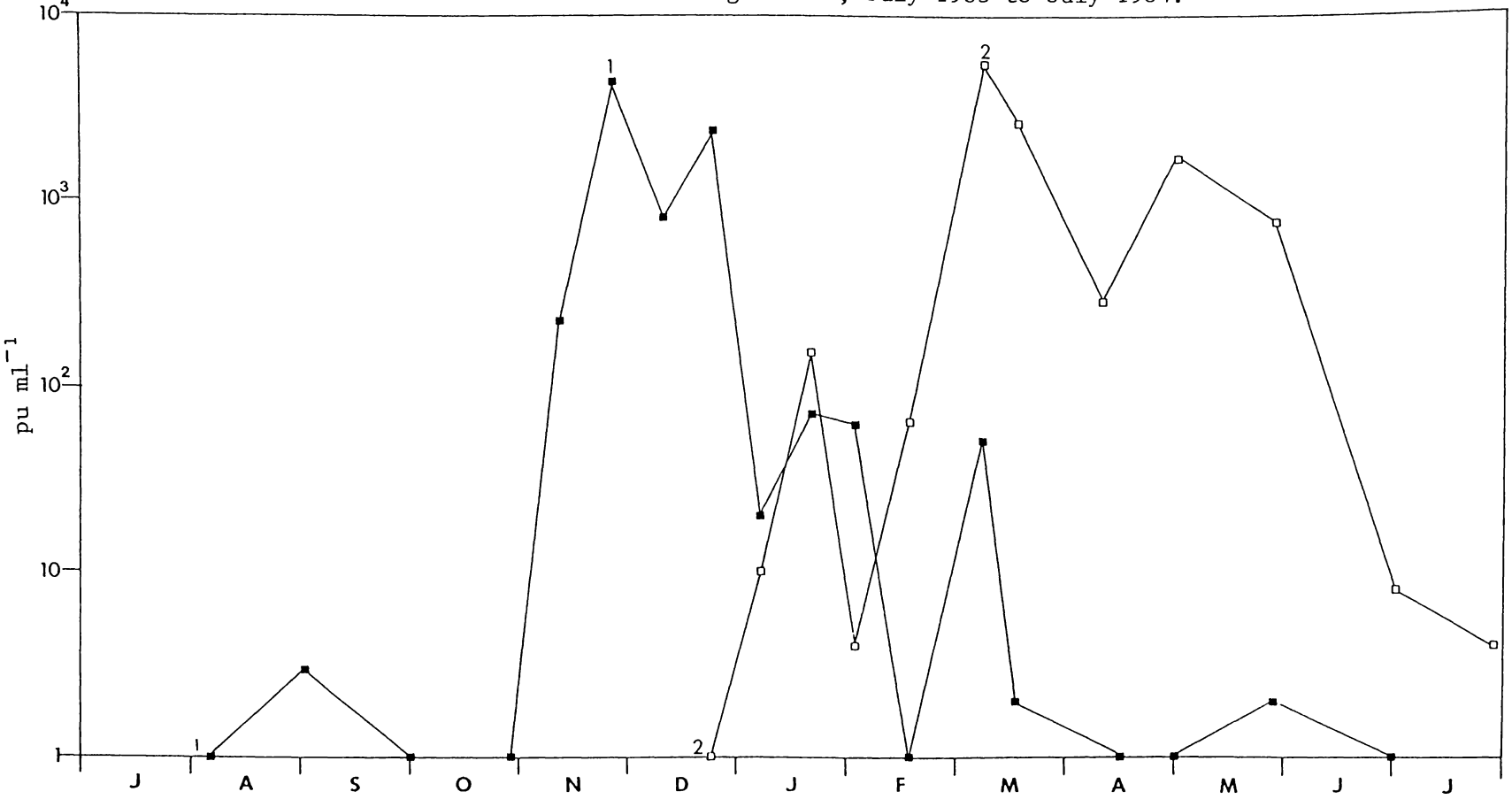


Fig. 6/12 Temporal variations in the densities (pu ml^{-1}) of *Asterionella formosa* and *Acanthoceras zachariasi* in Lake Mangakaware, July 1983 to July 1984.



Key:

1. = *Asterionella formosa*

2. = *Acanthoceras zachariasi*

TABLE 6/6 α diversity and Shannon-Wiener information index for each sampling date in Lake Mangakaware, July 1983 to July 1984.

Date	α Diversity		Shannon-Wiener Information Index
	s	d	
1983			
8.vii	32	9.35	1.45
5.viii	22	6.28	2.04
2.ix	50	12.48	1.15
30.ix	24	7.95	2.59
14.x	26	8.96	3.44
28.x	22	7.90	2.91
11.xi	24	8.16	3.32
25.xi	33	8.56	1.84
9.xii	54	15.20	3.41
23.xii	43	10.57	2.34
1984			
6.i	43	12.41	3.78
20.i	37	10.09	2.88
3.ii	23	5.98	1.72
17.ii	25	7.41	2.54
3.iii	21	5.51	0.88
16.iii	24	6.62	1.17
15.iv	25	8.27	2.72
30.iv	19	5.63	1.61
27.v	32	7.16	0.43
30.vi	23	6.58	2.01
27.vii	18	6.83	2.60

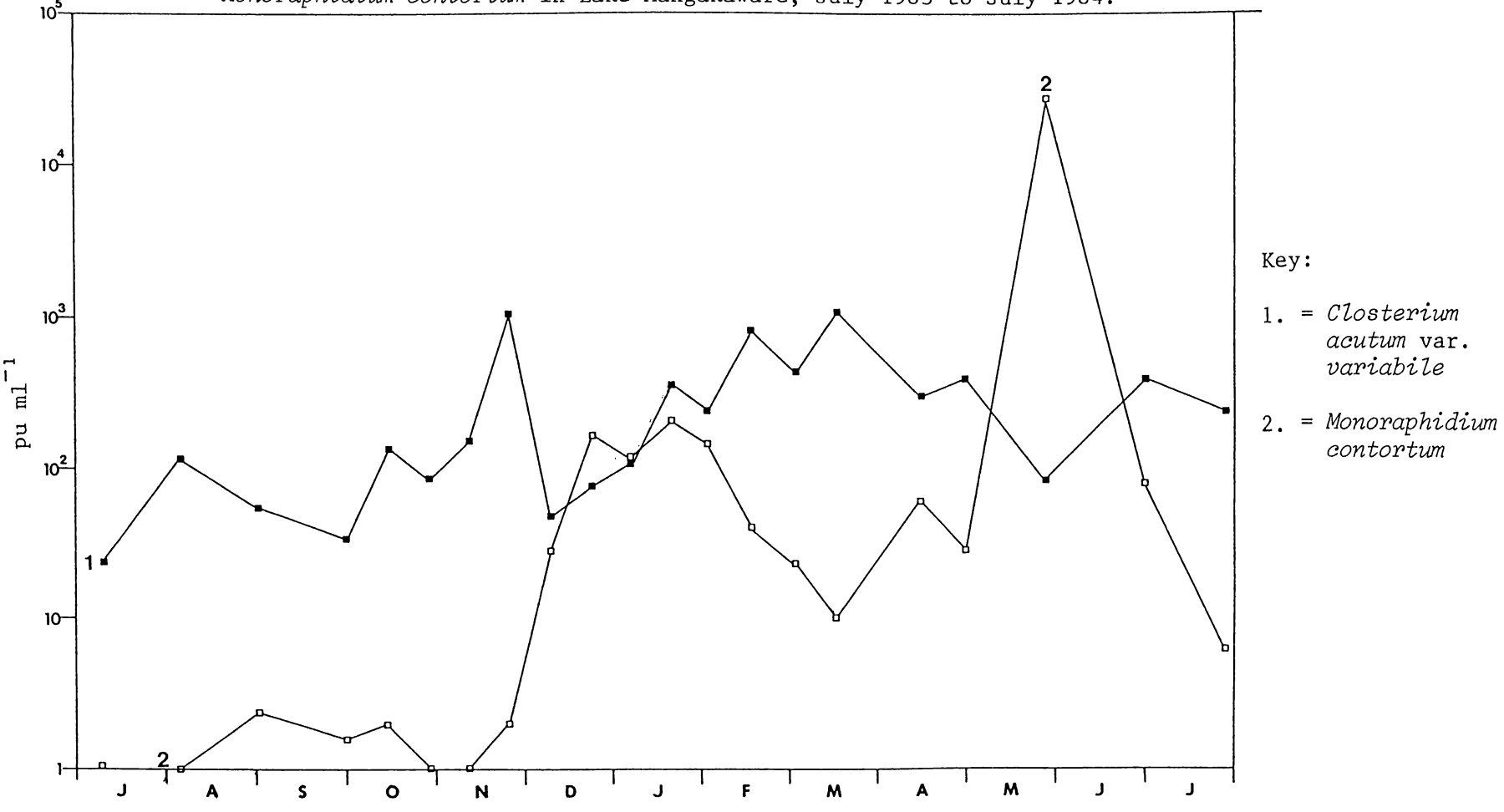
TABLE 6/7 Variation in the number of species (plus varieties) per 1 ml aliquot in Lake Mangakaware, July 1983 to July 1984.

Taxon	Number of Species			
	Maximum	Minimum	Mean ± 1 SD (n = 21)	Total
CHLOROPHYTA				
Euchlorophyceae	24	3	9.3 ± 4.9	46
Ulothricophyceae	1	0	0.04 ± 4.9	3
Zygophyceae	10	1	4.4 ± 2.3	23
CHROMOPHYTA				
Chrysophyceae	4	0	1.9 ± 1.1	6
Diatomophyceae	16	3	6.7 ± 3.1	41
Xanthophyceae	3	0	0.7 ± 0.9	4
CYANOPHYTA				
Cyanophyceae	4	0	1.1 ± 1.2	15
EUGLENOPHYTA				
Euglenophyceae	6	1	2.7 ± 1.9	20
PYRRHOPHYTA				
Cryptophyceae	3	0	1.7 ± 1.3	3
Dinophyceae	5	0	1.6 ± 1.5	7
RAPHIDOPHYTA				
Raphidophyceae	1	0	0.6 ± 0.5	1
ALL SPECIES	54	18	29.5 ± 10.3	170

TABLE 6/8 Percentage similarity indices of consecutive and other specified phytoplankton communites in Lake Mangakaware, July 1983 to July 1984.

Dates	Community Type	Percentage Similarity Index
1983		
8.vii/5.vii	consecutive	62
5.viii/2.ix	"	19
2.ix/30.ix	"	17
30.ix/14.x	"	29
14.x/28.x	"	40
28.x/11.xi	"	51
11.xi/25.xi	"	50
25.xi/9.xii	"	29
9.xii/23.xii	"	38
23.xii/6.i	"	21
1984		
6.i/20.i	"	35
20.i/3.ii	"	12
3.ii/17.ii	"	11
17.ii/3.iii	"	13
3.iii/16.iii	"	71
16.iii/15.iv	"	55
15.iv/30.iv	"	51
30.iv/27.v	"	4
27.v/30.vi	"	6
30.vi/27.vii	"	30
8.vii/14.x	winter-spring	30
14.x/6.i	spring-summer	17
6.i/15.iv	summer-autumn	23
15.iv/27.vii	autumn-winter	42
8.vii (1983)/ 27.vii (1984)	annual	4

Fig. 6/13 Temporal variations in the densities of *Closterium acutum* var. *variabile* and *Monoraphidium contortum* in Lake Mangakaware, July 1983 to July 1984.



6.1.4 Lake Maratoto

6.1.4.1 Temporal Variations in Total Phytoplankton Density and Biomass

Total density and biomass both fluctuated markedly throughout the sampling period (Figs. 6/14 and 6/15, respectively). Total density ranged from 1150 (1.9.83) to 54,246 pu ml^{-1} (16.2.84) (mean 6677 pu ml^{-1} [n = 20]). However, if the exceptionally high maximum density, (due largely to a brief appearance of *Chlamydomonas* sp. C) is excluded from the analysis, the mean density was 4130 pu ml^{-1} (n = 19).

The mean biomass was 72 g m^3, the highest recorded during the present study, and more than twice that of Lake Ngaroto, which ranked second (Table 7/1). *Botryococcus braunii* was largely responsible for the variations in total biomass, with its two extremes of density (1.9.83 and 22.12.83, respectively) (Fig. 6/16) and the maximum (244 g m^3) and minimum (15 g m^3) values coinciding.

6.1.4.2 Temporal Variations in the Composition of the Total Phytoplankton Standing Crop

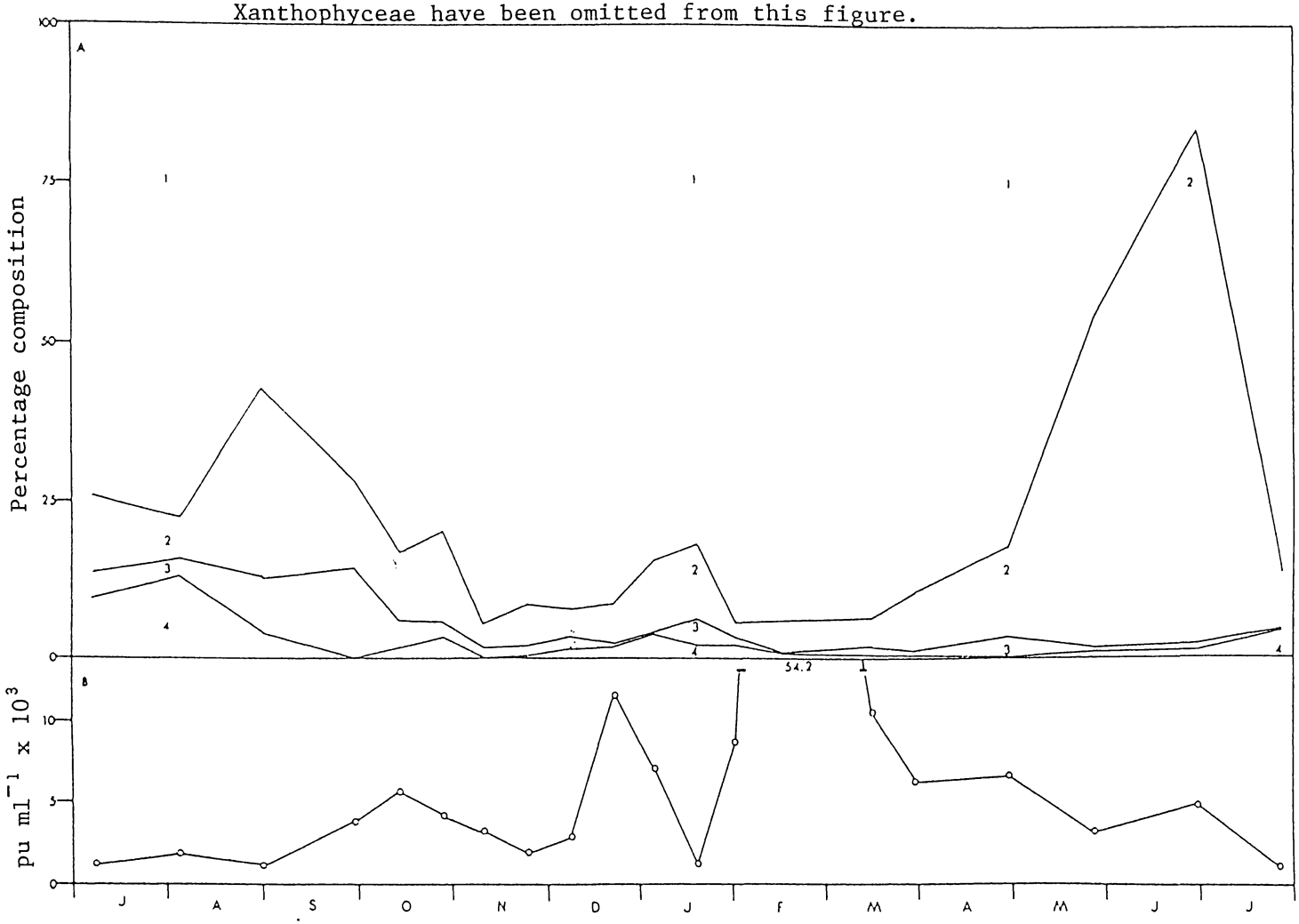
Quantitatively, the Euchlorophyceae dominated the community throughout the entire year, except for a brief period in winter (26.5.84 to 29.6.84), when a dramatic increase in numbers of *Closterium acutum* var. *variabile* (Fig. 6/17) resulted in high zygophycean proportions (52 and 80%, respectively). Cryptophytes and diatoms, with maximal proportions of 13 and 14%, respectively, played minor roles. The Euchlorophyceae (mainly because of the high densities of *Botryococcus braunii* (Fig. 6/16), and its large biovolume [23,425 μm^3]), comprised almost the entire biomass. Its maximum and minimum proportions were 98.7 (29.9.83) and 99.9% (29.3.84).

The Diatomophyceae had the second largest proportion, a remarkably low 1.3% (29.9.83), and it also was comprised of almost only one species (*Tabellaria flocculosa*) (Fig. 6/16).

6.1.4.3 Temporal Variations in Phytoplankton Species Diversity

Generally, species richness decreased during summer (lowest species number [9] 19.1.84) (Table 6/9). The mean Shannon-Wiener index was 1.3 ± 0.5, and both the lowest and highest values (0.46 and 2.17,

Fig. 6/14 Temporal variations in: (a) phytoplankton class composition, in terms of abundance; (b) total number of pu ml^{-1}, in Lake Maratoto, July 1983 to July 1984. The Chrysophyceae, Cyanophyceae, Dinophyceae, Raphidophyceae and Xanthophyceae have been omitted from this figure.



Key:

1. = Euchlorophyceae
2. = Zygophyceae
3. = Diatomophyceae
4. = Cryptophyceae

Fig. 6/15 Temporal variations in total phytoplankton biomass (g m^3 x 10) in Lake Maratoto, July 1983 to July 1984.

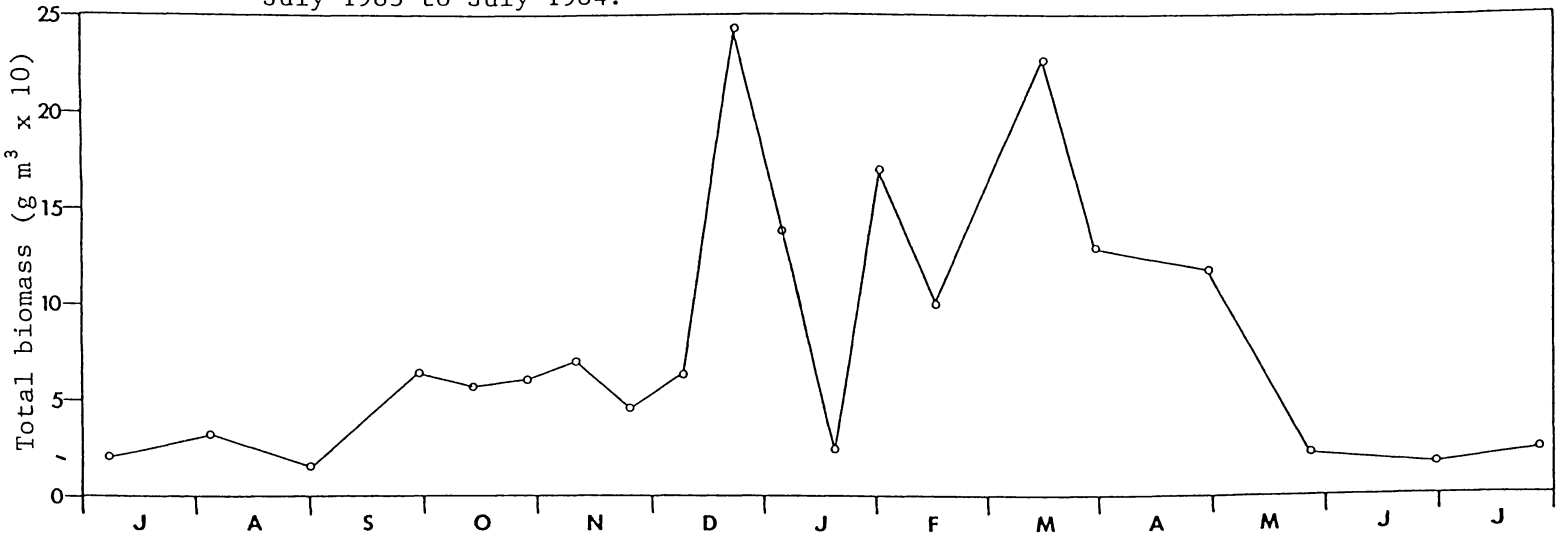


Fig. 6/16 Temporal variations in the densities (pu ml^{-1}) of *Botryococcus braunii*, *Tabellaria flocculosa* and *Aulacosira granulata* var. *angustissima* in Lake Maratoto, July 1983 to July 1984.

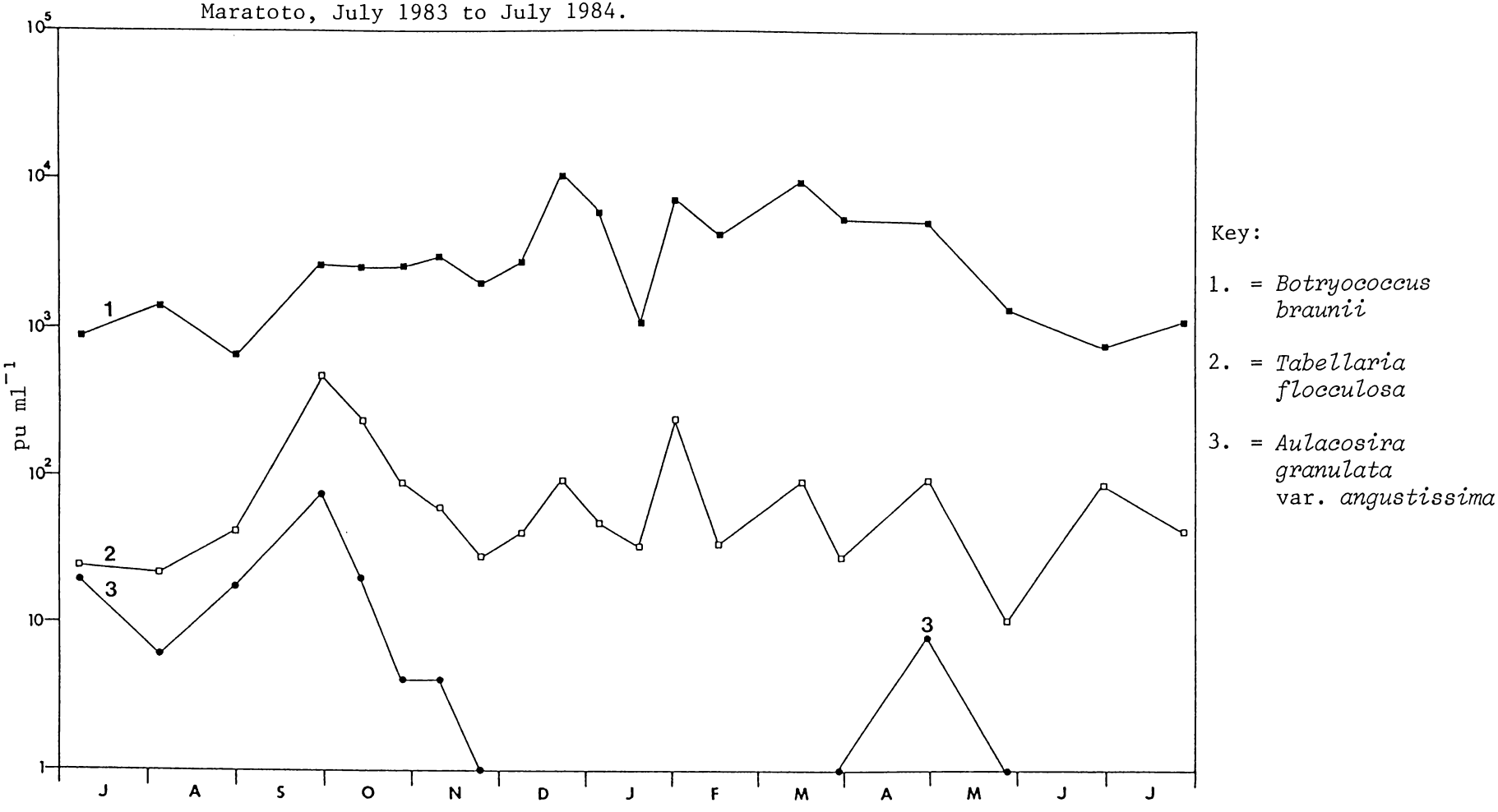


Fig. 6/17 Temporal variations in the densities (pu ml^{-1}) of *Monoraphidium tortile*, *Staurastrum* sp.B, *Closterium acutum* var. *variabile* and *Chlamydomonas* sp.C in Lake Maratoto, July 1983 to July 1984

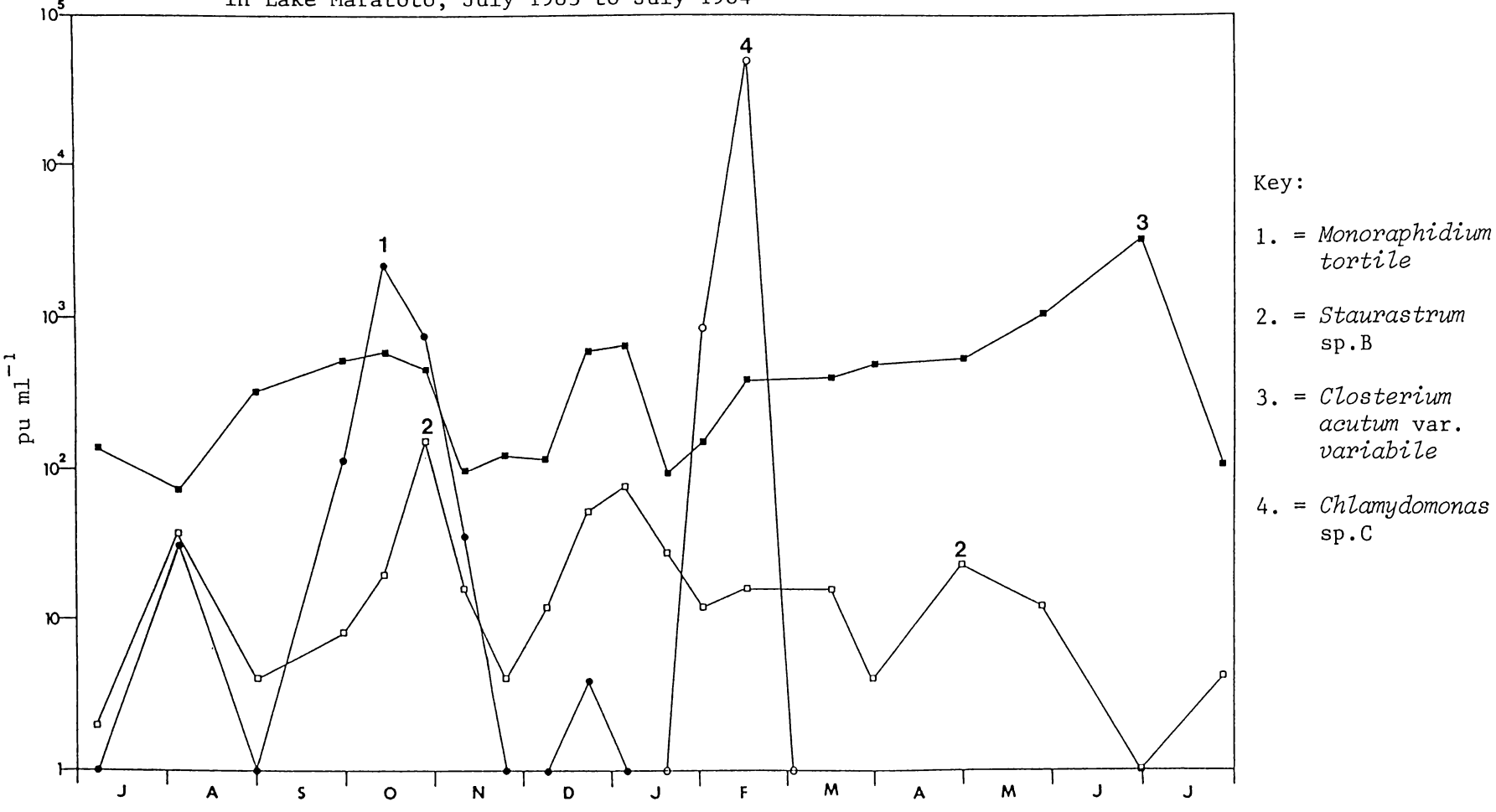


TABLE 6/9 α diversity and Shannon-Wiener information index for each sampling date in Lake Maratoto, July 1983 to July 1984.

Date	α Diversity		Shannon-Wiener Information Index
	s	d	
1983			
7.vii	14	4.54	1.46
4.viii	25	7.65	1.42
1.ix	21	6.86	1.87
29.ix	21	5.84	1.44
13.x	16	4.26	1.77
27.x	14	3.86	2.17
10.xi	15	4.25	0.94
24.xi	11	3.31	0.91
8.xii	17	4.90	1.16
22.xii	21	5.17	0.61
1984			
5.i	14	3.64	1.16
19.i	9	2.90	1.19
2.ii	15	3.80	1.09
16.ii	14	2.96	0.46
15.iii	25	6.21	0.70
29.iii	22	5.77	0.93
29.iv	28	7.33	1.39
26.v	27	7.67	2.06
29.vi	21	5.69	1.49
26.vii	21	6.71	1.50

respectively) occurred when only 14 species were recorded. The former coincided with the maximum density of *Chlamydomonas* sp. C (16.2.84 [Fig. 6/17]), and the highest value resulted from the co-occurrence in reasonable numbers of some of the less important taxa (e.g., *Monoraphidium tortile*, *Staurastrum* sp. B, *Aulacosira granulata* var. *angustissima* and *Vacuolaria* sp.) with the major phytoplankters (*Botryococcus braunii*, *Closterium acutum* var. *variabile*, *Tabellaria flocculosa* and *Cryptomonas* spp.) (Figs. 6/16 to 6/18).

The number of species per sample ranged from 9 to 28 (Table 6/10). The mean, the lowest of the nine study lakes, was 18 ± 5. Despite relatively high numbers of diatom and euchlorophyte species, little continuity was apparent. Their mean numbers of species per sample were 3 and 5, respectively, contrasting markedly with the Cryptophyceae, which was represented almost continuously by two of its three species.

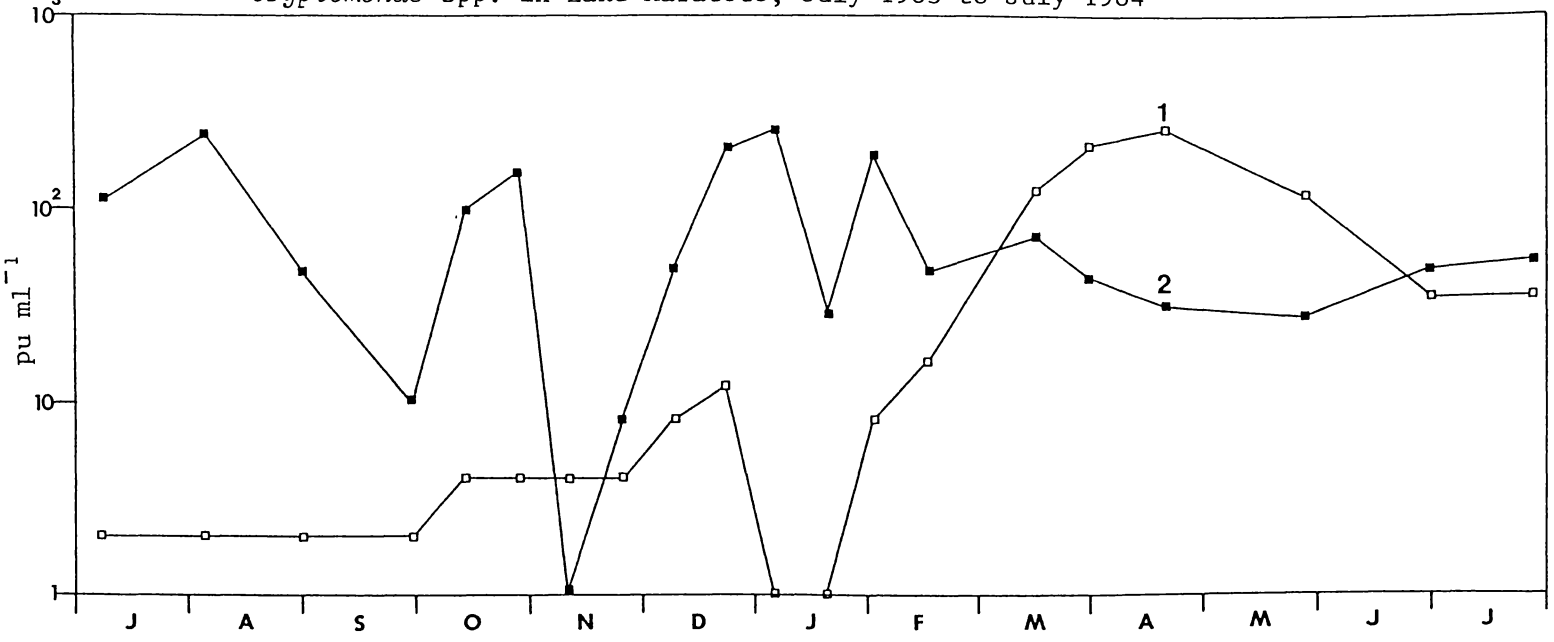
6.1.4.4 Percentage Similarity of the Phytoplankton Communities

Consecutive communities were, with three exceptions, remarkably similar (mean 70 ± 27% [n = 19]) (Table 6/11), especially throughout late spring and early summer. For example, between 10.11.83 and 19.1.84 (five consecutive communities), indices ranged from 91 to 97%. The 2.2.84/16.2.84 and 16.2.84/15.3.84 samples were the most dissimilar (18 and 19%, respectively), which is not unexpected because of the density of *Chlamydomonas* sp. C on 16.2.84 (Fig. 6/17). The 29.6.84/26.7.84 samples also showed little similarity (26%), largely because of the major difference between the densities of *Closterium acutum* var. *variabile* on these two occasions (Fig. 6/17).

6.1.4.5 Species Periodicity

The key role in the dynamics of the Lake Maratoto community was played by *Botryococcus braunii* (Fig. 6/16). It maintained consistently high densities throughout the entire year; with one exception (19.1.84), these were higher in summer and autumn than at any other time. The two most significant peaks (10,444 and 9708 pu ml^{-1}) occurred in summer (22.12.83 and 15.3.84, respectively), while the minimum density (646 pu ml^{-1}) was recorded in early spring [1.9.83] (Fig. 6/16).

Fig. 6/18 Temporal variations in the densities (pu ml^{-1}) of *Trachelomonas volvocina* and *Cryptomonas* spp. in Lake Maratoto, July 1983 to July 1984



Key:

1. = *Trachelomonas volvocina*

2. = *Cryptomonas* spp.

TABLE 6/10 Variation in the number of species (plus varieties) per 1 ml aliquot in Lake Maratoto, July 1983 to July 1984.

Taxon	Number of Species			
	Maximum	Minimum	Mean ± 1 SD (n = 20)	Total
CHLOROPHYTA				
Euchlorophyceae	6	1	3.1 ± 1.4	26
Ulothricophyceae	1	0	0.05 ± 0.2	1
Zygophyceae	8	2	4.3 ± 1.5	17
CHROMOPHYTA				
Chrysophyceae	2	0	0.6 ± 0.7	5
Diatomophyceae	12	2	5.3 ± 3.1	41
Xanthophyceae	1	0	0.4 ± 0.5	3
CYANOPHYTA				
Cyanophyceae	3	0	1.1 ± 1.1	14
EUGLENOPHYTA				
Euglenophyceae	3	0	1.5 ± 0.8	13
PYRRHOPHYTA				
Cryptophyceae	3	0	2.0 ± 0.6	3
Dinophyceae	3	0	0.9 ± 1.0	6
RAPHIDOPHYTA				
Raphidophyceae	1	0	0.5 ± 0.5	1
ALL SPECIES	28	9	18.5 ± 5.4	130

TABLE 6/11 Percentage similarity indices of consecutive and other specified phytoplankton communites in Lake Maratoto, July 1983 to July 1984.

Dates	Community Type	Percentage Similarity Index
1983		
7.vii/4.viii	Consecutive	88
4.viii/1.ix	"	66
1.ix/29.ix	"	73
29.ix/13.x	"	63
13.x/29.x	"	75
27.x/10.xi	"	66
10.xi/24.xi	"	91
24.xi/8.xii	"	95
8.xii/22.xii	"	97
22.xii/5.i	"	91
1984		
5.i/19.i	"	93
19.i/2.ii	"	86
2.ii/16.ii	"	18
16.ii/15.iii	"	9
15.iii/29.iii	"	90
29.iii/29.iv	"	90
29.iv/26.v	"	61
26.v/29.vi	"	62
29.vi/26.vii	"	26
7.vii/13.x	winter-spring	57
13.x/5.i	spring-summer	54
5.i/29.iv	summer-autumn	88
29.iv/26.vii	autumn-winter	89
7.vii (1983)/ 26.vii 91984)	annual	89

The two most important diatoms were *Tabellaria flocculosa* and *Aulacosira granulata* var. *angustissima* (Fig. 6/16). The former was a permanent member of the plankton, reaching a maximum density (472 pu ml^{-1}) in late winter (29.9.83), and exhibiting a minor peak (240 pu ml^{-1}) in mid-summer (2.2.84). *A. g.* var. *angustissima* also reached its maximal density (76 pu ml^{-1}) in late spring but, with one exception, was not found from December 1983 onwards.

Both *Chlamydomonas* sp. C and *Monoraphidium tortile*, the only significant representatives of the Euchlorophyceae (apart from *Botryococcus braunii*), were temporary phytoplankters (Fig. 6/17), with marked abilities to increase rapidly in number. Their maxima were 49,478 (16.2.84) and 2246 pu ml^{-1} (13.10.83), respectively.

The two most important desmids were *Closterium acutum* var. *variabile* and *Staurastrum* sp. B (Fig. 6/17). The former showed irregular fluctuations throughout the sampling period, and had its maximum density (3316 pu ml^{-1}) in winter (29.6.84). *Staurastrum* sp. B however, while having a broadly similar pattern of periodicity throughout the spring and summer (albeit at lesser densities), did not continue to increase during early winter 1984 (maximum density 152 pu ml^{-1} [27.10.83]).

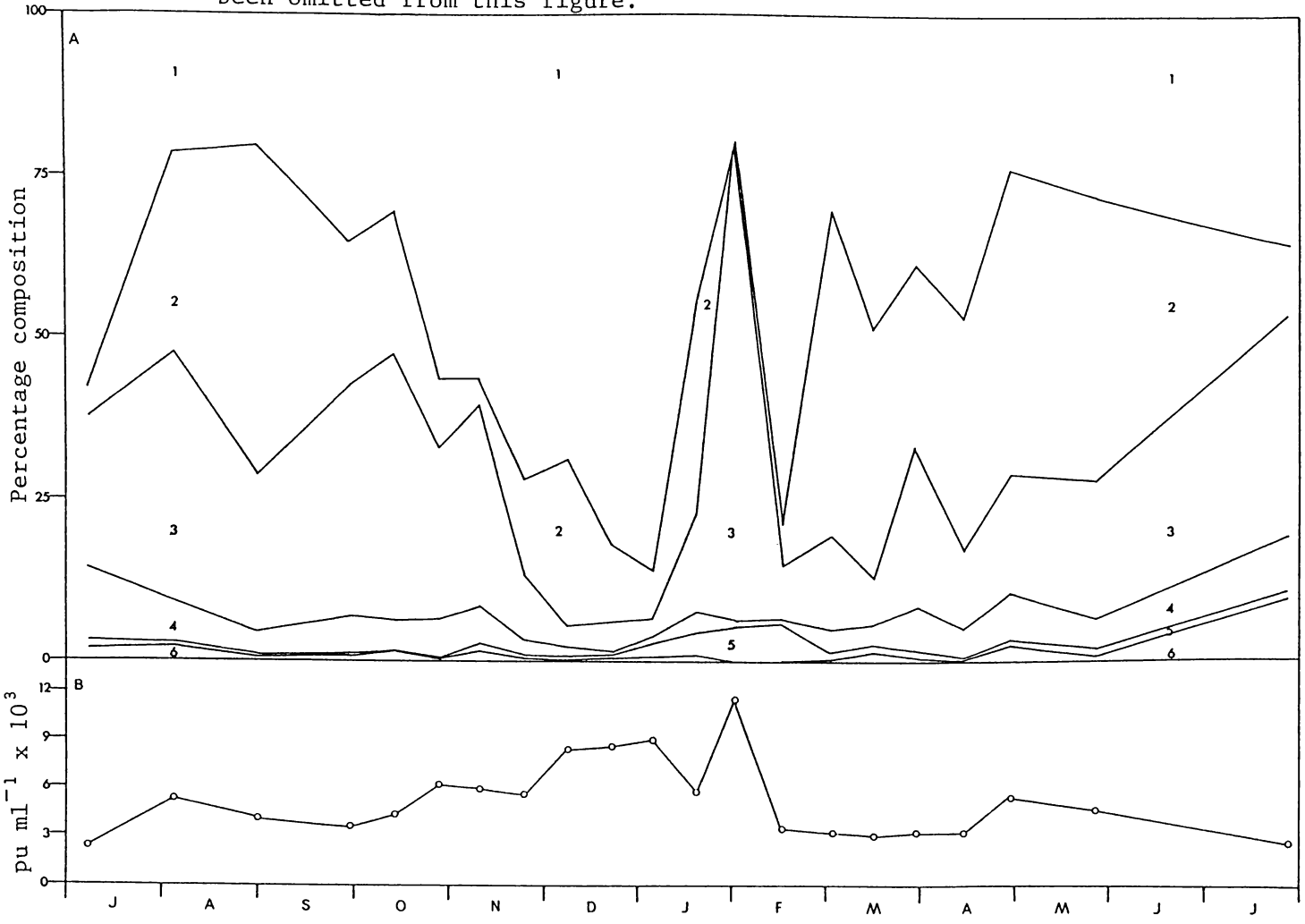
Trachelomonas spp. (*T. planctonica*, *T. playfairi* and *T. volvocina*) were unimportant from July 1983 to February 1984 (Fig. 6/18), but their densities commenced to increase rapidly (maximum 256 pu ml^{-1} [29.4.84] coincident with a decline in total phytoplankton numbers. The density of *Cryptomonas* spp. (*C. marssonii* and *C. ovata*) (Fig. 6/18) also fluctuated widely (range 0 to 256 pu ml^{-1}). Both early and mid-summer peaks occurred immediately after an increase in total phytoplankton numbers, but surprisingly, this trend was not apparent subsequent to the major peak of total phytoplankton in February 1984 (Fig. 6/14).

6.1.5 Lake Ngaroto

6.1.5.1 Temporal Variations in Total Phytoplankton Density and Biomass

The total density of phytoplankton ranged from 2373 (7.9.83) to 11,570 pu ml^{-1} (2.2.84) (mean 5330 pu ml^{-1} [n = 21]) (Fig. 6/19).

Fig. 6/19 Temporal variations in: (a) phytoplankton class composition, in terms of abundance; (b) total number of pu ml^{-1}, in Lake Ngaroto, July 1983 to July 1984. The Chrysophyceae, Dinophyceae, Xanthophyceae and Dinophyceae have been omitted from this figure.



Key:

1. = Diatomophyceae
2. = Cyanophyceae
3. = Euchlorophyceae
4. = Zygophyceae
5. = Euglenophyceae
6. = Cryptophyceae

Densities were relatively low in mid-winter 1983, and fluctuated erratically throughout the remainder of the sampling year.

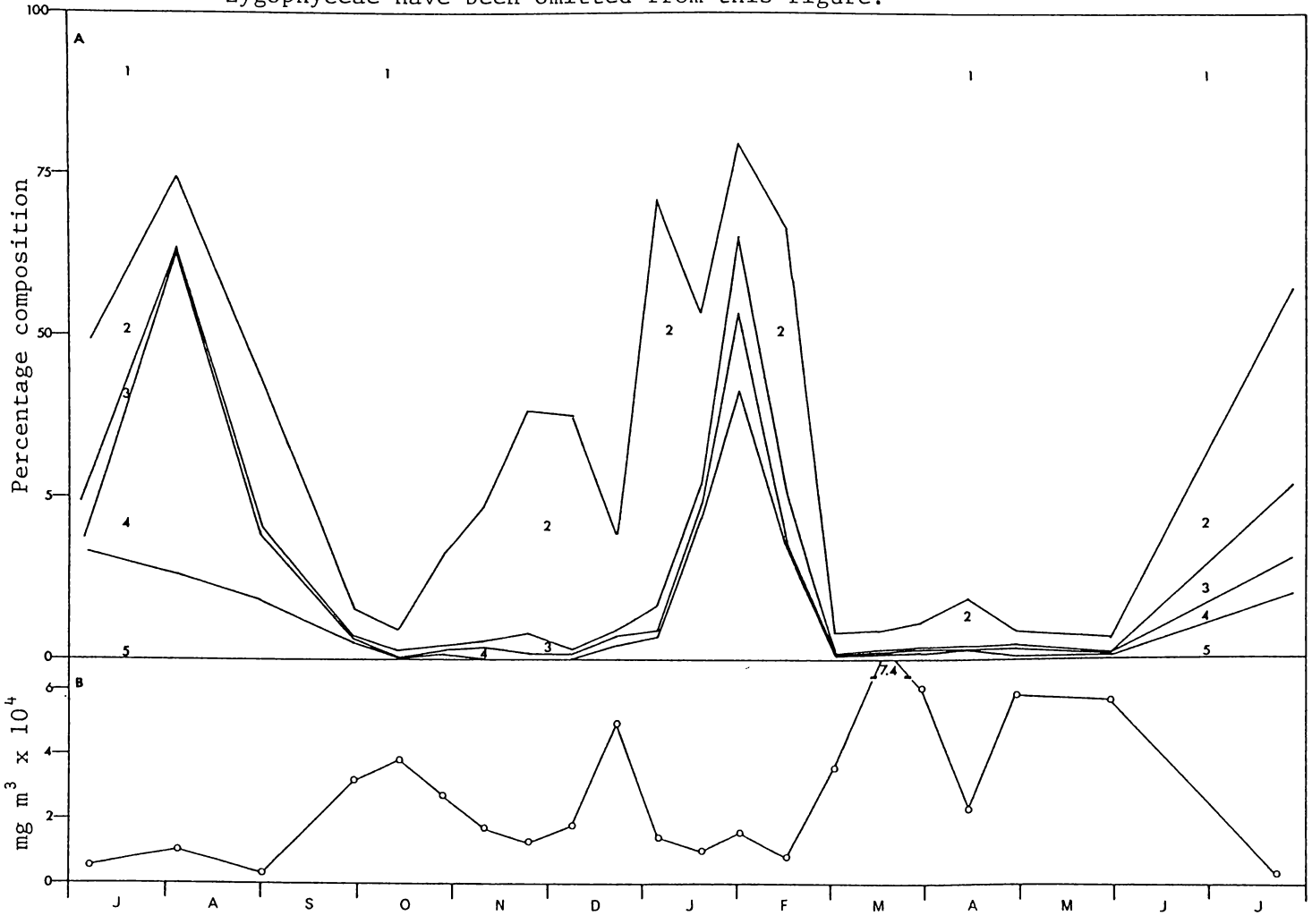
Total biomass also varied considerably (Fig. 6/20), with relatively low values being recorded during the colder months (minimum 3.1 g m^3 [26.7.84]). The maximum standing crop (74 g m^3) was recorded in late summer (15.3.84). The mean total biomass was 27.6 g m^3 (n = 21).

6.1.5.2 Temporal Variations in the Composition of the Total Phytoplankton Standing Crop

The seasonal dynamics of this community generally featured only three classes: the Diatomophyceae, Cyanophyceae and, to a lesser extent, the Euchlorophyceae (Fig. 6/19). Initially, the Diatomophyceae was numerically the most important class (54% [7.7.83]), but the Cyanophyceae and Euchlorophyceae generally dominated the plankton throughout both winter and spring 1983 (maximum proportions 51 and 41%, respectively). However, they were steadily replaced in early summer by the Diatomophyceae (85% [5.1.84]). The mid-summer period was characterised by a short euchlorophycean pulse (73% [2.2.84]), before further periods of dominance by the diatoms and cyanophytes (maximum proportions 77 [16.2.84] and 51% [29.4.84], respectively) in late summer-autumn and early winter 1984.

Because of the relatively large biovolumes of the major cyanophyte (*Microcystis aeruginosa* [65,449 μm^3]) and dinoflagellate species (*Peridinium cinctum* [39,250 μm^3]), the variations in total biomass (Fig. 6/20) differed markedly from those of abundance. Total biomass, with three exceptions, was dominated throughout the entire sampling period by the Cyanophyceae; its two highest proportions were recorded during late winter-spring 1983 (95%) and late summer-autumn 1984 (97%). The first interruption of this overwhelming dominance was apparent on 4.8.83 when the Euchlorophyceae and Dinophyceae accounted for 49 and 13% of the biomass, respectively. A second period of sub-dominance was recorded in mid-summer (2.2.84), and resulted from a dinophycean pulse (41%), combined with relatively minor but similar proportions of the Euchlorophyceae (12%), Diatomophyceae (15%) and Euglenophyceae (11%). A third exception was recorded in winter [26.7.84], when the Cyanophyceae shared dominance (30%) with the three previously mentioned classes, each of which was increasing in importance at the time.

Fig. 6/20 Temporal variations in: (a) phytoplankton class composition, in term of biomass; (b) total biomass (mg m^3 x 10^4), in Lake Ngaroto, July 1983 to July 1984. The Chrysophyceae, Cryptophyceae, Xanthophyceae and Zygophyceae have been omitted from this figure.



Key:

1. = Cyanophyceae
2. = Diatomophyceae
3. = Euglenophyceae
4. = Euchlorophyceae
5. = Dinophyceae

6.1.5.3 Temporal Variations in Phytoplankton Species Diversity

Species richness ranged from 22 (2.2.84) to 53 (7.7.83), but no seasonality was apparent (Table 6/12). The mean, the highest of the nine study lakes, was 41 ± 8 (n = 21). Despite considerable differences between total numbers of diatom (42) and cyanophyte species (24), their mean occurrences were remarkably similar (6 and 5 species, respectively). It is also of interest that although the Euchlorophyceae had only nine more species than the Diatomophyceae, its mean number of species per sample was markedly higher (17) (Table 6/13).

The Shannon-Wiener index displayed a considerable range (1.36 to 4.8) (Table 6/12). With one exception, five mid-summer communities (8.12.83 to 16.2.84) had the lowest values (mean 1.68), largely because of high densities of *Aulacosira granulata* var. *angustissima* (Fig. 6/23). The mean index was 2.66 ± 0.73.

6.1.5.4 Percentage Similarity of the Phytoplankton Communities

With two exceptions (29.4.84/26.5.84 [90%] and 22.12.83/5.1.84 [85%], consecutive communities were not markedly similar (Table 6/14). The mean index was 58 ± 19%, and there was little evidence of seasonality, with low indices occurring in mid-summer (27%), autumn (30%) and winter 1984 (38%). Summer/autumn and autumn/winter communities were also highly dissimilar (10 and 17%, respectively).

6.1.5.5 Species Periodicity

Aulacosira granulata var. *angustissima* was usually either the dominant or co-dominant phytoplankter (Fig. 6/23); however, although it was always present in relatively high densities (range 620 [26.7.84] to 7320 pu ml^{-1} [5.1.84), several other taxa exhibited marked seasonal periodicity.

Three of these species (*Anabaena tenericaulis*, *Raphidocelis contorta* and *Monoraphidium contortum*) were more abundant throughout winter and spring, than at any other time (Fig. 6/21). The maximum density of *A. tenericaulis* (2020 pu ml^{-1}), the most important in quantitative terms, was recorded on 1.9.83, and was followed successively by maxima of *Monoraphidium contortum* (608 pu ml^{-1} [29.9.83]) and *Raphidocelis contorta* (848 pu ml^{-1} [13.10.83]). All three taxa exhibited further peaks of abundance, but generally their

TABLE 6/12 α diversity and Shannon-Wiener information index for each sampling date in Lake Ngaroto, July 1983 to July 1984.

Date	α Diversity		Shannon-Wiener Information Index
	s	d	
1983			
7.vii	53	15.70	2.70
4.viii	48	12.89	2.84
1.ix	34	9.40	2.78
29.ix	33	9.27	3.23
13.x	35	9.63	3.80
27.x	43	11.34	2.90
10.xi	45	11.90	2.88
24.xi	41	10.93	2.09
8.xii	43	10.94	1.83
22.xii	48	12.18	1.47
1984			
5.i	42	10.60	1.36
19.i	50	13.29	2.93
2.ii	22	5.41	1.75
16.ii	30	8.43	1.99
2.iii	37	10.49	2.93
15.iii	42	11.62	2.63
29.iii	45	12.78	2.99
14.iv	31	8.81	2.19
29.iv	45	12.03	4.19
26.v	52	14.15	2.98
26.vii	47	13.72	3.44

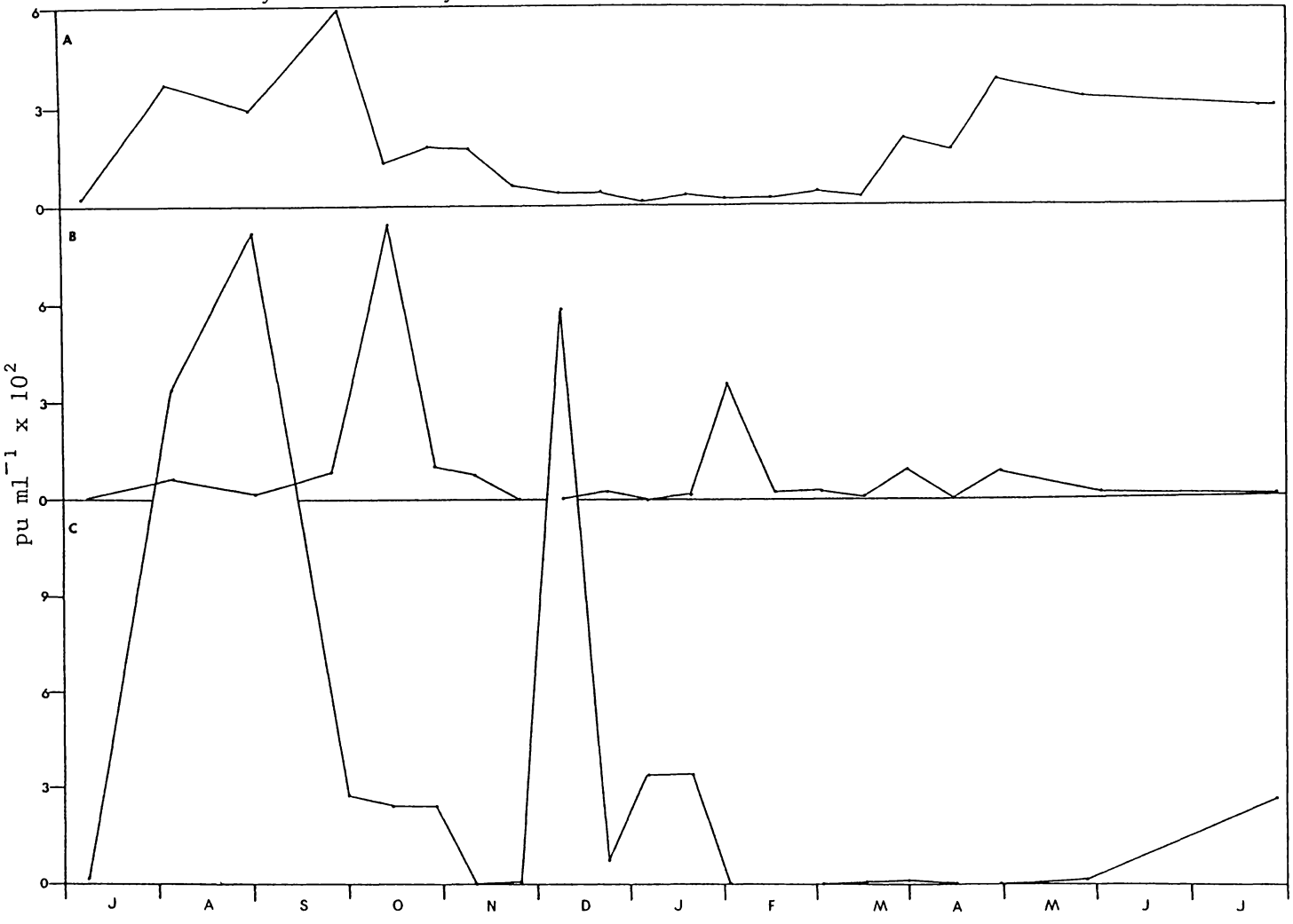
TABLE 6/13 Variation in the number of species (plus varieties) per 1 ml aliquot in Lake Ngaroto, July 1983 to July 1984.

Taxon	Number of Species			
	Maximum	Minimum	Mean ± 1 SD (n = 21)	Total
CHLOROPHYTA				
Euchlorophyceae	20	8	16.9 ± 3.0	51
Ulothricophyceae	1	0	0.05 ± 0.2	1
Zygophyceae	6	2	4.2 ± 1.1	16
CHROMOPHYTA				
Chrysophyceae	4	0	0.95 ± 1.1	7
Diatomophyceae	15	4	6.5 ± 2.9	46
Xanthophyceae	2	0	0.1 ± 0.5	2
CYANOPHYTA				
Cyanophyceae	9	3	5.3 ± 2.1	26
EUGLENOPHYTA				
Euglenophyceae	6	0	2.4 ± 1.8	18
PYRRHOPHYTA				
Cryptophyceae	2	0	1.8 ± 0.6	3
Dinophyceae	2	0	0.9 ± 0.5	4
ALL SPECIES	53	22	41.2 ± 8.0	174

TABLE 6/14 Percentage similarity indices of consecutive and other specified phytoplankton communites in Lake Ngaroto, July 1983 to July 1984.

Dates	Community Type	Percentage Similarity Index
1983		
7.vii/4.viii	Consecutive	42
4.viii/1.ix	"	71
1.ix/29.ix	"	47
29.ix/13.x	"	64
13.x/27.x	"	55
27.x/10.xi	"	72
10.xi/24.xi	"	68
24.xi/8.xii	"	74
8.xii/22.xii	"	74
22.xii/5.i	"	85
1984		
5.i/19.i	"	53
19.i/2.ii	"	27
2.ii/16.ii	"	29
16.ii/2.iii	"	43
2.iii/15.iii	"	63
15.iii/29.iii	"	70
29.iii/14.iv	"	30
14.iv/29.iv	"	58
29.iv/26.v	"	90
26.v/26.vii	"	38
7.vii/13.x	winter-spring	46
13.x/5.i	spring-summer	36
5.i/14.iv	summer-autumn	10
14.iv/26.vii	autumn-winter	17
7.vii (1983)/ 26.vii (1984)	annual	45

Fig. 6/21 Temporal variations in the densities (pu ml^{-1} x 10^2) of *Monoraphidium contortum*, *Anabaena tenericaulis* and *Raphidocelis contorta* in Lake Ngaroto, July 1983 to July 1984.



Key:

A. = *Monoraphidium contortum*

B. = *Anabaena tenericaulis*

C. = *Raphidocelis contorta*

densities were relatively low during the warmer months.

In contrast, the peak densities of a further six major taxa (Fig. 6/22), representing four classes (Euchlorophyceae, Zygophyceae, Diatomophyceae and Cyanophyceae), were recorded in early summer. Generally, their cycles of abundance were broadly similar: slight increases in spring; major peaks in October-November 1983; declining numbers throughout mid- and late summer; and small increases in either autumn or winter 1984.

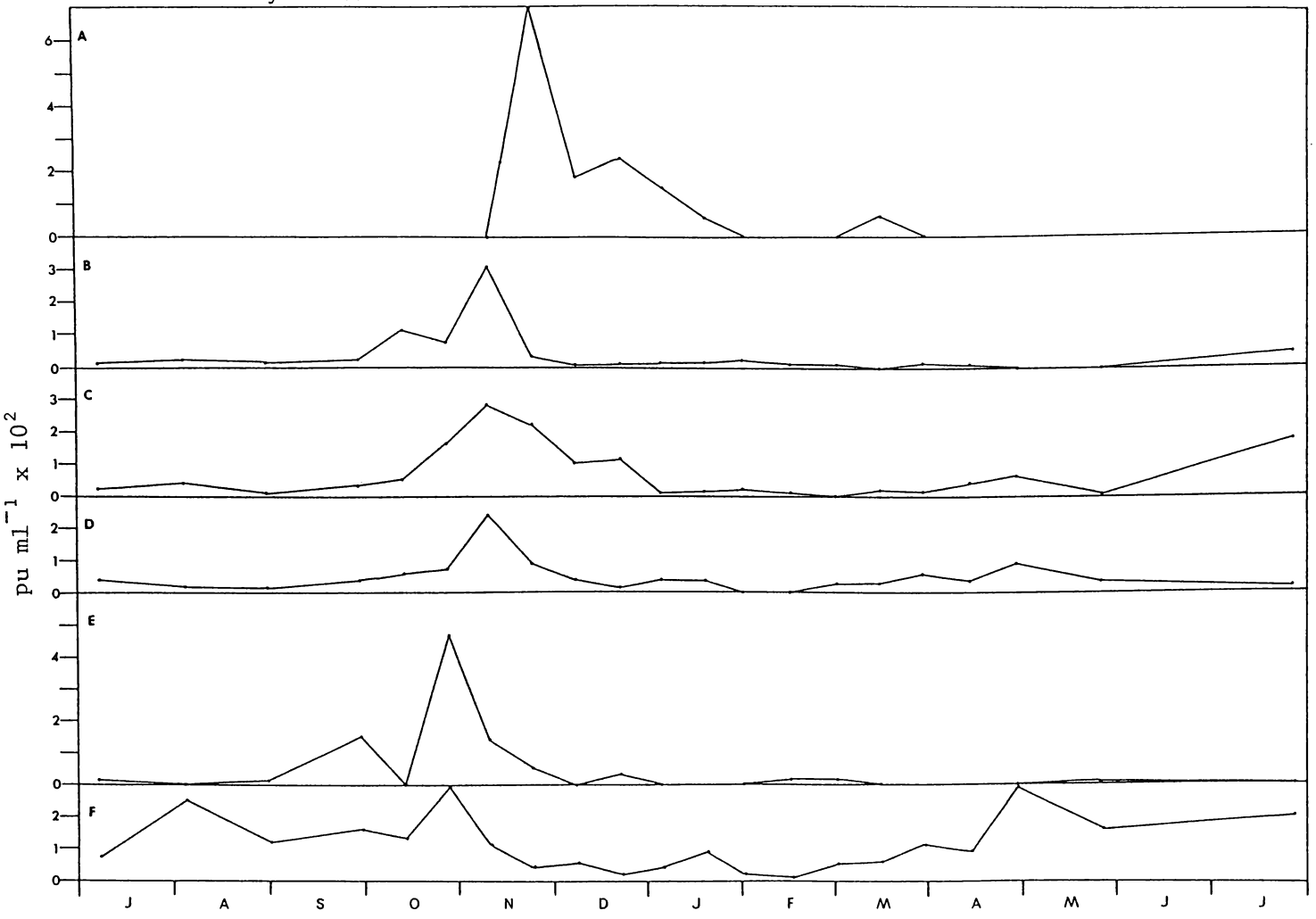
Of these six taxa, *Merismopedia minima* had the highest density (704 pu ml^{-1}), but was the most temporally restricted species. The maxima of *Tetrastrum triangulare* (468 pu ml^{-1}) and *T. staurogeniaforme* (316 pu ml^{-1}) were recorded on consecutive sampling dates (27.10.83 and 10.11.83, respectively), as were those of the two desmids, *Closterium acutum* var. *variabile* (292 pu ml^{-1} [27.10.83]) and *Staurastrum* sp. C (240 $puml^{-1}$ [10.11.83]). The maximum density of *Aulacosira distans* (284 pu ml^{-1}), the sixth member of this group, also was recorded on 10.11.83, although its subsequent decline was not as sharp as those of the other five taxa.

In mid-summer 1984, *Aulacosira granulata* var. *angustissima* dominated the community, but maxima of *Scenedesmus quadricauda*, *Trachelomonas volvocina* and *Asterionella formosa* were also recorded (Fig. 6/23). The former was a permanent member of the flora, with minimum and maximum densities of 620 (26.7.84) and 7320 pu ml^{-1} (5.1.84), respectively. Its numbers were lower throughout winter and spring than during the warmer months. At the time of its maximum abundance (5.1.84) it comprised 80% of the total community. The maximum density of *A. formosa* (404 pu ml^{-1}) was also recorded during this period. Diatom maxima were followed by peak densities of both *S. quadricauda* and *T. volvocina* (7608 and 648 pu ml^{-1}, respectively [2.2.84]).

Microcystis aeruginosa had minor pulses in early summer (560 pu ml^{-1} [27.10.83] and 616 pu ml^{-1} [12.12.83]) (Fig. 6/24) but its two largest peaks (1080 and 1444 pu ml^{-1}) were recorded in autumn (15.3.84) and early winter (29.4.84 and 26.5.84), respectively.

With the exception of a brief period in late summer (2.2.84 and 16.2.84), *Cryptomonas* spp. (*C. marssonii* and *C. ovata*) were permanent

Fig. 6/22 Temporal variations in the densities (pu ml^{-1} x 10^2) of *Merismopedia minima*, *Tetrastrum triangulare*, *T. staurogeniaforme*, *Aulacosira distans*, *Staurastrum* sp. C and *Closterium acutum* var. *variabile* in Lake Ngaroto, July 1983 to July 1984.



Key:

A. = *Merismopedia minima*

B. = *Tetrastrum triangulare*

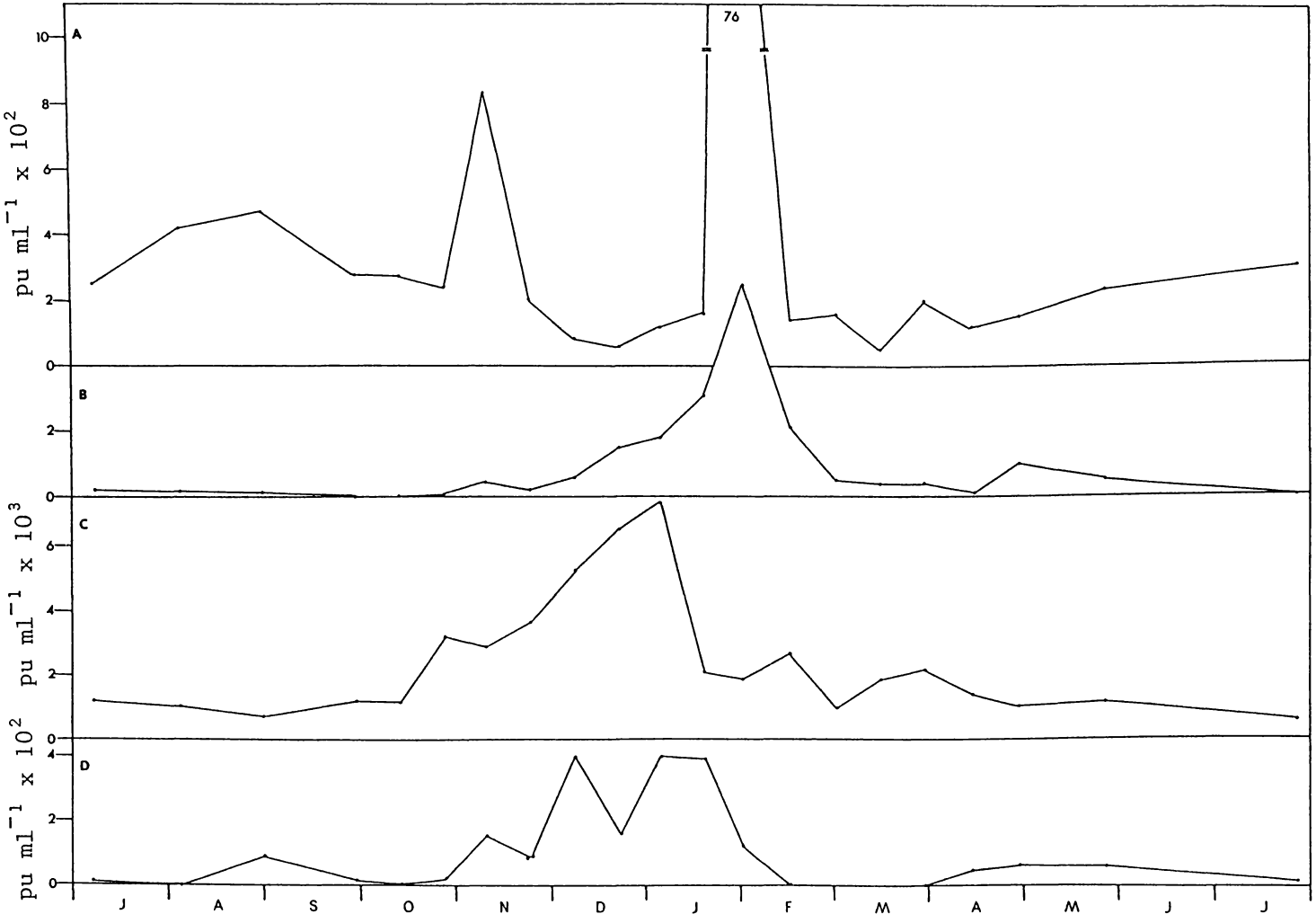
C. = *T. staurogeniaforme*

D. = *Aulacosira distans*

E. = *Staurastrum* sp. C

F. = *Closterium acutum* var. *variabile*

Fig. 6/23 Temporal variations in the densities (pu ml^{-1}) of *Scenedesmus quadricauda*, *Trachelomonas volvocina*, *Aulacosira granulata* var. *angustissima*, and *Asterionella formosa* in Lake Ngaroto, July 1983 to July 1984.



Key:

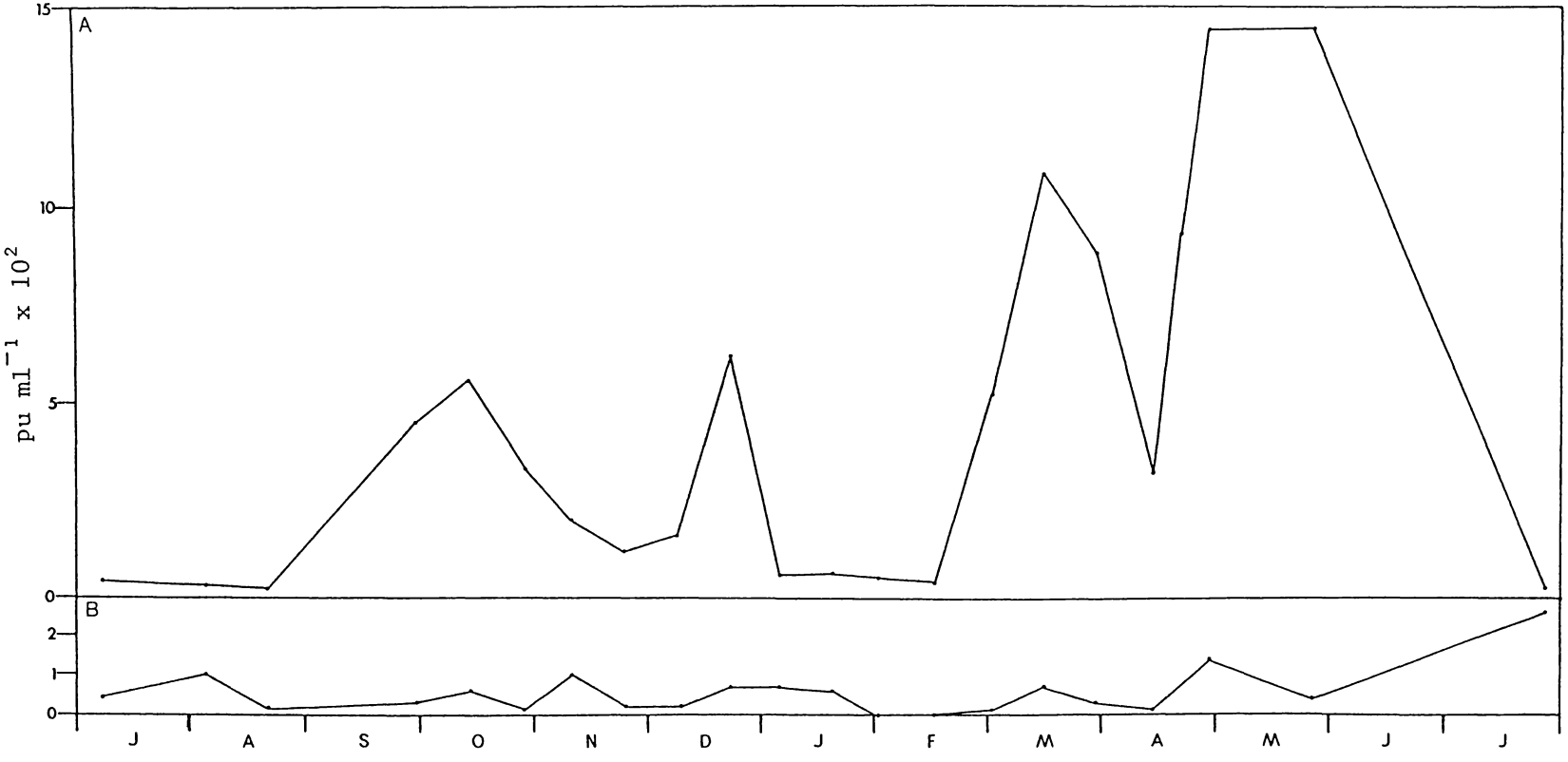
A. = *Scenedesmus quadricauda*

B. = *Trachelomonas volvocina*

C. = *Aulacosira granulata* var. *angustissima*

D. = *Asterionella formosa*

Fig. 6/24 Temporal variations in densities (pu ml^{-1} x 10^2) of *Microcystis aeruginosa* and *Cryptomonas* spp. in Lake Ngaroto, July 1983 to July 1984.



Key:

A. = *Microcystis aeruginosa*

B. = *Cryptomonas* spp.

members of the community (Fig. 6/24). Their numbers fluctuated erratically throughout the greater part of the year, but maxima occurred after autumn and early winter peaks of total phytoplankton biomass (140 [29.4.84] and 256 pu ml^{-1} [26.7.84], respectively) (Fig. 6/20).

6.1.6 Lake Rotokauri

6.1.6.1 Temporal Variations in Total Phytoplankton Density and Biomass

Total phytoplankton density fluctuated irregularly throughout the entire sampling year (Fig. 6/25). There was little evidence of seasonality, and both maximum (2190 pu ml^{-1}) and minimum (64 pu ml^{-1}) densities were recorded during the colder months (31.6.84 and 3.9.83, respectively). The mean density was 653 pu ml^{-1} (n = 22).

Total biomass also fluctuated dramatically (Fig. 6/26), ranging from 0.02 (28.7.84) to 2.3 g m^3 (4.2.84). Increased nutrient availability following aquatic macrophyte decomposition in mid-summer 1984 (Chapter 3.2), was undoubtedly responsible for the timing of the maximum biomass peak. The mean biomass, the lowest of the nine study lakes (Table 7/1), was 0.7 g m^3 (n = 22).

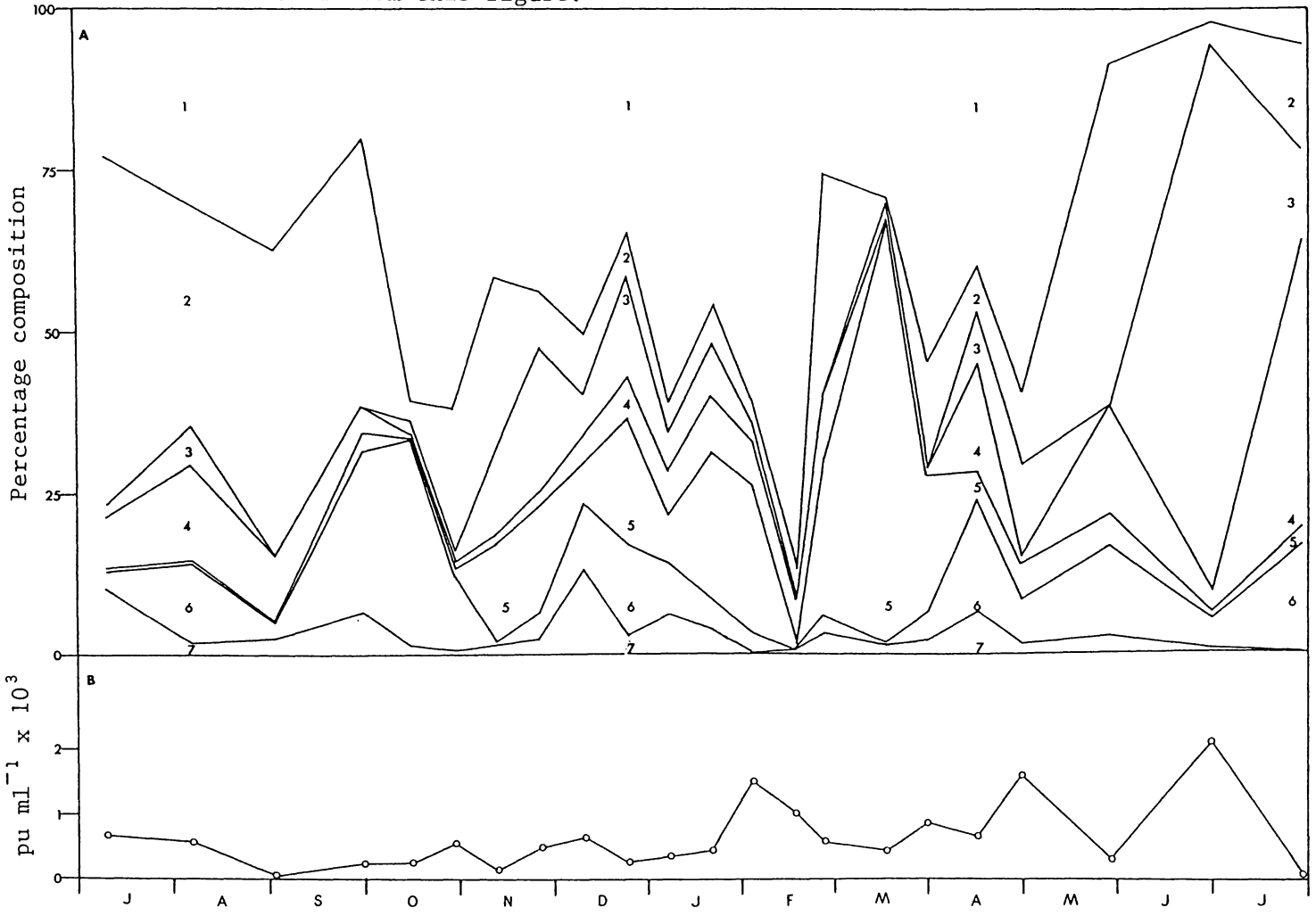
6.1.6.2 Temporal Variations in the Composition of the Total Phytoplankton Standing Crop

In terms of total density, two broad patterns were evident: first, the Diatomophyceae and Euchlorophyceae were the most important classes during winter-spring 1983 and summer-autumn 1984, respectively; secondly, other important taxa (Euglenophyceae, Chrysophyceae and Zygophyceae) each interrupted this dominance on one occasion, albeit briefly (Fig. 6/25).

Initially, the Diatomophyceae accounted for 54% of the mean total phytoplankton density, and its proportions remained relatively stable until 15.10.83 when, because of an increase in the Euchlorophyceae (61%), dominance changed. Between 15.10.83 and 27.2 84, the mean euchlorophyte proportion was 54% (n = 10). The maximum (86%) immediately preceded an increase in the importance of the Euglenophyceae. Euglenophyte dominance, however, was short-lived (maximum 65% [17.3.84]).

Both the Chrysophyceae and Zygophyceae rapidly increased in importance during winter (maximum proportions 85 [31.6.84] and 44%

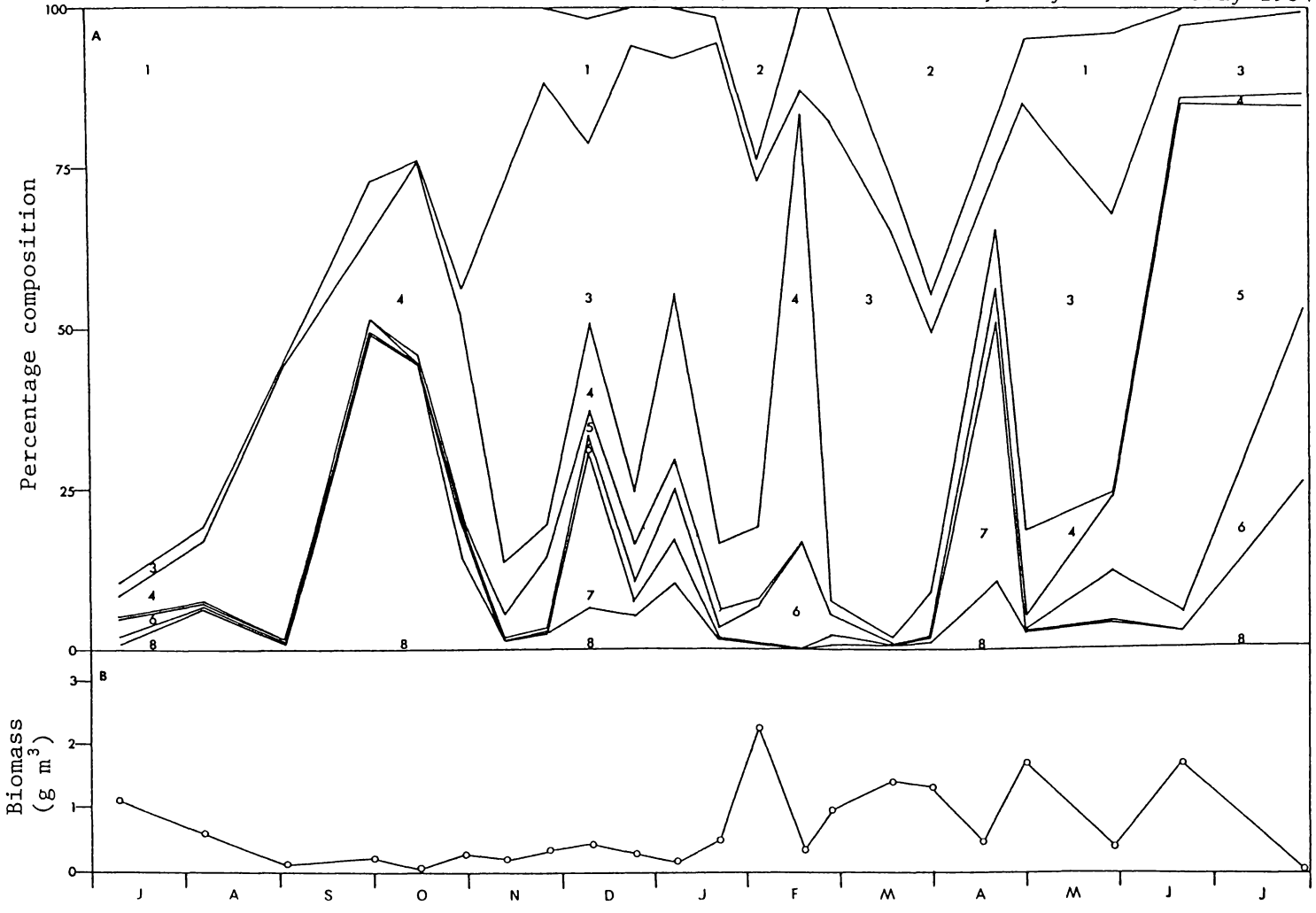
Fig. 6/25 Temporal variations in: (a) phytoplankton class composition, in terms of abundance; (b) total number of pu ml^{-1}, in Lake Rotokauri, July 1983 to July 1984. The Dinophyceae, Raphidophyceae and Ulothricophyceae have been omitted from this figure.



Key:

1. = Euchlorophyceae
2. = Diatomophyceae
3. = Chrysophyceae
4. = Zygophyceae
5. = Euglenophyceae
6. = Cryptophyceae
7. = Cyanophyceae

Fig. 6/26 Temporal variations in: (a) phytoplankton class composition, in terms of biomass; (b) total biomass (g m^3), in Lake Rotokauri, July 1983 to July 1984.



Key:

1. = Diatomophyceae
2. = Dinophyceae
3. = Euglenophyceae
4. = Euchlorophyceae
5. = Chrysophyceae
6. = Zygophyceae
7. = Cyanophyceae
8. = Cryptophyceae

[28.7.84], respectively).

In terms of total biomass, annual periodicity of the major classes was complicated (Fig. 6/26), largely due to the brevity of their periods of dominance. Initially, the Diatomophyceae, was the most important class (90% [9.7.83] and 81% [6.8.83]). However, in late spring and early summer 1983 it was gradually replaced by the Cryptophyceae and the Euchlorophyceae.

From November 1983 until June 1984, the major class, with two exceptions, was the Euglenophyceae. Its maximum and mean proportions during this period were 78 (21.1.84) and 50% (n = 14), respectively. The Euchlorophyceae and the Cyanophyceae briefly interrupted this long period of dominance, with respective proportions of 66 (18.2.84) and 41% (16.4.84). Euglenophytes also had two short periods of co-dominance, resulting from increases in importance of both the cyanophytes (24% [10.12.83]) and the dinoflagellates (44% [31.3.84]).

During late autumn and winter 1984, the Euglenophyceae was replaced by the Chrysophyceae (maximum proportion 80% [31.6.84]). Minor increases in the importance of both the Zygophyceae and Cryptophyceae were also recorded at the end of the sampling programme.

With one major exception, the cryptophytes generally showed an inverse relationship with total phytoplankton biomass, their highest proportions occurring in late spring-early summer 1983 (50 and 44%, respectively) and winter 1984 (25%), following rapid decreases in both diatom and chrysophyte biomass. However, the major mid-summer peak in total biomass was not followed by a cryptophyte pulse, possibly because decomposition of aquatic macrophytes (Chapter 3.2) produced abnormally high nutrient levels.

6.1.6.3 Temporal Variations in Phytoplankton Species Diversity

The number of species per sample (Table 6/15) ranged from 14 to 55 (mean 37.2 ± 12.1 [n = 22]). Generally, species richness was low during the colder months, but there were some exceptions; for example, 46 species were found on 9.7.83. More zygophyte, cyanophyte and euglenophyte species were found in Lake Rotokauri than any other study lake (Table 5/20), thus both the relatively low mean and maximum number per sample of these taxa are of special interest (Table 6/16). The mean Shannon-Wiener index (Table 6/15), the highest of the nine study lakes, was 3.57 ± 0.72 (range 1.51 to 4.76). Only three indices were ≤ 3.0, and no seasonality was apparent.

TABLE 6/15 α diversity and Shannon-Wiener information index for each sampling date in Lake Rotokauri, July 1983 to July 1984.

Date	α Diversity		Shannon-Wiener Information Index
	s	d	
1983			
9.vii	46	16.39	3.38
6.viii	37	13.39	3.53
3.ix	19	10.52	3.64
1.x	36	15.07	3.50
15.x	21	8.80	2.62
29.x	44	15.90	3.45
12.xi	34	15.56	4.15
26.xi	42	15.49	3.88
10.xii	55	19.44	4.76
24.xii	45	18.29	4.55
1984			
7.i	42	16.30	3.82
21.i	50	18.76	4.20
4.ii	54	16.97	4.39
18.ii	40	13.26	3.30
27.ii	46	16.71	4.15
17.iii	29	10.86	3.07
31.iii	45	15.31	3.89
16.iv	31	11.01	3.37
1.v	47	14.71	2.63
28.v	16	6.55	3.62
31.vi	26	7.78	1.51
28.vii	14	7.54	3.21

TABLE 6/16 Variation in the number of species (plus varieties) per 1 ml aliquot in Lake Rotokauri, July 1983 to July 1984.

Taxon	Number of Species			
	Maximum	Minimum	Mean ± 1 SD (n = 22)	Total
CHLOROPHYTA				
Euchlorophyceae	18	2	12.5 ± 5.2	48
Ulothricophyceae	1	0	0.1 ± 0.3	2
Zygophyceae	13	2	5.9 ± 3.5	47
CHROMOPHYTA				
Chrysophyceae	3	0	1.3 ± 1.0	6
Diatomophyceae	11	1	6.6 ± 2.6	31
Xanthophyceae	1	0	0.1 ± 0.3	1
CYANOPHYTA				
Cyanophyceae	11	0	3.7 ± 2.4	29
EUGLENOPHYTA				
Euglenophyceae	12	0	4.7 ± 3.7	35
PYRRHOPHYTA				
Cryptophyceae	3	0	2.0 ± 0.6	3
Dinophyceae	3	0	0.9 ± 1.0	7
RAPHIDOPHYTA				
Raphidophyceae	1	0	0.2 ± 0.4	1
ALL SPECIES	55	14	37.2 ± 12.1	210

6.1.6.4 Percentage Similarity of the Phytoplankton Communities

The remarkably low mean index (34 ± 12%) (Table 6/17) and the lack of continuity (both the highest [55%] and lowest [12%] indices fell within three consecutive communities [21.1.84 to 27.3.84]), provide further evidence of the ephemeral nature of the Lake Rotokauri phytoplankton populations.

6.1.6.5 Species Periodicity

With the exception of the diatoms, the seasonal cycles of the major phytoplankters were not clearly defined. Initially, the two most important species were *Gomphonema truncatum* and *Fragilaria ulna*; their maximal densities (240 and 73 pu ml^{-1}, respectively) were both recorded during winter 1983, and throughout the remainder of the sampling year they were insignificant members of the flora (Fig. 6/27).

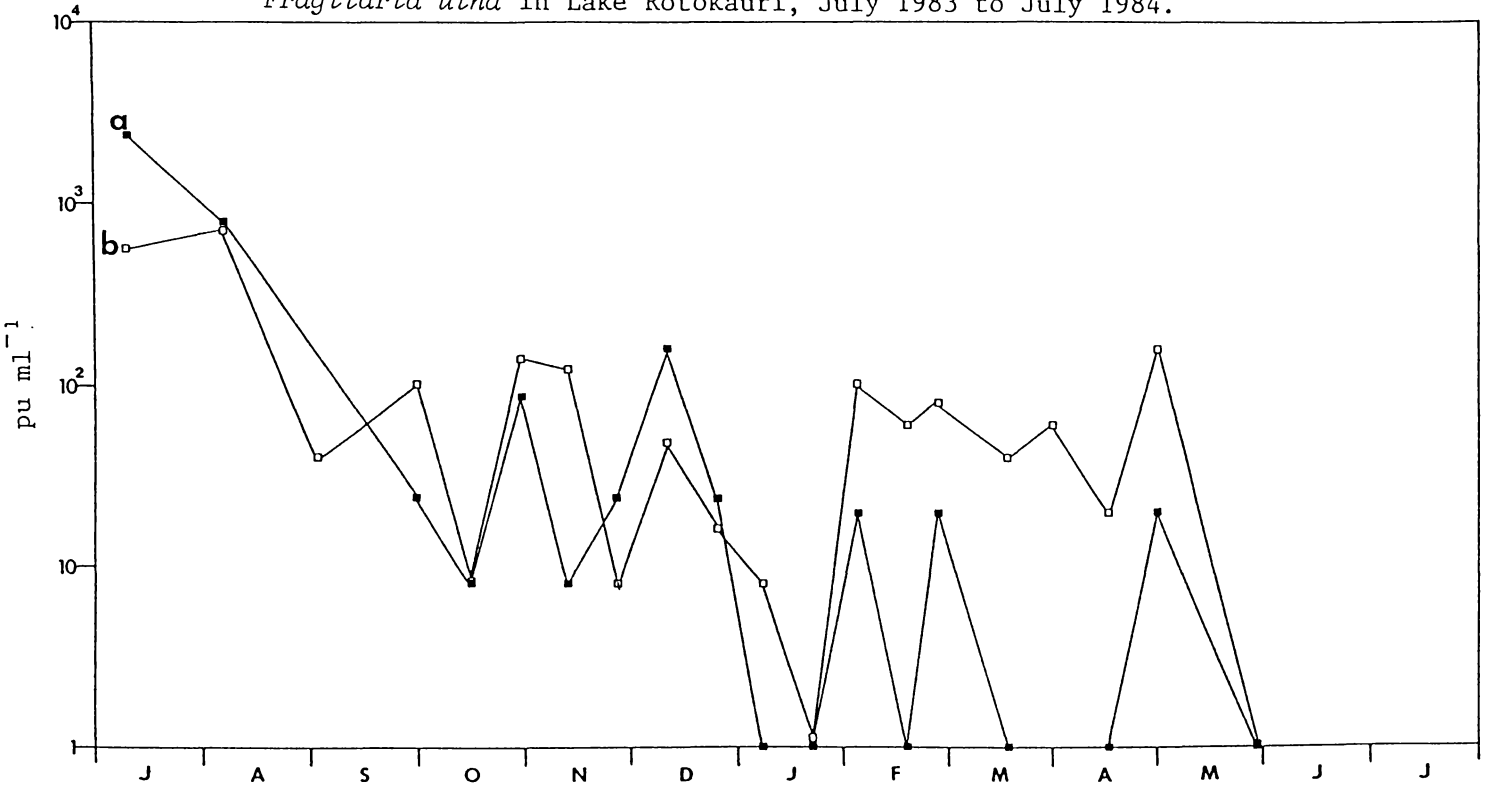
In spring and summer the major taxa were *Ankistrodesmus* spp., but generally their peaks were unpredictable (Fig. 6/28) and not confined to this period. The density of *A. falcatus* fluctuated erratically, peaking at 142 (29.10.83) and 157 pu ml^{-1} (26.11.83). *A. bibraianus* became dominant in mid-summer (Fig. 6/30), with peaks of 266 and 312 pu ml^{-1} (4.2.84 and 18.2.84, respectively) and, in a pattern similar to *A. gracilis*, showed a further increase at the beginning of winter 1984.

Periodicity was complex throughout autumn and winter 1984, with taxa from four classes becoming important. The maximal densities of *Trachelomonas planctonica, T. playfairi* and *T. volvocina* (222 pu ml^{-1}), and *Cryptomonas marssonii*, plus *C. ovata* (114 pu ml^{-1}), after showing broadly similar cycles throughout the entire sampling year (with one exception [17.3.84]) were recorded at this time (Fig. 6/29). *Monoraphidium contortum* (142 pu ml^{-1}) and *Mallomonas akrokomos* (1614 pu ml^{-1}) (Fig. 6/30) also peaked during this period, and the latter is of special interest because it was not found prior to 31.6.84.

TABLE 6/17 Percentage similarity indices of consecutive and other specified phytoplankton communites in Lake Rotokauri, July 1983 to July 1984.

Dates	Community Type	Percentage Similarity Index
1983		
9.vii/6.viii	consecutive	36
6.viii/3.ix	"	34
3.ix/1.x	"	27
1.x/15.x	"	30
15.x/29.x	"	46
12.xi/26.xi	"	35
26.xi/10.xii	"	33
10.xii/24.xii	"	26
24.xii/7.i	"	37
1984		
7.i/21.i	"	55
21.i/4.ii	"	59
4.ii/18.ii	"	42
18.ii/27.ii	"	12
27.ii/17.iii	"	23
17.iii/31.iii	"	35
31.iii/16.iv	"	45
16.iv/1.v	"	30
1.v/28.v	"	27
28.v/31.vi	"	27
31.vi/28.vii	"	16
9.vii/15.x	winter-spring	6
15.x/7.i	spring-summer	19
7.i/16.iv	summer-autumn	33
16.iv/28.vii	autumn-winter	28
9.vii (1983)/ 28.vii (1984)	annual	4

Fig. 6/27 Temporal variations in the densities (pu ml^{-1}) of *Gomphonema truncatum* and *Fragilaria ulna* in Lake Rotokauri, July 1983 to July 1984.

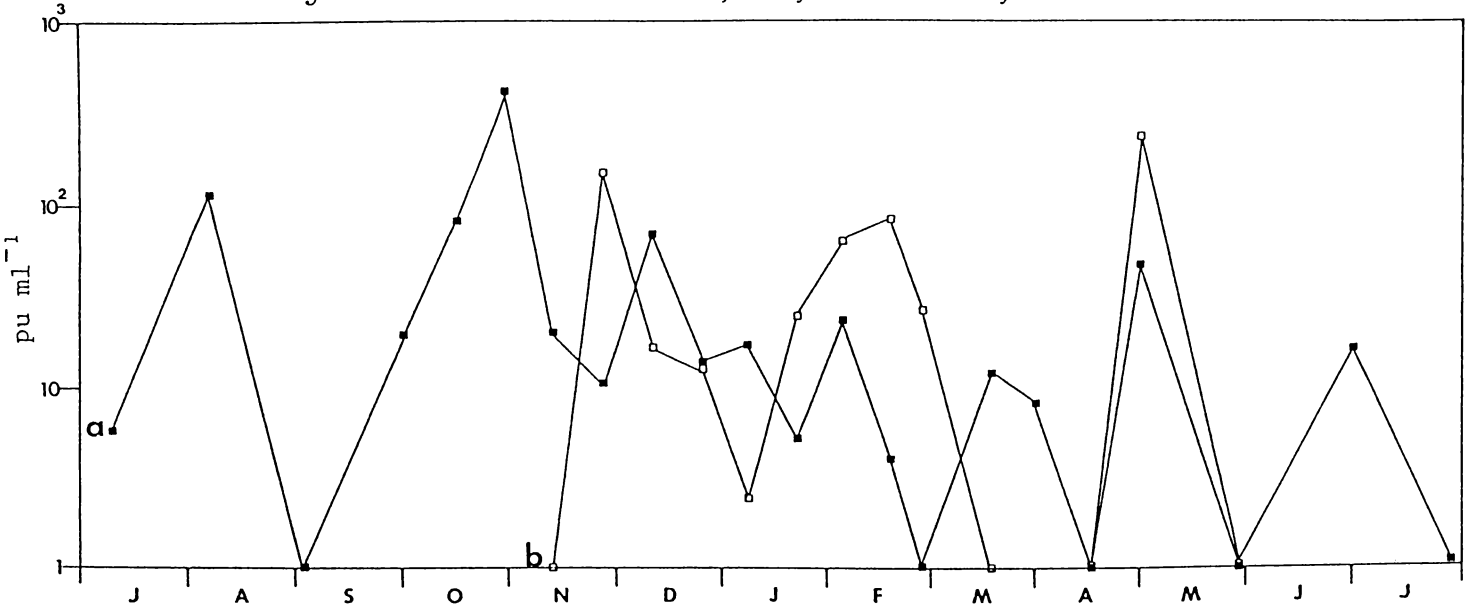


Key:

a. = *Gomphonema truncatum*

b. = *Fragilaria ulna*

Fig. 6/28 Temporal variations in densities (pu ml^{-1}) of *Ankistrodesmus falcatus* and *A. gracilis* in Lake Rotokauri, July 1983 to July 1984.

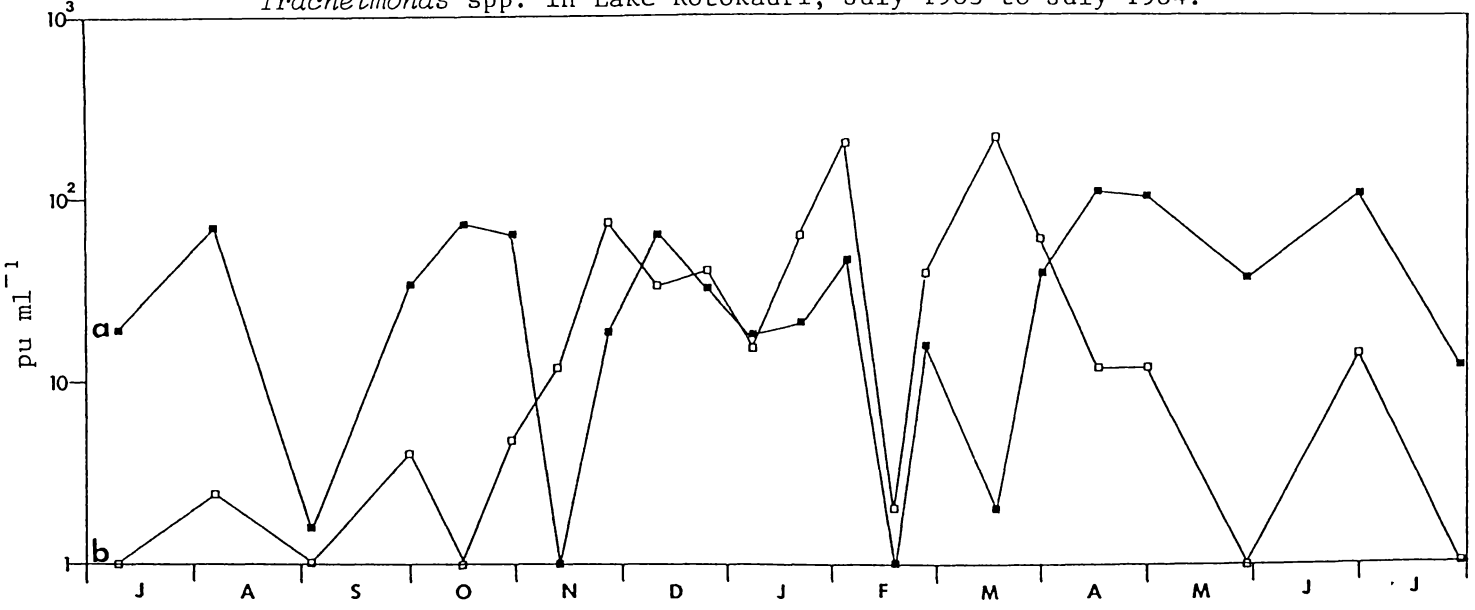


Key:

a. = *Ankistrodesmus falcatus*

b. = *A. gracilis*

Fig. 6/29 Temporal variations in the densities (pu ml^{-1}) of *Cryptomonas* spp. and *Trachelmonas* spp. in Lake Rotokauri, July 1983 to July 1984.

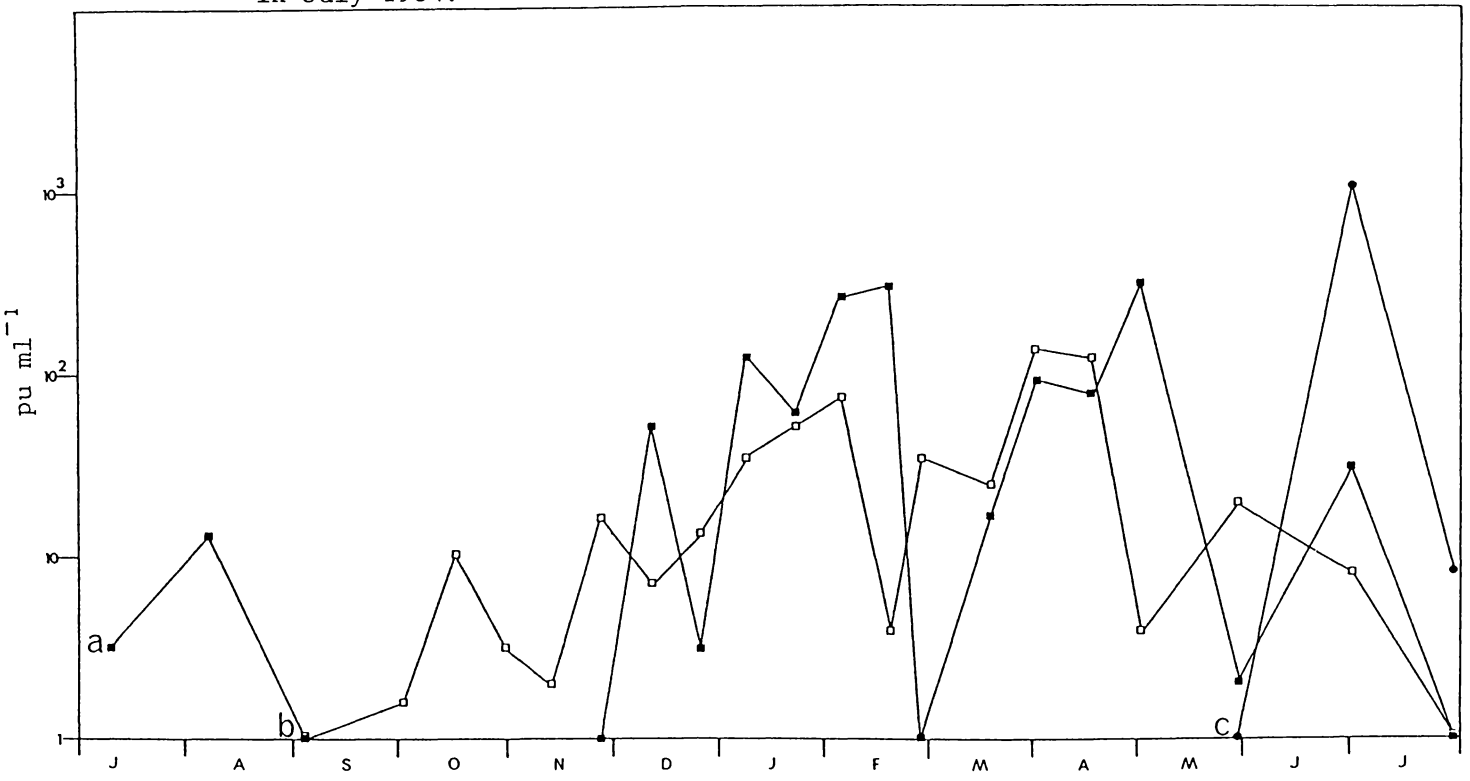


Key:

a. = *Cryptomonas* spp.

b. = *Trachelomonas* spp.

Fig. 6/30 Temporal variations in the densities (pu ml^{-1}) of *Ankistrodesmus bibraianus*, *Monoraphidium contortum* and *Mallomonas akrokomos* in Lake Rotokauri, July 1983 in July 1984.



Key:

a. = *Ankistrodesmus bibraianus*

b. = *Monoraphidium contortum*

c. = *Mallomonas akrokomos*

6.1.7 Lake Rotomanuka North

6.1.7.1 Temporal Variations in Total Phytoplankton Density and Biomass

Generally, total phytoplankton density peaked in winter and showed little variation during the remainder of the year (range 144 to 1186; mean 414 pu ml^{-1} [n = 21]) (Fig. 6/31). The densities of the two winter peaks were 1206 (4.8.83) and 1186 pu ml^{-1} (26.7.84), respectively, and with one exception, (526 pu ml^{-1} [13.10.83], densities were low throughout the remainder of the sampling period (range 139 [1.9.83] to 362 pu ml^{-1} [26.5.84]).

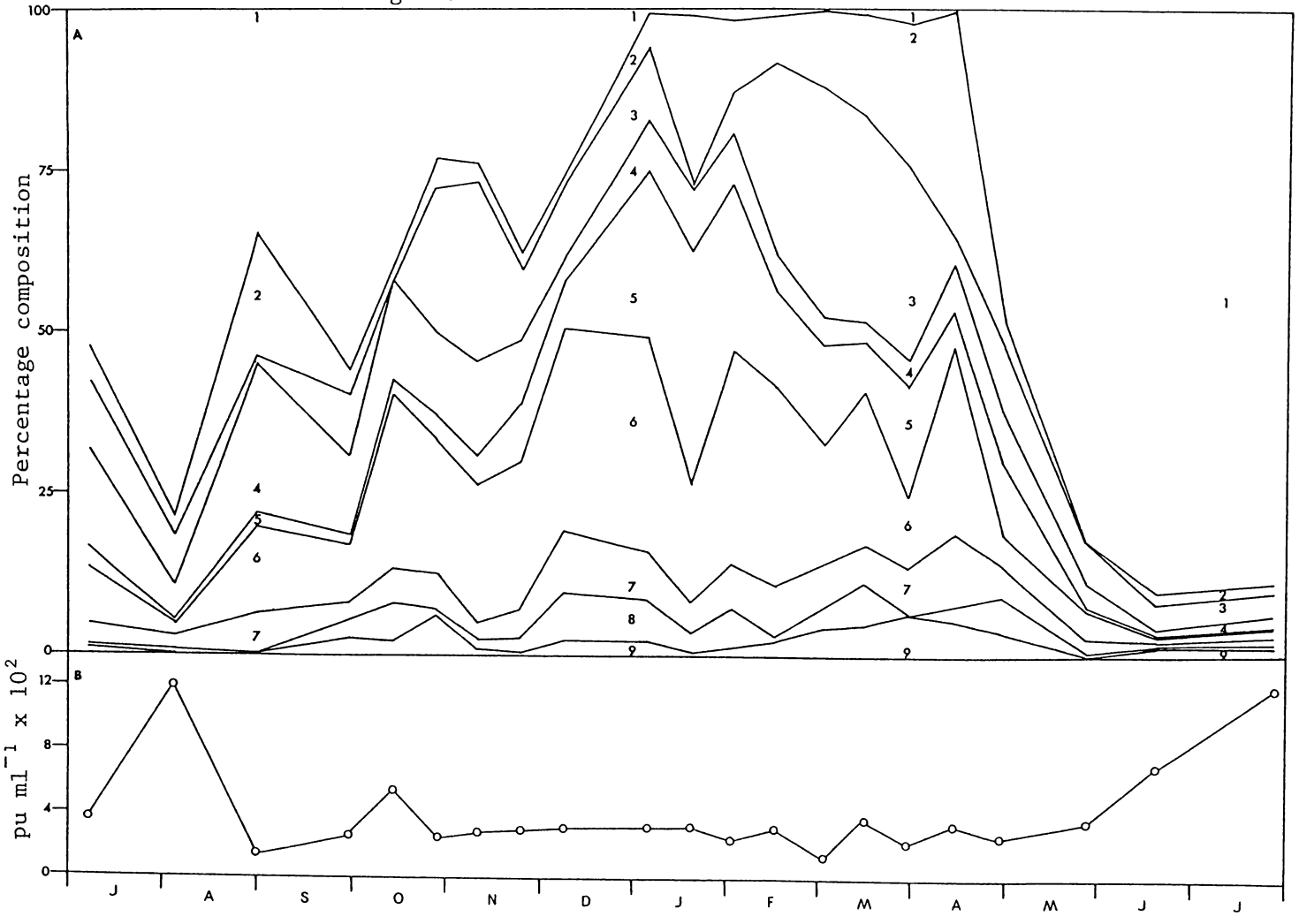
Total biomass ranged from 0.3 to 5.2 g m^3 (mean 1.7 g m^3 [n = 21]) (Fig. 6/32), and peaked once during each season (winter 1983, 1.5 g m^3; spring, 1.8 g m^3; summer 1984, 3.1 g m^3; and autumn 5.2 g m^3).

6.1.7.2 Temporal Variations in the Composition of the Total Phytoplankton Standing Crop

Numerically, all classes generally displayed marked seasonality (Fig. 6/31). The Chrysophyceae dominated the winter-spring 1983 and late autumn-winter 1984 communities (maximum proportions 78 and 85%, respectively). However, during the remainder of the sampling year, dominance was shared between all other classes, excluding the Zygophyceae, Cyanophyceae and Raphidophyceae. The highest diatom proportion (23%) was recorded in early spring (1.9.83), prior to well-developed stratification (Fig. 3/18). In contrast, the most important period for both the Euglenophyceae (36%) and the Euchlorophyceae (31%) was mid-summer (19.1.84 and 16.2.84, respectively), while for the Cryptophyceae (35%) and Dinophyceae (32%) it was late summer and autumn (2.3.84 and 14.4.84, respectively).

The major taxa also displayed marked seasonality in biomass (Fig. 6/32), although in comparison to total density, dominance during the warmer months was less evenly distributed. The Dinophyceae was the most important class throughout both winter-spring 1983 and mid-summer to July 1984 (maximum proportions 90 and 93%, respectively). The Euchlorophyceae and Cyanophyceae were the only other significant classes; the former comprised 52, 49 and 36% of the community on 10.11.83, 5.1.84 and 2.2.84, respectively, while the latter was co-dominant with the euchlorophytes in early summer (13.10.83 [38%] and 8.12.83 [39%]).

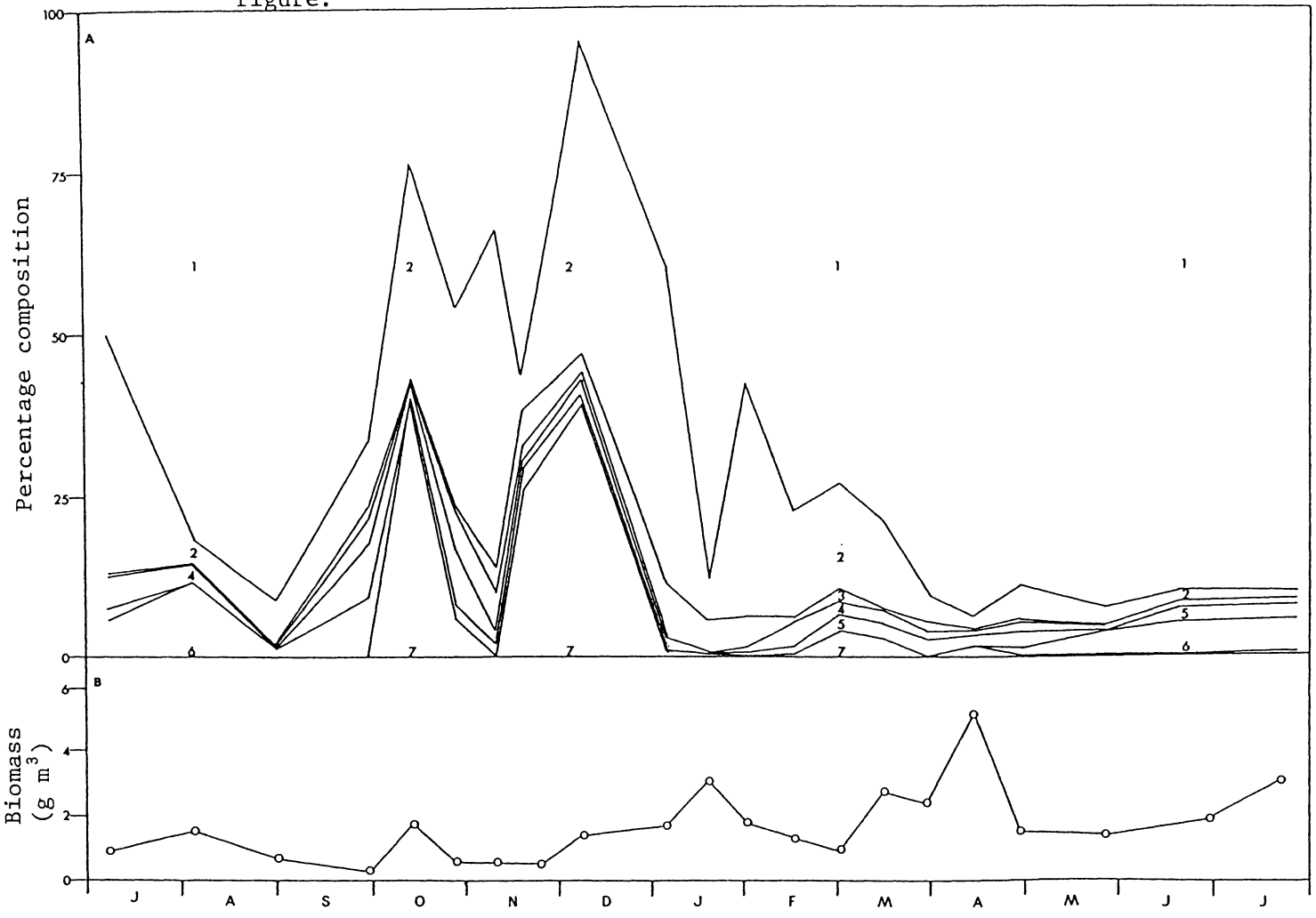
Fig. 6/31 Temporal variations in: (a) phytoplankton class composition, in terms of abundance; (b) total number of pu ml^{-1}, in Lake Rotomanuka North, July 1983 to July 1984. The Ulothricophyceae and Xanthophyceae have been omitted from this figure.



Key:

1. = Chrysophyceae
2. = Dinophyceae
3. = Cryptophyceae
4. = Diatomophyceae
5. = Euglenophyceae
6. = Euchlorophyceae
7. = Zygophyceae
8. = Cyanophyceae
9. = Raphidophyceae

Fig. 6/32 Temporal variations in: (a) phytoplankton class composition, in terms of biomass; (b) total biomass (g m^3), in Lake Rotomanuka North, July 1983 to July 1984. The Diatomophyceae and Zygophyceae have been omitted from this figure.



Key:

1. = Dinophyceae
2. = Euchlorophyceae
3. = Euglenophyceae
4. = Cryptophyceae
5. = Raphidophyceae
6. = Chrysophyceae
7. = Cyanophyceae

6.1.7.3 Temporal Variations in Phytoplankton Species Diversity

Species richness was high in mid-summer 1984 (maximum 46 [5.1.84], and generally markedly lower during the colder months (e.g., 20 [29.6.84] and 24 species [7.7.83]) (Table 6/18). The mean α diversity was 33.8 ± 8.4 (n = 21). Overall, the community displayed low species continuity (Table 6/19). The cryptophytes, dinoflagellates and the sole raphidophyte (*Vacuolaria* sp.) were the most consistent members of the flora, in contrast to both the Euchlorophyceae and Diatomophyceae which, despite high numbers of species, had low mean occurrences per sample (10 [17%] and 5 [14%], respectively).

The Shannon-Wiener indices (Table 6/18) were both relatively high and remarkably similar (range 2.88 to 3.84; mean 3.19 ± 0.14 [n = 21]), except for three lower values in mid-winter. The increased abundance of the Chrysophyceae (particularly *Dinobryon cylindricum* [Fig. 6/31]) at the end of the sampling programme was largely responsible for these low indices (1.67 [26.5.84], 0.97 [29.6.84], and 1.28 [26.7.84]).

6.1.7.4 Percentage Similarity of the Phytoplankton Communities

With few exceptions, consecutive communities were moderately similar throughout the sampling year (mean 56% ± 15 [n = 20]) (Table 6/20). The two most dissimilar periods (40%) occurred in early and mid-summer (13.10.83/27.10.83 and 8.12.83/5.1.84, respectively), and were largely due to major changes in the abundance of the chrysophytes (particularly *Dinobryon cylindricum*) (Fig. 6/31). This class also was largely responsible for high winter (1984) indices (26.5.84/29.6.84 [85%] and 29.6.84/26.7.84 [92%]). On a seasonal basis, communities also displayed moderate similarity, excluding spring/summer (20%), which coincided with both of the previously mentioned changes in chrysophyte abundance (Table 6/20).

6.1.7.5 Species Periodicity

With the exception of the ubiquitous *Cryptomonas* spp., the major phytoplankters displayed distinct seasonal periodicity. Both *Cyclotella stelligera* and *Dinobryon cylindricum* had peak densities in winter 1983 (74 [7.7.83] and 930 pu ml^{-1} [4.8.83], respectively), followed by rapid losses throughout early spring (Fig. 6/33). Although

TABLE 6/18 α diversity and Shannon-Wiener information index for each sampling date in Lake Rotomanuka North, July 1983 to July 1984.

Date	α Diversity		Shannon-Wiener Information Index
	s	d	
1983			
7.vii	24	8.73	2.74
4.viii	39	12.66	3.24
1.ix	29	13.52	2.88
29.ix	27	11.08	3.74
13.x	45	16.43	3.73
27.x	31	12.95	3.72
10.xi	37	15.06	3.72
24.xi	36	14.51	3.62
8.xi	44	17.51	3.84
1984			
5.i	47	18.74	3.71
19.i	44	17.57	3.65
2.ii	37	15.53	3.77
16.ii	37	14.81	3.59
2.iii	27	12.51	3.36
15.iii	46	17.89	3.56
29.iii	26	10.96	3.44
14.iv	21	8.27	3.34
29.iv	35	14.52	3.45
26.v	26	10.16	1.67
29.vi	20	7.02	0.97
26.vii	32	10.41	1.28

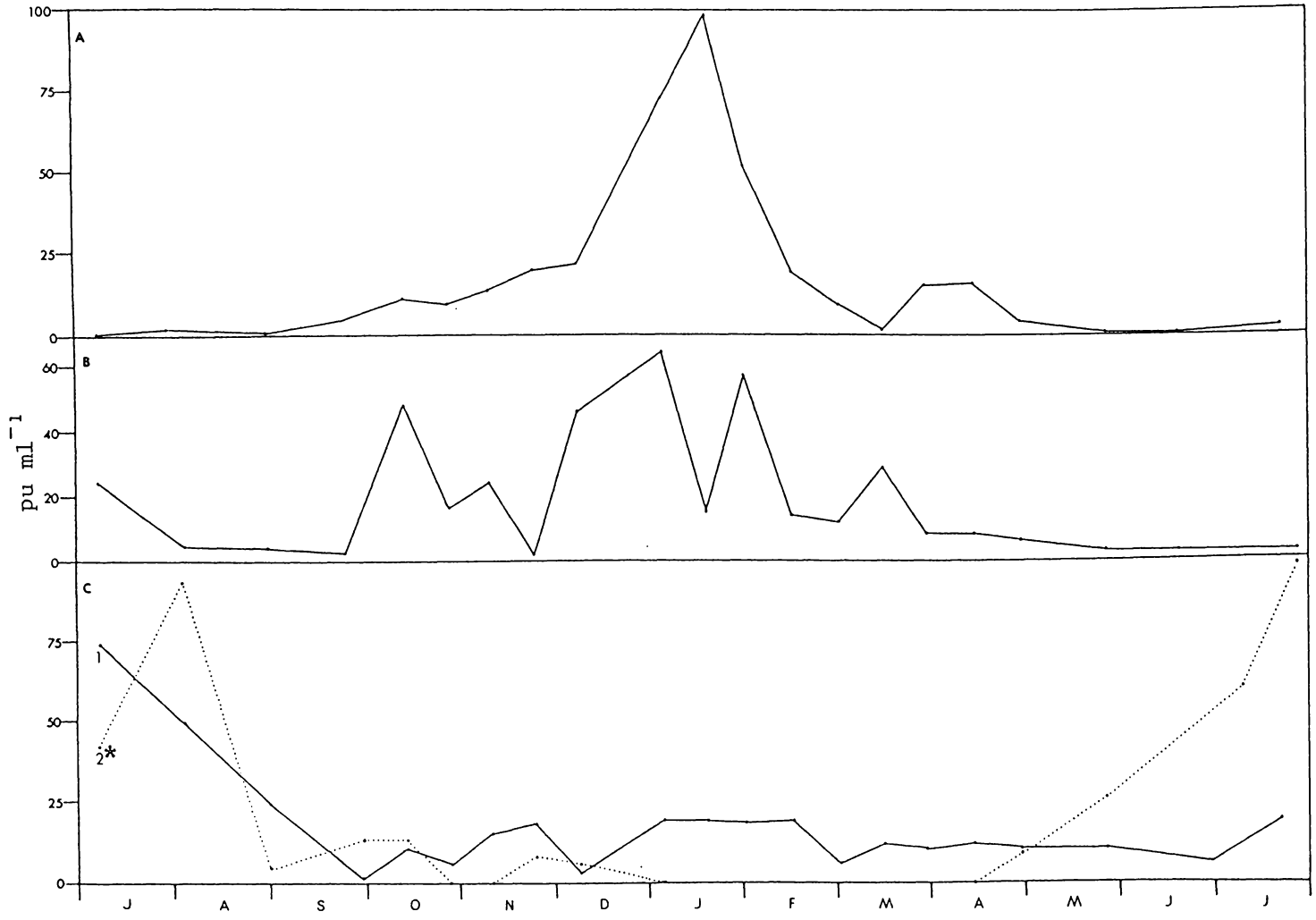
TABLE 6/19 Variation in the number of species (plus varieties) per 1 ml aliquot in Lake Rotomanuka North, July 1983 to July 1984.

Taxon	Number of Species			
	Maximum	Minimum	Mean ± 1 SD (n = 21)	Total
CHLOROPHYTA				
Euchlorophyceae	16	5	9.6 ± 3.4	60
Ulothricophyceae	1	0	0.09 ± 0.3	1
Zygophyceae	8	1	3.3 ± 1.8	26
CHROMOPHYTA				
Chrysophyceae	6	0	2.4 ± 1.8	13
Diatomophyceae	12	1	5.1 ± 3.1	35
Xanthophyceae	2	0	0.2 ± 0.5	2
CYANOPHYTA				
Cyanophyceae	6	0	2.9 ± 1.7	23
EUGLENOPHYTA				
Euglenophyceae	11	1	5.1 ± 3.7	31
PYRRHOPHYTA				
Cryptophyceae	0	3	2.1 ± 0.6	3
Dinophyceae	5	2	3.3 ± 0.9	8
RAPHIDOPHYTA				
Raphidophyceae	1	0	0.9 ± 0.4	1
ALL SPECIES	47	20	33.8 ± 8.4	203

TABLE 6/20 Percentage similarity indices of consecutive and other specified phytoplankton communites in Lake Rotomanuka North, July 1983 to July 1984.

Dates	Community Type	Percentage Similarity Index
1983		
7.vii/4.viii	consecutive	58
4.viii/1.ix	"	45
1.ix/29.ix	"	44
29.ix/13.x	"	49
13.x/27.x	"	40
27.x/10.xi	"	56
10.xi/24.xi	"	47
24.xi/8.xii	"	46
8.xii/5.i	"	40
1984		
5.i/19.i	"	45
19.i/2.ii	"	53
2.ii/16.ii	"	44
16.ii/2.iii	"	63
2.iii/15.iii	"	71
15.iii/29.iii	"	69
29.iii/14.iv	"	66
14.iv/29.iv	"	45
29.iv/26.v	"	56
26.v/29.vi	"	85
29.vi/26.vii	"	92
7.vii/13.x	winter-spring	48
13.x/5.i	spring-summer	20
5.i/29.iv	summer-autumn	53
29.iv/26.vii	autumn-winter	49
7.vii (1983)/ 26.vii (1984)	annual	52

Fig. 6/33 Temporal variations in the densities (pu ml^{-1}) of *Trachelomonas volvocina*, *Botryococcus braunii*, *Cyclotella stelligera*, and *Dinobryon cylindricum* in Lake Rotomanuka North, July 1983 to July 1984.



Key:

A. = *Trachelomonas volvocina*

B. = *Botryococcus braunii*

C_1 = *Cyclotella stelligera*

C_2 = *Dinobryon cylindrcum*

* = pu ml^{-1} x 10

the former was a permanent member of the community, no further pulses were recorded, and subsequent to its initial decline, its density did not exceed 20 pu ml^{-1}. In marked contrast, *Dinobryon cylindricum*, although not found throughout mid- and late summer 1984, increased in abundance throughout late autumn and early winter (maximum density 9972 pu ml^{-1} [26.7.84]).

Both *Botryococcus braunii* and *Trachelomonas volvocina* had maximal densities (65 [5.1.84] and 98 pu ml^{-1} [19.1.84], respectively) in summer 1984 (Fig. 6/33). *Peridinium cinctum* had one minor pulse (61 pu ml^{-1}) in summer (19.1.84) (Fig. 6/34), and its maximum density (100 pu ml^{-1}) was recorded in late autumn (14.4.84).

The cryptomonads (*Cryptomonas marssonii* and *C. ovata*) displayed little seasonality (Fig. 6/34), with peaks of abundance occurring in winter 1983 (90 pu ml^{-1}), and both early and late summer 1984 (79 and 118 pu ml^{-1}, respectively).

6.1.8 Lake Rotomanuka South

6.1.8.1 Temporal Variations in Total Phytoplankton Density and Biomass

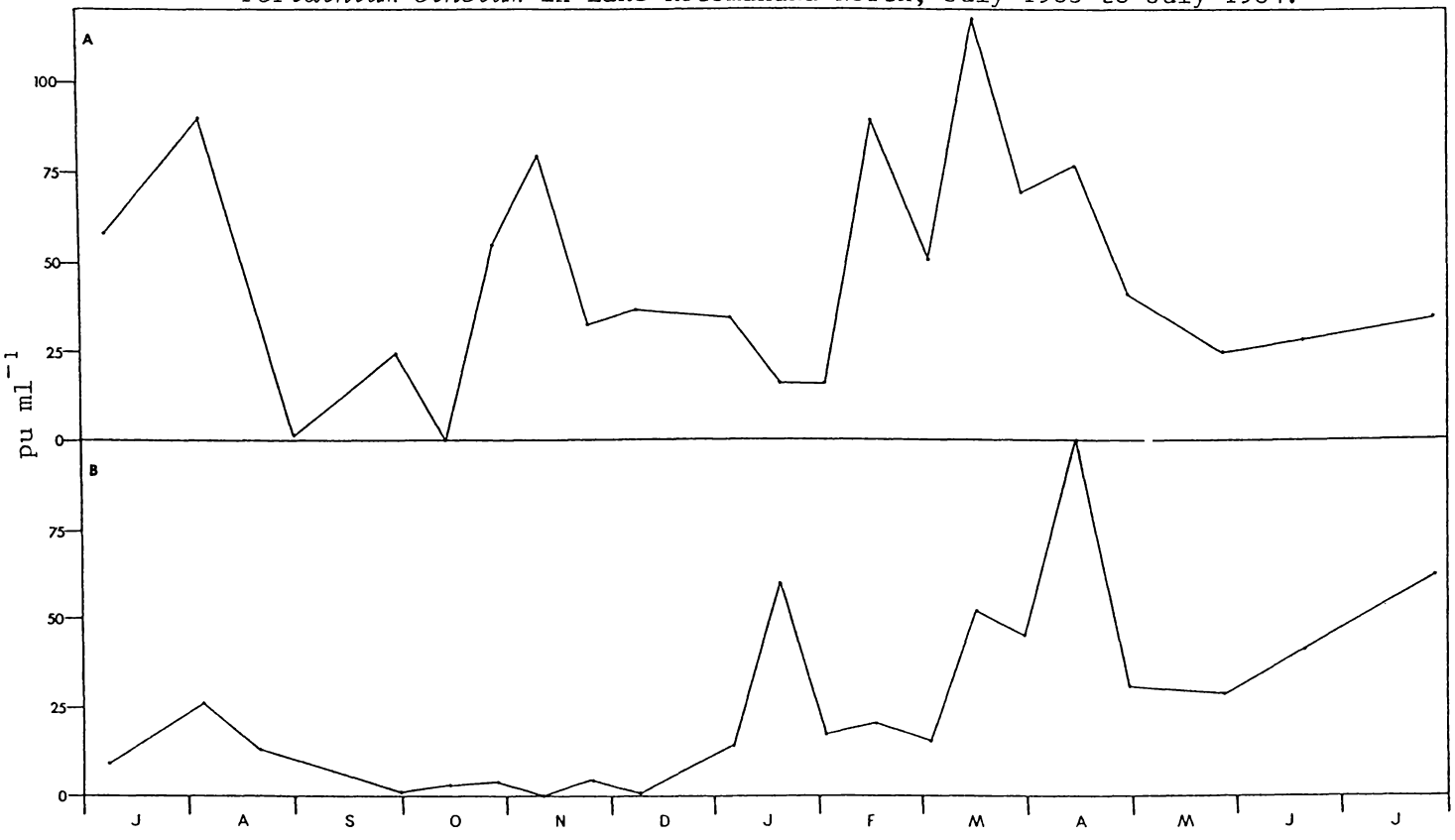
Despite a wide range in total density (755 [15.3.84] to 19,777 pu ml^{-1} [24.11.83]), the community appeared remarkably stable for lengthy periods (Fig. 6/35). An exceptionally high total density (due almost entirely to a sharp increase in numbers of *Closterium acutum* var. *variabile*) was recorded in November 1983. Mean densities, including and excluding this sample, were 3109 and 1919 pu ml^{-1}, respectively.

In contrast, total biomass (Fig. 6/36) gradually increased throughout both summer and autumn, peaking (because of a bloom of *Microcystis aeruginosa*) on 14.4.84 (92.4 g m^3). Minimum biomass (3.7 g m^3) was recorded in early summer (27.10.83); the mean was 32.3 g m^3 (n = 15).

6.1.8.2 Temporal Variations in the Composition of the Total Phytoplankton Standing Crop

Quantitatively, the community displayed three distinct phases: first, a spring-early summer period of zygophycean domination (maximum proportion 98% [24.11.83]); secondly, a mid-summer to late autumn

Fig. 6/34 Temporal variations in the densities (pu ml^{-1}) of *Cryptomonas* spp. and *Peridinium cinctum* in Lake Rotomanuka North, July 1983 to July 1984.

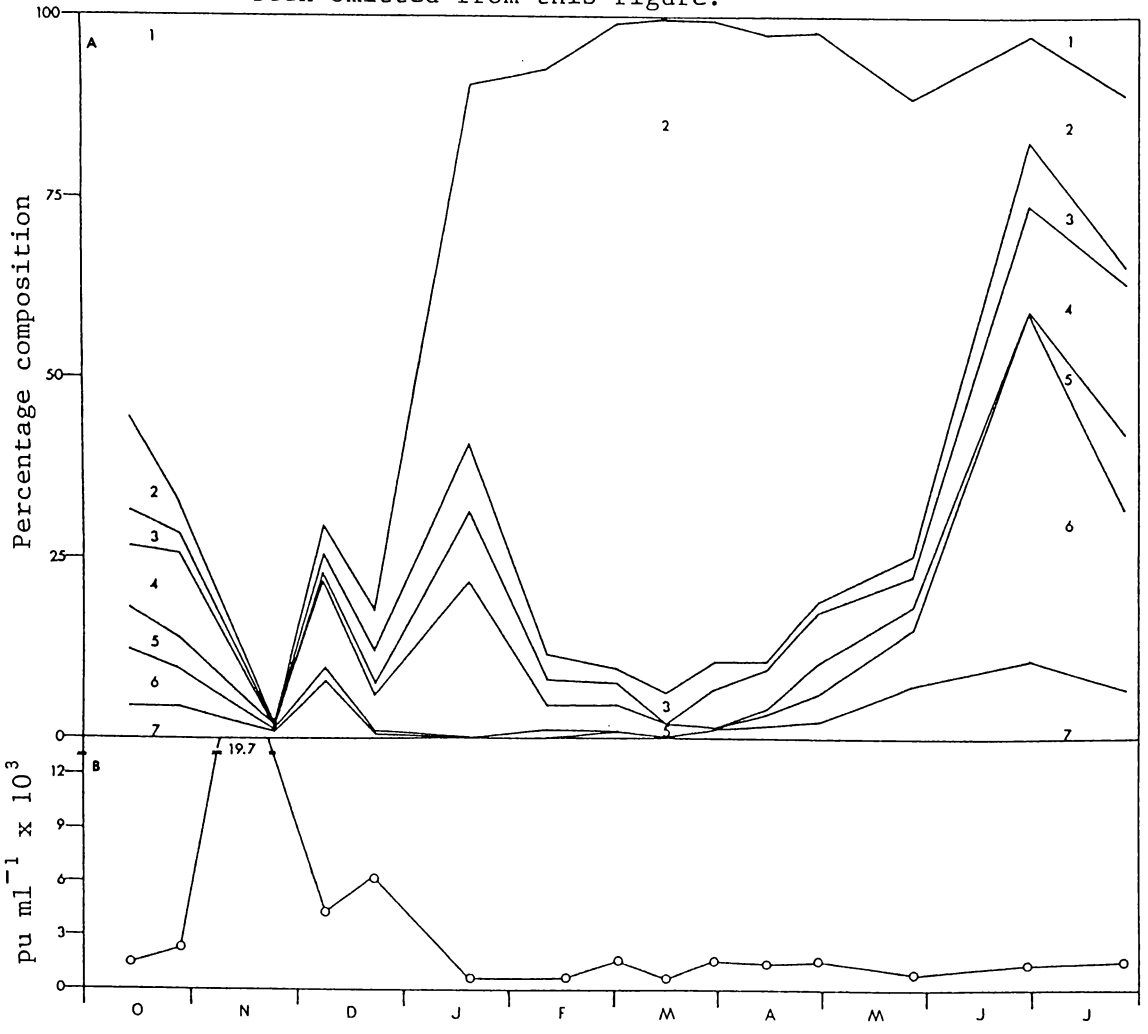


Key:

A. = *Cryptomonas* spp.

B. = *Peridinium cinctum*

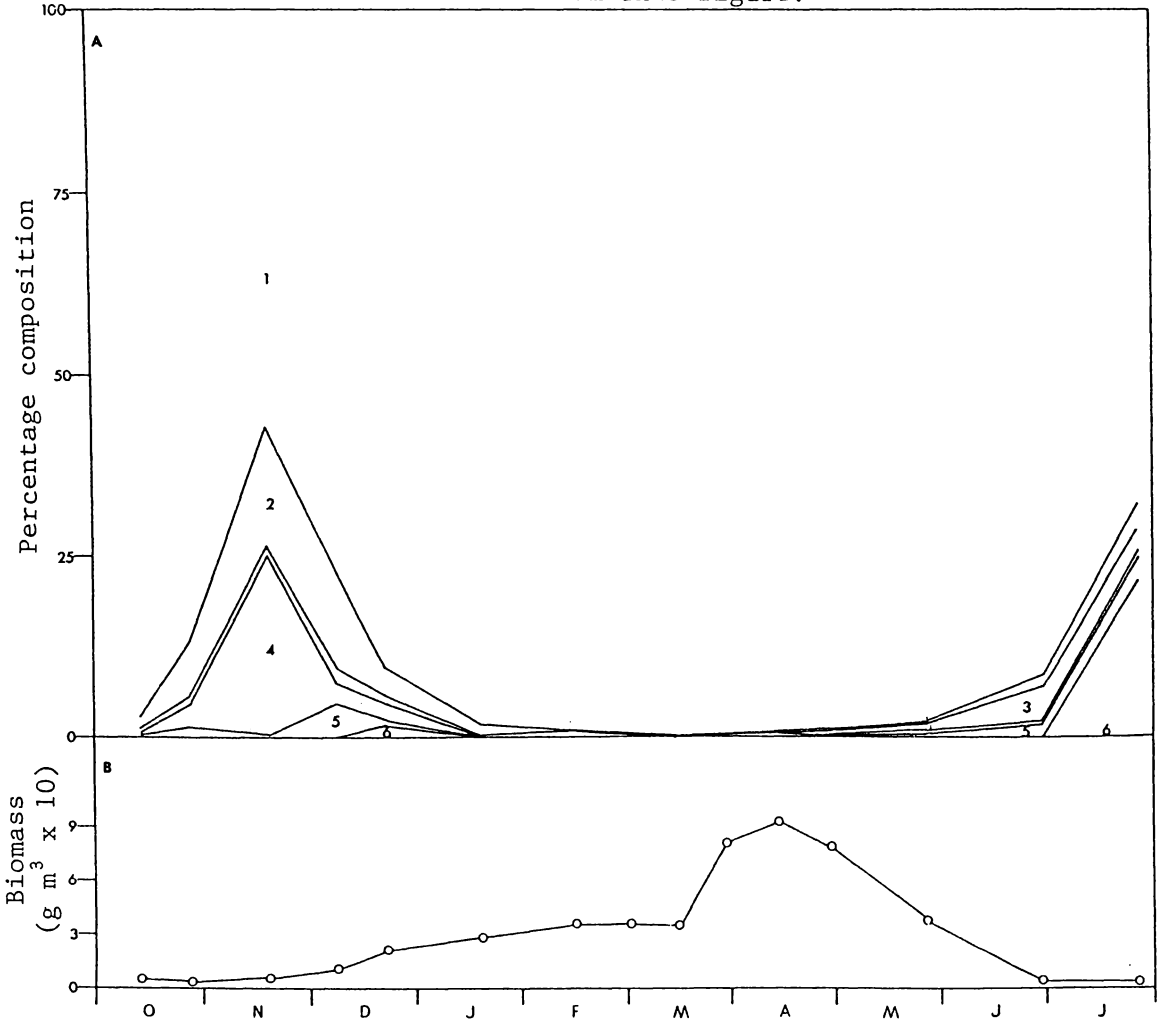
Fig. 6/35 Temporal variations in: (a) phytoplankton class composition, in terms of abundance; (b) total number of pu ml^{-1} x 10^3, in Lake Rotomanuka South, October 1983 to July 1983. The Dinophyceae and Xanthophyceae have been omitted from this figure.



Key:

1. = Zygophyceae
2. = Cyanophyceae
3. = Diatomophyceae
4. = Euchlorophyceae
5. = Euglenophyceae
6. = Chrysophyceae
7. = Cryptophyceae

Fig. 6/36 Temporal variations in: (a) phytoplankton class composition, in terms of biomass; (b) total biomass (g m^3 x 10), in Lake Rotomanuka South, October 1983 to October 1984. The Euchlorophyceae and Chrysophyceae have been omitted from this figure.



Key:

1. = Cyanophyceae
2. = Euglenophyceae
3. = Diatomophyceae
4. = Zygophyceae
5. = Cryptophyceae
6. = Dinophyceae

cyanophycean phase (mean proportion 79 ± 16% [n = 8]; and thirdly, a winter period when chrysophytes were dominant (45 [29.6.84] and 25% [26.7.84]), although some other classes were also important at this time (Fig. 6/35).

In terms of total biomass, the seasonal pattern was very simple (Fig. 6/36), because of the remarkably high cyanophyte proportions throughout the entire period (range 57 to 99.9%) (Plate 9; following p. 23). The Euglenophyceae and Zygophyceae were only significant in early summer (24.11.83 [16 and 25%, respectively]), but were still sub-dominant to the Cyanophyceae. The Dinophyceae, although comprising 21% of the mid-winter (26.7.84) standing crop, was rarely found during the remainder of the sampling period.

6.1.8.3 Temporal Variations in Phytoplankton Species Diversity

The Shannon-Wiener index (Table 6/21) was markedly variable throughout the sampling period (range 0.14 [24.11.83] to 3.66 [26.7.84]; mean 2.04 ± 0.85). High densities of *Closterium acutum* var. *variabile* and *Microcystis aeruginosa* were responsible for low indices on 24.11.83 and 22.12.83 (0.14 and 1.45, respectively), and also throughout late summer and autumn 1984 (1.32 to 1.8, respectively). Conversely, values were higher in winter than at any other time.

The total number of species per sample varied greatly (Table 6/21), with the minimum number (7) coinciding with the lowest phytoplankton density (15.3.84) (Fig. 6/35). Relatively high numbers were found during both cold and warmer periods; for example, 35 and 32 species were recorded on 8.12.83 and 26.7.84, respectively. Numbers of species within each class also varied considerably. With the exception of the Diatomophyceae and the Cyanophyceae, all classes lacked representation on at least one occasion, including the Euchlorophyceae (total species 35). The mean number of species per sample was 23.7 ± 6.7 (Table 6/22).

6.1.8.4 Percentage Similarity of the Phytoplankton Communities

The percentage similarity indices (Table 6/23) reflect the three consecutive phases of domination by the Zygophyceae, Cyanophyceae and Chrysophyceae (Chapter 6.8.2). Indices for the first five consecutive communities (13.10.83 to 22.12.83) ranged from 65 to 80%, coincident with domination by the zygophytes. The lowest index (16%

TABLE 6/21 α diversity and Shannon-Wiener information index for each sampling date in Lake Rotomanuka South, October 1983 to July 1984.

Date	α Diversity		Shannon-Wiener Information Index
	s	d	
1983			
13.x	27	8.47	2.83
27.x	23	6.85	1.95
24.xi	16	3.72	0.14
8.xii	35	9.67	2.09
22.xii	26	6.85	1.45
1984			
19.i	20	6.92	2.55
16.ii	26	8.98	2.02
2.iii	20	6.21	1.67
15.iii	7	2.43	1.32
29.iii	24	7.49	1.71
14.iv	27	8.47	1.55
29.iv	23	7.16	1.80
26.v	21	7.08	2.63
29.vi	28	8.93	3.20
26.vii	32	10.01	3.66

TABLE 6/22 Variation in the number of species (plus varieties) per 1 ml aliquot in Lake Rotomanuka South, October 1983 to July 1984.

Taxon	Number of Species			
	Maximum	Minimum	Mean ± 1 SD (n = 15)	Total
CHLOROPHYTA				
Euchlorophyceae	11	0	6.5 ± 3.2	35
Zygophyceae	8	0	3.5 ± 1.8	17
CHROMOPHYTA				
Chrysophyceae	4	0	1.7 ± 1.5	5
Diatomophyceae	15	3	6.1 ± 3.1	28
Xanthophyceae	1	0	0.1 ± 0.3	1
CYANOPHYTA				
Cyanophyceae	4	1	2.7 ± 0.9	15
EUGLENOPHYTA				
Euglenophyceae	4	0	1.9 ± 1.1	14
PYRRHOPHYTA				
Cryptophyceae	2	0	0.8 ± 0.6	2
Dinophyceae	3	0	0.4 ± 0.9	3
ALL SPECIES	35	7	23.7 ± 6.7	120

TABLE 6/23 Percentage similarity indices of consecutive and other specified phytoplankton communites in Lake Rotomanuka South, October 1983 to July 1984.

Dates	Community Type	Percentage Similarity Index
1983		
13.x/27.x	consecutive	73
27.x/24.xi	"	65
24.xi/8.xii	"	71
8.xii/22.xii	"	80
22.xii/19.i	"	16
1984		
19.i/16.ii	"	58
16.ii/2.iii	"	54
2.iii/15.iii	"	58
15.iii/29.iii	"	86
29.iii/14.iv	"	74
14.iv/29.iv	"	77
29.iv/26.v	"	71
26.v/29.vi	"	31
29.vi/26.vii	"	44
13.x/19.i	spring-summer	27
19.i/29.iv	summer-autumn	51
29.iv/26.viii	autumn-winter	17

[22.12.83/19.1.84]) marks an intermediate point between phase one and two. Throughout the period of cyanophyte dominance (19.1.84 to 26.5.84) the indices ranged from 54 to 86% (mean 68 ± 11% [n = 7]). Similarity during the chrysophycean phase (26.5.84/26.7.84) was markedly lower (31 and 44%) than during the previous periods, because of increased contributions of other classes, particularly the Cryptophyceae and the Euchlorophyceae. The mean index was 61 ± 20%.

6.1.8.5 Species Periodicity

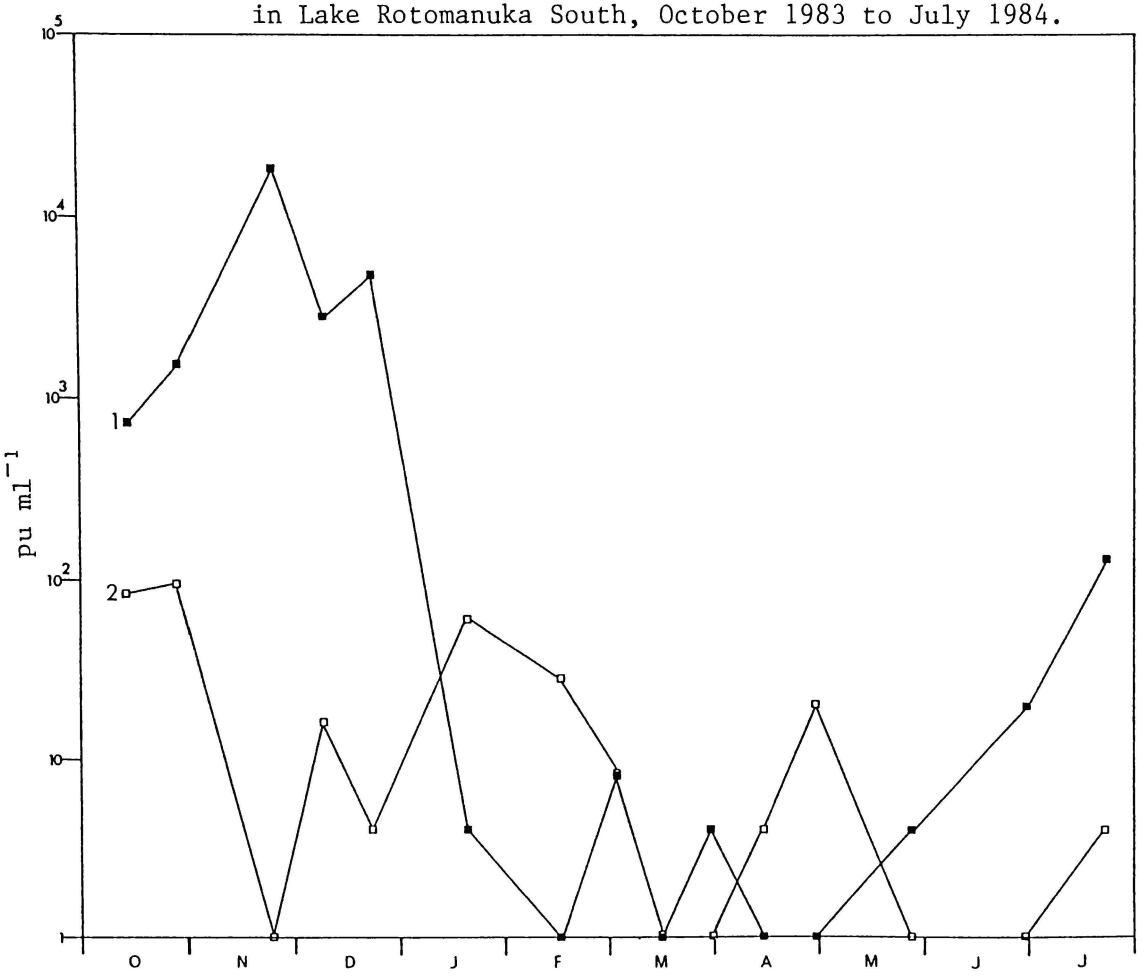
The absence of major euchlorophytes, despite their high species representation (Table 6/22), was the most conspicuous feature of the seasonal dynamics of this community. The dominant phytoplankter throughout late spring and early summer was *Closterium acutum* var. *variabile*. Its initial density was 748 pu ml^{-1} and its maximum (19,364 pu ml^{-1}) was recorded in early summer (24.11.83) after a period of very rapid increase (Fig. 6/37). Its densities were low throughout both mid-summer and autumn, but were increasing when sampling ceased (132 pu ml^{-1} [26.7.84]). The maximum density (96 pu ml^{-1}) of *Staurastrum* sp. C, the only other important zygophyte, also was recorded in early summer (27.10.83), but neither of these desmids was a permanent member of the community.

Maxima of *Trachelomonas* spp. (*T. planctonica* and *T. volvocina*), *Cryptomonas* spp. (*C. erosa* and *C. ovata*) and the major diatoms, rapidly followed those of the desmids (Fig. 6/38). Peaks of *Trachelomonas* spp. (484 pu ml^{-1}) and cryptomonads (138 and 200 pu ml^{-1}, respectively) coincided on 8.12.83, prior to general declines throughout the remainder of summer. *Cryptomonas erosa* was not found again, unlike *C. ovata*, which increased in abundance throughout autumn and winter 1984.

Peak densities of *Tabellaria flocculosa*, *Cyclotella stelligera* and *Acanthoceras zachariasi* (100, 156, and 124 pu ml^{-1}, respectively) were recorded in late December 1983, but densities decreased in mid-summer, and these species were either not found, or were of minor importance, during the remainder of the sampling period (Fig. 6/39).

The late summer-autumn communities were dominated by *Anabaena tenericaulis* and *Microcystis aeruginosa* (maximal densities 1024

Fig. 6/37 Temporal variations in the densities (pu ml^{-1}) of *Closterium acutum* var. *variabile* and *Staurastrum* sp. A in Lake Rotomanuka South, October 1983 to July 1984.

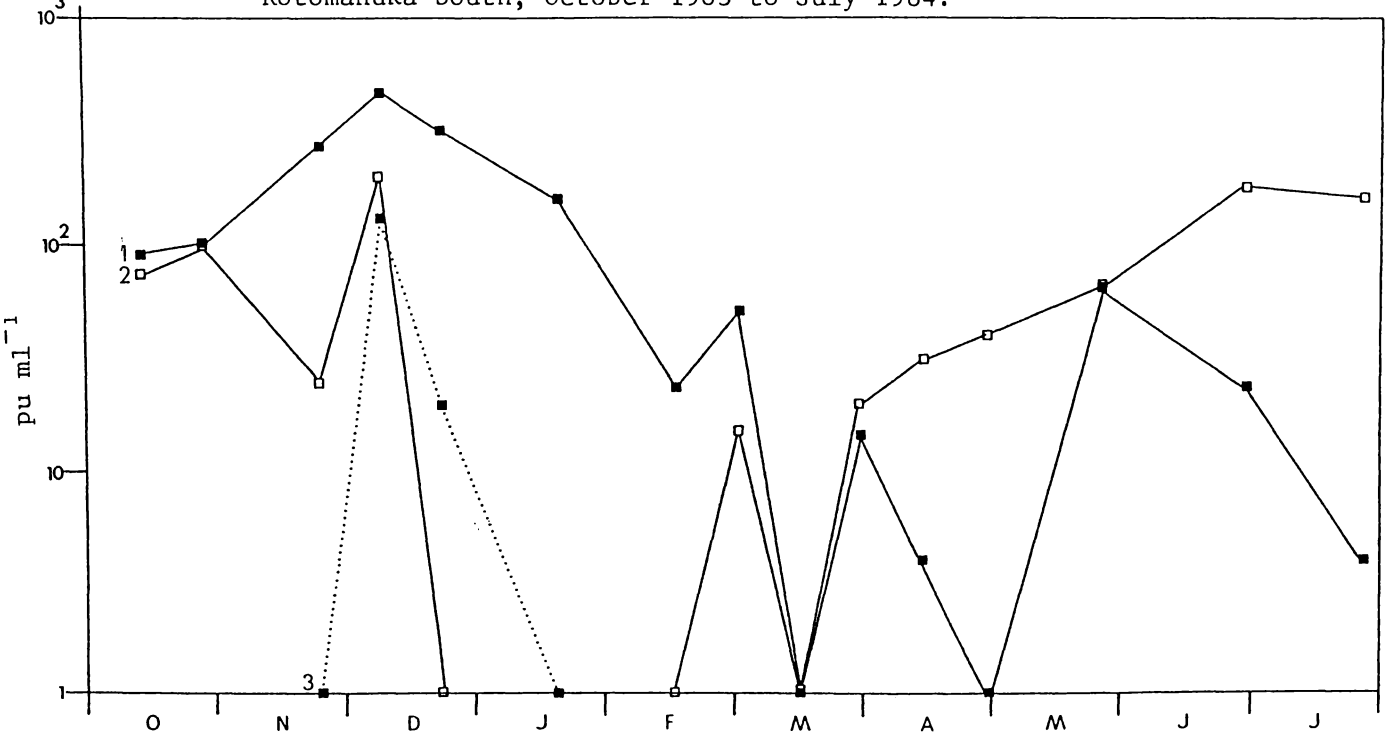


Key:

1. = *Closterium acutum* var. *variabile*

2. = *Staurastrum* sp. A

Fig. 6/38 Temporal variations in the densities (pu ml^{-1}) of *Trachelomonas volvocina*, *T. planctonica*, *Cryptomonas ovata* and *C. erosa* in Lake Rotomanuka South, October 1983 to July 1984.



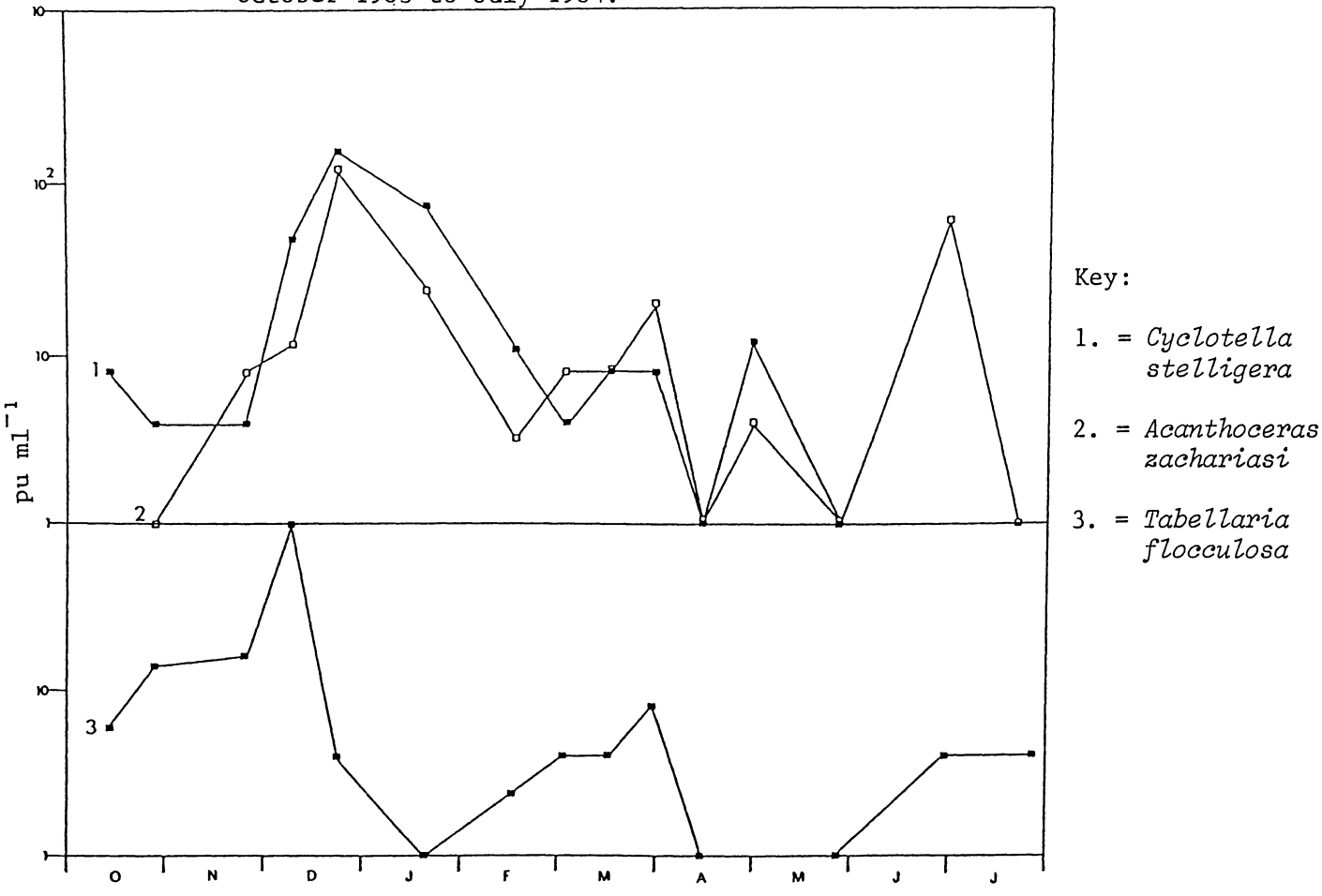
Key:

1. = *Trachelomonas volvocina* and *T. planctonica*

2. = *Cryptomonas ovata*

3. = *C. erosa*

Fig. 6/39 Temporal variations in the densities (pu ml^{-1}) of *Cyclotella stelligera*, *Acanthoceras zachariasi* and *Tabellaria flocculosa* in Lake Rotomanuka South, October 1983 to July 1984.



Key:

1. = *Cyclotella stelligera*

2. = *Acanthoceras zachariasi*

3. = *Tabellaria flocculosa*

[2.3.84] and 1224 pu ml^{-1} [29.4.84], respectively) (Fig. 6/40). The former was not found in the 1983 samples, in contrast to *M. aeruginosa*, which was a permanent member of the community (minimum density 20 pu ml^{-1}).

The winter phase was dominated by *Synura uvella* and *Dinobryon cylindricum*. Both were present in the October-November 1983 samples, but were not found from mid-summer to June 1984. Their highest densities were 564 (29.6.84) and 208 pu ml^{-1} (26.7.84), respectively (Fig. 6/40).

6.1.9 Lake Rotoroa

6.1.9.1 Temporal Variations in Total Phytoplankton Density and Biomass

With the exception of a large, sharp increase in late spring-early summer, phytoplankton densities showed only small-scale changes, and thus no evidence of seasonality (Fig. 6/41). Total density ranged from 276 (1.5.84) to 13,552 pu ml^{-1} (15.10.84) (mean 1913 pu ml^{-1} [n = 22]).

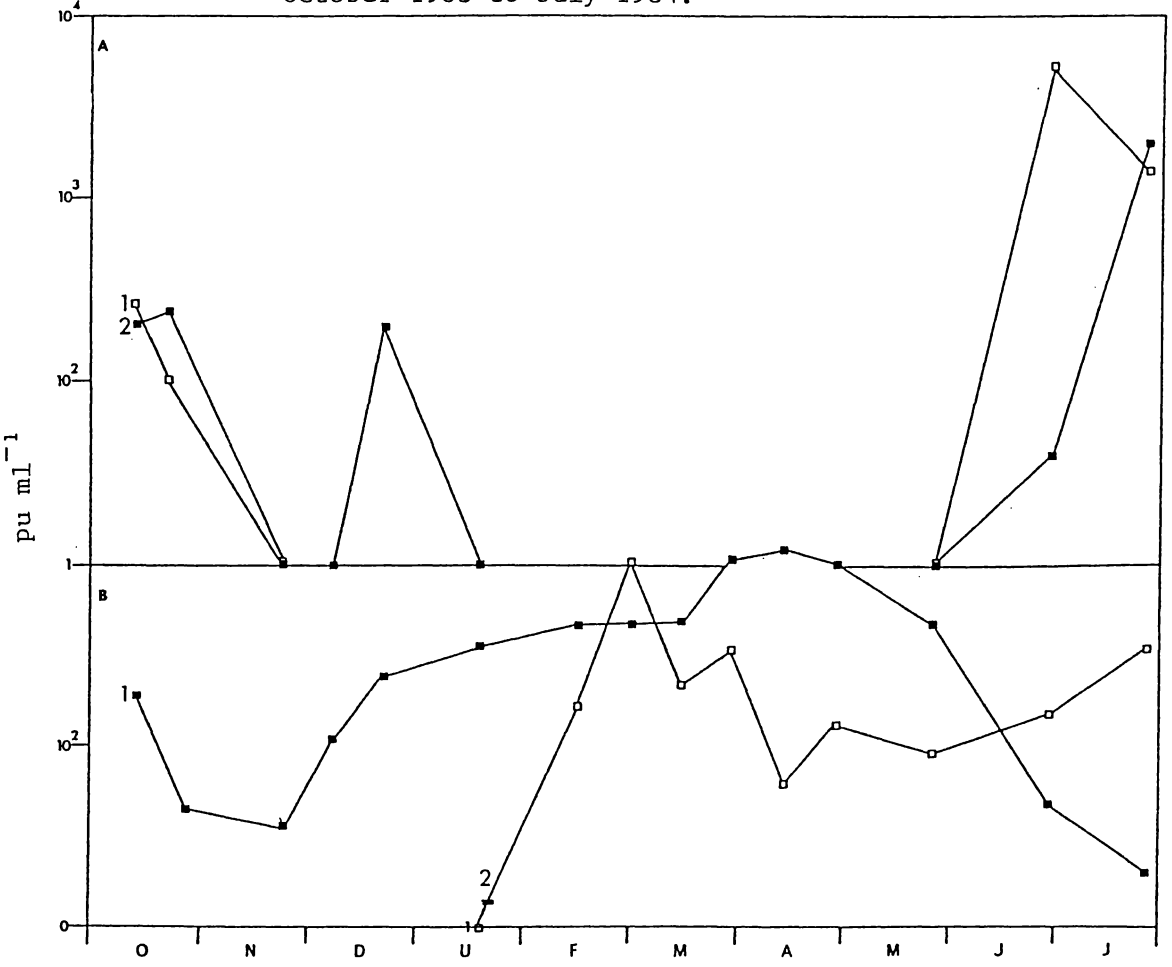
Total biomass ranged from 0.3 to 5.1 g m^3 (mean 1.8 [n = 22]) (Fig. 6/42) and also increased markedly in early summer (5.1 g m^3 [1.10.83]). Two smaller peaks were recorded in mid-summer (4.7 g m^3 [7.1.84]) and winter (2.6 g m^3 [31.6.84]).

6.1.9.2 Temporal Variations in the Composition of the Total Phytoplankton Standing Crop

Numerically, the annual cycle consisted of long phases of relatively equal proportions of the majority of classes, briefly interrupted by phases of domination by only one (Fig. 6/41). The Chrysophyceae dominated the community on three occasions (58% [9.7.83], 69% [12.11.83] and 66% [31.6.84]), albeit for short periods, the Euchlorophyceae during early summer (87% [15.10.83] and 86% [29.10.83]), and the Cyanophyceae was the most important class in autumn (51% [16.4.84]).

In contrast, the Dinophyceae accounted for most of the biomass throughout the entire year (range 45 [10.12.83] to 95% [7.1.84]) (Fig. 6/42). However, with the exception of the Zygophyceae, Xanthophyceae and Cyanophyceae, all other classes were sub-dominants at some stage. The maximum proportions of the Euchlorophyceae, Chrysophyceae and Diatomophyceae were 26% (28.5.84), 36% (12.11.83) and 25% (24.12.83),

Fig. 6/40 Temporal variations in the densities (pu ml^{-1}) of *Synura uvella*, *Dinobryon cylindricum*, *Microcystis aeruginosa* and *Anabaena tenericaulis* in Lake Rotomanuka South, October 1983 to July 1984.



Key:

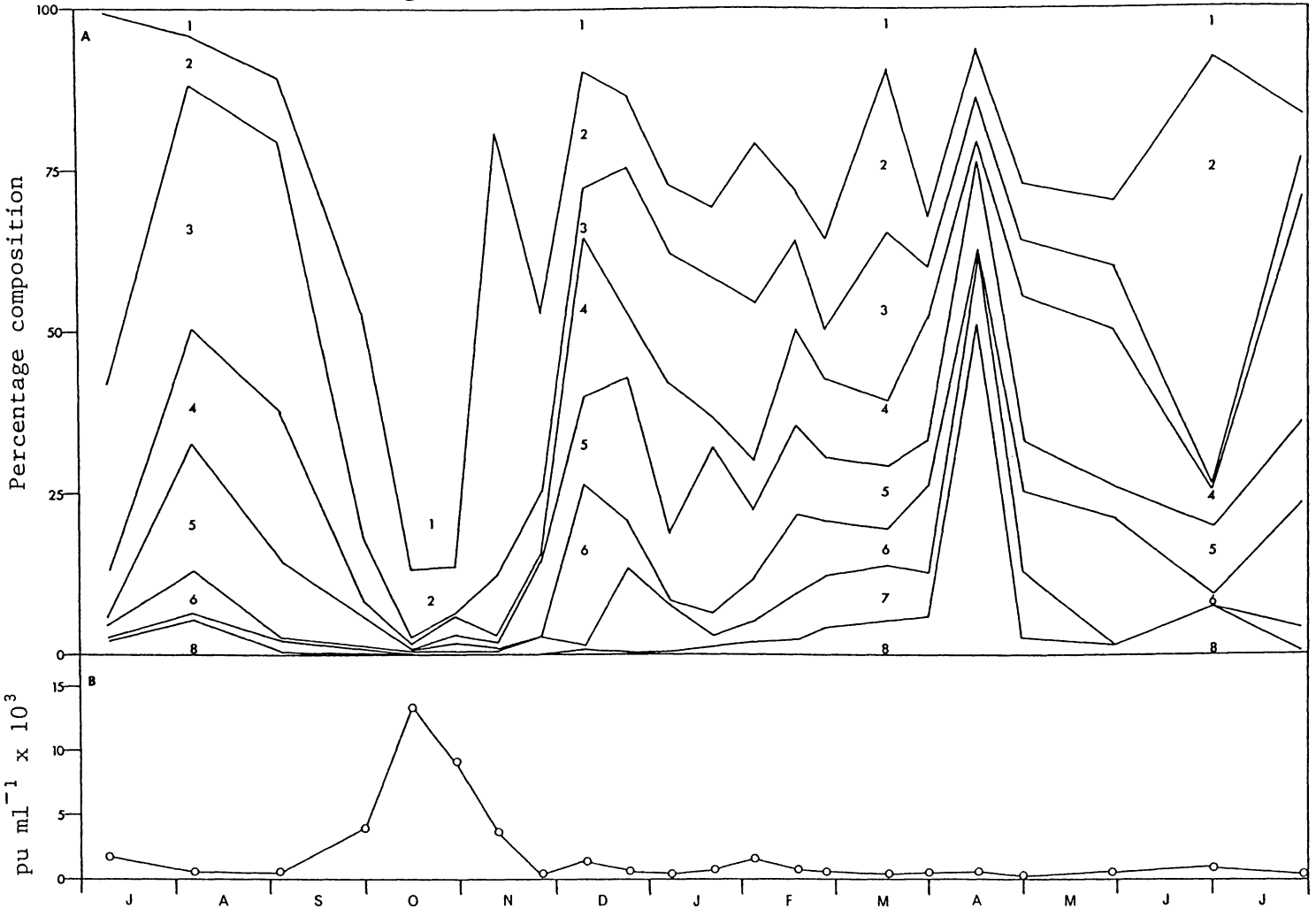
A1 = *Synura uvella*

A2 = *Dinobryon cylindricum*

B1 = *Microcystis aeruginosa*

B2 = *Anabaena tenericaulis*

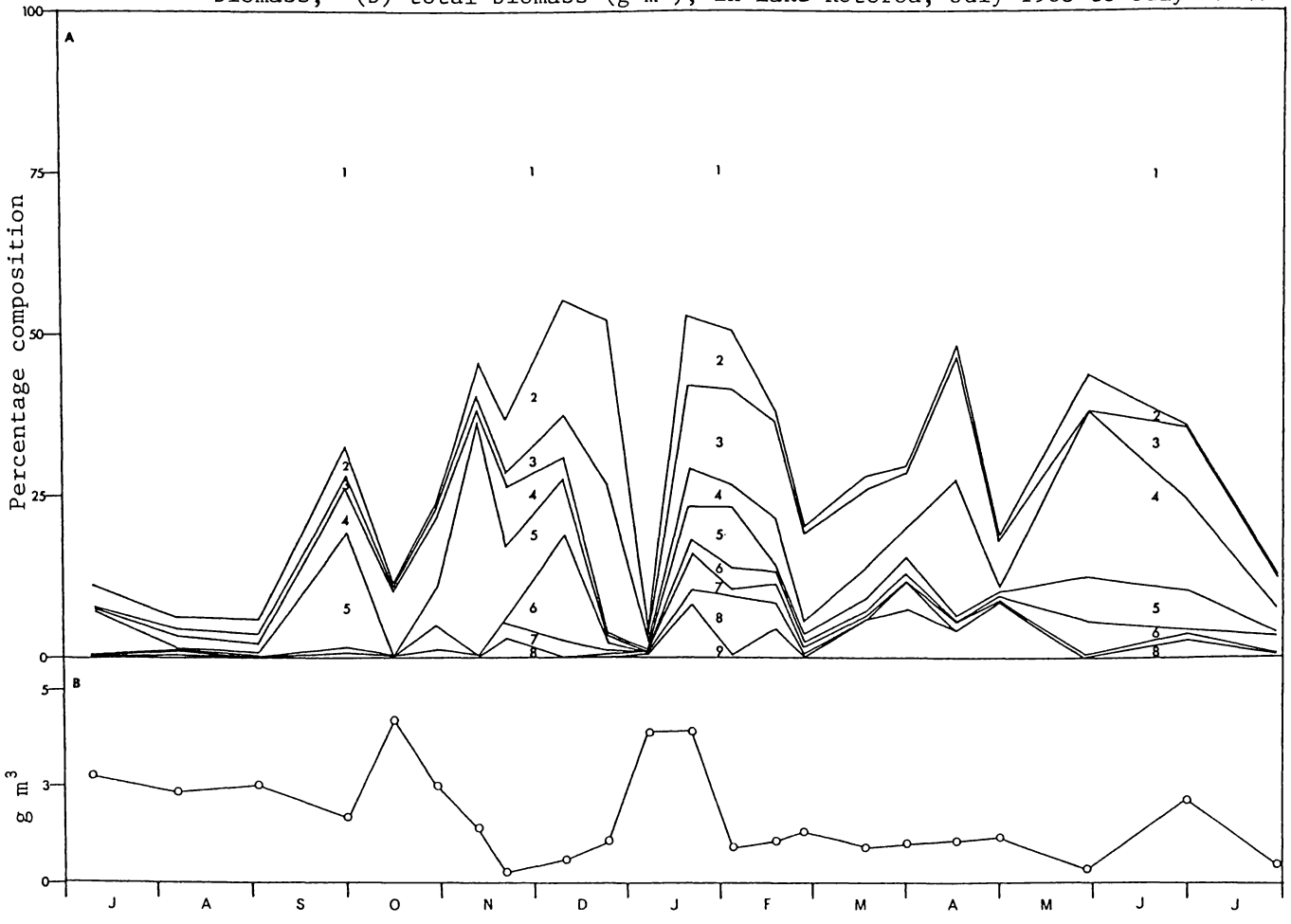
Fig. 6/41 Temporal variations in: (a) phytoplankton class composition, in terms of abundance; (b) total number of pu ml^{-1} x 10^3, in Lake Rotoroa, July 1983 to July 1984. The Ulothricophyceae and Xanthophyceae have been omitted from this figure.



Key:

1. = Euchlorophyceae
2. = Chrysophyceae
3. = Diatomophyceae
4. = Dinophyceae
5. = Zygophyceae
6. = Cryptophyceae
7. = Euglenophyceae
8. = Cyanophyceae

Fig. 6/42 Temporal variations in: (a) phytoplankton class composition, in terms of biomass; (b) total biomass (g m^3), in Lake Rotoroa, July 1983 to July 1984.



Key:

1. = Dinophyceae
2. = Diatomophyceae
3. = Euglenophyceae
4. = Euchlorophyceae
5. = Chrysophyceae
6. = Cryptophyceae
7. = Zygophyceae
8. = Xanthophyceae
9. = Cyanophyceae

respectively. The euglenophytes and cryptophytes (maximum proportions 23 and 17%, respectively) were most important after the decline of the major biomass peak (24.12.83 and 10.12.83, respectively). The Xanthophyceae, although generally unimportant in all other study lakes, comprised 9% of the community on 4.2.84.

6.1.9.3 Temporal Variations in Phytoplankton Species Diversity

Species richness ranged from 15 (28.7.84) to 35 (10.12.83) and, with one exception (16 species [29.10.83]), numbers of species were high throughout summer and declined during the colder months of 1984 (Table 6/24). The highest Shannon-Wiener indices (Table 6/24) were recorded from mid-summer to autumn (particularly 24.12.83 to 1.5.84), with the maximum (3.83) coinciding with a period when, in terms of abundance, the highest proportion of any class was 26%. The high proportions of the Euchlorophyceae in early summer (86% [29.10.83] and 87% [15.10.83]), were largely responsible for low indices at that time (0.72 and 0.81, respectively). The mean index was 2.7 ± 0.8 (n = 22). Despite high numbers of both euglenophyte and diatom species, their mean numbers per sample were relatively low (Fig. 6/25), with cryptophytes and dinoflagellates displaying much greater species continuity. The mean number of species per sample was 25.7 ± 5.9 (n = 22).

6.1.9.4 Percentage Similarity of the Phytoplankton Communities

The episodic nature of the phytoplankton communities is reflected in a low mean percentage similarity index (45 ± 16%). The highest value (93% [15.10.83/29.10.83) occurred when the euchlorophyte proportions were both high and almost identical (87 and 86%, respectively [Fig. 6/41]). However, other consecutive communities did not display such a marked degree of similarity (Table 6/26). For example, the second highest index was only 61% (21.1.84/4.2.84). Low indices (23, 25 and 26%), coincided with periods of change from a reasonably equal distribution of numbers to dominance by one taxon (or vice versa) (31.6.84/28.7.84, 29.10.83/12.11.83 and 31.3.84/16.4.84, respectively).

TABLE 6/24 α diversity and Shannon-Wiener information index for each sampling date in Lake Rotoroa, July 1983 to July 1984.

Date	α Diversity		Shannon-Wiener Information Index
	s	d	
1983			
9.vii	25	7.78	2.24
6.viii	32	11.62	2.88
3.ix	24	8.68	2.71
1.x	23	6.41	2.27
15.x	24	6.06	0.81
29.x	16	4.49	0.72
12.xi	23	8.43	1.50
26.xi	26	8.30	2.66
10.xii	35	12.42	2.67
24.xii	31	11.00	3.35
1984			
7.i	31	11.47	3.56
21.i	29	9.81	2.87
4.ii	30	9.36	3.11
18.ii	31	10.76	3.35
27.ii	32	11.66	3.83
17.iii	33	12.37	3.93
31.iii	25	9.51	3.24
16.iv	22	7.78	3.19
1.v	17	6.96	3.17
28.v	24	9.42	2.69
31.vi	17	5.67	1.90
28.vii	15	6.01	2.82

TABLE 6/25 Variation in the number of species (plus varieties) per 1 ml aliquot in Lake Rotoroa, July 1983 to July 1984.

Taxon	Number of Species			
	Maximum	Minimum	Mean ± 1 SD (n = 22)	Total
CHLOROPHYTA				
Euchlorophyceae	13	3	7.3 ± 2.8	42
Ulothricophyceae	1	0	0.05 ± 0.2	1
Zygophyceae	9	2	4.2 ± 1.9	24
CHROMOPHYTA				
Chrysophyceae	5	1	2.4 ± 1.1	9
Diatomophyceae	11	1	5.2 ± 2.5	31
Xanthophyceae	1	0	0.8 ± 1.0	3
CYANOPHYTA				
Cyanophyceae	5	0	1.5 ± 1.2	15
EUGLENOPHYTA				
Euglenophyceae	4	0	2.0 ± 1.2	18
PYRRHOPHYTA				
Cryptophyceae	3	0	2.0 ± 0.6	3
Dinophyceae	4	1	2.6 ± 0.7	5
ALL SPECIES	35	15	25.7 ± 5.9	151

TABLE 6/26 Percentage similarity indices of consecutive and other specified phytoplankton communites in Lake Rotoroa, July 1983 to July 1984.

Dates	Community Type	Percentage Similarity Index
1983		
9.vii/6.viii	consecutive	44
6.viii/3.ix	"	60
3.ix/1.x	"	38
1.x/15.x	"	58
15.x/29.x	"	93
29.x/12.xi	"	25
12.xi/26.xi	"	52
26.xi/10.xi	"	31
10.xii/24.xii	"	40
24.xii/7.1	"	39
1984		
7.1/21.i	"	54
21.i/4.11	"	61
4.ii/18.ii	"	56
18.ii/27.ii	"	42
27.ii/17.iii	"	50
17.iii/31.iii	"	53
31.iii/16.iv	"	26
16.iv/i.v	"	30
1.v/28.v	"	40
28.v/31.vi	"	40
31.vi/28.vii	"	23
9.vii/15.x	winter-spring	7
15.x/7.i	spring-summer	44
7.i/16.iv	summer-autumn	26
16.iv/28.vii	autumn-winter	22
9.vii(1983)/ 28.vii (1984)	annual	15

6.1.9.5 Species Periodicity

Patterns of abundance of the major species were generally complicated, and characterised by short, sporadic density changes. Initially, *Cyclotella stelligera* (Fig. 6/43) and *Dinobryon cylindricum* (Fig. 6/44) were the dominant species. The former, after a major peak (459 pu ml^{-1}) on 9.7.83, maintained relatively high densities throughout early spring before undergoing major losses in October 1983. Throughout summer its pattern was one of marked instability, featuring two further periods of relatively high densities (334 [12.11.83] and 380 pu ml^{-1} [4.2.84], followed immediately by sudden declines, and it remained unimportant throughout autumn and winter 1984. *D. cylindricum* also displayed an unstable cycle, its density ranging from 10 (28.7.84) to 2512 pu ml^{-1} (12.11.83), but more importantly, its abundance peaks were not confined to particular seasons (451 pu ml^{-1}, 9.7.83; 2512 pu ml^{-1}, 12.11.83; 358 pu ml^{-1}, 4.2.84; and 656 pu ml^{-1}, 3.6.84). *D. bavaricum* also displayed marked phases of both accelerated growth and decline (Fig. 6/44).

Two of the major summer species, *Tetrastrum triangulare* and *Oocystis lacustris*, had broadly similar patterns of abundance, albeit at different scales (Fig. 6/45). The maximum density of *T. triangulare* (11,704 pu ml^{-1}) was recorded on 15.10.83, after which time it gradually declined (36 pu ml^{-1} [7.1.84]). A minor upsurge (182 pu ml^{-1}) was recorded in mid-summer, but its abundance was low throughout the remainder of the sampling period. The density of *O. lacustris* also fluctuated rapidly, and its major peaks (82 and 76 pu ml^{-1}) were recorded on 1.10.83 and 4.2.84, respectively.

Closterium acutum var. *variabile*, a permanent member of the community (Fig. 6/44), had its maximum density (207 pu ml^{-1}) in mid-summer but, like other major phytoplankters, displayed peaks of abundance throughout the entire year (166 pu ml^{-1} [1.10.83]; 170 pu ml^{-1} [10.12.83]; 207 pu ml^{-1}, [21.1.84]; and 88 pu ml^{-1} [1.6.84]).

The annual periodicities of *Cryptomonas* spp. (*C. marssonii* and *C. ovata*), *Peridinium* spp. (*P. cinctum* and *P.* sp. A) and *Trachelomonas* spp. (*T. planctonica* and *T. volvocina*) also were characterised by

Fig. 6/43 Temporal variations in the densities (pu ml^{-1}) of *Cyclotella stelligera*, *Cryptomonas* spp., *Peridinium* spp. and *Trachelomonas* spp. in Lake Rotoroa, July 1983 to July 1984.

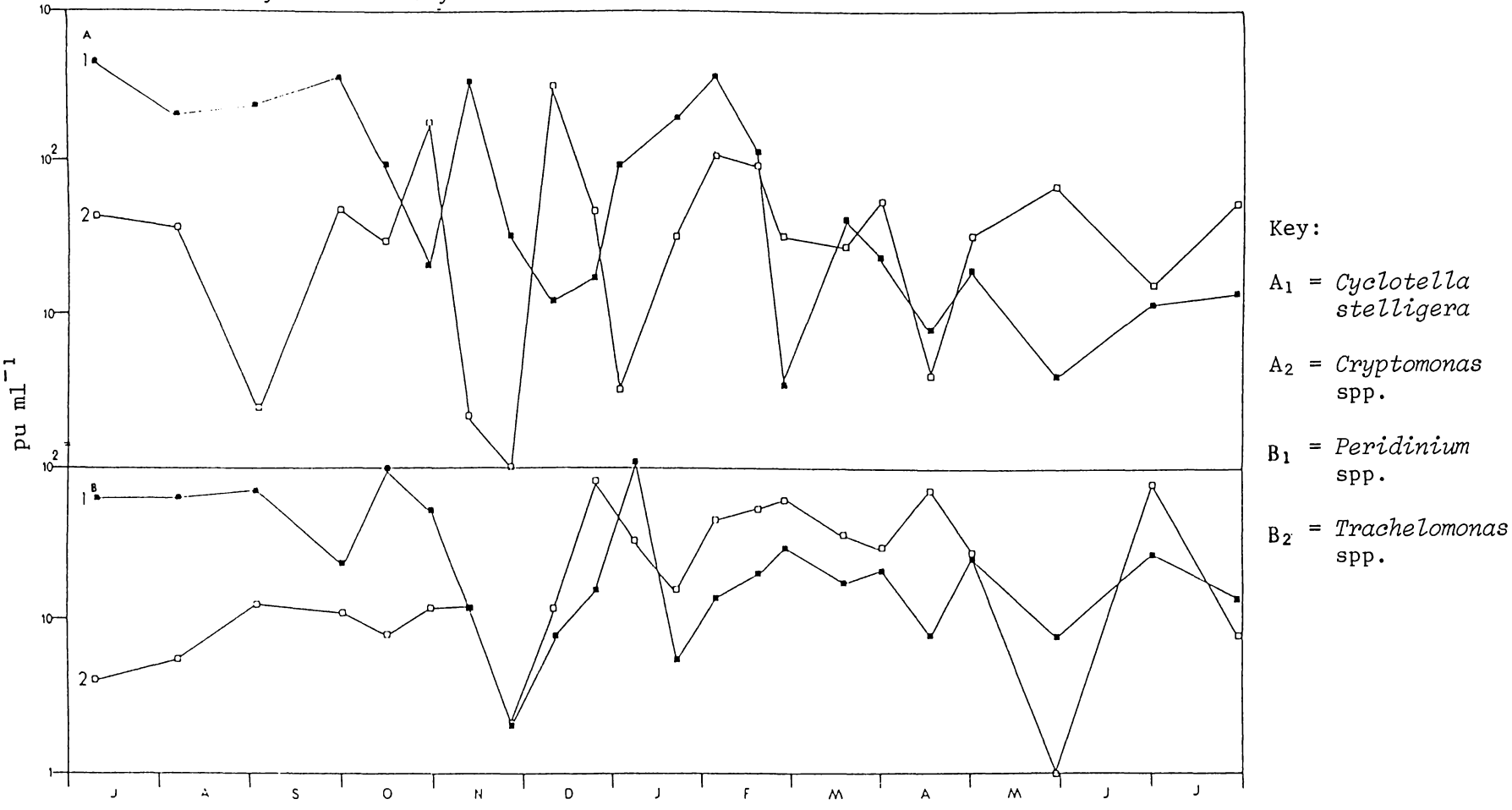
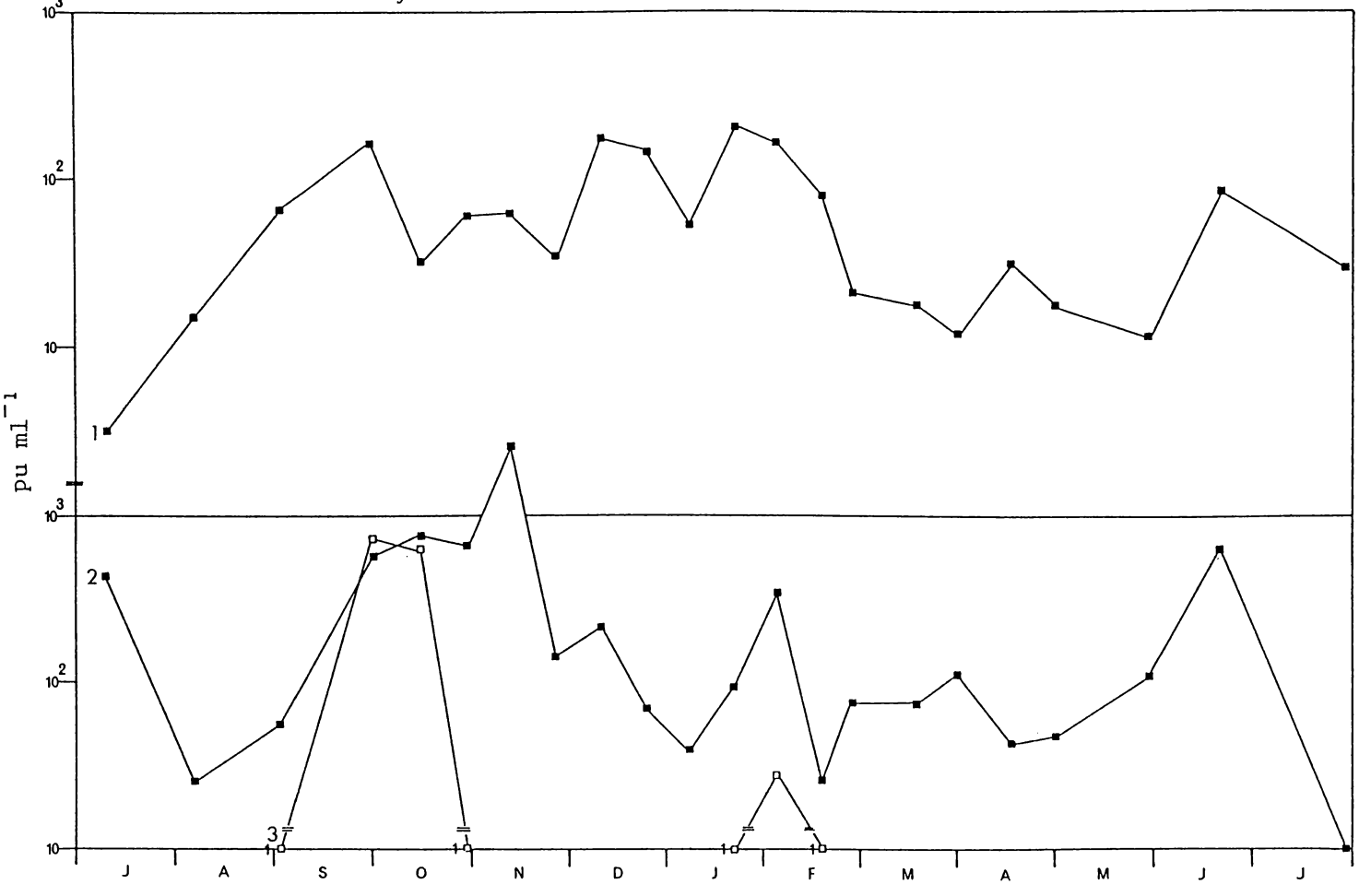


Fig. 6/44 Temporal variations in the densities (pu ml^{-1}) of *Closterium acutum* var. *variabile*, *Dinobryon cylindricum* and *D. bavaricum* in Lake Rotoroa, July 1983 to July 1984.



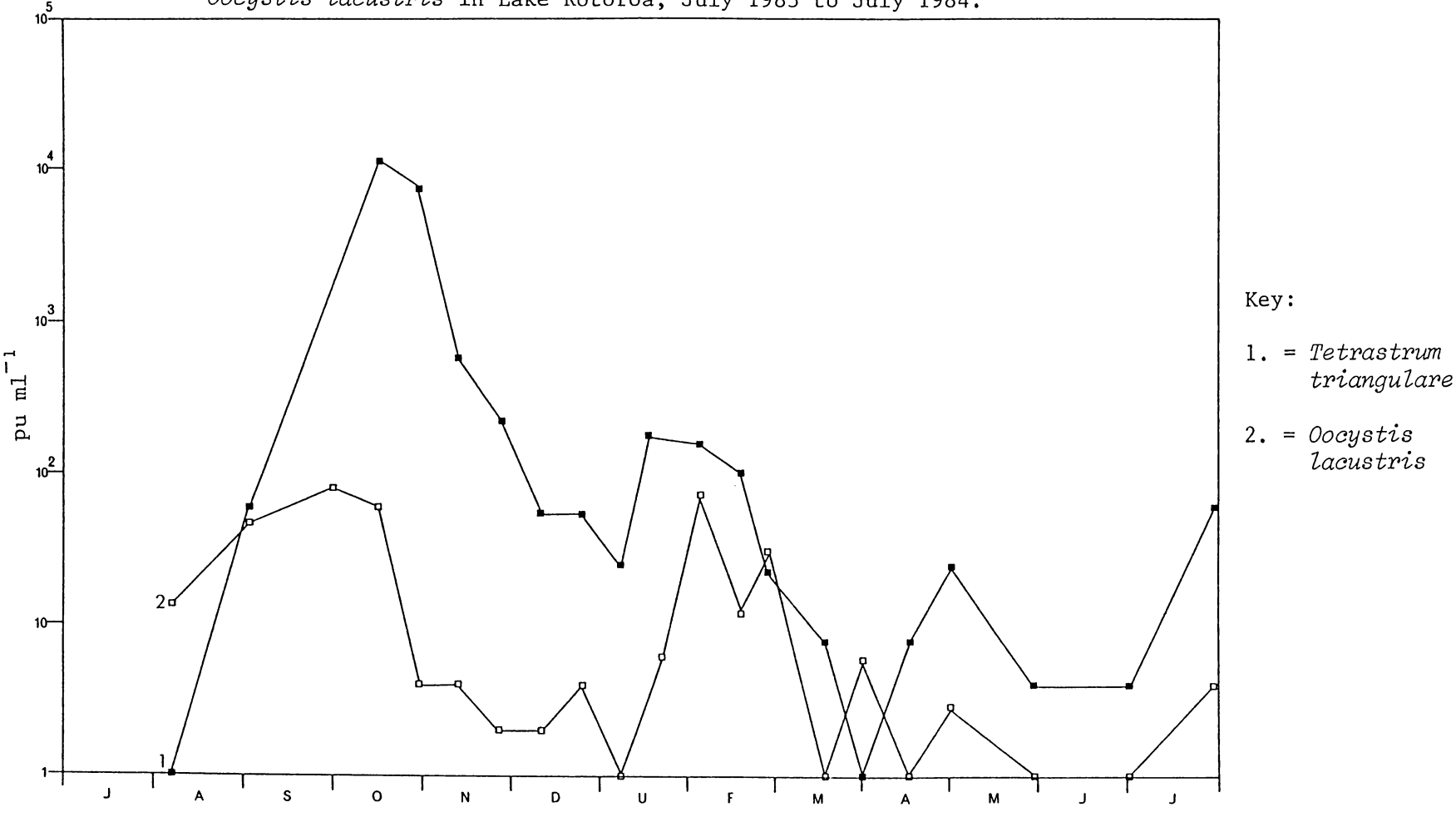
Key:

1. = *Closterium acutum* var. *variabile*

2. = *Dinobryon cylindricum*

3. = *D. bavaricum*

Fig. 6/45 Temporal variations in the densities (pu ml^{-1}) of *Tetrastrum triangulare* and *Oocystis lacustris* in Lake Rotoroa, July 1983 to July 1984.



short, sharp pulses and showed little evidence of seasonality (Fig. 6/43). Maximum densities of both *Cryptomonas* spp. and *Trachelomonas* spp. (324 and 84 pu ml^{-1}, respectively), were recorded immediately after the period of maximum total phytoplankton density in late spring-early summer (Fig. 6/41), but their densities fluctuated markedly throughout the remainder of the sampling programme. In broad terms, *Peridinium* spp. were a less ephemeral component of the community during winter and early spring (mean density 62 pu ml^{-1} [9.7.83 to 29.10.83] [n = 6]), than at any other time, although their highest density (114 pu ml^{-1}) was recorded in mid-summer (7.1.84).

6.2 SEASONAL DYNAMICS

Comparisons of temporal variations in the composition of the phytoplankton standing crops of the nine study lakes show that there were major differences in the seasonal dynamics of the various communities. In general, three temporal patterns were evident: dominance by one (sometimes two) class/es throughout the entire year; a series of brief, unpredictable periods of domination by successive taxa; and marked seasonality.

The first pattern was evident in Lakes Maratoto (Group I), Kainui (Group II), Ngaroto and Rotomanuka South (Group IV), the four lakes with both the highest mean total phytoplankton biomasses (Chapter 7.1.1) and, not unexpectedly, the highest concentrations of dominance (Chapter 5.4); the key taxa were Euchlorophyceae (*Botryococcus braunii*), Zygophyceae (*Staurodesmus* spp.) and Cyanophyceae (*Microcystis aeruginosa*), respectively. However, the absence of marked inter-group similarities, in terms of their dominant class/es, is noteworthy. Furthermore, while the Cyanophyceae was a major class in both Group IV lakes, these two communities differed with regard to their second dominant taxon (Diatomophyceae, Lake Ngaroto [Fig. 6/19]; Zygophyceae, Lake Rotomanuka South [Fig. 6/35]).

The mean PScs of consecutive communities of these four lakes were higher than those of other study lakes (grand mean 65 ± 6%), a further indication of the less ephemeral nature of their communities. In addition, except for Lake Ngaroto, their mean numbers of species per sample and mean Shannon-Wiener indices, were also lower than others

(grand means 21.1 ± 2.5 and 1.5 ± 0.4, respectively).

In contrast, the dominant taxa in Lakes Mangahia (Group I), Mangakaware (Group II), Rotokauri and Rotoroa (Group III), generally changed frequently and unpredictably throughout the entire year, their populations appearing to operate on truncated time scales. Again, in terms of dominant taxa, there were few signs during any particular season of compositional similarity, at either the inter- or intra-group level. The brevity and episodic nature of these associations are evidenced by a low grand mean PSc of consecutive communities (43 ± 13%) and, not unexpectedly, the grand mean Shannon-Wiener index was higher than that of the previous four lakes (2.7 ± 0.7), as was the mean number of species per sample (28.9 ± 6.2).

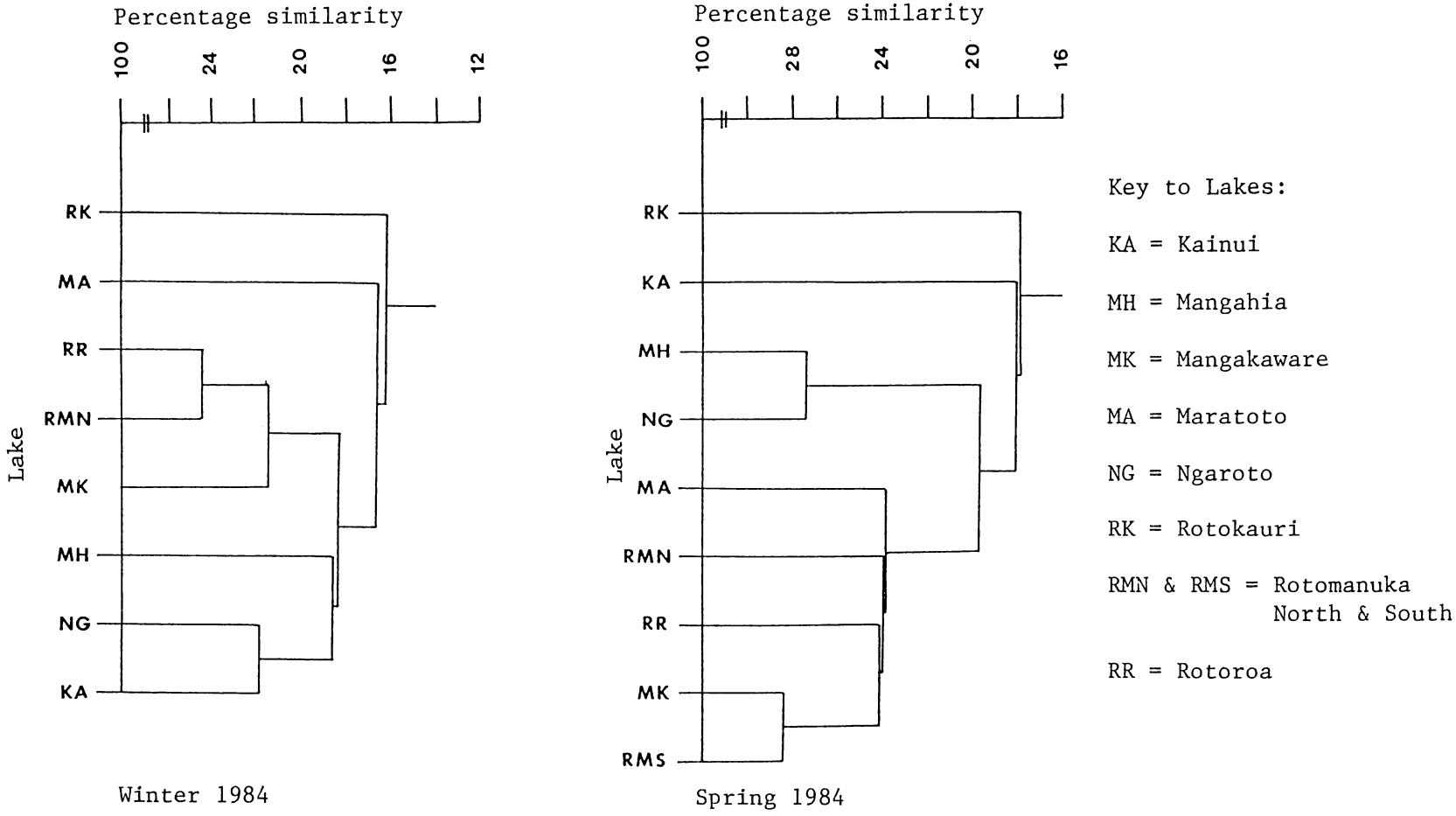
Marked seasonal periodicity, however, was clearly evident in Lake Rotomanuka North (Group III). Here the dominant taxa were those of Reynolds' typical mesotrophic sequence (Chapter 7.2), and both diatoms and euchlorophytes, although numerically less important, displayed the expected increases during late winter and early summer, respectively. Seasonal stability of the thermal regime (Chapter 3.1) permitted several periods of very similar community composition, which explains the high mean Shannon-Wiener Index (32). The mean number of species per sample (33.8) was relatively high, and once more may be attributed to an increased niche potential during marked stratification (as in Chapter 5).

Results of clustering presence-absence data on a seasonal basis (winter, July 1983; spring, October 1983; summer, January 1984; and autumn, April 1984) (Figs. 6/46 and 6/47) also reflect low overall similarity between lakes at both the inter- and intra-group levels. The low similarity between the Lake Rotokauri community and others, despite its high α diversity (Chapter 4.1.6.1), is especially noteworthy. The associations of Lakes Rotomanuka North and Rotoroa (Group III) were consistently the most alike, but similarity was still low.

6.3 PHYTOPLANKTON STRATEGIES

While the population sizes of some phytoplankters remained remarkably constant throughout the sampling period, the majority displayed distinct fluctuations. In order to interpret the ecological significance of these variations in life cycle strategy, the C.V. and SK of the ten most abundant species per study lake were calculated.

Fig. 6/46 Dendrograms of presence-absence data (Coefficient of community) of the nine* study lakes from winter and spring samples 1983 (* winter sample omits RMS).



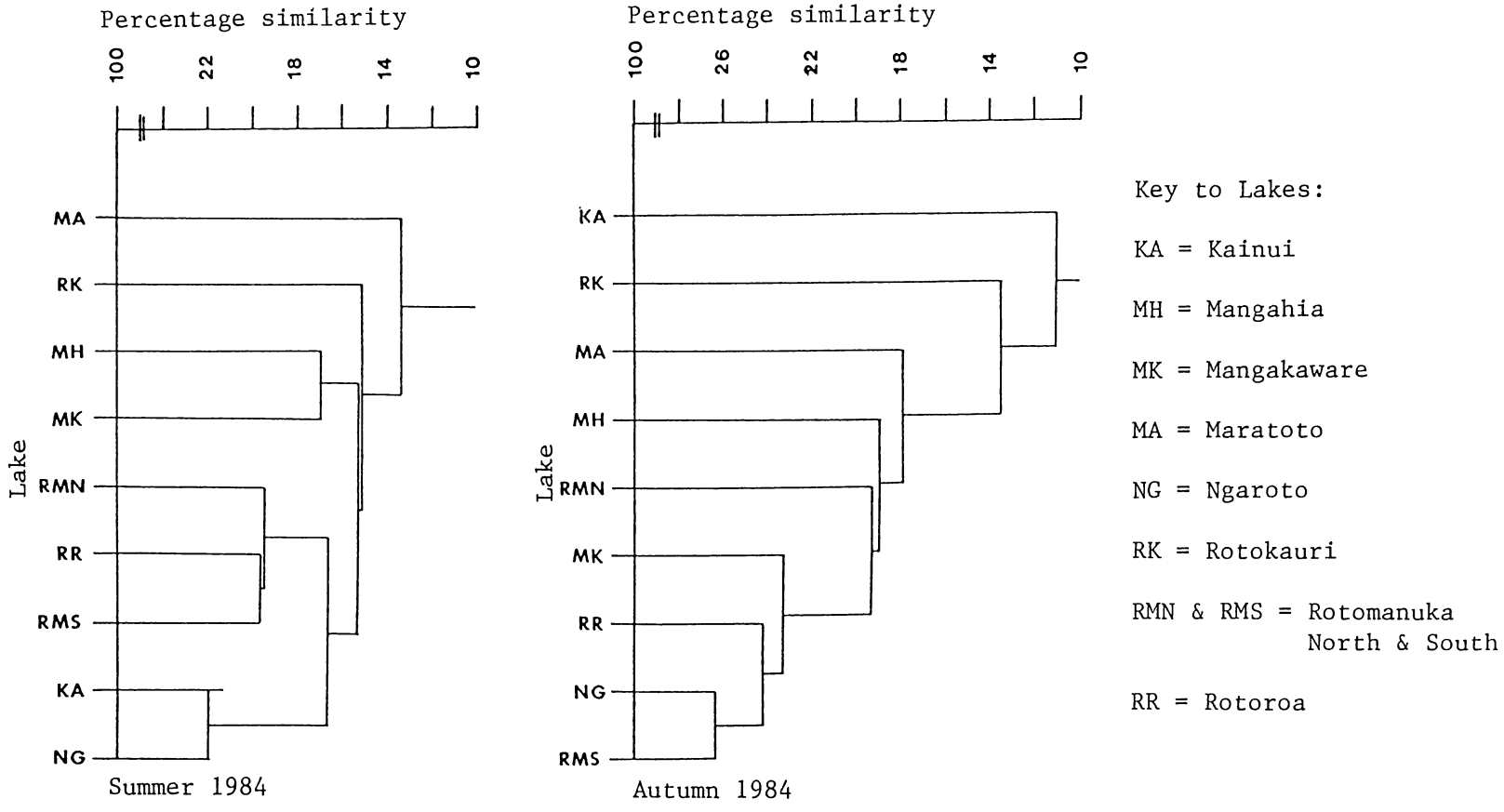


Fig. 6/47 Dendrograms of presence-absence data (Coefficient of community) of the nine study lakes from summer and autumn samples 1984.

These two statistics showed a highly significant correlation, with r ranging from 0.71 ($p \leq 0.05$) (Lake Maratoto) to 0.86 ($p = \leq 0.01$) (Lake Mangakaware) (log transformed data) (Tables 6/27 to 6/35).

The abundance distribution of the majority of these species was skewed, with 72% of their SKs ≥ 1.5. Eleven of these species (23%) displayed very pronounced skew and, of these, the SKs of five were ≥ 3 (*Chlamydomonas* sp. C, *Closterium acutum* var. *variabile*, *Dinobryon cylindricum*, and *Anabaena tenericaulis*), while those of a further six species were ≥ 4. The latter were either small greens (*Monoraphidium contortum*, *M. tortile*, *Rhombocystis complanata* and *Scenedesmus quadricauda*) or chrysophytes (*Mallomaonas akrokomos* and *Synura uvella*).

A few species exhibited low SKs. For example, *Cryptomonas* spp. (*C. marssonii* and *C. ovata*) and *Trachelomonas* spp. (*T. planctonica*, *T. playfairi* and *T. volvocina*) had mean SKs of 1.6 ± 0.4 (n = 8) and 2.0 ± 0.8 (n = 7), respectively. Some other large species, although scoring as one of the ten most abundant phytoplankters in fewer lakes, also had consistently low SKs: *Microcystis aeruginosa*, 1.6 in both Lakes Ngaroto and Rotomanuka South; *Botryococcus braunii*, 1.5 and 1.7 in Lakes Rotomanuka North and Maratoto, respectively; and *Peridinium cinctum*, 1.5 and 1.7 in Lakes Rotoroa and Rotomanuka North, respectively. Desmids generally displayed less skew than many other abundant species, making up 46% of the species with SKs less than 1.5. However, *Closterium acutum* var. *variabile*, one of the ten most abundant phytoplankters in all study lakes, except Rotokauri, displayed a particularly wide range of SKs (1.4 [Lakes Ngaroto and Rotoroa] to 3.6 [Lake Kainui]; mean 2.3 ± 0.9), suggesting that wide tolerance limits and a flexible life history strategy are key aspects of its autecology.

6.4 DISCUSSION

In Lake Rotomanuka North, an autogenic succession comprising euchlorophytes (largely *Monoraphidium* spp. [generally *M. contortum* and *M. tortile*]) → euglenophytes (*Trachelomonas volvocina*) → dinoflagellates (*Peridinium* spp. [largely *P. cinctum*]) (Fig. 6/31) was

TABLE 6/27 Mean density (pu ml^{-1}), coefficient of variation (C.V.) and skewness statistic (SK) of each of the ten most abundant phytoplankton species in Lake Kainui, July 1983 to July 1984 (n = 20).

Taxon	Mean Density (pu ml^{-1})	Standard Deviation	C.V.* (%)	SK*
Staurodesmus spp.	5192.0	6538.0	125	1.4
Staurastrum sp.C	2863.1	3541.6	124	1.2
Closterium acutum var. *variabile*	991.0	2446.8	247	3.6
Staurastrum brachiatum	918.1	1916.6	209	2.0
Scenedesmus quadricauda	595.3	1761.4	296	3.2
Staurastrum chaetopus?	220.7	269.6	122	1.4
Staurastrum arcuatum	211.3	544.3	257	2.7
Ankistrodesmus gracilis	124.6	360.5	289	3.2
Ankistrodesmus bibraianus	102.5	238.9	233	2.6
Cryptomonas spp.	65.3	57.9	89	1.8

* $r = 0.913$; $p \leq 0.001$ (log transformed data)

TABLE 6/28 Mean density (pu ml^{-1}), coefficient of variation (C.V.) and skewness statistic (SK) of each of the ten most abundant phytoplankton species in Lake Mangahia, July 1983 to July 1984 (n = 22).

Taxon	Mean Density (pu ml^{-1})	Standard Deviation	C.V.* (%)	SK*
Aulacosira distans	2284.7	3467.5	152	2.2
Closterium acutum var. *variable*	1508.2	3734.1	247	2.6
Chlorella sp.	1034.7	3733.0	360	3.6
Aulacosira granulata var. *angustissima*	345.7	849.9	246	2.9
Trachelomonas volvocina	330.0	480.7	144	1.9
Closterium gracile	181.9	384.4	211	3.3
Scenedesmus quadricauda	110.0	152.3	138	2.4
Cryptomonas spp.	91.2	144.3	165	2.0
Raphidocelis contorta	63.2	108.2	158	1.8
Monoraphidium tortile	63.2	123.3	199	3.1

* $r = 0.794$; $p \leq 0.02$ (log transformed data)

TABLE 6/29 Mean density (pu ml^{-1}), coefficient of variation (C.V.) and skewness statistic (SK) of each of the ten most abundant phytoplankton species in Lake Mangakaware, July 1983 to July 1984 (n = 21).

Taxon	Mean Density (pu ml^{-1})	Standard Deviation	C.V.* (%)	SK*
Monoraphidium contortum	1346.1	5964.0	443	4.0
Acanthoceras zachariasi	541.7	1353.2	250	2.8
Trachelomonas spp.	399.5	1026.1	257	3.8
Asterionella formosa	380.1	1063.5	280	3.0
Monoraphidium tortile	376.3	1702.9	453	4.0
Closterium acutum var. *variabile*	286.5	306.0	107	1.8
Dinobryon cylindricum	227.4	466.8	205	2.0
Dictyosphaerium subsolitarium?	179.0	538.3	301	2.8
Palmodictyon viride	149.3	684.3	458	3.6
Rhombocystis complanata	140.7	639.6	454	4.0

* $r = 0.862$; $p \leq 0.01$ (log transformed data)

TABLE 6/30 Mean density (pu ml^{-1}), coefficient of variation (C.V.) and skewness statistic (SK) of each of the ten most abundant phytoplankton species in Lake Maratoto, July 1983 to July 1984 (n = 20).

Taxon	Mean Density (pu ml^{-1})	Standard Deviation	C.V.* (%)	SK*
Botryococcus braunii	3050.5	2931.6	83	1.7
Chlamydomonas sp. C	2516.8	11055.1	439	3.8
Closterium acutum var. *variabile*	514.7	709.9	138	3.2
Monoraphidium tortile	159.9	520.0	325	3.3
Tabellaria flocculosa	90.2	109.4	121	2.4
Cryptomonas spp.	86.0	79.8	93	1.3
Closterium gracile	71.2	173.4	243	2.3
Trachelomonas spp.	42.6	75.3	176	2.1
Staurastrum sp. B	25.0	35.2	141	2.9
Staurastrum inflexum	18.1	18.8	103	1.2

*r = 0.709; $p \leq 0.05$ (log transformed data)

TABLE 6/31 Mean density (pu ml^{-1}), coefficient of variation (C.V.) and skewness statistic (SK) of each of the ten most abundant phytoplankton species in Lake Ngaroto, July 1983 to July 1984 (n = 21).

Taxon	Mean Density (pu ml^{-1})	Standard Deviation	C.V.* (%)	SK*
Aulacosira granulata var. *angustissima*	2413.1	1887.2	78	1.7
Scenedesmus quadricauda	590.0	1617.5	274	4.0
Microcystis aeruginosa	402.0	457.9	114	1.6
Anabaena tenericaulis	333.2	608.3	183	3.4
Trachelomonas volvocina	186.8	145.3	163	2.2
Monoraphidium contortum	166.4	162.7	98	2.6
Chroococcus limneticus	138.9	312.1	225	2.1
Anabaena circinalis	136.3	331.7	243	2.7
Closterium acutum var. *variabile*	117.0	84.2	72	1.4
Asterionella formosa	93.3	127.5	137	1.9

* $r = 0.804$, $p \leq 0.01$ (log transformed data)

TABLE 6/32 Mean density (pu ml^{-1}), coefficient of variation (C.V.) and skewness statistic (SK) of each of the ten most abundant phytoplankton species in Lake Rotokauri, July 1983 to July 1984 (n = 22).

Taxon	Mean Density (pu ml^{-1})	Standard Deviation	C.V.* (%)	SK*
Mallomonas akrokomos	73.8	344.0	466	4.3
Ankistrodesmus bibraianus	63.0	103.3	164	1.7
Cryptomonas spp.	41.3	35.8	87	1.3
Trachelomonas spp.	37.6	61.5	163	1.3
Ankistrodesmus gracilis	28.9	62.5	216	2.1
Ankistrodesmus falcatus	27.9	39.4	141	1.8
Monoraphidium contortum	26.7	39.9	149	2.0
Scenedesmus acutiformis	25.2	43.1	171	2.2
Synura uvella	23.9	69.6	291	2.7
Acanthoceras zachariasi	22.4	49.1	219	2.0

* $r = 0.824$; $p \leq 0.01$ (log transformed data)

TABLE 6/33 Mean density (pu ml^{-1}), coefficient of variation (C.V.) and skewness statistic (SK) of each of the ten most abundant phytoplankton species in Lake Rotomanuka North, July 1983 to July 1984 (n = 21).

Taxon	Mean Density (pu ml^{-1})	Standard Deviation	C.V.* (%)	SK*
Dinobryon cylindricum	139.8	295.8	176	2.2
Cryptomonas spp.	46.7	31.1	66	1.4
Peridinium cinctum	26.4	25.9	98	1.7
Botryococcus braunii	18.6	18.9	101	1.5
Trachelomonas volvocina	17.9	25.8	143	2.1
Cyclotella stelligera	17.3	16.4	94	2.4
Closterium acutum var. *variabile*	10.5	6.6	63	1.5
Synura uvella	8.6	21.8	256	2.5
Vacuolaria sp.	7.9	6.4	81	1.0
Fragilaria delicatissima	7.5	15.0	199	2.4

* $r = 0.772$; $p \leq 0.01$ (log transformed data)

TABLE 6/34 Mean density (pu ml^{-1}), coefficient of variation (C.V.) and skewness statistic (SK) of each of the ten most abundant phytoplankton species in Lake Rotomanuka South, October 1983 to July 1984 (n = 15).

Taxon	Mean Density (pu ml^{-1})	Standard Deviation	C.V.* (%)	SK*
Closterium acutum var. *variabile*	1962.4	5010.8	255	3.2
Microcystis aeruginosa	352.0	297.9	95	1.6
Anabaena tenericaulis	170.4	266.0	156	2.2
Trachelomonas spp.	108.4	144.3	133	1.6
Cryptomonas ovata	62.1	70.3	113	1.1
Synura uvella	50.5	147.1	291	2.8
Chrysococcus rufescens	22.3	26.8	120	0.9
Cyclotella stelligera	21.8	41.5	190	2.4
Staurastrum sp. A	21.6	32.1	148	1.5
Monoraphidium tortile	18.9	56.1	296	3.0

* $r = 0.856$; $p \leq 0.002$ (log transformed data)

TABLE 6/35 Mean density (pu ml^{-1}), coefficient of variation (C.V.) and skewness statistic (SK) of each of the ten most abundant phytoplankton species in Lake Rotoroa, July 1983 to July 1984 (n = 22).

Taxon	Mean Density (pu ml^{-1})	Standard Deviation	C.V.* (%)	SK*
Tetrastrum triangulare	1042.8	2196.9	280	2.8
Dinobryon cylindricum	325.0	545.5	168	3.1
Cyclotella stelligera	123.7	144.3	117	1.6
Closterium acutum var. *variabile*	68.3	61.3	90	1.4
Dinobryon bavaricum	63.4	199.2	314	2.7
Cryptomonas spp.	56.6	72.7	128	2.4
Peridinium cinctum	32.6	31.2	96	1.5
Trachelomonas volvocina	28.7	26.4	92	1.3
Synura uvella	22.3	95.3	427	4.1
Oocystis lacustris	16.2	25.8	158	1.7

* $r = 0.849$; $p \leq 0.002$ (log transformed data)

apparent throughout early spring and summer, when stratification was most pronounced (Fig. 3/18), and was similar to that recorded during the same period in 1979 (Etheredge, 1983). These phytoplankters display a range of adaptations which enable them to prolong residency in the euphotic zone: *Monoraphidium* and *Trachelomonas* are both small with concomitant large surface area to volume ratios, and the latter is motile; *Peridinium* can perform diel vertical migrations to lower stations in the water column where entrainment of nutrients may occur (Wetzel, 1975; Sherr *et al.*, 1982), has well-documented capacities for luxury consumption and intracellular storage of phosphorus (Serruya & Berman, 1975; Wynne & Berman, 1980; Elgavish *et al.*, 1982), and is well-protected from herbivory by its large size, and thecal structure and composition.

Dinoflagellate dominance in Lake Rotomanuka North ended abruptly when mixing commenced in April 1984 (Fig. 3/0), and a rapid shift (allogenic change) to a chrysophyte community (largely *Dinobryon cylindricum*) was recorded. Chrysophyte maxima also coincided with periods of holomixis in Lakes Rotokauri (Fig. 3/1), Rotomanuka South (Fig. 3/8), and Rotoroa (Fig. 3/7). In some respects, such timing is enigmatic because both colonial and unicellular chrysophytes are generally considered responsive to increased stability of the water column (Reynolds, 1984a), and maxima of *Dinobryon* in temperate, stratified lakes elsewhere have frequently been noted to follow those of diatoms and precede those of euchlorophytes (Pearsall 1930, 1932; Hutchinson, 1944; Rodhe, 1948; Bamforth, 1958). However, some aspects of the ecology of *Dinobryon* are contradictory (Lehman, 1976); for example, although inverse correlations between its abundance and dissolved phosphate concentrations are attributed to extremely efficient nutrient uptake at low concentrations (Schelske & Stoermer, 1972; Lehman, 1976), there is also evidence of luxuriant growth in waters with high phosphate concentrations (Lehman, 1976), and in addition, the growth of some species is known to be enhanced by enrichment (Lefèvre & Farrugia, 1958; Talling, 1962).

It is thus of interest that in Lakes Rotomanuka North and South, Rotoroa, and Rotokauri chrysophyte maxima occurred immediately after major peaks of total phytoplankton biomass suggesting that, despite holomixis, phosphorus concentrations were probably low. Similar

periodicity has been noted in mesotrophic Lake Rotokakahi (Flint, 1977).

In addition, Pearsall's (1932) observations that this genus is favoured by high nitrate to phosphate ratios are also of relevance to the present study. Markedly higher ratios occurred in Lakes Rotomanuka North and Rotoroa, than in those lakes with high proportions of diatoms (Table 3/9).

There is also evidence of a clear relationship between the abundance of *Dinobryon cylindricum* and silica concentrations; for example, Lakes Rotomanuka North and Rotoroa had both the lowest silica concentrations and the highest mean numbers of *D. cylindricum* (39 and 20% of mean total phytoplankton densities, respectively). Conversely, Lakes Mangahia, Mangakaware and Ngaroto, in which diatoms were key floral components, had markedly higher silica concentrations (Table 6/36).

It is highly probable that water temperature also influenced the periodicity of *D. cylindricum* for, with one exception (12.11.83; Lake Rotoroa), abundance peaks were recorded in winter (range of surface temperatures 11 - 12°C), adding support to Moore's (1981b) suggestion that this species generally prefers colder temperatures.

Other allogenic changes or shifts in community structure were common in the lakes with unstable thermal regimes, and where brief periods of stratification alternated with either equally short periods of holomixis or weakly developed stratification (e.g., Lakes Mangahia, Mangakaware and Rotoroa [Chapter 3]). Such intermittent shifts in the physico-chemical environment resulted in sharp transitions between consecutive communities (Figs. 6/4, 6/8, 6/41, respectively), with repeated replacements of existing populations by assemblages of species better adapted to the new regimes.

Thus, in Lake Mangakaware during early summer, the maximum difference between surface to bottom waters was 3.5°C (Fig. 3/6) and diatoms, especially *Asterionella formosa*, were dominant. This population exhibited rapid density increases, which are typical of its life history strategy elsewhere, and largely attributable to its physiological properties, summarised by Reynolds (1984a) as high photosynthetic efficiency and capacity, and efficient carbon assimilation at low irradiance levels. However, in mid-summer when stratification was well developed, a sharp change to a community

TABLE 6/36 Silica concentrations (g m^3) and mean proportions of the Chrysophyceae and the Diatomophyceae in the six study lakes in which one or other of these taxa was dominant, July 1983 to July 1984.

Lake	Silica (g m_3)		Chrysophyceae		Diatomophyceae	
	Sept. 1983	Nov. 1983	No.	Proportion (%)	No.	Proportion (%)
Mangahia	13.0	2.8	60	0.9	2677	42.3
Mangakaware	7.0	7.5	387	7.7	1153	22.9
Ngaroto	5.9	2.6	21	0.4	2600	47.5
Rotokauri	3.0	3.1	117	17.9	106	16.2
Rotomanuka North	0.9	1.0	159	42.1	30	7.9
Rotoroa	0.4	0.7	417	21.8	148	7.7

dominated by small euchlorophytes (largely *Monoraphidium contortum* and *Tetrastrum triangulare*) occurred. In late summer, these dominants were also replaced, equally rapidly, by *Acanthoceras zachariasi*, the transition coinciding with the weakening and eventual breakdown of stratification. This reversion to a diatom dominated community, although involving a different key species, gives support to Reynolds' (1984a) suggestion that assemblages contain several potential dominants.

Allogenic changes were equally conspicuous in Lake Mangahia (Fig. 6/4); an abrupt replacement of diatoms (largely *Aulacosira distans*, *A. granulata* var. *angustissima* and *Tabellaria flocculosa*) by chlorophytes (*Closterium acutum* var. *variabile* and small greens) occurred at about two monthly intervals, coinciding with periods of holomixis (and/or weakly developed stratification) and more stable stratification, respectively (Fig. 3/5).

The influence of reduced circulation was equally dramatic in Lakes Rotomanuka South and Ngaroto where it was accompanied by immediate shifts from zygophycean (*Closterium acutum* var. *variabile* to cyanophyte (*Microcystis aeruginosa* and *Anabaena tenericaulis*), and diatoms (*Aulacosira granulata* var. *angustissima*) to euchlorophyte (largely *Scenedesmus quadricauda* and *Actinastrum hantzschii*) dominated communities, respectively.

Conversely, the absence of intermittent shifts in the mixing pattern of Lake Maratoto (Fig. 3/2) probably explains the consistent dominance by one class (Euchlorophyceae [*Botryococcus braunii*]) throughout almost the entire year (Fig. 6/14), an upsurge in numbers of *Closterium acutum* var. *variabile*, in winter 1984, being the only exception. Despite the absence of well-developed stratification in Lake Maratoto, the Diatomophyceae remained numerically unimportant throughout the entire year (Table 4/17; Fig. 6/14), as was the case in 1979 (Etheredge, 1983), although the diatom species diversity (36 [29%]) was the highest of the series. This conforms with their unimportant role in several dystrophic lakes elsewhere (e.g., Nygaard, 1949; Berg & Petersen, 1956; Hansen, 1962). Lake Kainui, with one exception, was also holomictic or weakly stratified throughout the entire year (Fig. 3/3), and displayed a similar pattern of almost

continuous domination by one class (Zygophyceae) (Fig. 6/0).

Cryptophytes are eurytopic species (Hutchinson, 1967; Rosén, 1981; Reynolds *et al.*, 1982), and frequently found permanently in the plankton. They are favoured by increasing stability of the water column (Etheredge, 1983), undoubtedly because of their ability to undergo regular vertical migrations which give access to nutrient-rich waters (Tilzer, 1973; Salonen *et al.*, 1984).

In the present study, *Cryptomonas* spp. (*C. marssonii* and *C. ovata*) had one of the ten highest ISIs in seven lakes, with the three highest indices occurring in Group III lakes, especially Rotomanuka North, and Rotokauri (Table 5/15), the two with the most stable stratification (Chapter 3). It is noteworthy, however, that the highest mean densities occurred in the most darkly-stained waters (Mangahia [Table 4/5]; Maratoto [Table 4/15]), with both Lakes Mangakware (Table 4/10) and Kainui (Table 4/0) (Group III), ranking third and fourth, respectively. This is in agreement with their well-documented tolerance of low light regimes (see Stewart & Wetzel, 1986).

However, they were seasonally unselective in all study lakes, with abundance peaks consistently following maxima of other taxa, and thus coincident with periods of decomposition. Similar timings have been reported from many other lakes elsewhere (e.g., Ramberg, 1976; Ringelberg & Kersting, 1978; Schwartz *et al.*, 1981). As *Cryptomonas* spp. are both facultative heterotrophs and auxotrophic, such pulses probably result directly from increased quantities of both dissolved and/or particulate organic matter and vitamins, produced during decomposition (Stewart & Wetzel, 1986).

Compositional and structural changes in planktonic communities may be interpreted as functions of particular life history strategies of their component populations. The concept of r- and K- selection (MacArthur & Wilson, 1967), and later extensions of the concept by Pianka (1970, 1972), is the most generally accepted theory concerning the strategies of both plants and animals. In broad terms, r-selection favours small-sized, short-lived species (fugitive, colonising, opportunistic, pioneer, or weedy species [see Grassle & Grassle, 1974]), with high growth rates and considerable reproductive potential. K- selected species (constants, equilibrium, or

autochthonous species), however, are larger with pronounced anti-herbivorous devices. They have lower growth rates, divert less energy and resources to reproduction than r- strategists, and exhibit superior competitive abilities and utilisation of resources; such selection obviously reduces niche overlap. In addition, the mortality characteristics of the two strategists differ, being catastrophic and density-independent, and density-dependent, respectively.

Despite a blanket characterisation by population biologists of all phytoplankters as highly selected r-strategists (Kilham & Kilham, 1980), recent authors (Kilham & Kilham, 1980; Sommer, 1981; Reynolds, 1984a) have clearly demonstrated that a full range of life history strategies is present within phytoplankton communities.

Coefficients of variation and skewness statistics yield information which can be interpreted in terms of r- and K- selection. Phytoplankters with low Cs.V. and SKs, do not have rapid growth surges, thus conforming to K- selection; and conversely, those with high Cs.V. and SKs, increase rapidly within narrow bands of favourable conditions, thus exhibiting radical density changes, and fit the profile of r- selected species (Lewis, 1977).

Clearly, shifts along the continuum from r- to K- selected species occur throughout the annual cycles of lakes which develop stable stratification. Sommer (1981), for example, analysed the most abundant species within the phytoplankton community of Lake Constance, in terms of their rates of increase and sizes, and concluded that species of the same growth- and size-classes were generally associated with each other. From spring until August, shifts from both the fast-growing to slow-growing classes and smallest to largest size-classes were observed, with the reverse trends apparent throughout autumn.

However, in the present study, seasonality of the most abundant r- and K- strategists was, not unexpectedly, only apparent in Lake Rotomanuka North, where small diatoms (e.g., *Cyclotella stelligera* and *Fragilaria delicatissima*) with high SKs (both 2.4; Table 6/33) were common only during winter and early spring, respectively; and conversely, the large dinoflagellate (*Peridinium cinctum*; see above for adaptive factors) was present throughout the entire year, but increased in numbers only throughout summer and autumn (SK = 1.66; Table 6/33). The instability of the water columns in Lakes Mangahia, Mangakaware and Rotoroa (Chapter 3), precluded such seasonal progressions, and instead small r- strategists occurred sporadically

throughout the year; for example, diatoms such as *Asterionella formosa*, *Tabellaria flocculosa* and *Cyclotella stelligera*, achieved peak densities throughout mid- to late summer in Lakes Mangakaware, Mangahia and Rotoroa, respectively.

Conversely, in those study lakes which were almost permanently holomictic or had a transient period of weakly developed stratification (Maratoto, Kainui, and Ngaroto [Chapter 3]), large K-strategists (*Botryococcus braunii*, *Microcystis aeruginosa* and *Aulacosira granulata* var. *angustissima* dominated for lengthy periods, and many of the r- strategists were, when considered in terms of SKs, 'highly' r- selected; for example, *Scenedesmus quadricauda* (4.0; Lake Ngaroto), *Chlamydomonas* sp. C (3.8; Lake Maratoto), *Closterium acutum* var. *variabile* (3.6; Lake Kainui), *Anabaena tenericaulis* (3.4; Lake Ngaroto) and *Monoraphidium tortile* (3.3; Lake Maratoto).

Success as a K- strategist requires low vulnerability to herbivory, an ability to sequester, and maximum exploitation of resources; motility is usually a prerequisite for the latter, although in the context of the mixing patterns of the study lakes under discussion, this is probably of minor importance. In terms of anti-herbivorous devices *Botryococcus braunii* is both large and unmanageable (stressed as important by Porter [1977]), occurring as an irregular colony of numerous cells embedded in an oily matrix, and with a distinctive rubbery texture (Belcher, 1968). Its sequestering abilities are excellent (for details see Wake & Hillen [1981]; Wolf & Cox, 1982]), and it may remain alive for a period of at least ten months when placed at a constant temperature of 25°C (Belcher, 1968). Efficient light utilisation is obviously of paramount importance to phytoplankton in darkly-stained waters, and the numerical success of *B. braunii* in Lake Maratoto is further evidence of its adaptability, particularly because the heavy pigmentation within the colony matrix must greatly reduce the quantity of light reaching the chromatophore at the base of the cell (Belcher, 1968).

Microcystis aeruginosa, like *Botryococcus braunii*, exhibits considerable physiological, biochemical and behavioural flexibility. Its annual cycle, described in detail by Reynolds *et al.*, (1981),

typifies that of a 'highly' selected K- species. Although, sometimes it may exist, like other K- strategists, almost as a monoculture, in Lake Ngaroto it was sub-dominant to *Aulacosira granulata* var. *angustissima*. This narrow form is considered to resist stressful conditions, especially either high pH (see Chapter 3) or large populations of cyanophytes unfavourable to *A. granulata* (Prowse & Talling, 1958); in addition, it is chiefly this variety which co-exists with cyanophycean blooms in Lake George (Talling, 1965).

Thus, in the study lakes, fundamental changes in phytoplankton community structure were inextricably inter-related to changes in mixing patterns i.e. Round's (1971) 'shock periods'. However, biological factors such as parasitism, grazing, and allelopathy, also interact with the physico-chemical regime to influence periodicity.

Fungal parasites (Order - Chytridiales; see Sparrow [1960]) reached epidemic proportions in Lakes Mangakaware (*Rhizophydium planktonicum*? on *Asterionella formosa* [Chapter 6.1.3.5]) and Kainui (unidentified chytrids and/or biflagellates [Order - Lagenidales] on *Staurastrum brachiatum* [Chapter 6.1.3.1]). As well, *Rhizophydium deformans* Jaag and Nipkow (on *Oscillatoria limosa*), and other unidentified fungi were observed very infrequently on the following species in other study lakes: *Ankistrodemsus bibraianus; Aulacosira granulata; Botryococcus braunii; Microcystis aeruginosa; Nephrocytium agardhianum; Peridinium willei*; and *Staurastrum leptocladum* var. *insigne*.

Several detailed studies have been made of the effects of *Rhizophydium planktonicum* on the population dynamics of *Asterionella formosa* (Canter & Lund 1948, 1951; Koob, 1966), as well as their specific host/parasite interactions (Canter & Jaworski 1978, 1979). Canter & Lund (1951) concluded that parasitism may both delay the timing and decrease the size, of *Asterionella formosa* maxima, and suggested that parasitism of one species may alter community dynamics by permitting the development of another. However, in the present study, it is difficult to assess quantitatively the influence of the parasite on the decline of *A. formosa*, because it was coincident with an abrupt change in water temperature and turbulence (Fig. 3/6). For

example, the surface water temperature was 21°C, at the time of its maximum abundance, but during the following 14 days increased to 26°C, a temperature which is considerably higher than the optimum given by Hutchinson (1967) (range 10 - 20°C).

Desmids are also frequently parasitised, and ecological effects are similar to those on diatoms (Canter & Lund, 1969). In Lake Kainui, a marked upsurge of *Closterium acutum* var. *variabile* followed the rapid decline of parasitised *Staurastrum brachiatum*, but once more, other factors may have been partially responsible.

These are the first records of major fungal infections of phytoplankton in New Zealand, although the presence during winter of *Rhizophydium planktonicum* on *Asterionella formosa*, has been noted in Lake Waikaremoana (Cassie, 1978).

A detailed discussion on the influence of grazing on phytoplankton community composition and biomass is given in Chapter 8.

The distinct seasonal periodicity of total phytoplankton biomass generally observed in Northern Hemisphere warm monomictic lakes (see Hutchinson, 1967; Wetzel, 1975) was not apparent in Lakes Rotomanuka North and Rotokauri (Figs. 6/32 and 6/26, respectively). Viner & White (1987), using chlorophyll data as a basis for comparative analyses, have reported similar deviations in other New Zealand lakes, and also, in some instances, inter-annual differences. Such variations, brought about largely by the reduced annual temperature range of New Zealand lakes compared with continental ones (Chapter 3), obviously have important implications for zooplankton life cycles. However, further detailed analyses of phytoplankton (particularly small species) and zooplankton population dynamics are a prerequisite to a greater understanding of their interactions (Chapman & Green, 1987).

The β diversity for the composite phytoplankton community of the nine study lakes was remarkably high (14.35) compared to other groups of lakes elsewhere; for example, Lewis (1978b) gave values of 6.4 and 3.0 for twelve tropical lakes and fifteen Austrian and south German alpine lakes, respectively. High β diversity is only possible in lakes lacking uniform physico-chemical regimes, and thus is to be expected in the present study where, superimposed on top of the major differences between the lakes in terms of morphometry, concentrations of DHM and nutrient concentrations (Chapters 1 and 3), were variations

in mixing regimes which permitted the previously discussed combination of autogenic succession and numerous allogenic changes.

CHAPTER SEVEN

COMPARATIVE ANALYSES OF THE TROPHIC STATUS OF THE NINE STUDY LAKES

7.1 TROPHIC INDICES

7.1.1 Maximum and Mean Standing Crops

Lake trophic classifications based on a variety of general characteristics are given in Table 7/0.

In terms of maximum phytoplankton biomass, all lakes belonging to Groups I, II and IV (Chapter 3) were highly eutrophic. Of the Group III lakes, Rotokauri was mesotrophic, and both Rotomanuka North and Rotoroa were eutrophic (Table 7/1). Except for Group I, intra-group maximum biomasses were broadly similar. Inter-group maximum biomasses, however, differed by two orders of magnitude (2.3 g m^3 [Lake Rotokauri] to 244 g m^3 [Lake Maratoto]). The remarkably high maximum biomass in the latter (Fig. 6/15), was not an isolated occurrence, with values exceeding 10 g m^3 on all sampling occasions. High total biomasses were also recorded for considerable periods in Lakes Ngaroto (Fig. 6/20) and Rotomanuka South (Fig. 6/36) (Group IV), exceeding 10 g m^3 on 86 and 71% of sampling occasions, respectively.

Group III lakes also had the three lowest mean phytoplankton biomasses (wet weight) (Table 7/1). Using this criterion, Lake Rotokauri was oligotrophic, both Lakes Rotomanuka North and Rotoroa were mesotrophic, Lake Maratoto (Group I) and Group IV lakes were hyper-eutrophic, and Lake Kainui (Group II) was bordering on hyper-eutrophy. Both Lakes Mangahia (Group I) and Mangakaware (Group II) were meso-eutrophic.

When trophic status was considered in terms of mean total phytoplankton biomass expressed as mg C m^3 (Heyman, 1983) (Table 7/0), Lake Rotokauri (Group III) was oligotrophic, Lakes Rotomanuka North and Rotoroa (Group III) and Mangahia (Group I) were mesotrophic, and the remainder were eutrophic (Table 7/1).

Mean phytoplankton densities ranged from 0.4 (Lake Rotomanuka North) to 11.6 pu l^{-1} (Lake Kainui), and the lowest values were also recorded in the Group III lakes (0.4 [Rotomanuka North], 0.7 [Rotokauri] and 1.9 pu l^{-1} [Rotoroa]). The highest mean densities were recorded in the most darkly-stained lakes (Maratoto (6.7 pu l^{-1}), Mangahia (6.3 pu l^{-1}) and Kainui (11.6 pu l^{-1}) (Table 7/1).

TABLE 7/0 Some general characteristics of lakes of various trophic status.

Trophic Status	Maximum[1] Phytoplankton Biomass ($g\ m^3$)	Mean[2] Phytoplankton Biomass ($g\ m^3$)	Phytoplankton[3] Biomass ($mg\ C\ m^3$)*	Dominant[4] Phytoplankton and GALD[5]	Total Phosphorus[6] ($\mu g\ l^-$)
Ultra-oligotrophic		⩽ 0.5	< 50		
OLIGOTROPHIC	< 1	0.5 - 1.0	20 - 100	*Staurodesmus*, *Staurastrum* or *Cyclotella*, *Tabellaria* or *Dinobryon*, some *Mallomonas* < 30 μm	< 10
MESOTROPHIC		1.0 - 2.0	100 - 300		10 - 20
Meso-eutrophic		2.0 - 4.0			
EUTROPHIC	3 - 5	4.0 - 8.0	> 300	*Asterionella*, *Fragilaria crotonensis*, *Synedra*, *Stephanodiscus*, *Melosira granulata* > 30 μm	> 20

Hyper-eutrophic	> 10	> 8.0	*Microcystis* *Aphanizomenon* *Anabaena*

[1] After Vollenweider (1968)
[2] After Vollenweider *et al.*, (1974)
[3] After Likens (1975)
[4] After Wetzel (1975)
[5] After Hillbricht-Ilkowska (1977)
[6] After Vollenweider (1965)
[*] Method after Heyman (1983)

TABLE 7/1 Some biological and chemical indices of trophic status of the nine study lakes, July 1983* to July 1984.

	Group I Lakes		Group II Lakes		Group III Lakes			Group IV Lakes	
Index	MA	MH	KA	MK	RK	RMN	RR	NG	RMS
Maximum total phytoplankton biomass ($g\ m^3$)	244.0	10.1	16.8	17.9	2.3	5.2	5.1	74.0	92.4
Mean total phytoplankton biomass ($g\ m^3$)	72.0	2.5	7.9	3.5	0.7	1.7	1.8	27.6	32.3
Mean total phytoplankton biomass ($mg\ C\ m^3$)	7920	275	869	385	77	187	198	3036	3553
Maximum number pu l^{-1}	54.2	23.5	21.1	29.4	2.2	1.2	13.5	11.6	19.8
Mean number pu l^{-1}	6.7	6.3	11.6	5.0	0.6	0.4	1.9	5.3	3.2

Highest ISI ($x10^3$), and taxon responsible	4.1 *Botryococcus braunii*	3.6 *Aulacosira distans*	4.5 *Staurodesmus* spp.	2.3 *Monoraphidium contortum*	0.6 *Ankistrodesmus bibraianus*	2.3 *Dinobryon cylindricum*	4.7 *Tetrastrum triangulare*	4.4 *Aulacosira granulata* var. *angustissima*	4.7 *Closterium acutum* var. *variabile*
Highest concentration of one taxon (pu l^{-1}), and taxon responsible	49.5 *Chlamydomonas* sp.C	17.0 *Chlorella* sp.	11.1 *Closterium acutum* var. *variabile*	27.4 *Monoraphidium contortum*	0.3 *Ankistrodesmus bibraianus*	1.0 *Dinobryon cylindricum*	11.7 *Tetrastrum triangulare*	7.3 *Aulacosira granulata* var. *angustissima*	19.4 *Closterium acutum* var. *variabile*
Highest mean biomass of one taxon (g m^3) and taxon responsible	*Botryococcus braunii*	*Aulacosira distans*	*Staurodesmus* spp.[1]	*Trachelomonas* spp.[2]	*Trachelomonas armata* var. *inevoluta*	*Peridinium cinctum*	*Peridinium* spp.[3]	*Microcystis aeruginosa*	*Microcystis aeruginosa*
Mean 'edible'** proportion (%) of the mean total phytoplankton biomass	0.3	56.5	1.8	34.9	15.4	3.5	9.1	1.9	1.3
Compound Quotient	3.56	5.47	3.59	4.31	2.67	4.74	4.11	6.47	4.19

Total phosphorus (mg m^3) (mean spring and early summer)	27.0	40.5	41.0	61.5	13.0	16.5	15.5	86.5	91.0***
Total nitrogen (mg m^3) mean spring and early summer)	1382.5	1815	1027.5	1105	437.5	645	950	1530	3180***

Key:

KA = Kainui
MA = Maratoto
MH = Mangahia
MK = Mangakaware
NG = Ngaroto
RK = Rotokauri
RMN = Rotomanuka North
RMS = Rotomanuka South
RR = Rotoroa

[1] Includes *S. cuspidatus*
S. dejectus
S. mammillatus

[2] Includes *T. planctonica*
T. playfairi
T. volvocina

[3] Includes *P. cinctum*
P. sp. A

* RMS October 1983 to July 1984; ** GALD ≤ 20 μm fraction; *** Early summer only.

7.1.2 Compound Quotients

The Compound Quotient (CQ) (Nygaard, 1949) where

$$CQ = M + Cl + Ce + E / D$$

and

M	=	number of species of Myxophyceae
Cl	=	number of species of Chlorococcales
Ce	=	number of species of Centrales
E	=	number of species of Euglenieae
D	=	number of species of Desmidiaceae

was calculated for each study lake (Table 7/1).

The criteria used for interpreting CQs are:-

< 1	=	oligotrophic
1 to 2.5	=	mesotrophic or slightly eutrophic
3 to 5	=	moderately eutrophic
> 5	=	highly eutrophic

The CQs suggest that Lakes Ngaroto (Group IV) and Mangahia (Group I) were hyper-eutrophic, and the remaining seven were eutrophic.

Of the above taxonomic groups, the greens showed marked correlations with standing crop. For example, chlorophyte generic and specific richness were negatively correlated with both maximum total biomass ($r = -0.736$; $p \leq 0.05$; $n = 9$ and $r = -0.761$; $p \leq 0.05$; $n = 9$, respectively) and mean total biomass ($r = 0.798$; $p = \leq 0.05$; $n = 9$ and $r = -0.769$; $p \leq 0.05$; $n = 9$, respectively), as was desmid species richness ($r = -0.629$; $p = \leq 0.01$; $n = 9$ and $r = -0.617$; $p = \leq 0.01$; $n = 9$, respectively).

7.1.3 Size Fractions

The nine study lakes had remarkably similar numbers of taxa within the various size fractions, larger species being the most common (Fig. 7/0). For example, the proportion of phytoplankters in each study lake with GALDs $\geq$ 21 μm ranged from 83 (Lake Kainui) to 89% (Lake Mangakaware) (mean 85.9 $\pm$ 1.9% [n = 9]).

Inter-group differences were apparent, however, when the ten most important (ISI) phytoplankters per lake (Table 5/15) were categorised according to their GALDs (Fig. 7/1). First, only Group I lakes had

Fig. 7/0 Relative proportions (percentages) of phytoplankton species in each of six size fractions in the nine* study lakes, July 1983 to July 1984. (* Lake Rotomanuka South October 1983 to July 1984).

Key to Lakes:

Group I - 1. Maratoto
- 2. Mangahia

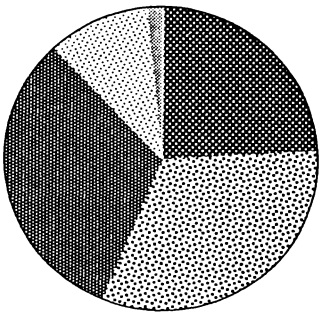
Group II - 3. Kainui
- 4. Mangakaware

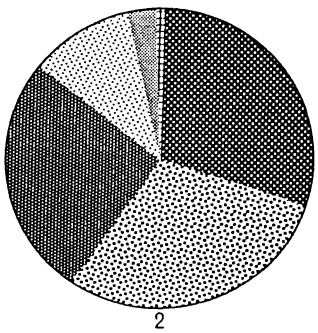
Group III - 5. Rotokauri
- 6. Rotomanuka North
- 7. Rotoroa

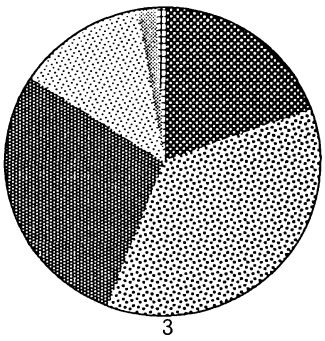
Group IV - 8. Ngaroto
- 9. Rotomanuka South

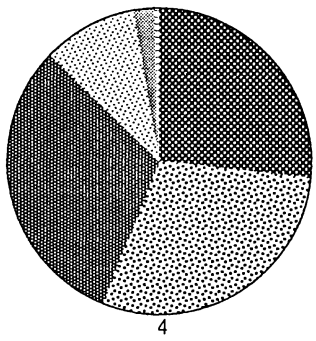
Key to Symbols: (um)

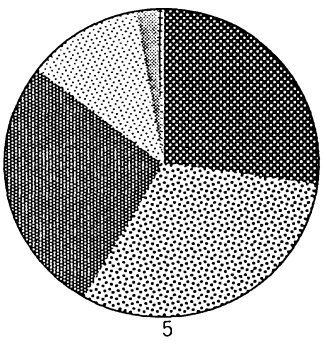
Fig. 7/0

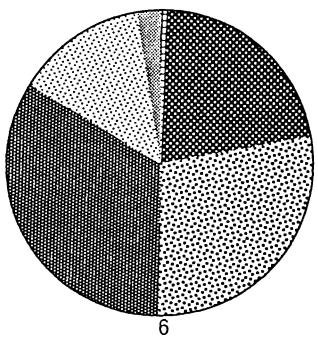


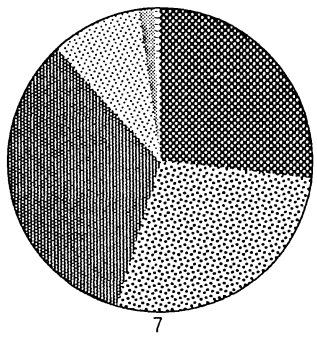


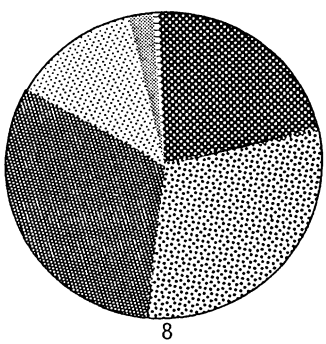












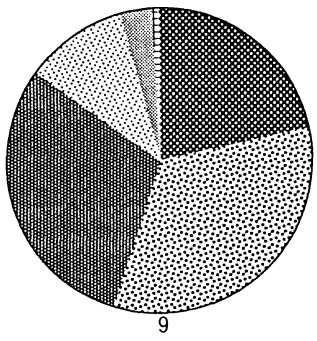


Fig. 7/1 Relative proportions (percentages) of the phytoplankton species with the highest ISIs in each of six size fractions in the nine* study lakes, July 1983 to July 1984. (* Lake Rotomanuka South October 1983 to July 1984).

Key to Lakes:

Group I - 1. = Maratoto
- 2. = Mangahia

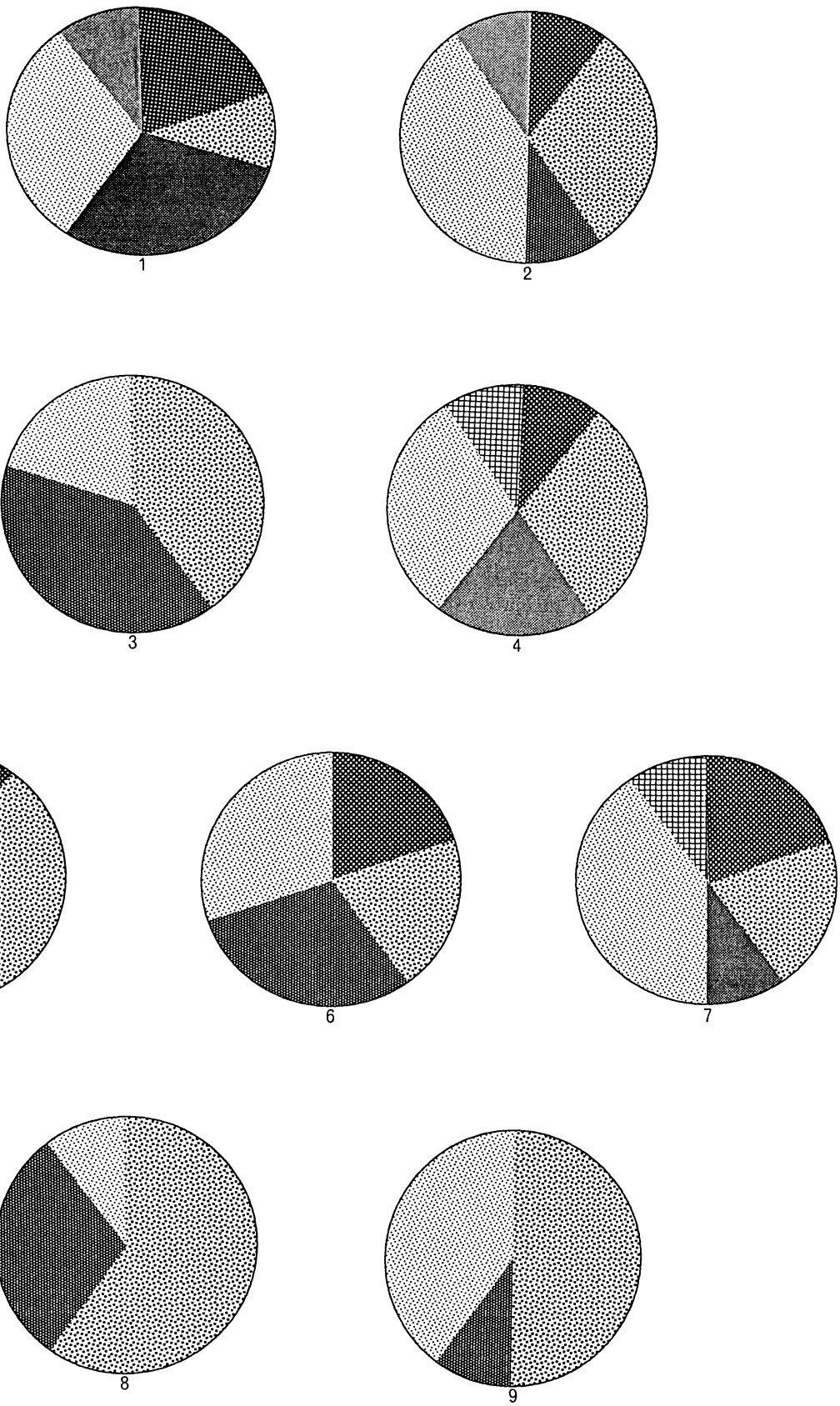
Group II - 3. = Kainui
- 4. = Mangakaware

Group III - 5. = Rotokauri
- 6. = Rotomanuka North
- 7. = Rotoroa

Group IV - 8. = Ngaroto
- 9. = Rotomanuka South

Key to Symbols: (um)

Fig. 7/1



important species within the 6 to 10 μm fraction; and secondly, only Group IV lakes had ≥ 50% of their important species in the 41 to 63 μm fraction, but none had GALDs ≥ 64 μm. In terms of numbers of important species with GALDs > 21 μm (and generally considered unavailable to zooplankton grazers because of size [Chapter 8]), the Group I lakes were very similar (Maratoto 60%; Mangahia 50%), but other intra-group differences were marked; for example, in Group IV, 90% (Lake Ngaroto) and 60% (Lake Rotomanuka South) of important species were inedible.

Group I lakes had more major biomass species with GALDs ≥ 64 μm than any other group (Maratoto 25%; Mangahia 30%) (Fig. 7/2), although the proportions in the Group III lakes were also broadly similar and relatively high (Rotokauri 21%; Rotomanuka North 20%; Rotoroa 25%). In contrast, low numbers were recorded in the Group IV lakes (Ngaroto 11%; Rotomanuka South 0%). Numbers of major biomass species within the smaller fractions also varied considerably. For example, major phytoplankters belonging to the 6 to 10 μm fraction were recorded only in Group I lakes (Maratoto [0.2%] and Mangahia [17%]) and one of the Group III lakes (Rotoroa [21%]). The only major species belonging to the ultraplankton was recorded in Lake Mangakaware (Group II; 2.5%). However, numbers of major biomass species with GALDs ≥ 21 μm were very high in all nine lakes (mean 81.8 ± 7.1%).

There were considerable intra-group differences in the relative proportions of various size fractions expressed in terms of mean total biomass of major species, except in Group IV (Fig. 7/3). The 21 to 40 μm size range was the most important in Lake Maratoto (Group I [99.5%]) and Mangakaware (Group II [81.4%]), and of about equal importance as the 41 to 63 μm size fraction in Lake Kainui (30.6 and 30.8%, respectively), the other Group II lake. However, in the Group III and IV lakes, the major species belonging to the 41 to 63 μm size fraction accounted for the majority of the biomass (range 50% [Lake Rotokauri] to 98.7% [Lake Rotomanuka South]; mean 77.9 ± 20.1% [n = 5]). Interestingly, Lake Mangahia (Group I) had the highest proportions of the ≥ 64 μm (18%), 11 to 20 μm (57%) and 6 to 10 μm size fractions (1.2%). The < 5 μm size fraction was recorded in Lake Rotoroa only.

Fig. 7/2 Relative proportions (percentages) of six size fractions, expressed in terms of numbers of major* biomass species in the nine** study lakes, July 1983 to July 1984. (* A major species is defined as one with a mean contribution of ⩾ 0.1% of the mean total biomass [Chapter 4]; ** Lake Rotomanuka South October 1983 to July 1984).

Key to Lakes:

Group I - 1. = Maratoto
- 2. = Mangahia

Group II - 3. = Kainui
- 4. = Mangakaware

Group III - 5. = Rotokauri
- 6. = Rotomanuka North
- 7. = Rotoroa

Group IV - 8. = Ngaroto
- 9. = Rotomanuka South

Key to Symbols: (um)

Fig. 7/2

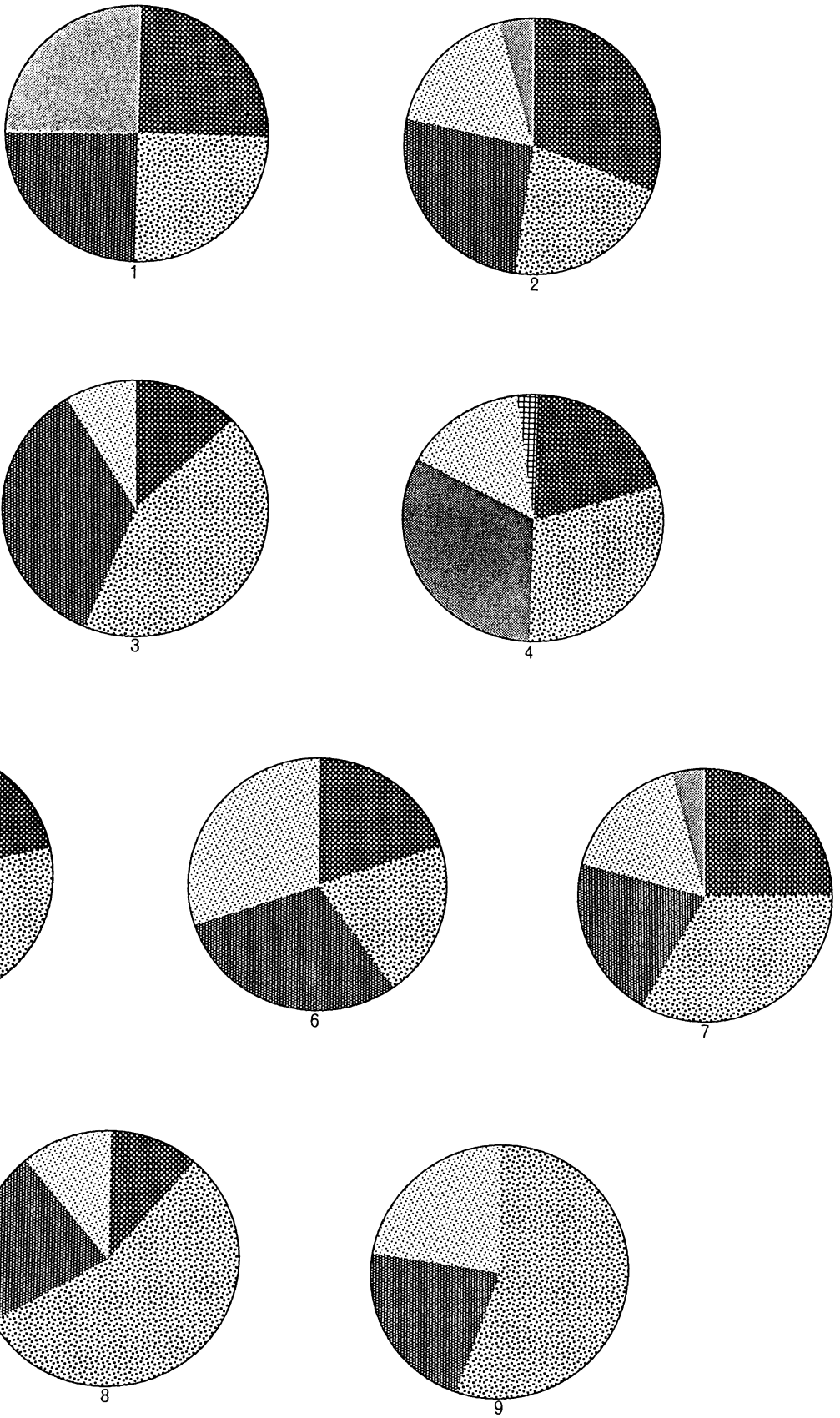


Fig. 7/3 Relative proportions (percentages) of six size fractions expressed in terms of mean total biomass of major* biomass species in the nine** study lakes, July 1983 to July 1984. (* A major species is defined as one with a mean contribution ≥ 0.1% of the mean total biomass [Chapter 4]; ** Lake Rotomanuka South October 1983 to July 1984).

Key to Lakes:

Group I - 1. = Maratoto
- 2. = Mangahia

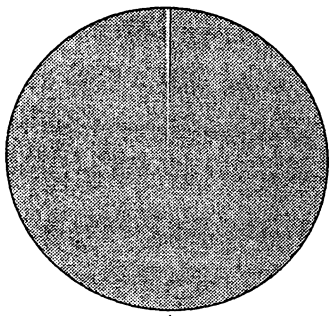
Group II - 3. = Kainui
- 4. = Mangakaware

Group III - 5. = Rotokauri
- 6. = Rotomanuka North
- 7. = Rotoroa

Group IV - 8. = Ngaroto
- 9. = Rotomanuka South

Key to Symbols: (um)

Fig. 7/3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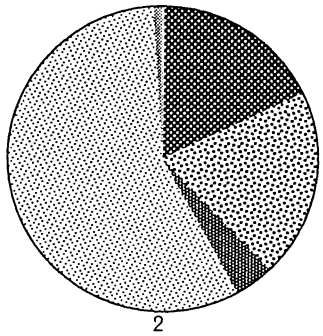
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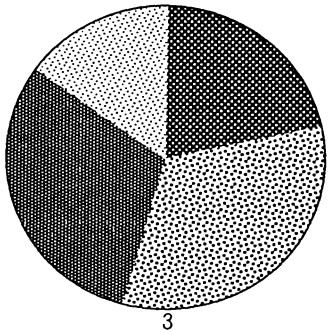
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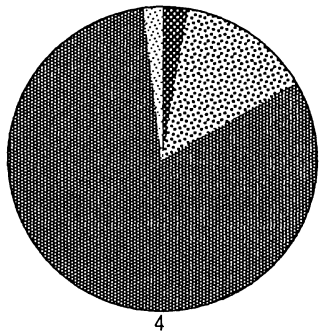
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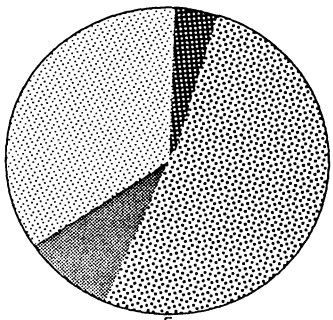
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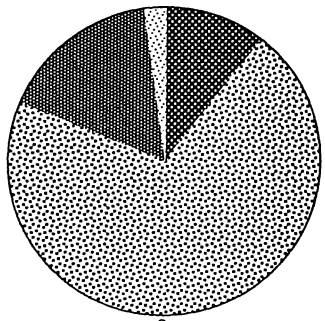
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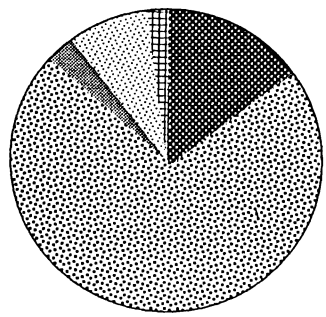
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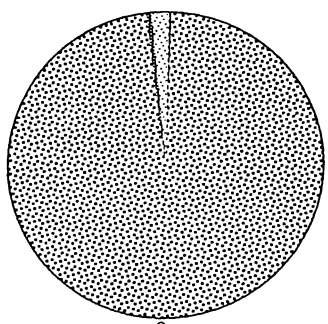
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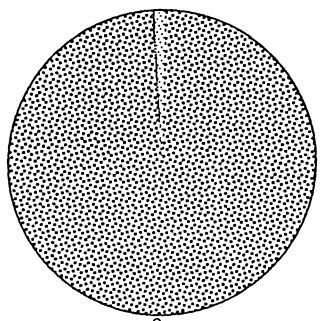
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7.1.4 Trophic Indicator Species

Of those species which had one of the ten highest ISIs per study lake (Table 5/15), 75% have either been recorded as 'dominant' in one or more eutrophic/meso-eutrophic New Zealand lakes, or are regarded as key indicators of such waters elsewhere (Table 7/2). The remainder are less common in New Zealand (e.g., *Monoraphidium tortile* is a new New Zealand record [Appendix VIII]), and their ecological preferences are generally poorly documented. However, *Monoraphidium contortum* and *M. tortile* are usually found in eutrophic and meso-eutrophic waters, respectively (Huber-Pestalozzi *et al.*, 1983). The desmid species are problematical because although initially *Staurastrum* spp. were regarded as clearly indicative of oligotrophy (e.g., Rawson, 1956), other studies have shown that their ecological requirements are very heterogeneous (Teiling, 1955; Brook 1959, 1965).

Four genera containing important species (*Asterionella*, *Dinobryon*, *Cyclotella* and *Tabellaria*) have been listed by some authors as oligotrophic indicators (Table 7/2).

7.2 PHYTOPLANKTON TYPES AND SPECIES ASSOCIATIONS

Although the provisional classification of twelve phytoplankton types by Hutchinson (1967) was derived mainly from typically dimictic, temperate Northern Hemisphere lakes, several categories are appropriate for some of the study lakes (Table 7/3).

The Lake Maratoto community differed from others within the series, and can be categorised as a *Botryococcus braunii* plankton. The ecology of this plankton, however, is probably the least well understood of any type. Although *B. braunii* has been noted in dystrophic lakes elsewhere (e.g., Denmark [Nygaard, 1949], and in Lake Hakojärvi, an oligotrophic darkly-stained Finnish lake where it comprised as much as 80% of the total biomass [Ilmavirta, 1982]), it is by no means restricted to them. Belcher (1968), for example, considered it grew successfully in natural waters ranging from pH 4.5 to 8. In addition, a summary of its distribution worldwide (living and fossil) (Aaronson *et al.*, 1983) indicates that it is possibly one of the most cosmopolitan phytoplankters known, inhabiting not only temperate lakes and reservoirs of varying trophic status, but also both tropical and alpine lakes, and brackish and saline waters.

TABLE 7/2 A list of phytoplankton taxa with the highest Important Species Indices (ISIs) (ten per study lake) and other New Zealand lakes in which they have been recorded as dominant algae, together with the trophic status of the lake at the time of the study.
Key: E = eutrophic; DE = dystrophic-eutrophic; HE = highly eutrophic; M = mesotrophic; ME = meso-eutrophic; O = oligotrophic; OM = oligo-mesotrophic; DO = dystrophic-oligotrophic.

Taxon	Study Lake/s*	ISI Rank	Other N.Z. lakes in which Taxon has been recorded as a Dominant	Trophic Status at time of study	Reference	Trophic Indicator	Reference
Euchlorophyceae							
Ankistrodesmus	KA	10	as *A.* spp			as *A.* spp.	
bibraianus	RK	1	Tomahawk Lagoon	E	Flint (1975)	E	Palmer (1969)
			Horseshoe	M	"		Hörnström (1981)
			Selfe	"	"		
			Small Spectacles	"	"		
A. falcatus	RK	5	as above	as above	as above	as above	as above
						as *A. falcatus*	
						E	Palmer (1969)
Botryococcus	MA	1	Tomahawk Lagoon	E	Flint (1975)		
braunii	RMN	4	Ida	M	"		
			Large Spectacles	M	"		
			Tripp	M	"		
			Waikaremoana	O	Cassie (1978)		
Chlamydomonas	MA	3				as *C.* spp.	
sp. C						E	Palmer (1969)
Chlorella sp.	MH	5	as *Ch.* spp.			as *Ch.* spp.	
			Rotowhero	E	Flint (1975)	E	Palmer (1969)
			as *Ch.* sp.				

			Ida	M	Flint (1975)		
			Rotokakahi	M	Flint (1975,1977)		
			Small Spectacles	M	Flint (1975)		
Monoraphidium contortum	MK	1					
	NG	5					
	RK	4					
	RMN	9					
M. tortile	MA	6					
	MH	9					
	MK	7					
Oocystis lacustris	RR	8	Okaro	E	Flint (1975,1977)		
Raphidocelis contorta	MH	10					
	NG	7=					
Scenedesmus acutiformis	RK	6	as *S.* spp.			as *S.* spp.	
			Tomahawk Lagoon	E	Flint (1975)	E	Palmer (1969)
S. quadricauda	KA	4				E	Palmer (1969)
	MH	7				ME	Rosén (1981)
	NG	2					
Tetrastrum triangulare	MK	9					
	RR	1					
Zygophyceae							
Closterium acutum var. *variabile*	KA	3	Johnson	HE	Burns & Mitchell (1974)	E	Teiling (1955)
	MA	2				E	Coesel (1975, 1983)
	MH	2					Rosén (1981)
	MK	3					
	RMN	7					
	RMS	1					
C. gracile	MA	9				M	Coesel (1975)
	MH	5					
Staurastrum arcuatum	KA	7					
St. brachiatum	KA	6					
St. chaetopus?	KA	5					

St. inflexum	MA	10						
St. sp. A	RMS	7						
	RR	9						
St. sp. B	MA	8						
St. sp. C	KA	2						
Staurodesmus spp.[1]	KA	1					*St. cuspidatus*	
							E	Coesel (1975)
							M	Rosén (1981)
Chrysophyceae								
Chrysococcus rufescens	RMS	10						
Dinobryon bavaricum	RR	7	Rotoehu	E	Cassie (1978)		O	Hutchinson (1967)
D. cylindricum	MK	6	Ngapouri	E	Flint (1977)		OM	Rosén (1981)
	RMN	1	Rotokakahi	ME	"		OM	Rosén (1981)
			as *D.c.* var. *alpinum* (Imhof) Bachm.				O	Hutchinson (1967)
			Rotoiti	E	Cassie (1978)			
			Rotoma	OM	"			
Mallomonas akrokomos	RK	7	as *M.* sp.					
			Sarah	M	Flint (1975)			
Synura uvella	MK	10	as *S.* sp.					
	RK	9	Rotorua (near Kaikoura)	E	Flint (1975)			
	RMS	8						
Diatomophyceae								
Acanthoceras zachariasi	MK	4						
	RMS	9					DE	Järnefelt (1952)
							E	Teiling (1955)

Asterionella formosa	MK NG	5 7=	Ngapouri	E	Flint (1975,1977)	O	Lawson (1956)
			Rotoiti	E	Cassie (1974,1978)	OM E	Rosén (1981) Hutchinson (1967)
			Rotorua	E	"		
			Grasmere	M	Flint (1975)		
			Howard	M	"		
			Rotorua (Nelson)	M	"		
			Selfe	M	"		
			Taylor	M	"		
			Tripp	M	"		
			Aviemore	O	"		
			Benmore	O	"		
			Benmore	See ref.	Duthie & Stout (1986)		
			Pukaki	"			
			Tekapo	"	"		
Aulacosira distans (= *Melosira distans* (Ehrenberg) Kützing)	MH	1	Ngapouri	E	Flint (1975)		
			Rotoiti	E	Cassie (1974,1978) Vincent *et al.*, (1984)		
			Rotorua	E	"		
			Okataina	M	Flint (1975)		
			Aviemore	O	"		
			Benmore	O	"		
			Waitaki	O	"		
			Benmore (Ahuriri arm only)	See ref.	Duthie & Stout (1986)		
A. granulata var. *angustissima* (= *Melosira granulata* var. *angustissima* (Müller)	MH NG	4 1	Hakanoa	E	Flint (1975)	E	Hörnström (1981)
			Ngahewa	E	Forsyth & McColl (1977)	E	Rosén (1981)
			Okaro	E	Flint (1977)	E	Brook (1982)
					Dryden & Vincent (1986)	E	Kilham & Kilham (1975)

			Ohakuri	E	Cassie (1969)		
			Rotoehu	E	Cassie (1978)		
			Rotoiti	E	Cassie (1974,1978)		
			Rotoiti (near Kaikoura)	E	Flint (1975)		
			Rotorua (near Kaikoura)	E	"		
			Tutira	E	"		
			Waitawa	E	"		
Cyclotella	MK	8	Rotoiti	E	Cassie (1978)	as *C.* spp	
stelligera	RMN	6	Rotorua	E	Cassie (1974)	O	Hutchinson (1967)
	RMS	6	Horseshoe	M	Flint (1975)		
	RR	3	Ida	M	"	O	Stockner (1971)
			Parson	M	"	O	Shero *et al.*, (1978)
			Rotokakahi	M	Flint (1977)	O	Rosén (1981)
			Haupiri	O	Paerl *et al.*, (1979)		
			Okareka	O	Flint (1977)		
			Ototoa	O	Flint (1975) Green (1976b)		
			Waikaremoana	O	Cassie (1978) Howard-Williams *et al.*, (1986)		
Fragilaria ulna	RK	10	as *Synedra ulna* (Nitzsch) Ehr.			as *Synedra ulna*	
			Rotorua	E	Cassie (1974)	E	Palmer (1969)
			Grasmere	M	Flint (1975)		
Gomphonema truncatum	RK	8				as *G.* spp. E	Palmer (1969)
Tabellaria flocculosa	MA	5				O	Lawson (1956)
						O	Hutchinson (1967)

Cyanophyceae							
Anabaena circinalis	NG	9	Rotorua	E	Cassie (1974)	as A. spp.	
						E	Lawson (1956)
						E	Hutchinson (1967)
						E	Wetzel (1975)
						as *A. circinalis*	
						E	Teiling (1955)
						E	Rosén (1981)
A. tenericaulis	NG	4	Koutu	E	Etheredge (unpubl. data)		
	RMS	3					
			Orakai	E	Flint (1975)		
Chroococcus limneticus	NG	10	Rotorua	E	Cassie (1974)	M	Rosén (1981)
	RR	10					
Microcystis aeruginosa	NG	3	Hakanoa	E	Flint (1975)	E	Teiling (1955)
	RMS	2	Horowhenua	E	"		
			Koutu	E	Etheredge (unpubl. data)		
			Okaro	E	Dryden & Vincent (1986)		
			Pupuke	E	Cassie (1979)		
			Rotoiti	E	Cassie (1974)		
			Rotoiti (near Kaikoura)	E	Flint (1975)		
			Tutira	E	McColl (1978)		
			Waiparera	E	Flint (1975)		
			Waitawa	E	"		
Euglenophyceae							
Trachelomonas spp.[2]	KA	9	as *T. volvocina*			as *T. volvocina*	
	MA	7	Ngahewa	E	Flint (1975)	E	Rosén (1981)
	MH	3	Rotoiti	E	Cassie (1974)		
	MK	2	Rotorua (near Kaikoura)				
	NG	6		E	Flint (1975)		
	RK	3					
	RMN	5					
	RMS	4					
	RR	6					

Cryptophyceae							
Cryptomonas spp.[3]	KA	8	as *C. ovata*				
	MA	4	Rotoehu	E	Cassie (1978)		
	MH	8	as *C.* sp.				
	RK	2	Rotorua (near Kaikoura)				
	RMN	2		E	Flint (1975)		
	RMS	4	Ida	M	"		
	RR	5	Large Spectacles	M	"		
			Small Spectacles	M	"		
			Matheson	DO	"		
Dinophyceae							
Ceratium hirundinella	RMN	9	Okaro	E	Flint (1975,1977)	E	Hutchinson (1967)
			as *C.h.f. furcoides* (Schrod.) Hub-Pest.			ME	Rosén (1981)
			Rotoma	O	Cassie (1978)		
			as *C.h.f. scotticum* Bachm.				
			Waikaremoana	O	Cassie (1978)		
Peridinium cinctum (includes *P.* sp. A in RR)	RMN	3				E	Hutchinson (1967)
	RR	5				ME	Rosén (1981)
Raphidophyceae							
Vacuolaria sp.	RMN	8					

Key To Study Lakes: KA = Kainui; MA = Maratoto; MH = Mangahia; MK = Mangakaware; NG = Ngaroto; RK = Rotokauri; RMN = Rotomanuka North; RMS = Rotomanuka South; RR = Rotoroa

[1] Includes *S. cuspidatus*, *S. dejectus*, *S. mammillatus*

[2] Includes *T. planctonica*, *T. playfairi*, *T. volvocina* in Lakes MA, MK, and RK; *T playfairi*, *T. volvocina* in Lake RR; and only *T. volvocina* in Lakes KA, MH, NG, RMN, and RMS.

[3] Includes *C. marssonii*, *C. ovata* in all lakes except RMS where ISI refers to *C. ovata* only.

TABLE 7/3 Phytoplankton types of eight of the nine study lakes according to the provisional classification of Hutchinson (1967).

Phytoplankton Type	Dominant Species	Trophic Status	Study Lake
Botryococcus braunii	*Botryococcus braunii*	Variable	Maratoto (Group I)
Dinoflagellate	*Peridinium* and sometimes *Ceratium* spp.	Meso- or eutrophic	Rotomanuka North (Group III) Rotoroa (Group III)
Diatom	*Asterionella* spp., *Fragilaria crotonensis*, *Synedra* spp., [1] *Stephanodiscus* spp., *Melosira* spp.[2]	Eutrophic	Mangahia (Group I) Mangakaware (Group II)
Desmid	*Staurastrum* spp.	Meso- or eutrophic	Kainui (Group (II)
Myxophycean	*Anacystis* spp.,[3] *Aphanizomenon* spp., *Anabaena* spp.	Eutrophic	Ngaroto (Group IV) Rotomanuka South (Group IV)

[1] = *Fragilaria* spp. in the present study
[2] = *Aulacosira* spp. in the present study except for *Melosira varians*
[3] = *Microcystis* spp. in the present study

It has been dominant in several New Zealand lakes, apart from Maratoto (Table 7/2), none of which was categorised as dystrophic at the time of the study. Consequently, the fact that it was of such importance in the Lake Maratoto (Group I) community, but not in the other study lakes, except for Rotomanuka North (Group III) (Table 5/15), is enigmatic. It was also a major species in both these lakes during 1979, being ranked first and fourth in terms of biomass, respectively (Etheredge, 1983). It has been shown experimentally that nitrogen deficiency favours lipid production in *B. braunii* (Belcher, 1968), and consequently nitrogen must play a key role in its autecology; however, more detailed chemical analyses than are available from the present study would be needed to decide whether a relationship exists between its distribution and abundance, and nitrogen concentrations in the study lakes.

The dinoflagellate type is appropriate for both Lakes Rotomanuka North and Rotoroa (mean proportions of mean total biomass 74 [Table 4/32] and 78% [Table 4/37], respectively), but not for Lake Rotokauri (mean proportion 10% [Table 4/27], the third Group III lake. The Dinophyceae was also the most important taxon in terms of both biomass and number, in Lake Rotomanuka North during 1979 (mean proportions 91 and 23%, respectively [Etheredge, 1983]). This plankton type is not common in New Zealand and, despite the eurytopic classification of *Peridinium cinctum* by Hutchinson (1967), it has been found in only four other lakes (Tomarata, Sarah, Johnson and Hayes [Cassie, 1984c]). However, it has been recorded as a major species in both Lakes Hayes and Johnson (Burns & Mitchell, 1974). *Ceratium hirundinella* is a common and widespread dinoflagellate (Dodge & Crawford, 1970; Bruno & McLaughlin, 1977; Harris *et al.*, 1979), particularly in eutrophic, temperate lakes (Moore, 1981a). Consequently, it is of special significance that it has been recorded only once in the South Island (Lake Ohau [Thomasson, 1980]) (as *C. h. f. carinthiacum* (Zederbauer) Bachmann). It occurs in several North Island lakes (see Cassie, 1984c), and has been dominant in three (see Table 7/2).

The communities of Lakes Mangahia (Group I) and Mangakaware (Group II) can be broadly categorised as diatom planktons. In Lake Mangahia, diatoms accounted for 42 and 50% of the mean total phytoplankton number and biomass, respectively (Table 4/7). However, there were some

marked differences from Hutchinson's definition. For example, although *Aulacosira* = *Melosira* spp. (*Aulacosira distans* and *A. granulata* var. *angustissima*) together comprised 41 and 47% of the mean total phytoplankton number and biomass, respectively (Table 4/8), neither *Fragilaria* nor *Stephanodiscus* was found, and *Asterionella formosa* was insignificant (Table 4/5). *Aulacosira distans* has been dominant in several eutrophic New Zealand lakes, and also the Waitaki lakes (Table 7/2), which have been categorised as oligotrophic (Flint, 1975), although this is questionable (see Duthie & Stout, 1986). Similarly, *A. granulata* var. *angustissima* has been dominant in numerous eutrophic lakes throughout both the North and South Island. As *Melosira granulata*, it has been described as perhaps the best indicator of eutrophy (Nygaard, 1956).

In Lake Mangakaware, diatoms, particularly *Asterionella formosa* and *Acanthoceras zachariasi*, were numerically important, but so also were *Monoraphidium contortum* and *Trachelomonas* spp. (Table 4/13). Consequently, the characterisation of its plankton as a diatom one is, as for Lake Mangahia (but for different reasons), only approximate. *Asterionella formosa*, unlike *Acanthoceras zachariasi*, has been frequently documented as an important species in many New Zealand lakes of varying trophic status (Table 7/2). The first record of *A. zachariasi* in New Zealand, however, was in Lake Rotomanuka North (Etheredge, 1983) and, during the present investigation, it was found in all study lakes, except for Kainui (Appendix VII). It was the dominant phytoplankter in Lake Mangakaware throughout 1985 (Greenwood, 1987). There are surprisingly few references to its ecological preferences in the literature, but it has been considered an indicator of dystrophic-eutrophic and eutrophic waters by Järnefelt (1952) and Teiling (1955), respectively.

As noted in Chapter 5, the Lake Kainui phytoplankton community was unlike that of any other study lake, but it is generally similar to Hutchinson's No. 9 plankton type i.e. meso- or eutrophic desmid plankton, although *Staurodesmus* spp. were about twice as abundant as *Staurastrum* spp. (Table 4/3). There have been no other reports of such extremely high densities of *Staurodesmus* spp. (maximum 18,040 pu ml^{-1} [Fig. 6/3]) in New Zealand, although densities of *Staurastrum* spp. (*S.*

bibrachiatum, *S. manfeldtii* and *S. paradoxum*) of 8400 cells ml^{-1} have been recorded in eutrophic Lake Johnson (Burns & Mitchell, 1974). However, such extraordinary concentrations are rare, desmids usually making only small contributions to total biomass in eutrophic lakes (Brook, 1981).

The Myxophycean plankton type is an apt description of the communities in the two Group IV lakes, Ngaroto and Rotomanuka South. Although *Microcystis* and *Anabaena* have been dominant in many other New Zealand lakes (Table 7/2), it is of special interest that *Aphanizomenon flos-aquae*, the third member of Hutchinson's type, has been reported as an important species only once (in Lake Rotoehu [Cassie, 1978]), despite its presence in many New Zealand lakes (Etheredge & Pridmore, in press) (Appendix I).

Such plankton types obviously include a variety of associations combined primarily on a taxonomic basis, but they are not necessarily equivalent to formations in a strict phytosociological sense. However, Reynolds (1980, 1982, 1984a, b), after thorough analyses (using methods similar to those employed by terrestrial plant ecologists [e.g., Braun-Blanquet, 1964]) of both natural and experimental systems (Lund Tubes), has provided a generalised seasonal sequence of species associations typical of temperate waters of varying trophic status.

The occurrence of several of these assemblages within the large communities of the study lakes gives support to Reynolds' (1980) prediction that, although his analyses were based on stratifying systems, they may apply equally well to shallow, mixed lakes. First, an association of *Monoraphidium*, *Scenedesmus* and *Tetrastrum*, a typical early summer grouping in hyper-eutrophic lakes, was present in both Lakes Mangahia (Fig. 6/6) and Ngaroto (Figs. 6/21 to 6/23). Both lakes also had a grouping comparable to Reynolds' No. 8 summer association in eutrophic lakes. In Lake Mangahia it was restricted to *Aulacosira* and *Closterium* (Fig. 6/7) but, in Lake Ngaroto, *Asterionella formosa* was also important (Fig. 6/23). A third association, consisting of *Microcystis*, *Closterium*, *Aulacosira* and *Cryptomonas*, also developed in Lake Ngaroto in late summer-autumn (Figs. 6/22 to 6/24), representing a mix of Reynolds' Nos. 8 and 9 groupings.

The more stable stratification present in Lake Rotomanuka North

resulted, not unexpectedly, in a series of species assemblages closely matching Reynolds' mesotrophic sequence; *Cyclotella* (No. 1) was replaced successively by *Dinobryon* (Nos. 4/5), and *Peridinium* and *Ceratium* (No. 10). Cryptomomads were also an important component of each association. There was little evidence of distinct seasonal assemblages in the remainder of the study lakes.

7.3 DISCUSSION

Assessment of a lake's trophic status is of practical and theoretical value to limnologists (Brook, 1965). Any one, or a combination of trophic indicators may be used, but classifications are to some degree arbitrary (Lewis *et al.*, 1984) because of marked fluctuations exhibited by many of the criteria, and satisfactory categorisation demands thorough, frequent investigations. The trophic status suggested for each study lake, together with classifications given by other authors, are listed in Table 7/4.

Group III lakes were the least productive, with Rotomanuka North and Rotoroa showing broadly similar values, particularly in terms of both maximum and mean total phytoplankton biomass, highest mean biomass of one taxon (and taxon responsible), compound quotients, and total phosphorus and nitrogen concentrations. Lake Rotokauri, however, was more difficult to categorise. Although it had mean total phosphorus concentrations similar to other Group III lakes, it differed from them in other respects. First, its maximum and mean biomasses, and mean total nitrogen concentrations, were distinctly lower (Table 7/1). Secondly, its most important phytoplankton species (ten highest ISIs [Table 5/15]) were markedly different from those of the other two lakes (and all other study lakes). This is enigmatic because of the presence of dense aquatic macrophyte beds in all Group III lakes (Chapter 1.4.2), their broadly similar morphometries, water clarities and pHs (Table 3/10). Thirdly, nine of its ten most important species (ISI) are either regarded as eutrophic indicators or commonly found in eutrophic waters (Table 7/2) but, despite this, its maximum ISI, and highest number and mean biomass of one taxon, were markedly lower than those of any other lake (Table 7/1). At present there is no satisfactory explanation for these differences.

Group I and II lakes were eutrophic or highly eutrophic, but not to the same degree as those of Group IV. The maximum and mean

TABLE 7/4 Suggested trophic status of the nine study lakes, July 1983* to July 1984, and comparisons with categorisations from other studies.

Study Lake**	Trophic Status			
	Present study	Other Studies	Major Criteria Used in Other Studies	Reference
Group I	Hyper-eutrophic	Slightly eutrophic	Maximum & mean phytoplankton biomass and numbers	Etheredge (1983)
MA		Eutrophic	Chlorophyll *a*, total phosphorus PO_4-P	Boswell *et al.*, (1985)
MH	Eutrophic	Eutrophic	Chlorophyll *a*, total phosphorus PO_4-P	Boswell *et al.*, (1985)
Group II				
KA	Hyper-eutrophic			
MK	Hyper-eutrophic	Eutrophic	Chlorophyll *a*, total phosphorus PO_4-P	Boswell *et al.*, (1985)
		Eutrophic or hyper-eutrophic	Maximum & mean numbers of dominant phytoplankton, chlorophyll *a*	Greenwood (1987)
Group III				
RK	Mesotrophic			
RMN	Meso-eutrophic	Slightly eutrophic	Maximum & mean phytoplankton biomass	Etheredge (1983)
		Mesotrophic	Chorophyll *a*, total phosphorus PO_4-P	Boswell *et al.*, (1985)

RR	Meso-eutrophic	Mesotrophic	Chlorophyll *a*, total phosphorus PO_4-P	Boswell *et al.*, (1985)
Group IV				
NG	Hyper-eutrophic	Eutrophic	Chlorophyll *a*	Howard-Williams & Vincent (1984)
		Hyper-eutrophic	Chlorophyll *a*, total phosphorus PO^4-P	Boswell *et al.*, (1985)
RMS	Hyper-eutrophic			

* Rotomanuka South October 1983 to July 1984.

** Key to Study Lakes: KA = Kainui; MA = Maratoto; MH = Mangahia; MK = Mangakaware; NG = Ngaroto; RK = Rotokauri; RMN = Rotomanuka North; RMS = Rotomanuka South; RR = Rotoroa

biomasses of Lake Mangahia were lower than others in these two groups, due to the smaller biovolumes of its major biomass species. For example, *Aulacosira distans* and *Trachelomonas volvocina*, which together accounted for 53% of its mean total biomass, had mean biovolumes of 350 and 1767 μm^3, respectively, which contrast markedly with those of the larger, dominant biomass species in the other Group I and II lakes (*Botryococcus braunii* 23,425 μm^3 [Maratoto]; *Peridinium* spp. 39,269 μm^3 [Mangakaware]; *Staurodesmus* spp. 5192 μm^3 [Kainui]). It should be noted that both total phosphorus and nitrogen concentrations in Lake Mangahia were higher than those in Lake Maratoto. Despite the highly productive nature of the Group I and II lakes, none of the species with the ten highest ISIs from these lakes (Table 7/1) is considered a key eutrophic indicator, suggesting that other factors such as humic content, morphometry and biological influences may have been equally, if not more important, than nutrient levels in determining dominance.

It is of interest, however, that *Anabaena circinalis* and *Microcystis aeruginosa*, which are very characteristic of highly eutrophic waters (Teiling, 1955), have been abundant in the Group II lakes since 1984. In the present study, *Microcystis aeruginosa* was rarely found in Lake Kainui (mean proportion of total biomass 0.5%) [Table 4/3]), but in January 1985 it formed a mixed bloom with *Anabaena spiroides* var. *tumida* (maximum biomasses 2017 and 143 mg m^3, respectively; unpublished data). *Anabaena circinalis* was similarly important, although not dominant, in Lake Mangakaware during late summer 1986 (Greenwood, 1987), with a maximum biomass of 563 mg m^3 (unpublished data). These two examples give further support to the hyper-eutrophic classification given to these lakes (despite the lack of eutrophic species indicators in the present study), and also serve to illustrate the pitfalls associated with assigning trophic classifications to New Zealand lakes on the basis of short-term sampling programmes and/or indicator species only. Inter-annual variation of this nature has also been noted in Lake Johnson, where *Anabaena flos-aquae* bloomed in two successive summers (January 1970 [approximately 26,000 cells ml^{-1}] and December 1970 [96,000 cells ml^{-1}], but was either very rare or absent during the following summer (Burns & Mitchell, 1974).

Group IV lakes were hyper-eutrophic, with very similar highest ISIs, mean total biomasses, and mean numbers of pu l^{-1}. In addition, their highest mean biomasses recorded for one species were almost identical (26.3 g m^3 [Lake Ngaroto] and 26.4 g m^3 [Lake Rotomanuka South]; *Microcystis aeruginosa*) (Table 7/1). This classification is supported by their mean total phosphorus and nitrogen concentrations (Table 7/1). The high mean phosphorus concentration in Lake Ngaroto was remarkably similar to that obtained during summer 1981 (86 mg m^3 [n = 10])(Boswell *et al.*, 1985).

Comparisons with other quantitative phytoplankton studies (Table 7/5) indicate that, in terms of both maximum and mean biomass, and density, Lakes Maratoto, Ngaroto and Rotomanuka South are the most productive recorded in New Zealand to date. In addition, the maximum total biomass of Lake Maratoto was very much higher than values reported from other eutrophic, humic lakes elsewhere; for example, in two series of highly productive, darkly-stained Finnish lakes, maximum total biomass has been reported to range from 1.2 to 2 (Järnefelt, 1956) and 0.05 to 26.9 g m^3 (Heinoen, 1982). However, it is important to note that biovolumes calculated for *Botryococcus braunii*, were based on measurements of colonies, and thus included the oily matrix, whereas those of all other species excluded mucilaginous sheaths (and spines) (Chapter 2.4.1).

In the study lakes, nutrients generally considered responsible for high levels of productivity probably come mainly from agricultural activities, as is generally the case elsewhere in New Zealand (White, 1977). In many New Zealand lakes the limiting nutrient is nitrogen (Vincent, 1982; White, 1983; White *et al.*, 1986), unlike many lakes in North America and northern Europe, where phosphorus controls algal production (Vollenweider, 1968; Schindler, 1977; Taub, 1984). Mean spring and early summer nitrogen concentrations in both the eutrophic and hyper-eutrophic study lakes were higher (except in Lake Mangakaware) (Table 7/1) than those listed by White (1983) for a number of other eutrophic New Zealand lakes, and this may partially explain their high productivity. It is of interest, however, that the mean nitrogen concentration for these lakes (1673 mg m^3) was still distinctly lower than that reported for eutrophic lakes in the OECD (1982) study (2367 mg m^3).

The influence of DHM on phytoplankton growth has been the focus of

TABLE 7/5 A comparison of maximum and mean phytoplankton biomass (g m^3) and density (pu l^{-1}) in some New Zealand lakes of varying trophic status.

Lake	Trophic Status	Biomass (g m^3)		Density (pu l^{-1})		Reference
		Maximum	Mean	Maximum	Mean	
Ototoa	Oligotrophic	0.4	0.18	0.8	nd	Green (1976a)
Rerewhakaaitu						
Main lake	Mesotrophic	nd	nd	4.67	nd	Chapman *et al.*, (1981)
Crater	Mesotrophic	nd	nd	2.35	nd	" " "
Rotorua	Eutrophic	nd	nd	>5.0	nd	Cassie (1969)
Hayes*	Eutrophic	7.49	1.93	65.0**	6.0**	Burns & Mitchell (1974)
Johnson*	Eutrophic	58.19	9.37	117.6*	11.0**	Burns & Mitchell (1974)
Maratoto	Eutrophic	17.4	2.8	9.47	0.99	Etheredge (1983)
Rotomanuka North	Eutrophic	29.5	2.7	1.39	0.4	Etheredge (1983)
Mangakaware***	Eutrophic to Hyper-eutrophic	nd	nd	6.69	1.28	Greenwood (1987)

Key:

* Trophogenic zone only
** Cells l^{-1}
*** Dominant species only
nd No data

numerous studies. Low concentrations are considered to have stimulatory effects (Nechutova & Tichy, 1970; Hoeffner & Manahan, 1980; Toledo *et al.*, 1980). The results of the present study, however, do not support this view, because the most darkly-stained and acidic of the nine lakes (Maratoto [Table 3/10]) and the almost clear-water lakes (Group III) were the most and least productive lakes, respectively (Table 7/1). However, the negative effects of high concentrations of DHM on productivity are not well understood (Prakash & MacGregor, 1983), although there is evidence that in some instances they can depress primary productivity (Jackson & Hecky, 1980). The chelating ability of DHM is usually considered responsible for both stimulated growth rates (Lange, 1970; Huntsman & Sunda, 1980), and enhanced total yields (Prakash *et al.*, 1973) at low concentrations, but clearly more information is required. The direct effects of DHM on both permeability and biochemistry of algal cells should not be discounted (Hunstman & Sunda, 1980).

With one exception (*Staurodesmus* spp. [Lake Kainui]), each species responsible for the highest mean biomass recorded in one of the eutrophic or hyper-eutrophic lakes (Table 7/1), has one or more particular features enabling it to remain in the euphotic zone for considerable periods of time: for example, *Microcystis aeruginosa* (gas vacuole regulation); *Botryococcus braunii* (aberrant fat metabolism [lipids constitute between 30 and 40% of dry weight (Belcher, 1968; Fogg, 1975; Wake & Hillen, 1981]); *Trachelomonas* spp. (flagella); *M. aeruginosa* and *B. braunii* (copious quantities of mucilage); *Aulacosira distans* (small size which, in a shallow and extensively mixed lake, such as Mangahia, would allow rapid resuspension of such a diatom from the sediments).

Generally, there was little agreement between classifications suggested by CQs and those of other trophic indices. The Lake Rotokauri CQ (2.67) was the lowest of the series (as were other indices for this lake), but those of the other Group III lakes were high, particularly that of Lake Rotomanuka North (4.74), which was marginally higher than that of hyper-eutrophic Rotomanuka South (4.19). Despite assertions that CQs can allow successful assessments of trophic status to be made from single samples (Round, 1981), these results are not unexpected, because of the obvious limitations in the use of such quotients. Precise discrimination between euplanktonic and

pseudo- or tychoplanktonic forms is essential for the success of CQs and furthermore, the possibility of pelagic adulteration must be extremely high in the study lakes, because of their shallowness (Table 1/0) and susceptibility to frequent mixing (Chapter 3). Other problems associated with such phytoplankton quotients are discussed by Kalff & Knoechel (1973).

It has been shown, using published data sets from a number of lakes of varying trophic status, that if total phytoplankton biomass is used as a criterion for trophic status, then increasing trophy is accompanied by increasing nannoplankton biomass, but a decrease in its relative proportion (Watson & Kalff, 1981; results based on data sets employing definitions of nannoplankton ranging from $\leqslant$ 20 to < 64 μm). (Initially, 'nannoplankton' referred to all phytoplankters not retained by a tow net [Hutchinson, 1967], but the use of plankton nets with widely differing mesh openings, or other criteria [e.g., specified GALDs or ingestibility], has resulted in a bewildering range of size delimitations for this group [Table 7/6]). In terms of plankton size and energy flow, lakes have been classified into two basic groups: first, eutrophic lakes in which energy flows from large inedible algae (> 30 μm), to detritus, and on to small zooplankton; and secondly, oligotrophic lakes, characterised by a direct flow of energy from small algae (< 30 μm) to larger, herbivorous zooplankton (Hillbricht-Ilkowska, 1977). This classification is supported by other investigations; for example, a negative correlation was found between the nannoplankton biomass (< 30 μm size fraction) and total phosphorus concentration (taken as the most appropriate measure of lake productivity) in 37 lakes in Ontario (Sprules & Knoechel, 1984). Such results are extensions of work by Pavoni (1963) and Findenegg (1965), who examined the role of nannoplankton in total biomass and primary productivity, respectively, and also Nauwerck's (1963) investigations into the regulation of nanno- and net plankton populations.

Although none of the study lakes was categorised as oligotrophic, it is still reasonable to expect that the importance of the nannoplankton would decrease within the series as trophy increased, because of the marked variation which was recorded in terms of mean total biomass (two orders of magnitude [Table 7/1]). However, although the four most highly eutrophic lakes, in terms of biomass (Maratoto, Rotomanuka South, Ngaroto and Kainui), had the lowest mean proportions of small edible phytoplankton (<20 μm; see Chapter 8), the reverse

TABLE 7/6 Size (μm) of mesh opening of plankton nets or GALD of phytoplankton used by various authors to define nannoplankton in freshwaters.

Size of Mesh Opening of Plankton Net or GALD of Phytoplankton (μm)	Reference
10	Gelin (1971,, 1975)
	Manny (1972)
20	Rosemarin (1975)
	Paerl & McKenzie (1977)
	Gelin & Ripl (1978)
25	Lohmann (1911)
30	Pavoni (1963)
	Spodniewska (1978, 1979)
50	Gliwicz (1967)
	Kristiansen (1971)
	Gliwicz & Hillbricht-Ilkowska (1972)
	Welch *et al.*, (1975)
60	Granberg (1970)
64	Kalff (1972)
	Sheath & Munawar (1974)
80	Nauwerck (1963)
100	Rodhe (1958)

trend was not apparent in the least productive lakes (Group III) (Table 7/1); for example, the mean proportions recorded in both Lakes Mangahia and Mangakaware were considerably higher than those of the Group III lakes. However, this is may be explainable in terms of the differing physico-chemical regimes; for example, Lakes Rotomanuka North and Rotokauri, in particular, stratified for longer than either of the other two lakes, which in turn appeared to permit higher numbers of large species, such as *Peridinium* spp., *Ceratium*, and *Trachelomonas armata* var.*inevoluta*. On the other hand, Lakes Mangahia and Mangakaware, had unstable thermal regimes with only transient stratification, which favoured small r- selected species (see Chapter 6.4).

CHAPTER EIGHT

EXPERIMENTAL INVESTIGATION: THE INFLUENCE OF ZOOPLANKTON GRAZING ON PHYTOPLANKTON COMMUNITY STRUCTURE IN LAKES ROTOMANUKA NORTH AND MARATOTO

8.1 INTRODUCTION

Herbivorous zooplankton exert a selective mortality on some phytoplankton species and simultaneously regenerate vital inorganic nutrients (Lehman, 1984). Consequently, interactions between algae and herbivorous zooplankton are central to an understanding of phytoplankton community structure and dynamics.

Phytoplankton-zooplankton interactions in the marine environment have been of interest for a considerable time (e.g., Harvey *et al.*, 1935; Riley, 1946), but a detailed understanding of these relationships in freshwater has been slow to develop, despite an appreciation of their importance (Reynolds, 1984b). Reasons for this are: first, early methods of collection, preservation and examination were inadequate and resulted in easily identifiable (but less edible) net plankton becoming the focus of community studies; secondly, despite a late recognition of the importance of nannoplankton as producers (e.g., Lund, 1961; Pavoni, 1963; Kristiansen, 1971; Happey-Wood, 1976) and a food source for herbivorous zooplankton (e.g., Gliwicz, 1967; Burns, 1968), only nutritional adequacy received attention during initial investigations of algal food quality (e.g., Richman, 1958; Schindler, 1968), and the importance of factors such as manageability and toxicity has only recently been recognised (e.g., Porter 1973, 1975, 1976, 1977; Porter & Orcutt, 1980); thirdly, phytoplankton seasonal periodicity was initially explained largely in terms of changes in physico-chemical regimes and although recently there has been an increased awareness of biological factors, there has been an imbalance between the emphasis given to algal growth compared to loss processes such as grazing (Kalff & Knoechel, 1978); fourthly, many early studies of filter-feeding by zooplankton were performed under controlled laboratory conditions, and their relevance to filtering rates in nature is debatable (Haney, 1973), because of the number of factors now known to affect filtration.

Recently, however, there has been a substantial increase in the number of detailed studies on the impacts of zooplankton grazing on

both phytoplankton community structure (e.g., McCauley & Briand, 1979; Lynch & Shapiro, 1981; Vyhnálek, 1983; Benndorf *et al.*, 1984; Schoenberg & Carlson, 1984; Bergquist *et al.*, 1985; Havens & DeCosta, 1985; Knisely & Geller, 1986; Sarnelle, 1986), and the release and cycling of nutrients between algae and herbivores (e.g., Lehman, 1980a, 1984; Henry, 1985).

In New Zealand, despite the distinctive nature of the zooplankton communities (low species diversity, an absence of many types of predators and generally little regional differentiation [Chapman & Green, 1987]), there is little information about phytoplankton-zooplankton interactions. An absence of predators (e.g., *Chaoborus* and carnivorous cladocerans) and low densities of facultative carnivorous cyclopoids, suggest that algal food supply (and thus competitive interaction) is largely responsible for regulating zooplankton numbers (Chapman *et al.*, 1975; Chapman & Green, 1987). Small clutch sizes compared to those of Northern Hemisphere populations, and a lack of seasonal variation in clutch size, are further evidence of food limitation (Chapman, 1973; Green, 1976a; Chapman *et al.*, 1985). Under such circumstances, it is highly probable that zooplankton herbivory has a major impact on both phytoplankton floristics and seasonal dynamics in most lakes. It has been estimated that specific grazing rates could have been at least 50% of specific phytoplankton loss rates for most of a year in Lakes Hayes and Johson (Mitchell & Burns, 1981). However, zooplankton grazing was dismissed as a regulator of the major phytoplankton species (*Anabaena oscillarioides*, *Synedra ulna*, *Chlorella vulgaris* and *Cyclotella meneghiniana*) in Lake Rotongaio (Viner & Kemp, 1983), but more detailed investigations are required, because there is evidence that zooplankton utilise both *C. vulgaris* and *C. meneghiniana* (see Chapman & Green, 1987).

Generally, planktonic suspension/filter-feeding crustaceans do not use particles with GALDs $\geqslant$ 20 μm (Nadin-Hurley & Duncan, 1976; Gelin & Ripl, 1978). However, variations can occur because of differences in particle morphology and rigidity (Hall *et al.*, 1976); and Brooks & Dodson's (1965) generalisation of a positive correlation between competitive ability and zooplankton body length has been questioned (Dodson, 1974; Neil, 1975; Hall *et al.*, 1976; Bogdan & Gilbert, 1984).

Zooplankton feeding experiments (using spherical plastic beads) have shown that small-sized particles are preferred by some New Zealand populations (Chapman & Green, 1987). For example, the mean particle size selected by *Calamoecia lucasi* Brady was 9.5 μm (Green, 1975b), which is remarkably similar to the mean diameter (8.5 μm) of the dominant phytoplankter (*Cyclotella stelligera*) found in the gut after natural feeding activities in Lake Ototoa (Green, 1976b). *Boeckella* spp. also select relatively small-sized particles, although they are generally slightly larger than those selected by *C. lucasi* (Green, unpublished data; Whitehouse, 1980).

The aim of this experimental study was to investigate the regulation of phytoplankton community composition and biomass by herbivorous zooplankton in a dystrophic and an almost clear-water lake (Maratoto [Group I; Chapter 3] and Rotomanuka North [Group III; Chapter 3], respectively).

These experiments were initiated because analyses of the phytoplankton communities of Lakes Maratoto and Rotomanuka North during 1979 (Etheredge, 1983), showed marked differences in numbers of edible algae (i.e. GALD $\leq$ 20 μm) available to herbivorous zooplankton. For example, in Lake Maratoto, none of the species comprising 95% of both the mean total phytoplankton biomass and the mean total number of pu ml^{-1}, had a GALD $\leq$ 20 μm, compared to 38% in Lake Rotomanuka North.

It is possible that zooplankton grazing pressure in Lake Maratoto kept edible algae to minimal numbers throughout the entire year. Such grazing pressure would presumably be high in this lake because of the absence of small predators (e.g., smelt *Retropinna retropinna* Richardson) to act as zooplankton community regulators. Presumably, if such grazing pressure was reduced, edible algae would increase in number (due to lower mortality rates) and provide strong competition for larger species, because of their larger surface area to volume ratios, high maximum growth rates (Fenchel, 1974; Banse, 1976) and slower sinking rates (Smayda, 1970; Walsby & Reynolds, 1980). Alternatively, the dystrophic, and thus stressful conditions prevailing in Lake Maratoto (Etheredge, 1983), may have been unsuitable for the development of large populations of small algae.

To test these possibilities, two experiments using limnocorrals (LCs) were designed. The hypotheses were:

(1) that phytoplankton community composition is not influenced by zooplankton grazing in Lakes Rotomanuka North and Maratoto;

(2) that phytoplankton community biomass is not influenced by zooplankton grazing in Lakes Rotomanuka North and Maratoto.

Experiment I was performed in both Lakes Rotomanuka North and Maratoto and tested both hypotheses. A reduction in zooplankton herbivory was achieved by filtering zooplankton from the lake water as it entered the LCs. The sampling interval was shorter than in Experiment II, and both phyto- and bacterioplankton were counted, the latter as a possible indicator of an alternative zooplankton food source. Experiment II also tested both hypotheses, but because it was not performed in Lake Maratoto, its results were for comparative purposes only. It also differed from Experiment I in that fish densities were manipulated to reduce zooplankton grazing pressure, the sampling interval was longer, and numbers of bacterioplankton were not monitored.

8.2 EXPERIMENT I

8.2.1 Experimental Design

A set of four transparent, polyethylene (gauge 0.125 mm) LCs was installed in both Lakes Rotomanuka North and Maratoto. Each LC (Plate 10) (diameter 1.0 m; depth 1.5 m; volume c. 1200 l) was sealed at the bottom, supported internally by a well-inflated, tractor inner-tube (diameter $\leq$ 1.0 m), and partially closed at the top by means of a nylon draw-cord inserted through a 10 cm wide casing. The LCs were made by heat sealing.

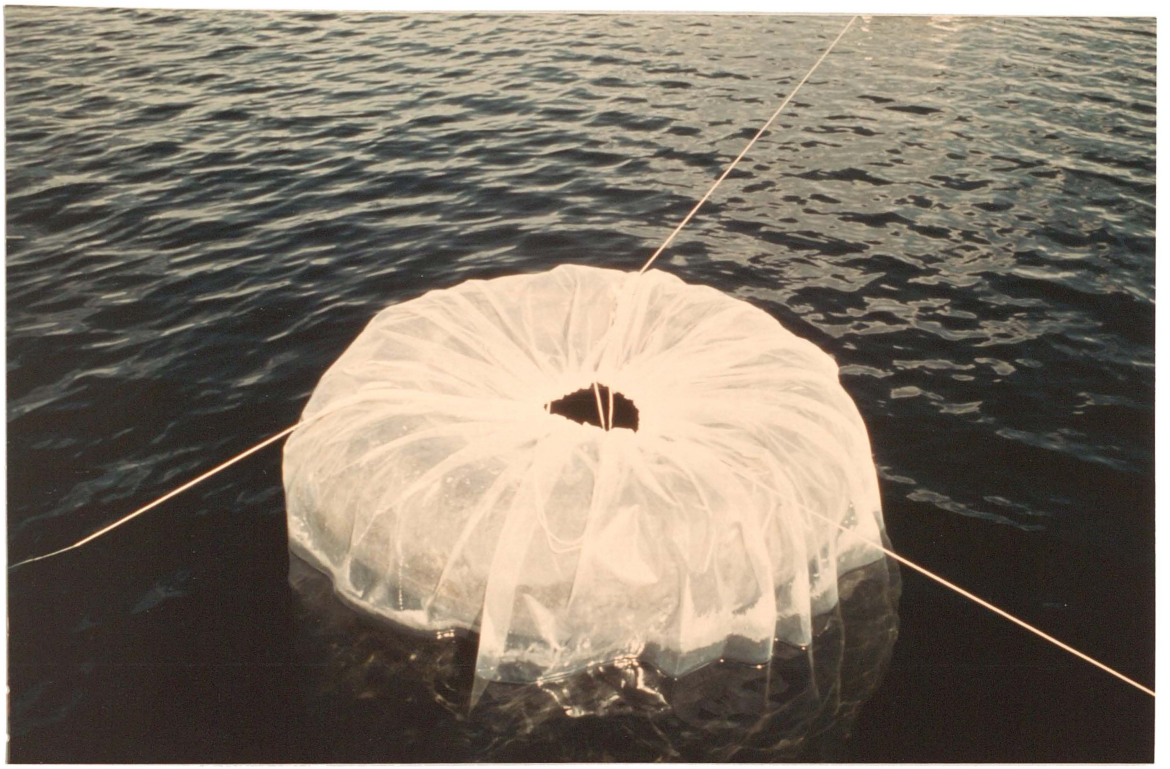
Each LC was filled by pump with lake water from 1.5 m. Water entering three LCs of each set was passed through a zooplankton net (mesh size 0.47 μm) and most zooplankton, except for nauplii and small rotifers, were excluded. These three LCs are referred to as zooplankton-exclosures. Because the net also retained some large phytoplankton species, all zooplankton retained by the net were killed with CO_2 (dry ice [c. 2 cm^2 per 50 ml sample]), prior to being returned, together with live large phytoplankton which were not affected by this treatment, to the LC. (Preliminary tests had established both the quantity of dry ice and the time required to kill all zooplankton in a 50 ml sample. Because *Peridinium* spp. were affected by the dry ice they were omitted from the phytoplankton counts, but were numerically insignificant at the time). The fourth LC

Plate 10

1. Design of limnocorrals used in Experiments I and II.

2. Limnocorrals anchored at southern end of Lake Maratoto during Experiment I.

Plate 10



of each set was filled with unfiltered lake water and thus became the zooplankton-enclosure.

After filling, the four LCs were towed a short distance into the deepest area of each lake (8 m, Rotomanuka North; 7 m, Maratoto). Each LC was positioned at a corner of a square (*c.* 9 m^2), individually anchored, and also secured to its two neighbours. Three upward facing loops glued to the inner side of each inner-tube, and equidistant from each other, provided attachment points for the anchoring system (Plates 10 and 11).

8.2.2 Sampling Techniques

Samples were collected at 3 day intervals (6.3.85 to 21.3.85 Lake Maratoto; 8.3.85 to 21.3.85 Lake Rotomanuka North) between *c.* 0700 and 1100 h. Temperature, oxygen and pH measurements were made using the methods described in Chapter 2.1. Water samples for phytoplankton analyses were collected in triplicate from each LC using the methods described in Chapter 2.2.1.

Water samples (120 ml) for bacterial enumeration were collected in triplicate from each LC at 0.5 m, following a thorough stirring of the contents. Samples were fixed immediately with formalin (2% final concentration) and stored in the dark at 4°C.

At the end of the experiment, zooplankton in each LC were sampled by means of a vertical net haul (diameter 20 cm; length 93 cm; mesh size 0.47 μm) taken through the water column and preserved with formalin (4% final concentration).

8.2.3 Laboratory Techniques

Methods employed for both phytoplankton enumeration and biomass calculations are described in Chapters 2.3. and 2.4. A 9-day running average was used in the calculations of mean total biomass.

Zooplankton were counted by Ms T.L. Greenwood, using the methods described in Greenwood (1987).

Bacteria were counted within 21 days of collection by epifluorescent microscopy, using the following techniques (based largely on those of Thomsen & Cooper [1980]):

(i) Filter Preparation

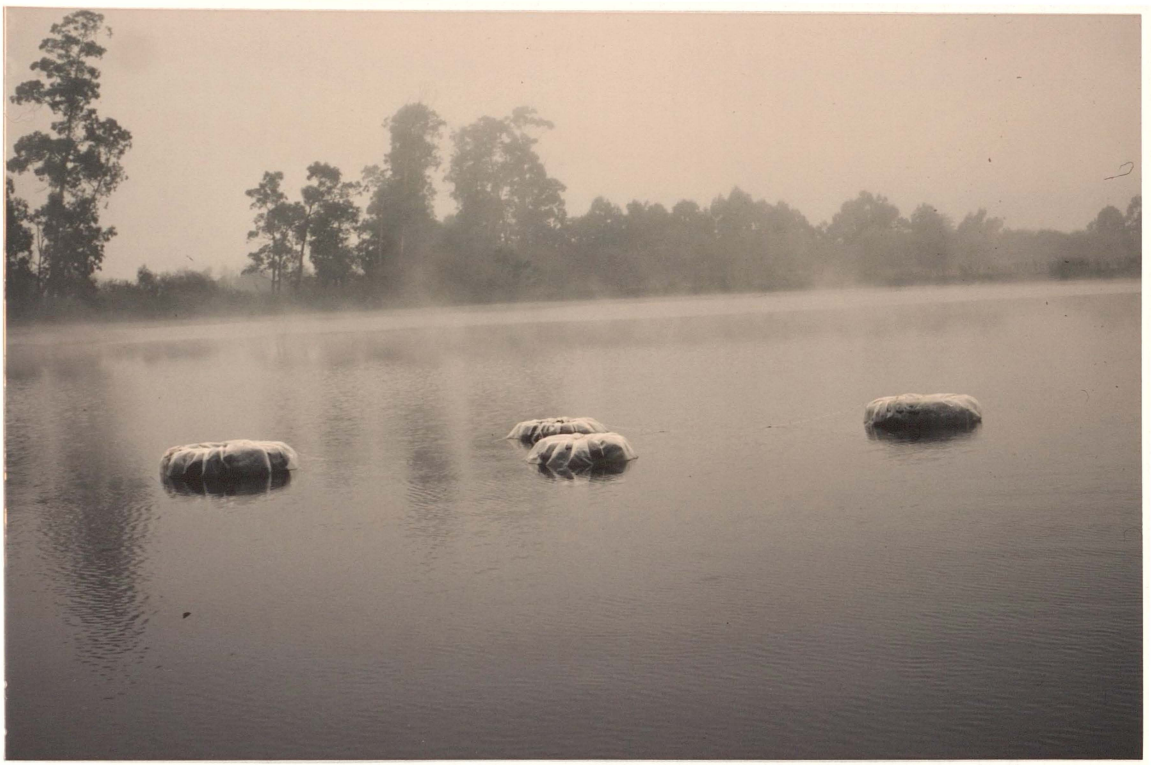
Nuclepore polycarbonate membrane filters (diameter 25 mm; pore size 0.22 μm) were stained for a minimum of 24 h in 66 mg l^{-1} Sudan Black-B in 50:50, v/v, 0.22 μm filtered water/ethanol. After removal

Plate 11

1. Limnocorrals anchored near the centre of Lake Rotomanuka North during Experiment I.

2. Arrangement of limnocorrals in Lake Rotomanuka North during Experiment II. Two limnocorrals were nutrient- enriched and are not discussed in the present study.

Plate 11



from the stain, each filter was individually rinsed twice in 0.22 μm filtered water and stored in the dark in formalin treated (2% final concentration) 0.22 μm filtered water.

(ii) Filtration Unit

The filtration unit consisted of a 30 ml glass filter tower and a 20 mm porous sintered glass filter. A Whatman cellulose nitrate membrane filter (diameter 25 mm; pore size 0.45 μm) was placed across the glass filter to act as a support filter and a small quantity of 0.22 μm filtered water was run through the system to ensure that the filters were flat. Between samples, the filter tower was sterilised with 70% ethanol, rinsed thoroughly with 0.22 μm filtered water and the prestained Nuclepore filter was placed on the damp, cellulose filter.

(iii) Sample Filtration, Staining and Destaining

Initially, a pre-filter diluent (5 or 8 ml 0.22 μm filtered water) was pipetted onto the filter, followed by an appropriate volume of sample to give a total volume of 10 ml. The following solutions were added for the stated lengths of time and removed by application of vacuum:

(a) 2 ml 0.1M phosphate buffer, pH 8.2, run through immediately;

(b) 1 ml acridine orange stain (Sigma practical grade) at 0.4 g l^{-1} in 0.1M phosphate buffer, pH 8.2, 2 minutes;

(c) 2 ml 0.1M phosphate buffer, pH 7.2, run through immediately;

(d) 2 ml 0.1M phosphate buffer, pH 4.6, run through immediately.

To prevent contamination, all solutions had formalin (2% final concentration) added, were stored at 4°C and, except for Sudan Black B, were filtered (0.22 μm) prior to use.

Each sample was filtered in triplicate and test blanks were run at the commencement of each filtering session.

(iv) Filter Mounting

Immediately after filtration, the Nuclepore membrane was placed on a small drop of epifluorescent microscopy oil (Olympus Optical Co. Ltd.; index nd = 1.404) on a microscope slide, and a further drop of immersion oil was placed on top, followed by a coverslip.

(v) Observation

Enumeration was completed within 1 h of preparation, using a Reichert-Jung Polyvar microscope in the epifluorescent mode, equipped with a mercury lamp (200 W), a LP 520 barrier filter, a BP 450-495 exciter filter and a D 5510 dichroic mirror. A magnification of x1200

was attained using a Plan Apo x100 oil immersion objective. 400 bacteria were counted per sample by means of a grid, thus enabling 95% confidence limits to be calculated as bacteria per ml ± 10% (Lund *et al.*, 1958).

8.3 RESULTS: EXPERIMENT I

Data obtained from day 10 onwards from two of the zooplankton-exclosures in Lake Rotomanuka North were not included in the analyses because of contamination by shag (*Phalacrocorax melanoleucos* Vieillot) faeces.

8.3.1 Physico-chemical

There were no significant differences (t test; $p \geq 0.05$) between the zooplankton-exclosures and -enclosure within each lake, in surface and bottom temperatures, surface and bottom oxygen concentrations, and surface pH, but there were minor differences between lakes (Tables 8/0 and 8/1). In both lakes, the surface temperature of the water adjacent to and within the LCs was identical on each sampling occasion, indicating that enclosure did not affect water temperature. In Lake Rotomanuka North, the surface temperature was initially 22°C, but it decreased to 19°C (day 7) and then remained at 20°C until the end of the experiment. In Lake Maratoto, the pattern was similar except for a higher initial temperature (25°C). The surface pH of both lakes and both sets of LCs fluctuated slightly throughout the experiment, but there were no significant differences ($p \geq 0.05$) between individual lakes and the LCs. The median surface pH was 7.7 in Lake Rotomanuka North and 6.4 in Lake Maratoto.

8.3.2 Phytoplankton Species Diversity

8.3.2.1 Lake Rotomanuka North.

81 species, belonging to 52 genera, were found during Experiment I (Table 8/2). Initially, there was no significant difference between the mean number of species in the zooplankton-exclosures (16.1) and the -enclosure (16.3) (Table 8/3). After 7 days in the absence of zooplankton, however, the number of species increased (21.3), but later declined below the initial number (12.6 species [day 13]) and this differed significantly from the number in the zooplankton-enclosure (16.6) on day 13 (Table 8/3).

TABLE 8/0 pH range, and mean ± 1 SD and coefficient of variation (%) of other environmental variables within Lake Rotomanuka North zooplankton-enclosure and zooplankton-exclosures during Experiment I.

Environmental Variable	Mean ± 1 SD	Range	n	C.V. (%)
Zooplankton-enclosure				
Temperature (°C) - surface water	20.3 ± 1.1		5	5.3
- bottom water	20.3 ± 1.1		5	5.3
Oxygen (g m^3) - surface water	8.9 ± 0.1		5	10.8
- bottom water	8.6 ± 0.8		5	8.8
pH - surface water		7.5 - 8.2	5	
Zooplankton-exclosures				
Temperature (°C) - surface water	20.3 ± 1.1		15	5.3
- bottom water	20.3 ± 1.1		15	5.3
Oxygen (g m^3) - surface water	8.7 ± 1.4		11	16.6
- bottom water	8.5 ± 1.4		11	16.5
pH - surface water		7.3 - 8.1	15	

TABLE 8/1 pH range, and mean ± 1 SD and coefficient of variation (%) of other environmental variables within Lake Maratoto zooplankton-enclosure and zooplankton-exclosures during Experiment I.

Environmental Variable	Mean ± 1 SD	Range	n	C.V. (%)
Zooplankton-enclosure				
Temperature (°C) - surface water	21.0 ± 2.2		6	10.4
- bottom water	20.8 ± 2.2		6	10.5
Oxygen (g m^3) - surface water	8.4 ± 0.6		6	7.5
- bottom water	8.1 ± 0.6		6	7.5
pH - surface water		6.3 - 6.8	6	
Zooplankton-exclosures				
Temperature (°C) - surface water	21.0 ± 2.1		18	9.8
- bottom water	20.8 ± 1.9		18	9.0
Oxygen (g m^3) - surface water	8.4 ± 0.6			
- bottom water	8.1 ± 0.6			
pH - surface water		6.3 - 6.8	18	

TABLE 8/2 Phytoplankton taxa collected from Lake Rotomanuka North during Experiment I.
* = GALD ≤ 10 μm; + = SGALD ≤ 10μm; x = GALD ≤ 20 μm.

Taxon	Size Fraction		
CHLOROPHYTA			
Euchlorophyceae			
Actinastrum gracillimum			
A. fluviatile			
A. hantzschii			
Ankistrodesmus bibraianus			+
A. falcatus			+
A. gracilis			+
A. spiralis			+
Botryococcus braunii			
Chlamydomonas sp.		x	+
Coelastrum astroideum			
C. microporum		x	
C. reticulatum			
Crucigenia fenestrata	*	x	+
C. quadrata	*	x	+
Crucigeniella rectangularis	*	x	+
Elakatothrix gelatinosa		x	+
Eudorina elegans			
Gonium pectorale			
Kirchneriella obesa			
Micractinium pusillum			
Monoraphidium contortum			+
M. irregulare			+
M. komarkovae			+
M. minutum	*		+
Nephrocytium agardhianum			
Oocystis lacustris		x	
Pediastrum tetras			
Quadrigula lacustris		x	
Raphidocelis contorta			
Scenedesmus acuminatus			
S. acutus		x	+
S. ecornis		x	
S. obtusus		x	
S. quadricauda		x	
Tetrastrum staurogeniaeforme	*	x	+
T. triangulare	*	x	+
Tetraedron minimum	*	x	+
Westella botryoides	*	x	+
small unidentified greens	*	x	+
Zygophyceae			
Closterium acutum var. *variabile*			+
C. gracile			+
C. parvulum			+
C. pronum			+
Gonatozygon brebissonii			+
Micrasterias decemdentata			
Mougeotia sp.			+

TABLE 8/2 contd.

Staurastrum avicula			
S. leptocladum var. *insigne*			
S. muticum var. *victoriense*			
S. sp.		x	
Staurodesmus dejectus			
St. glaber var. *limnophilus*			
CHROMOPHYTA			
Chrysophyceae			
Dinobryon cylindricum			
Mallomonas acaroides ?			+
Synura uvella ?			
Diatomophyceae			
Acanthoceras zachariasi			
Achnanthes linearis		x	+
Aulacosira distans		x	+
A. granulata			+
Cocconeis placentula			
Cyclotella stelligera	*	x	+
Eunotia pectinalis			+
Fragilaria ulna			+
Hantzschia amphioxys			+
Navicula radiosa			+
Nitzschia acicularis			+
N. gracilis			+
Tabellaria flocculosa			
Xanthophyceae			
Pseudostaurastrum sp. A.			
P. sp. B			
CYANOPHYTA			
Cyanophyceae			
Anabaena minutissima ?			+
Lyngbya limnetica			+
Merismopedia elegans			
Microcystis aeruginosa			
Oscillatoria limnetica			+
O. splendida			+
EUGLENOPHYTA			
Euglenophyceae			
Lepocindis marssonii			
Trachelomonas volvocina		x	
PYRRHOPHYTA			
Cryptophyceae			
Cryptomonas marssonii		x	+
C. ovata		x	+
RAPHIDOPHYTA			
Raphidophyceae			
Vacuolaria sp.			

TABLE 8/3 Mean number of phytoplankton species ± 1 SD collected in Lake Rotomanuka North zooplankton-exclosures and zooplankton-enclosure throughout Experiment I.

Day	Zooplankton-enclosure Mean Number of Species ±1 SD (n = 3)	Zooplankton-exclosures Mean Number of Species ± 1 SD (n = 9)	t Test t	p
0	16.3 ± 1.1	16.1 ± 1.8	0.2	ns
4	16.0 ± 1.7	16.5 ± 2.6	0.4	ns
7	15.3 ± 1.5	21.3 ± 1.8	5.6	†
10	15.0 ± 1.7	16.6 ± 0.5*	0.2	ns
13	16.6 ± 1.5	12.6 ± 0.5*	4.24	†

* n = 3

† p = <0.05

8.3.2.2 Lake Maratoto

Initially, there was no significant difference between the mean species diversity in the zooplankton-exclosures (22.7) and the -enclosure (23.0), and this similarity continued despite the marked decreases in diversity that occurred in both treatments (Table 8/4). The final mean numbers of species (12.5 [zooplankton-exclosure] and 12.0 [zooplankton-enclosure]) are decreases of 46 and 47% respectively. 53 species belonging to 38 genera were found during the experiment (Table 8/5).

8.3.3 Dominant Taxa

8.3.3.1 Lake Rotomanuka North

Initially, *Microcystis aeruginosa* (biovolume 98,581 μm^3) made up 77% of the mean total biomass in the zooplankton-exclosures (Fig. 8/0). This proportion decreased to 9% (day 10), but then rose to 30% (day 13). In the zooplankton-enclosure, the initial mean contribution of *Microcystis aeruginosa* (77%) remained relatively unchanged throughout the experiment, except for an increase to 91% on day 10. In the presence of zooplankton, *Cyclotella stelligera* (biovolume 188 μm^3), the dominant species in the GALD $\leq$ 10 μm fraction, increased its mean proportion during the first four days (6 to 17%) (Fig. 8/1) but later declined, accounting for 8% of the mean total biomass on both days 10 and 13. However, in the absence of zooplankton, its mean proportion increased during the first seven days from 7 to 38% then, after a slight decline, increased markedly to 58% (day 13).

8.3.3.2 Lake Maratoto

Initially, *Closterium acutum* var. *variabile* (biovolume 99.8 μm^3), the dominant phytoplankter (Fig. 8/2), made up 21 and 23% of the mean total biomasses in both the zooplankton-exclosures and -enclosure respectively. By day 15, despite fluctuations, its biomass had *c.* tripled in all LCs.

8.3.4 Mean Phytoplankton Biomass

8.3.4.1 Lake Rotomanuka North

Initially, the biomasses in the zooplankton-exclosures and

TABLE 8/4 Mean number of phytoplankton species ± 1 SD collected in Lake Maratoto zooplankton-exclosures and zooplankton-enclosure throughout Experiment I.

Day	Zooplankton-enclosure Mean Number of Species ± 1 SD (n = 3)	Zooplankton-exclosures Mean Number of Species ± 1 SD (n = 9)	t Test t	p
0	22.7 ± 1.1	23.0 ± 3.6	0.24	ns
3	16.3 ± 2.5	20.0 ± 2.3	2.05	ns
6	18.6 ± 0.5	19.5 ± 2.7	1.09	ns
9	14.0 ± 1.0	15.4 ± 2.4	1.31	ns
12	10.0 ± 1.7	11.6 ± 2.1	1.36	ns
15	12.0 ± 1.4	12.5 ± 1.8	0.47	ns

TABLE 8/5 Phytoplankton taxa collected from Lake Maratoto during Experiment I.
* = GALD ≤ 10 μm; † = SGALD ≤ 10 μm; x = GALD ≤ 20 μm.

Taxon	Size Fraction		
CHLOROPHYTA			
Euchlorophyceae			
Botryococcus braunii			
Coelastrum indicum			
C. microporum		x	
Dictyosphaerium subsolitarium ?		x	
Elakatothrix gelatinosa		x	+
Kirchneriella obesa			
Monoraphidium contortum			+
Oocystis lacustris		x	
Pediastrum tetras			
Raphidocelis contorta			
Scenedesmus acutus		x	+
S. quadricauda		x	
Zygophyceae			
Closterium acutum var. *variabile*			+
C. parvulum			+
C. pronum			+
Staurastrum inflexum			
S. sp. A.		x	
S. sp. B.			
Staurodesmus glaber var. *limnophilus*			
CHROMOPHYTA			
Chrysophyceae			
Mallomonas acaroides	*	x	+
M. tonsurata			
Synura uvella			
Diatomophyceae			
Acanthoceras zachariasi			+
Achnanthes linearis		x	+
Aulacosira distans		x	+
A. granulata			+
Cocconeis placentula			
Cyclotella meneghiniana		x	
C. stelligera	*	x	+
Cymbella palustris			+
Epithemia sorex			

TABLE 8/5 contd.

Eunotia pectinalis		+
Fragilaria ulna		+
Gomphonema truncatum		
Navicula pupula		+
N. subtilissima		+
Rhizosolenia eriensis		+
Stenopterobia intermedia		+
Tabellaria flocculosa		
Xanthophyceae		
Pseudostaurastrum sp. A		
CYANOPHYTA		
Cyanophyceae		
Anabaena minutissima ?		+
Chroococcus turgidus	x	
Oscillatoria limnetica		+
O. splendida		+
EUGLENOPHYTA		
Euglenophyceae		
Euglena oxyuris		
Phacus hamatus		
P. helicoides		
P. pleuronectes		
Trachelomonas volvocina	x	
PYRRHOPHYTA		
Cryptophyceae		
Cryptomonas marssonii	x	+
C. ovata	x	+
RAPHIDOPHYTA		
Raphidophyceae		
Vacuolaria sp.		

Fig. 8/0 Changes in the proportions of *Microcystis aeruginosa* in the Lake Rotomanuka North limnocorrals throughout Experiment I.

Key: A. = Zooplankton - enclosure
B. = Zooplankton - exclosure

Fig. 8/1 Changes in the proportions of *Cyclotella stelligera* in the Lake Rotomanuka North limnocorrals throughout Experiment I.

Fig. 8/2 Changes in the proportions of *Closterium acutum* var. *variabile* in Lake Maratoto limnocorrals throughout Experiment I.

Key: A. = Zooplankton -exclosure
B. = Zooplankton -enclosure

Fig. 8/0

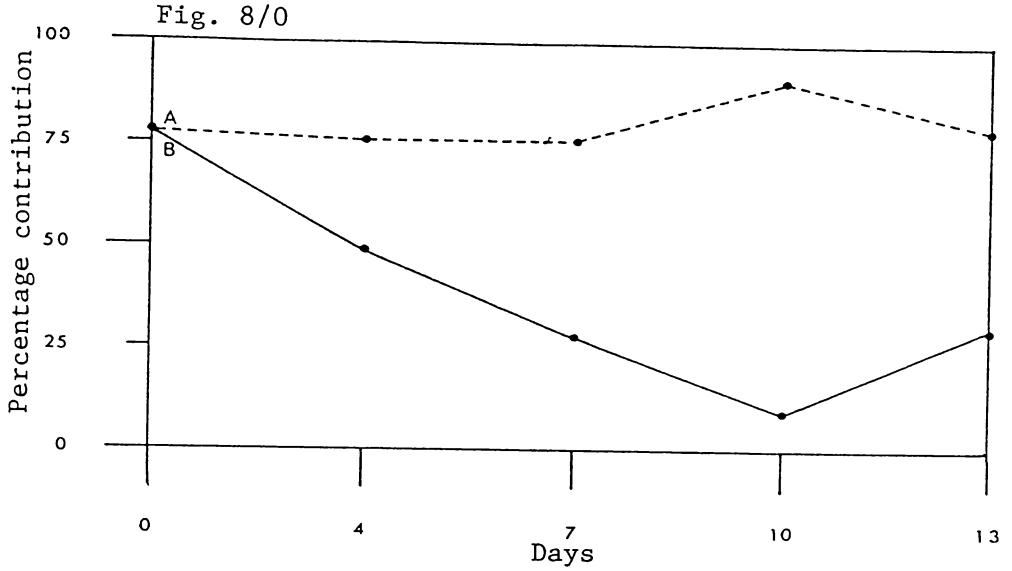


Fig. 8/1

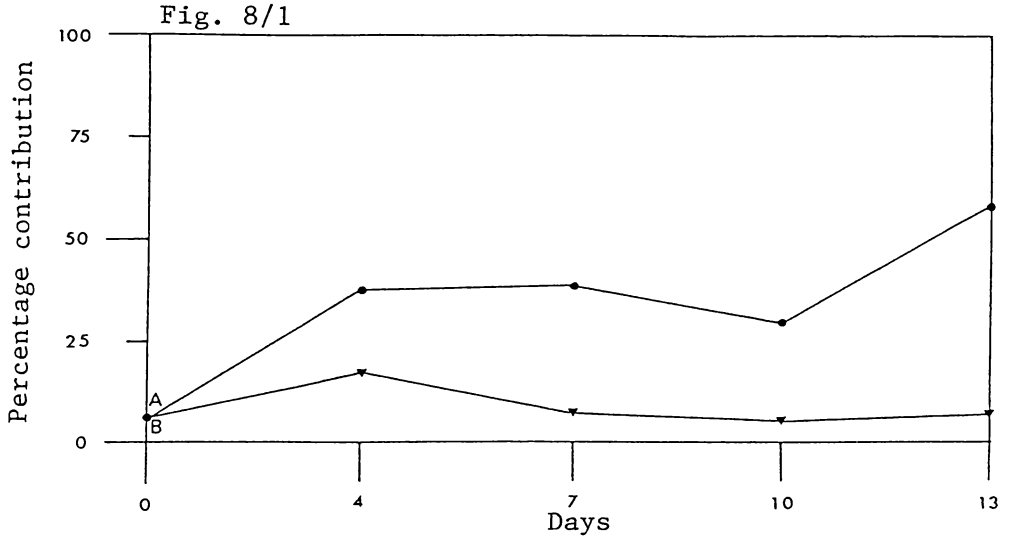
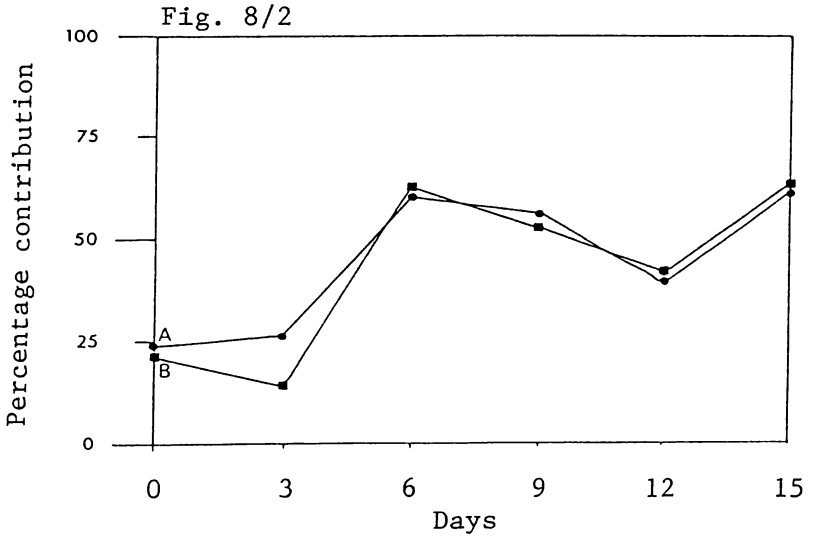


Fig. 8/2



zooplankton-enclosure were similar, but as the experiment progressed marked increases occurred in the absence of zooplankton. By day 4, total biomass had increased by c. 45%, and in the following two consecutive samples by 113 and 248%, respectively, the latter representing the maximum biomass (1897 mg m^3). By day 13 the biomass had decreased to 1724 mg m^3.

Biomass also increased in the zooplankton-enclosure, but to a much lesser extent; the maximum biomass (1202 mg m^3 [day 7]) represents an increase of 41%, but by day 13, it had decreased to 1003 mg m^3 (Fig. 8/3).

8.3.4.2 Lake Maratoto

During the first six days in the absence of zooplankton, biomass increased (maximum 1451 mg m^3). Thereafter levels declined (1197 mg m^3 [day 12]), but during the final three days a further increase was recorded (13,754 mg m^3 [day 15]). A similar pattern was apparent in the zooplankton-enclosure, albeit at slightly reduced levels (Fig. 8/4).

8.3.5 Mean Phytoplankton Biomass Of Specific Size Fractions

8.3.5.1 Lake Rotomanuka North

Taxa with GALDs $\leq$ 10 μm (10%), SGALDs $\leq$ 10 μm (49%) and GALD $\leq$ 20 μm (26%) are listed in Table 8/2.

In the absence of zooplankton, marked increases in the total biomass of these size fractions occurred (Table 8/6). The importance of the GALD $\leq$ 10 μm fraction in relation to the total biomass increased dramatically (7 to 59%), as did that of the SGALD $\leq$ 10 μm fraction (12 to 65%); the maximum biomasses of these fractions (1008 and 1118 mg m^3, respectively) were recorded on day 13. The proportion of the GALD $\leq$ 20 μm fraction also increased (15 to 68%), the maximum (711 mg m^3) also occurring on day 13.

These results contrast strongly with those from the zooplankton-enclosure, where the proportions of both the GALD $\leq$ 10 μm and SGALD $\leq$ 10 μm fractions increased only minimally (6 to 7 and 11.6 to 12.3%, respectively), and maximum biomasses (111 and 175 mg m^3, respectively) were recorded on day 7. The total biomass of the GALD $\leq$ 20 μm fraction fluctuated only slightly, and once more the maximum (192 mg m^3) was recorded on day 7.

Fig. 8/3 Changes in the mean total phytoplankton biomass in the Lake Rotomanuka North limnocorrals throughout Experiment I.

Key: A = Zooplankton-enclosure (n = 3)
B = Zooplankton-exclosure (n = 9 for days 0-7; n=3 for days 10-13)

Fig. 8/4 Changes in the mean total phytoplankton biomass in the Lake Maratoto limnocorrals throughout Experiment I.

Key: A = Zooplankton-enclosure (n = 3)
B = Zooplankton-exclosure (n = 9)

Fig. 8/3

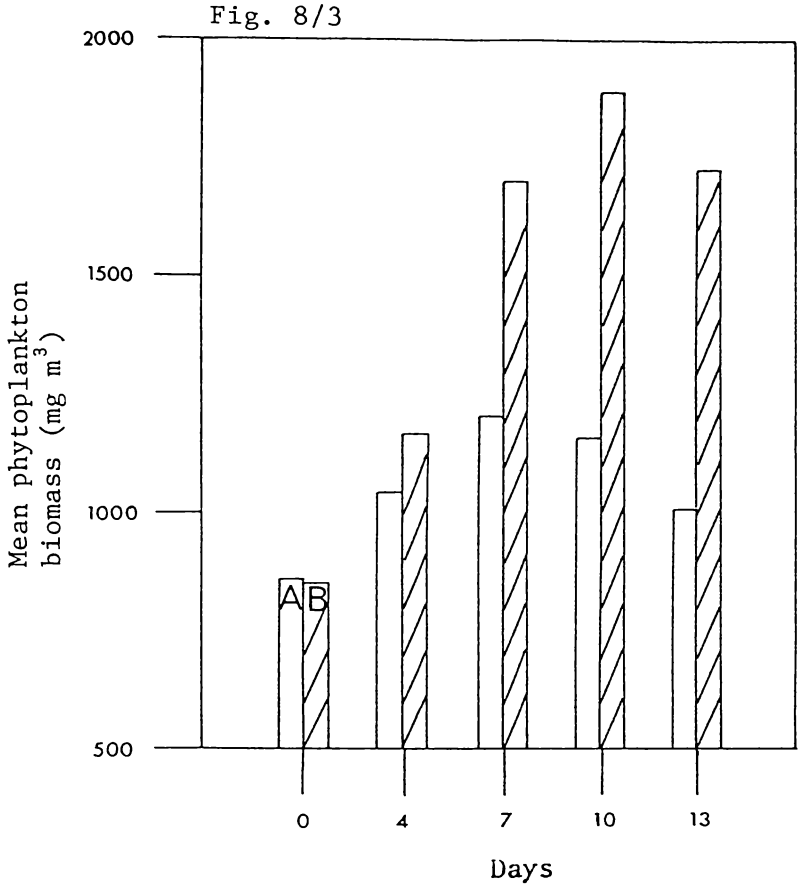

2000
1500
1000
500
Mean phytoplankton biomass (mg m^3)
A
B
0
4
7
10
13
Days

Fig. 8/4

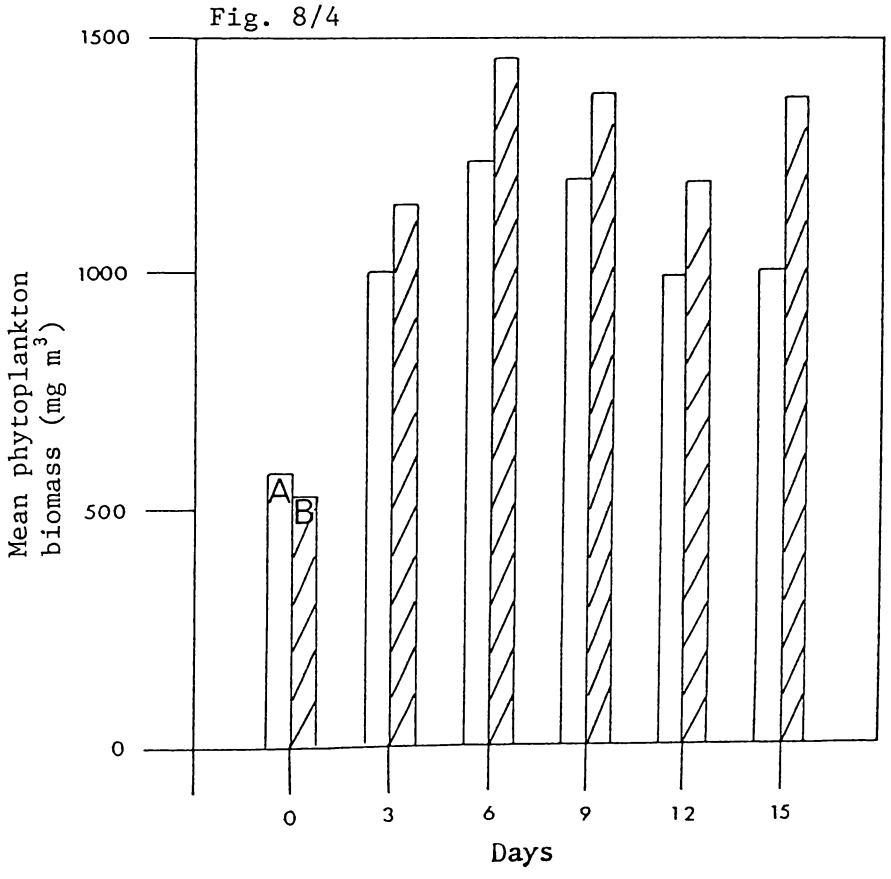

1500
1000
500
0
Mean phytoplankton biomass (mg m^3)
A
B
0
3
6
9
12
15
Days

TABLE 8/6 Mean phytoplankton biomass (mg m^3) of specific size fractions (GALD ≤ 10 μm; SGALD ≤ 10 μm; GALD ≤ 20 μm) and their percentage contribution to the mean total biomass in Lake Rotomanuka North zooplankton-exclosures and zooplankton-enclosure throughout Experiment I.

Day	Mean Phytoplankton Biomass (mg m^3)	Percentage Contribution to Mean Total Phytoplankton Biomass
Zooplankton-enclosure		
GALD ≤ 10 μm (n = 3)		
0	49.2	5.8
4	106.4	10.2
7	111.0	9.2
10	76.7	6.6
15	76.1	7.6
SGALD ≤ 10 μm (n = 3)		
0	99.3	11.6
4	159.2	15.3
7	175.3	14.6
10	141.3	12.2
13	123.8	12.3
GALD ≤ 20 μm (n = 3)		
0	108.6	12.7
4	181.0	17.4
7	192.1	16.0
10	134.2	11.6
13	123.0	12.3
Zooplankton-exclosures		
GALD ≤ 10 μm (n = 9)		
0	54.2	6.8
4	387.1	33.3
7	554.7	32.4
10	743.5*	39.2
13	1008.1*	58.5

TABLE 8/6 contd.

SGALD ⩽ 10 μm (n = 9)		
0	96.7	12.0
4	506.2	43.5
7	700.3	41.0
10	902.3*	47.6
13	1118.5*	64.9
GALD ⩽ 20 μm (n = 9)		
0	118.3	14.8
4	516.4	44.4
7	711.4	41.6
10	924.2*	48.7
13	1166.1*	67.6

* n = 3

8.3.5.2 Lake Maratoto

The GALD ≤ 10 μm, SGALD ≤ 10 μm and GALD ≤ 20 μm fractions were represented by 2 (4%), 24 (46%), and 16 (30%) taxa, respectively (Table 8/5). In both the zooplankton-exclosures and -enclosure, the GALD ≤ 10 μm fraction was unimportant, and fluctuations were similar (Table 8/7). In the zooplankton-exclosure, the GALD ≤ 20 μm fraction initially showed a minor increase, but the major trend during the experiment was one of gradual decline. With one exception, a similar trend occurred in the zooplankton-enclosure. The initial and final proportions of the GALD ≤ 20 μm fraction in the zooplankton-exclosures and -enclosures were (27 and 31%) and (10 and 11%). In contrast, a major alteration in the importance of the SGALD ≤ 10 μm fraction occurred in both treatments. In the zooplankton-enclosure, mean proportions on days 0 and 15 were 67% (391 mg m^3) and 98% (995 mg m^3), respectively. In the absence of zooplankton, this fraction initially accounted for 71% (371 mg m^3), but increased within six days to 80% (1158 mg m^3), and these high values continued (94% [day 12] and 90% [day 15]), largely as result of *Closterium acutum* var. *variabile* (Fig. 8/2).

8.3.6 Bacterial Densities

8.3.6.1 Lake Rotomanuka North

Although the mean densities of bacteria in the zooplankton-exclosures and -enclosure did not differ significantly on day 0, within three days substantial differences were apparent, and these continued until day 13 (Table 8/8). In the absence of zooplankton, an almost regular increase in mean bacterial concentrations was recorded, while densities in the zooplankton-enclosure declined steadily (Fig. 8/5).

8.3.6.2 Lake Maratoto

The general patterns observed in the Lake Rotomanuka North LCs were repeated in Lake Maratoto, albeit to a greater extent in the presence of zooplankton (56%) (Fig. 8/6). In the zooplankton-exclosures, mean numbers increased throughout the experiment (Table 8/9).

8.3.7 Zooplankton

8.3.7.1 Lake Rotomanuka North

No adult copepods and only minimal numbers of other zooplankters

TABLE 8/7 Mean phytoplankton biomass (mg m^3) of specific size fractions (GALD ≤ 10 μm; SGALD ≤ 10 μm; GALD ≤ 20 μm) and their percentage contribution to the mean total biomass in Lake Maratoto zooplankton-exclosures and zooplankton-enclosure throughout Experiment I.

Day	Mean Phytoplankton Biomass (mg m^3)	Percentage Contribution to Mean Total Phytoplankton Biomass
Zooplankton-enclosure		
GALD ≤ 10 μm (n = 9)		
0	1.6	0.3
3	2.4	0.3
6	2.1	0.2
9	1.1	0.09
12	0.7	0.09
15	0.3	0.03
SGALD ≤ 10 μm (n = 9)		
0	390.6	67.4
3	682.9	67.1
6	921.0	74.5
9	998.7	83.2
12	910.5	91.2
15	994.6	97.7
GALD ≤ 20 μm (n = 9)		
0	177.9	30.6
3	260.0	25.5
6	300.0	24.2
9	182.6	15.2
12	177.1	17.7
15	114.4	11.2
Zooplankton-exclosures		
GALD ≤ 10 μm (n = 9)		
0	1.8	0.3
3	2.9	0.3
6	2.4	0.2
9	1.2	0.09
12	0.5	0.04
15	0.7	0.05

TABLE 8/7 contd.

SGALD ≤ 10 μm (n = 9)		
0	371.5	71.2
3	902.7	78.8
6	1152.8	79.8
9	1142.9	82.4
12	1036.1	86.7
15	1237.2	90.0
GALD ≤ 20 μm (n = 9)		
0	141.1	27.0
3	366.1	31.9
6	392.1	27.0
9	284.0	20.5
12	156.7	13.0
15	133.3	9.6

TABLE 8/8 Mean bacterial concentrations ($10^5.ml^{-1}$ ± 1 SD) in Lake Rotomanuka North zooplankton-exclosures and zooplankton-enclosure throughout Experiment I.

Day	Zooplankton-enclosure Mean Bacterial Concentration ($10^5.ml^{-1}$ ± 1 SD) (n = 3)	Zooplankton-exclosures Mean Bacterial Concentration ($10^5.ml^{-1}$ ± 1 SD) (n = 9)	t-test t	p
0	19.43 ± 1.1	20.52 ± 1.8	1.21	>0.05
4	18.77 ± 1.1	22.54 ± 2.2	3.76	<0.01**
7	17.10 ± 1.7	24.84 ± 2.6	5.61	<0.01**
10	16.10 ± 1.7	24.83 ± 1.8*	5.97	<0.01**
13	17.10 ± 1.7	28.77 ± 2.5*	6.68	<0.01**

** highly significant

* n = 3

Fig. 8/5 Percentage changes from day 0 in mean concentrations of bacterioplankton in the Lake Rotomanuka North limnocorrals throughout Experiment I.

Key: A. = Zooplankton-exclosure (n = 9, days 0 - 7; n = 3, days 10 - 13)
B. = Zooplankton-enclosure (n = 3)

Fig. 8/6 Percentage changes from day 0 in mean concentrations of bacterioplankton in the Lake Maratoto limnocorrals throughout Experiment I.

Key: A. = Zooplankton-exclosure (n = 9)
B. = Zooplankton-enclosure (n = 9)

Fig. 8/5

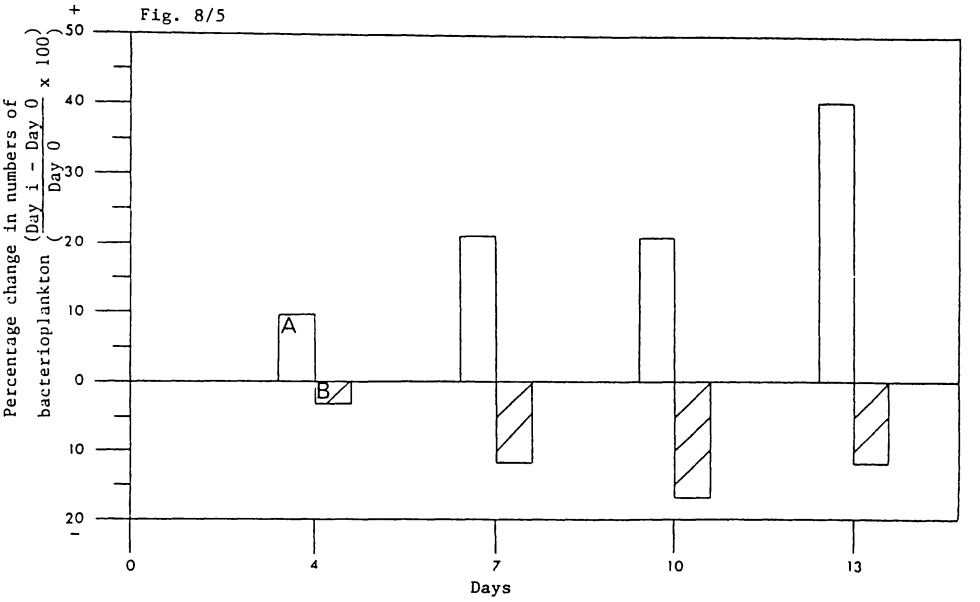

Percentage change in numbers of bacterioplankton ((Day i - Day 0 / Day 0) x 100)
+
50
40
30
20
10
0
10
20
A
B
0
4
7
10
13
Days

Fig. 8/6

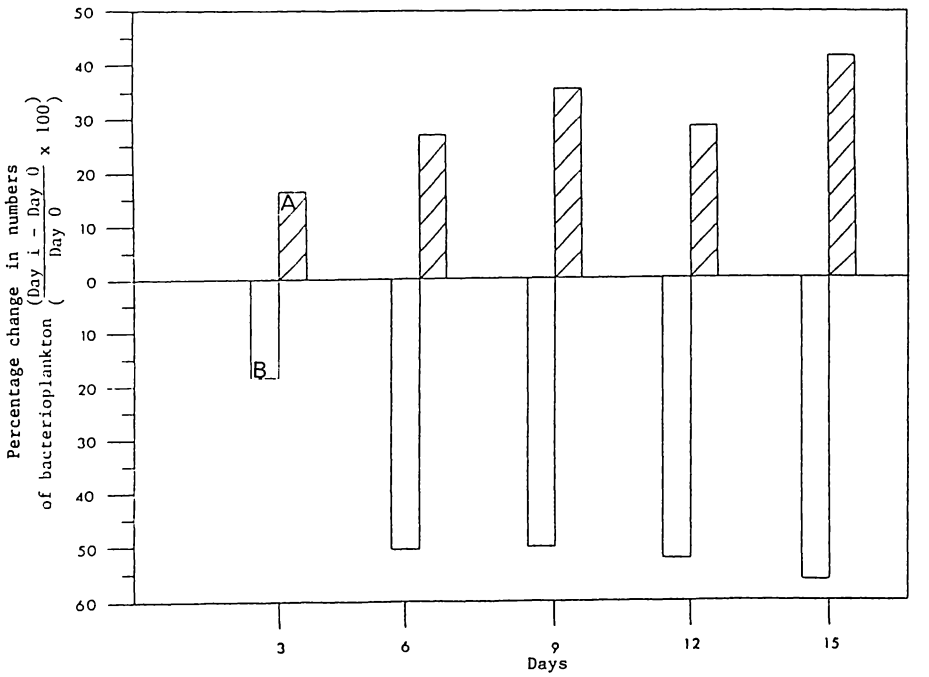

Percentage change in numbers of bacterioplankton ((Day i - Day 0 / Day 0) x 100)
50
40
30
20
10
0
10
20
30
40
50
60
A
B
3
6
9
12
15
Days

TABLE 8/9 Mean bacterial concentrations ($10^5.ml^{-1}$ ± 1 SD) in Lake Maratoto zooplankton-exclosures and zooplankton-enclosure throughout Experiment I.

Day	Zooplankton-enclosure Mean Bacterial Concentration ($10^5.ml^{-1}$ ± 1 SD) (n = 3)	Zooplankton-exclosures Mean Bacterial Concentration ($10^5.ml^{-1}$ ± 1 SD) (n = 9)	t test t	p
0	13.56 ± 0.5	13.10 ± 1.1	0.94	>0.05
3	11.00 ± 0.5	15.23 ± 1.7	6.55	<0.001***
6	6.66 ± 0.4	16.63 ± 1.7	15.34	<0.001***
9	6.73 ± 0.2	17.72 ± 2.7	11.94	<0.001***
12	6.43 ± 0.4	16.81 ± 3.1	9.69	<0.001***
15	5.93 ± 0.3	18.52 ± 3.4	10.72	<0.001***

*** very highly significant

were found in the zooplankton-exclosure at the end of the experiment (Table 8/10) and, not unexpectedly, rotifers (largely *Keratella cochlearis*) were the most abundant. In contrast, a total of 457.5 zooplankton per litre were recorded in the zooplankton-enclosure. The dominants were rotifers and a cladoceran, *Bosmina meridionalis*.

8.3.7.2 Lake Maratoto

Although all groups were present in the zooplankton-exclosures, numbers were negligible (Table 8/11). Rotifers and total nauplii were the most abundant. In the zooplankton-enclosure, total numbers were also low, although calanoid copepodites and a cladoceran (*Ceriodaphnia pulchella*) were the most abundant.

8.4 EXPERIMENT II

8.4.1 Experimental Design

Three transparent, polyethylene (gauge 0.25 mm) LCs (diameter 1.4 m; depth 6 m; volume c. 9000 l) were constructed, filled and anchored using the methods described in Chapter 8.2.1. Two small polyethylene sandbags were added to each LC to prevent flotation. Fish densities were manipulated on day 7 by adding three smelt of adult body form to one LC, and fifteen to a second, giving moderate and high densities, respectively. The smelt were captured in Lake Rotomanuka North with a 8 x 1.2 m seine net (mesh size 2.0 mm). The three LCs were subsequently called fish-enclosures 1 and 2, and fish-exclosure 3, respectively. At the conclusion of the experiment, the smelt were killed with rotenone and gut analyses were carried out by Dr M. Cryer.

8.4.2 Sampling Procedures and Field Techniques

The experimental unit (Plate 11) was installed on 8.3.84, sampling commenced on 15.3.84, and continued at approximately weekly intervals for six weeks. Generally samples were taken between 0800 and 1100 h.

Temperature and oxygen concentrations were measured in each LC using the methods described in Chapter 2.2. Phytoplankton sampling and preservation techniques are described in Chapter 2.3. Zooplankton samples were collected by Dr M. Cryer. A vertical haul net (diameter 20 cm; length 93 cm; mesh size 0.47 μm) was taken through the water column of each LC, and zooplankton were immediately narcotised with chloroform (to prevent egg loss) before preservation with formalin (4%

TABLE 8/10 Densities (numbers per litre) of zooplankton from limnocorrals in Lake Rotomanuka North on day 13, Experiment I.

Taxon	Density (Nos. l^{-1}) Zooplankton-exclosure	Zooplankton-enclosure
ARTHROPODA		
Copepoda		
Calanoida		
Adults	-	2.0
Copepodites	0.1	11.5
Cyclopoida		
Adults	-	0.03
Copepodites	-	2.3
Diplostraca		
Bosmina meridionalis	1.5	78.5
Ceriodaphnia pulchella	0.06	0.5
Total nauplii	0.2	34.0
ROTATORIA	30.6	329.1

TABLE 8/11 Densities (numbers per litre) of zooplankton from limnocorrals in Lake Maratoto on day 15, Experiment I.

Taxon	Mean Density (nos. l^{-1}) (n = 3) Zooplankton-exclosures	Density (nos. l^{-1}) Zooplankton-enclosure
ARTHROPODA		
Copepoda		
Calanoida		
Adults	0.1	0.9
Copepodites	0.6	5.4
Cyclopoida		
Adults	0.02	0.1
Copepodites	0.3	1.6
Diplostraca		
Bosmina meridionalis	0.05	0.3
Ceriodaphnia pulchella	0.2	3.2
Total nauplii	12.5	9.9
ROTATORIA	7.1	9.5

final concentration).

Sampling of fish-enclosure 1 ceased after 28 days because of a split along a fold in the polyethylene.

8.4.3 Laboratory Techniques

The methods used for both phytoplankton enumeration and biomass calculations are described in Chapter 2.3. Zooplankton counting was performed by Dr M. Cryer using the methods described in Cryer (1983), and data are expressed as numbers per haul. A 3-week running average was applied to all data.

8.5 RESULTS: EXPERIMENT II

8.5.1 Physico-chemical

A summary of the physico-chemical data for fish-enclosure 2 and fish-exclosure 3 is given in Table 8/12. At no time did the temperature and oxygen profiles obtained from either LC differ significantly from each other or from those obtained from the lake. Surface temperature decreased from 22°C (day 0) to 17°C (day 39).

8.5.2 Phytoplankton Species Diversity

A total of 75 species and 1 variety, belonging to 46 genera, were found (Table 8/13). On day 0, 31 and 28 species were found in fish-enclosure 2 and fish-exclosure 3, respectively. During the 14 days following manipulations in fish-enclosure 2, the number of species rose to 38, but by day 39 had declined to 27. However, in fish-exclosure 3, there was little variation in species diversity, except for a decrease to 22 on day 21 (Table 8/14).

8.5.3 Phytoplankton Biomass

On day 0, total biomasses within the LCs were remarkably similar, however, after manipulation, a substantial increase occurred, before a small decline in the latter part of the experiment. In contrast, the maximum biomass in fish-exclosure 3 was recorded on day 7, after which time it steadily declined (Fig. 8/7).

8.5.4 Phytoplankton Biomass Of Specific Size Fractions

All taxa with GALDs $\leq$ 10 μm (8% [Table 8/13]) belonged to the Euchlorophyceae, except *Cyclotella stelligera*. Initially, the proportions of the $\leq$ 10 μm fractions were similar (1.4%, fish-

TABLE 8/12 pH range, and mean ± 1 SD and coefficient of variation (%) of other environmental variables within Lake Rotomanuka North fish-enclosure 2 and fish-exclosure 3 during Experiment II.

Environmental Variable		Mean ± 1 SD	Range	n	C.V. (%)
Fish-enclosure 2					
Temperature (°C)	- surface water	20.2 ± 2.0		5	10.1
	- bottom water	18.3 ± 1.0		5	5.7
Oxygen (g m^3)	- surface water	8.9 ± 0.6		5	6.6
	- bottom water	0.4 ± 0.2		5	62.8
pH	- surface water		7.5 - 8.9	7	
Fish-exclosure 3					
Temperature (°C)	- surface water	20.2 ± 2.1			10.2
	- bottom water	17.6 ± 0.7			4.0
Oxygen (g m^3)	- surface water	8.4 ± 0.6			6.5
	- bottom water	0.4 ± 0.2			51.6
pH	- surface water		7.1 - 8.1	7	

TABLE 8/13 Phytoplankton taxa collected from Lake Rotomanuka North during Experiment II.
* = GALD ≤ 10 μm; + = GALD ≤ 20 μm.

Taxa	Size Fraction	
CHLOROPHYTA		
Euchlorophyceae		
Ankistrodesmus bibraianus		
A. falcatus		
A. gracilis		
A. spiralis		
Botryococcus braunii		
Chlamydomonas sp. A	*	+
C. sp. B	*	+
Coelastrum microporum		+
Elakatothrix gelatinosa		+
Eudorina elegans		
Kirchneriella obesa		
Monoraphidium contortum		
M. irregulare		
M. minutum	*	+
M. tortile		
Nephrocytium agardhianum		
Oocystis lacustris		
O. solitaria		
Pediastrum duplex		
P. tetras		
Pteromonas sp.		+
Scenedesmus acuminatus		+
S. ecornis		+
S. obtusus		+
Sorastrum spinulosum		
Tetraedron minimum	*	+
Tetrastrum triangulare	*	+
small unidentified greens	*	+
Zygophyceae		
Closterium acutum var. *variabile*		
C. gracile		
C. pronum		
Cosmarium perfissum		
Gonatozygon brebissonii		
Mougeotia sp. A		
M. sp. B		
Staurastrum leptocladum var. insigne		
S. subradians ?		
S. tohopekaligense var. *minus*		+
S. sp. A		
CHROMOPHYTA		
Chrysophyceae		

TABLE 8/13 cont.

Chrysococcus rufescens	*	+
Dinobryon cylindricum		
Mallomonas acaroides ?		
M. akrokomos		+
Synura uvella ?		
Diatomophyceae		
Achnanthes linearis		+
Amphora sp.		
Cyclotella stelligera	*	+
Cymbella aspersa		
Eunotia pectinalis		
Fragilaria capucina		
F. delicatissima ?		
F. ulna		
Frustulia rhomboides		
Nitzschia acicularis		
CYANOPHYTA		
Cyanophyceae		
Anabaena minutissima ?		
Lyngbya limnetica		
Microcystis aeruginosa		
Oscillatoria limnetica		
O. subbrevis		
O. tenuis		
EUGLENOPHYTA		
Euglenophyceae		
Cyclidiopsis acus		
Euglena acus		
Phacus agilis		+
P. glaber		
P. suecicus		
Trachelomonas armata		
T. a. var. *longispina*		
T. hispida		
T. sydneyensis		
T. volvocina		+
PYRRHOPHYTA		
Cryptophyceae		
Cryptomonas erosa		
C. ovata		+
Dinophyceae		
Ceratium hirundinella		
Peridinium cinctum		
P. inconspicuum		+
P. pusillum tab. *conjunctum*		
RAPHIDOPHYTA		
Raphidophyceae		
Vacuolaria sp.		

TABLE 8/14 Number of phytoplankton species and percentage of total number of species collected from fish-exclosure 3 and fish- enclosure 2 in Lake Rotomanuka North throughout Experiment II.

Day	Fish-enclosure 2		Fish-exclosure 3	
	Number of Species	Percentage	Number of Species	Percentage
0	31	41.3	28	37.3
7	32	42.7	30	40.0
14	37	49.3	29	38.7
21	38	50.7	22	29.3
28	34	45.3	27	36.0
33	28	37.0	25	33.3
39	27	36.0	27	36.0

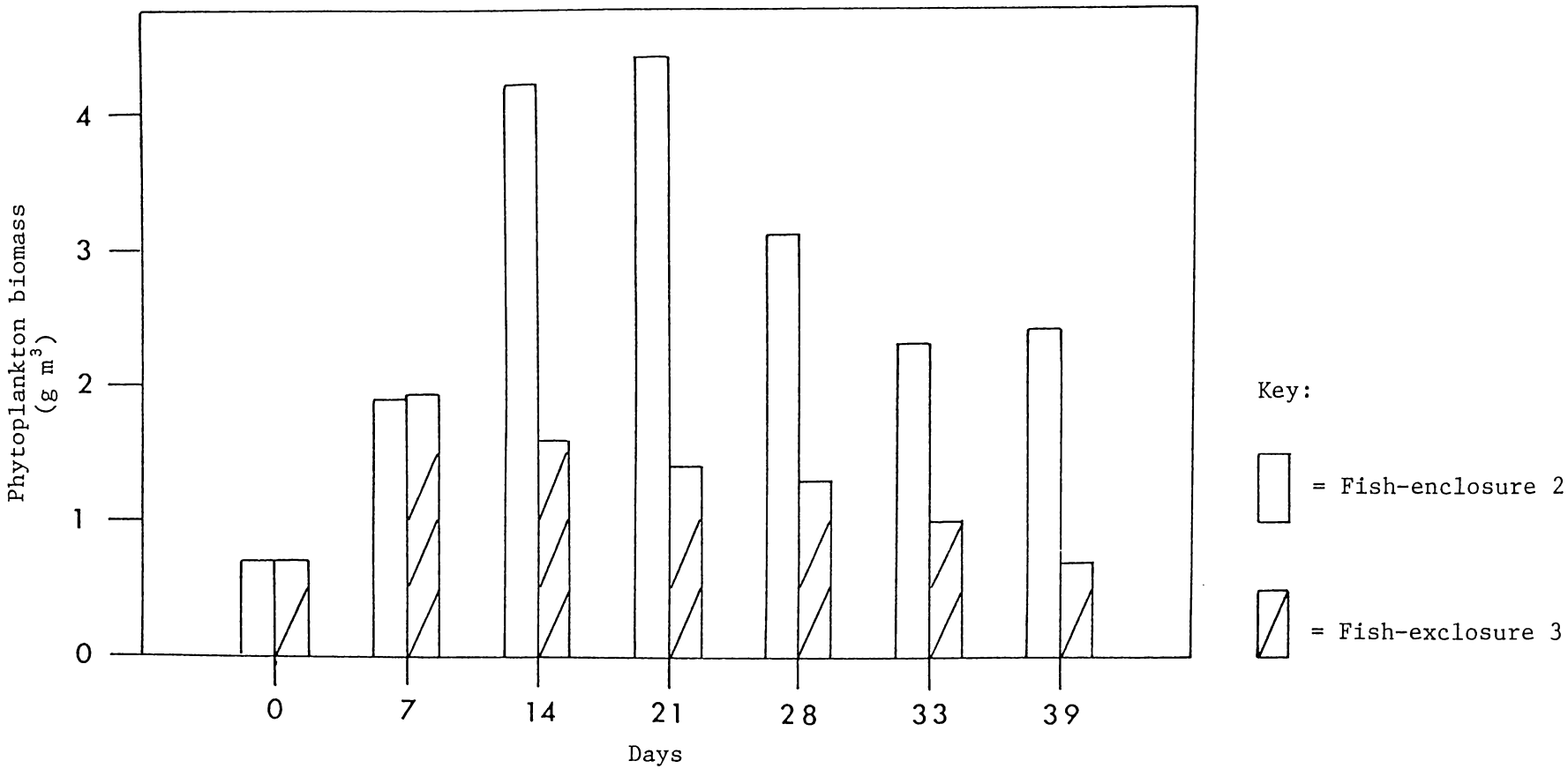


Fig. 8/7 Changes in total phytoplankton biomass in the limnocorrals throughout Experiment II.

enclosure 2; 1.0%, fish-exclosure 3) (Fig. 8/8), but this pattern did not continue. In the absence of fish, a small but steady decline occurred throughout the entire experiment. In fish-enclosure 2 however, after an initial decline the GALD $\leq$ 10 μm proportion increased, peaking on day 21, before a decline to 0.1% on day 39. In this LC the proportion of the GALD $\leq$ 20 μm fraction increased dramatically (13% [day 0] to 61% [day 33]), before a small decline to 37% by the end of the experiment. In fish-exclosure 3, the proportion of the GALD $\leq$ 20 μm fraction fluctuated, but at no time did it exceed the initial value (Fig. 8/9).

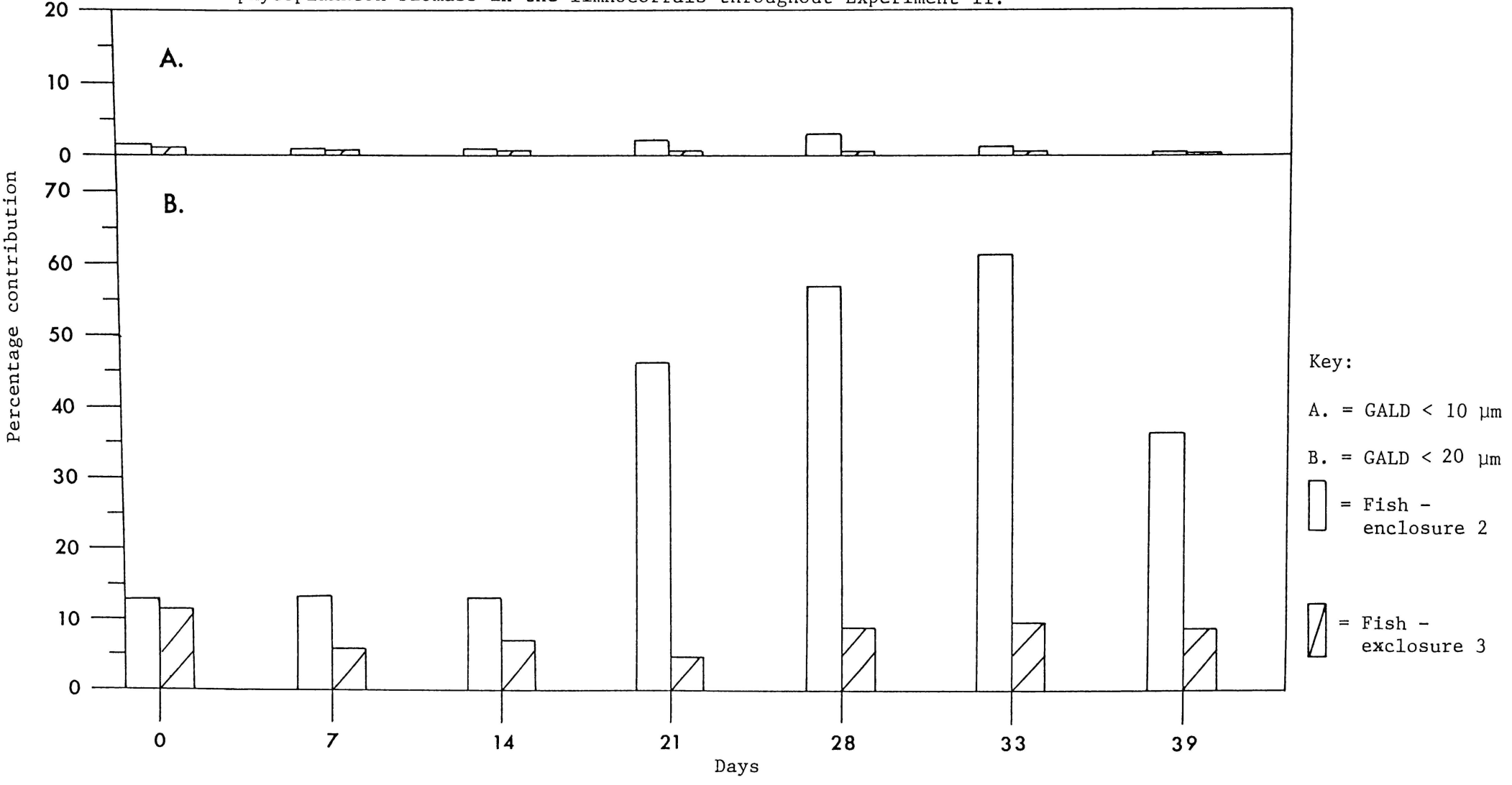
8.5.5 Zooplankton

A list of zooplankton taxa recorded during Experiment II is given in Table 8/15. The cladocerans (*Bosmina meridionalis* and *Ceriodaphnia* sp.), showed a positive response in both LCs, but especially in fish-exclosure 3 (Fig. 8/10). Both species increased most rapidly during the first seven days after manipulation. Slower rates of increase (e.g., *Ceriodaphnia*) or temporary decreases (e.g., *Bosmina*), coincided with declines in both total phytoplankton biomass (Fig. 8/7) and the proportion of the GALD $\leq$ 10 μm fraction of the phytoplankton to the total biomass (Fig. 8/8). In the absence of smelt, copepods (combined counts of nauplii, copepodids and adults) showed greatest increases in their contributions to total zooplankton numbers during the initial period, but different responses then occurred (Fig. 8/11). The relative importance of the cyclopoids increased until day 33, in contrast to that of the calanoids, which remained stable for 14 days after their initial peak, and then declined. In fish-enclosure 2, the relative importance of the cyclopoids also increased until day 28, albeit at a slower rate. However, 14 days after manipulation, the relative importance of the calanoids in fish-enclosure 2 was greater than that in fish-exclosure 3, and it continued to show a steady increase until the end of the experiment. The relative importance of rotifers declined in both the presence and absence of smelt, but particularly in fish-exclosure 3 (Fig. 8/12).

8.5.6 Fish

Nine smelt were recovered from fish-enclosure 2 at the end of the experiment. The gut contents of four (five did not contain

Fig. 8/8 Changes in percentage contributions of the GALD < 10 and 20 µm fractions to the total phytoplankton biomass in the limnocorrals throughout Experiment II.



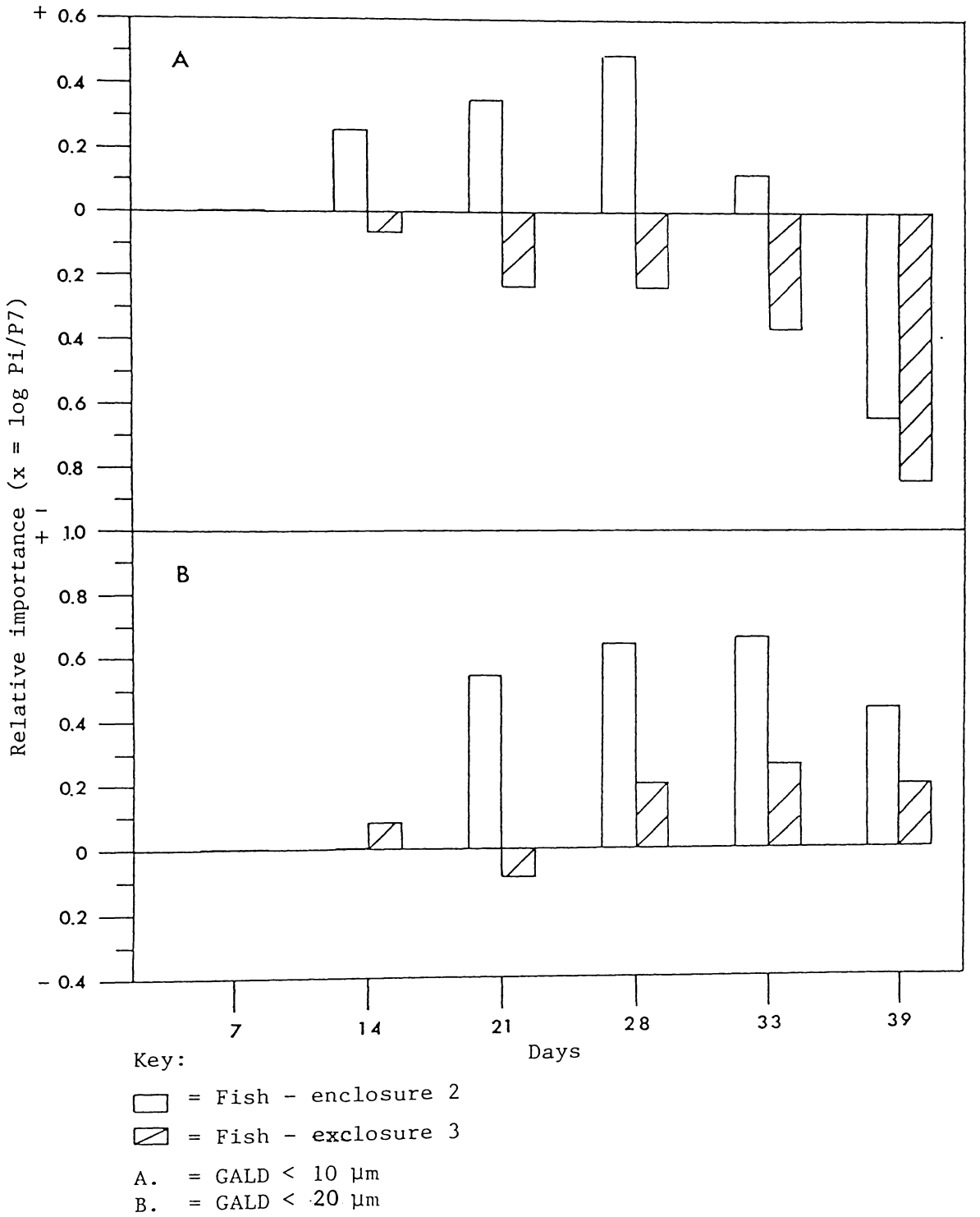


Fig. 8/9 Changes in relative importance of the GALD < 10 µm and 20 µm fractions of the total phytoplankton biomass in the limnocorrals throughout Experiment II.

TABLE 8/15 List of zooplankton species found during Experiment II (M. Cryer, pers. comm.).

ARTHROPODA

Crustacea
Copepoda
Calanoida
Calamoecia lucasi Brady

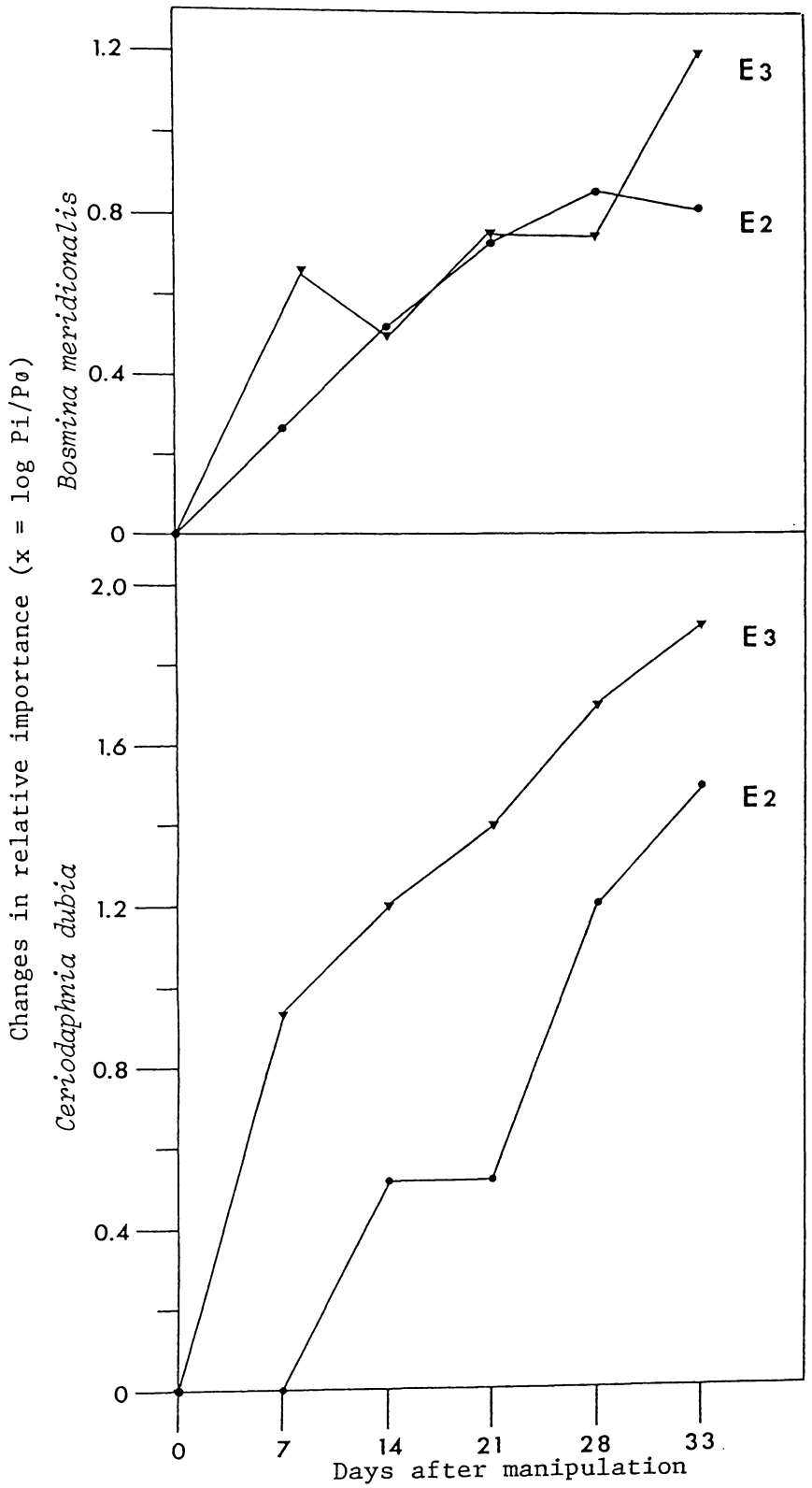
Cyclopoida
Mesocyclops leuckarti Claus
cyclopoid sp./spp.

Branchiopoda
Diplostraca
Alona sp.
Bosmina meridionalis Sars
Ceriodaphnia sp.
Chydorus sphaericus O.F. Müller

ROTATORIA

Monogononta
Ploima
Asplanchna priodonta Gosse ?
Brachionus quadridentatus Hermanns
Cephalodella sp.
Keratella cochlearis Gosse
K. procurva Thorpe
Lecane sp. ?
Mytilina sp.
Polyarthra dolichoptera Idelson
P. minor Voight ?
Proales sp.
Synchaeta pectinata Ehrenberg
S. sp.
Trichocerca sp.

Floscullariacea
Conochilus sp.
Filina terminalis Plate
Hexarthra mira Hudson



Key:

E_2 = Fish-enclosure 2
E_3 = Fish-exclosure 3

Fig. 8/10 Changes in relative importance of cladocerans in the limnocorrals throughout Experiment II.

Fig. 8/11 Changes in relative importance of copepods in the limnocorrals throughout Experiment II.

Fig. 8/12 Changes in relative importance of rotifers in the limnocorrals throughout Experiment II.

Key:

E_2 = Fish - enclosure 2

E_3 = Fish - exclosure 3

Fig. 8/11

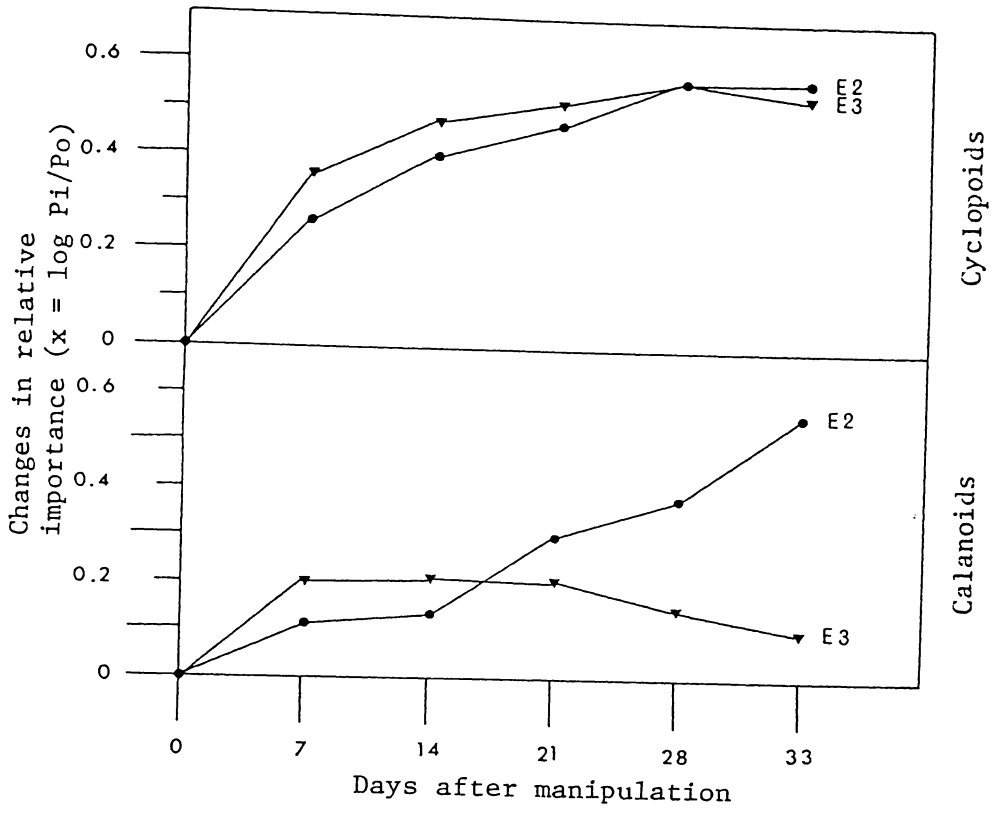
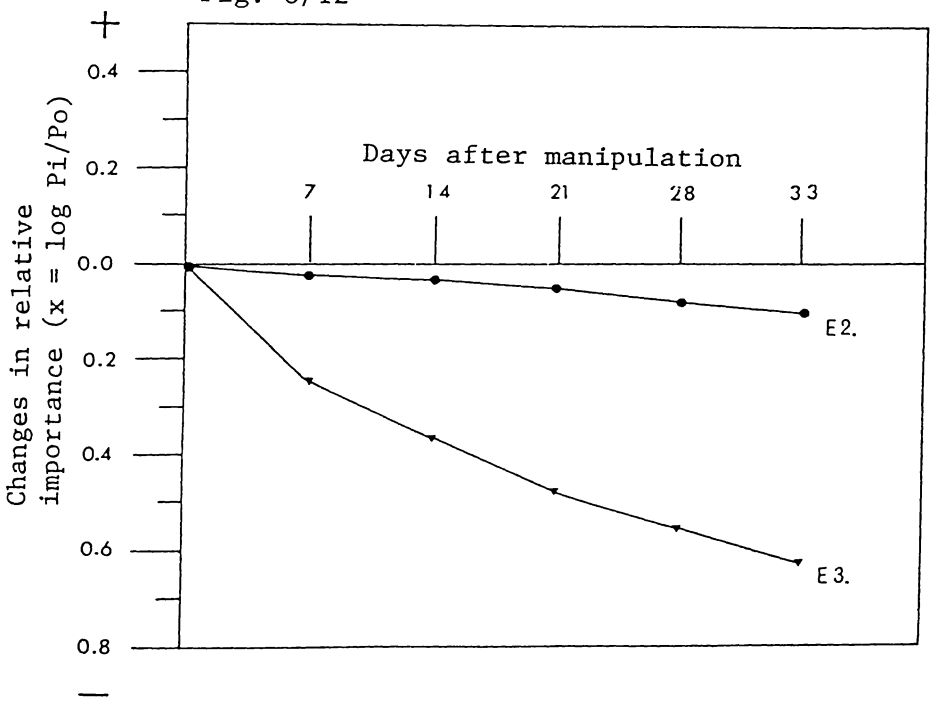


Fig. 8/12



identifiable remains) showed that cladocerans and copepods comprised 92.4 and 7.5% of the contents, respectively (Table 8/16).

8.6 ASSESSMENT OF METHODOLOGY

8.6.1 Containment

Assessment of the role zooplankton herbivory plays in structuring phytoplankton communities requires experimentation using a number of lakes (e.g., Stevenson, 1971) or *in situ* manipulations. Although the former is the ideal method, it is rarely practicable. Limnocorrals provide an acceptable alternative (Lund & Reynolds, 1982).

A wide variety of LCs (including both static and flow-through systems, and volumes varying by a factor of 10^9 [Schelske, 1984]) have been used for a broad range of investigations. However, none has an obvious advantage in relation to any other (Lund, 1978). The advantages of LCs are evident on a general basis (see Uehlinger *et al.*, 1984). The disadvantages include: a large expenditure of manpower; a decrease in natural turbulence and eddy diffusion (and increased stability of stratification); a change in light regime by the polyethylene walls and later by the development of aufwuchs (Uehlinger *et al.*, 1984).

Also, a key problem yet to be resolved is that of LC size. Whereas large LCs have a more favourable surface area to volume ratio, and consequently should be less influenced by wall effects, increasing size can also allow greater heterogeneity (Gamble & Davies, 1982). The horizontal distribution of plankton has been studied in three sizes of enclosure (Stephenson *et al.*, 1984), and no defined edge zone with respect to phytoplankton density or biomass occurred. Zooplankton population estimates varied slightly along distance gradients in their smallest enclosure (20,000 l), but no consistent patterned distribution was apparent.

In the present study, the volumes of both sets of LCs (Experiment I, 1200 l; Experiment II, 9000 l) were considerably less than those used by Stephenson *et al.*, and it was assumed that any heterogeneity was insignificant; also, Uehlinger *et al.*, (1984) considered that single samples from the centre of LCs are sufficient for studies of this type, provided they did not include ^{14}C measurements. For bacterial populations, the edge effect is considered to be minimised by volumes $\geq 10^3$ litres (Ferguson *et al.*, 1984). Larger LCs were

TABLE 8/16 Diet comparisons from gut analyses of four smelt (*Retropinna retropinna*) recaptured from fish-enclosure 2, Lake Rotomanuka North, on completion of Experiment II (Cryer, pers. comm.).

Taxon	Total Number	Mean Percentage of Gut Content ± SE
Cladocerans		
Bosmina meridionalis	1	0.13 ± 0.13
Ceriodaphnia sp.	104	12.2 ± 11.9
Chydorids	832	80.1 ± 18.8
Copepods		
Cyclopoids - nauplii	-	-
- copepodids	22	2.4 ± 2.0
- adults (male)	33	3.8 ± 3.5
(female)	5	0.55 ± 0.45
Calanoids - nauplii	-	-
- copepodids	6	0.7 ± 0.7
- adults (male)	-	-
(female)	1	0.13 ± 0.13

necessary in Experiment II because of the introduction of a third trophic level (Harris *et al.*, 1982).

Although at the commencement of *in situ* experiments the temperature profiles within LCs rapidly become similar to that of surrounding lake water (Boyce, 1974; Takahashi & Whitney, 1977), there is evidence that a reduction in circulation occurs with time (Steele *et al.*, 1977; Menzel & Steele, 1978), which may result in increased sedimentation rates, and consequently is of particular significance in communities dominated by diatoms (Davis & Gamble, 1979). However, it has also been shown that flexible enclosures, such as those used in the present study, not only allow horizontal movement of energy but also permit some vertical transport (Bröckel, 1982), thus reducing losses by sedimentation.

Despite technical difficulties in the use of LC experiments, however, they are still of considerable value, particularly if used as a complement to experimental studies investigating interactions between various trophic levels (Bloesch *et al.*, in press).

8.6.2 The Appropriateness Of The GALD As A Criterion For Grazing Response

Although GALDs and SGALDs of phytoplankton have been used frequently in zooplankton feeding selectivity investigations (e.g., Nadin-Hurley & Duncan, 1976; Lewis, 1979), it was recently concluded (Horn, 1985) that the greatest axial length was the least suitable parameter for characterising food particles; volume, projected particle area or form coefficient were considered more appropriate. Despite the obvious relationship between the volume of a particle and its dimensions, shape is sometimes thought to override such relationships (Lewis, 1979). Vogel's (1981) dimensionless surface area to volume ratio (square root of surface area/cube root of volume) permits investigations of the significance of shape during grazing and consequently was applied to the dominant 'increasers', and 'decreasers', in Experiments I and II. In Experiment I, taxa were placed in one or other of these categories if they showed a significant (t test; $p \leq 0.05$) increase or decrease in their mean contribution to the mean total biomass within the zooplankton-exclosure relative to that in the zooplankton-enclosure. In Experiment

II, statistically accurate categorisation was impossible because of the lack of replicates. Vogel's ratio ranged from 2.14 to 2.78 and GALD varied almost eightfold (Table 8/17). Other morphological characteristics (e.g., mucilaginous sheaths, spines or nature of the cell wall) probably were of some importance in determining algal response to zooplankton grazing pressure, but it is of special interest that the 'decreasers' had GALDs $\geqslant$ 35 μm and dimensionless surface area to volume ratios $\leqslant$ 2.44, whereas the respective values of the 'increasers' were $\leqslant$ 20 μm and $\leqslant$ 2.7. This suggests that algal size, and thus the GALD, is a major determinant of response to grazing pressure and supports the experimental results of Bergquist *et al.*, (1985).

8.6.3 The Acridine Orange Direct Count Method

The acridine orange direct count (AODC) method for the enumeration of aquatic bacteria is a widely adopted technique and has been extensively evaluated and modified by Francisco *et al.*, (1973), Jones (1974), Daley & Hobbie (1975), Jones & Simon (1975), Hobbie *et al.*, (1977), Meyer-Reil (1978) and Zimmermann *et al.*, (1978). However, it cannot be regarded as a routine procedure. Both Jones (1974) and Ramsay (1978) concluded that fluorescence techniques should be used cautiously, as slight technical variations can produce significantly different results. Uniform application is therefore more important than the particular choice of technique made from the numerous AODC methods that are available.

An analysis of variance performed on counts from a Lake Maratoto sample before preservation, and after both 10 and 21 storage days, indicated that no significant change ($p \geqslant 0.05$) occurred as a result of preservation and storage techniques. These results are similar to those of Cooper & Thomsen (1980), but contrary to the views of Ramsay (1978), who considered that fluorescence was sometimes poor when samples were stored fixed and unfiltered.

Nuclepore polycarbonate filters were chosen in preference to cellulose filters because they provide a single focal plane which greatly facilitates enumeration (Daley & Hobbie, 1975). Tests by Cooper & Thomsen (1980) showed that counts from cellulose filters were significantly lower than those on Nuclepore filters. Filtrate counts using Nuclepore filters, yielded similar values to blanks, therefore the lower counts on cellulose filters were considered to result from

TABLE 8/17 Responses of some phytoplankton from the zooplankton-exclosures relative to their contributions made to the total biomass in the zooplankton-enclosures throughout Experiment I. Taxa are arranged from shortest to longest GALD. I = increaser; D = decreaser; d S:V = dimensionless surface area to volume ratio.

Taxon	Category	d S:V	GALD
Scenedesmus ecornis	I	2.78	8.0
Cyclotella stelligera	I	2.38	8.3
Coelastrum microporum	I	2.21	20.0
Botryococcus braunii	D	2.14	35.0
Vacuolaria sp.	D	2.44	36.0
Microcystis aeruginosa	D	2.42	63.0

the trapping of bacteria within the filter meshwork.

The tendency of Sudan Black-B to precipitate from 50% ethanol after *c.* 48 h, necessitated a regular preparation of fresh solutions. This stain also needed to be completely dissolved in absolute ethanol prior to dilution with 0.22 μm filtered water.

Initially, the concentrations of bacteria in both lakes were such that a 5 ml sample was an appropriate volume for enumeration. However, as the experiment proceeded in Lake Rotomanuka North, a 2 ml sample became more suitable. For these samples, a total volume of 10 ml was chosen for filtration, because it has been shown that unless a sample is made up to a total volume of *c.* 6 ml with pre-filter diluent, bacterial distribution is nonrandom, with higher numbers occurring in the peripheral regions (Jones & Simon, 1985).

The distribution of bacteria on the Nuclepore filter was tested using Fisher's Index of Dispersion (Fisher, 1948), as defined by Lund *et al.*, (1958) and described in Chapter 2.5. Twenty filters (10 per study lake) were used and 5 random grids were counted per filter and the null hypothesis that the variance and the mean were equal was rejected twice (Table 8/18). In both instances, the uneven distribution was obvious prior to counting and thus during routine procedures such filters would have been discarded.

Staining with acridine orange 'on filter' (Ramsay, 1978; Zimmermann *et al.*, 1978; Thomsen & Cooper, 1980) was chosen in preference to the 'in solution' staining technique described by Jones (1974), Daley & Hobbie (1975) and Hobbie *et al.*, (1977). Ramsay (1978) obtained significantly higher counts when acridine orange was applied after filtration compared to 'in solution' staining, and Cooper & Thomsen (1980) also considered it to be more satisfactory. Meyer-Reil's (1978) principle of alkaline staining followed by acidic destaining, in combination with a 0.1M phosphate buffer system (Cooper & Thomsen, 1980), provided consistent results.

8.7 DISCUSSION

8.7.1 Experiment I: Hypothesis I - that phytoplankton community composition is not influenced by zooplankton grazing in Lakes Rotomanuka North and Maratoto.

The impact of zooplankton grazing on phytoplankton community composition can be analysed in terms of: (1) species diversity; (2)

TABLE 8/18 Test for random distribution of bacteria on the nuclepore filter: Fisher's index of dispersion (X^2) for counts from 10 filters (5 grids/filter) from Lake Rotomanuka North and Lake Maratoto.

Sample Number	Mean Number of Bacteria ± 1 SD	X^2	*
Lake Maratoto			
1	27.2 ± 2.2	0.69	
2	25.8 ± 4.3	2.9	
3	27.6 ± 8.3	9.9	*
4	27.4 ± 8.9	11.58	*
5	31.4 ± 2.7	0.92	
6	29.2 ± 4.2	3.28	
7	28.8 ± 3.3	1.49	
8	30.4 ± 3.4	1.55	
9	29.0 ± 2.9	1.17	
10	26.8 ± 5.8	3.99	
Lake Rotomanuka North			
1	47.8 ± 5.4	2.49	
2	46.6 ± 6.1	3.2	
3	47.4 ± 4.7	1.88	
4	45.4 ± 6.6	3.86	
5	47.2 ± 4.9	2.01	
6	49.2 ± 6.4	3.43	
7	46.8 ± 3.7	1.17	
8	49.0 ± 4.1	1.35	
9	45.2 ± 5.8	2.98	
10	46.0 ± 5.6	2.7	

Critical value ($p = 0.05$) is 9.488 with 4 degrees of freedom

number of taxa within specific size fractions; (3) species dominance; (4) number of taxa within major taxonomic groups.

The suggestion that zooplankton herbivory is a major factor in explaining the high phytoplankton species diversity so common in lakes was made by Hutchinson (1961), and supporting evidence has continued to be produced. McCauley & Briand (1979) tested the predation hypothesis using LCs in a low-nutrient Canadian lake, and concluded that a reduction in zooplankton grazing pressure produced a significant decrease in numbers of inedible phytoplankton species, whereas the diversity of edible taxa remained unaltered. They considered this to be the result of intensified competition for critical nutrients; smaller, more competitive edible species were considered to have excluded larger, inedible phytoplankton with lower utilisation efficiencies. This conclusion supports Menge & Sutherland's (1976) statement that 'predation is the major factor maintaining diversity at lower levels in trophically complex communities' (McCauley & Briand, 1979; p. 251). However, Lynch & Shapiro (1981), after studying the significance of both grazing and enrichment on phytoplankton species diversity in a eutrophic pond, produced strong evidence to the contrary. Their results suggested that a relaxation in grazing pressure increased the species diversity of both grazeable and non-grazeable taxa. However, they concluded that such results were not incompatible with McCauley & Briand's, because nutrients were not in limited supply.

In the Lake Rotomanuka North zooplankton-exclosures, the increase in mean species diversity throughout the first seven days suggests that during this time some phytoplankton which had previously formed part of the 'hidden flora' (Rahat & Dor, 1968) became quantitatively important because of reduced grazing pressure, and also that the community was not nutrient-limited; the latter is in agreement with the classification given to this lake (Etheredge, 1983; Chapter 7.2). The subsequent decrease in species diversity may be interpreted as a direct response to competition for nutrients within a presumably declining nutrient pool, brought about by a reduction in both mixing (compared to open water) and nutrient recycling by zooplankton (Rigler, 1973; Lehman, 1980a & b; Axler *et al.*, 1981; Henry, 1985). The reduction in mean total phytoplankton biomass after day 10 (Fig. 8/3) also suggests a dwindling nutrient supply. In contrast, there is no evidence to indicate that grazing had similar effects in Lake

Maratoto.

The changes in the number of taxa within specific size fractions in the zooplankton-exclosures in Lake Rotomanuka North, also suggest that zooplankton herbivory influenced phytoplankton community composition. For example, although initially there was no significant difference (t test; $p \geqslant 0.05$) between the mean number of taxa within the GALD $\leqslant$ 10 and 20 μm fractions in the zooplankton-exclosures and zooplankton-enclosure, by day 13 significant differences had occurred, with small edible phytoplankton having increased in the absence of zooplankton, but not the larger (GALD $\geqslant$ 20 μm) taxa (Table 8/19). However, such changes did not occur in Lake Maratoto, where the proportions of the smaller fractions declined in both treatments, except for the GALD $\leqslant$ 20μm fraction which, despite the presence of zooplankton, showed a minor increase from 22 to 25% (Table 8/20).

The results of Experiment I (Figs. 8/0 to 8/2) also suggest that herbivory was responsible for marked changes in both phytoplankton species dominance and numbers of species within the major taxonomic groups in Lake Rotomanuka North, but not Lake Maratoto. In Lake Rotomanuka North, the substantial decline in the importance of *Microcystis aeruginosa* and the increase in the importance of *Cyclotella stelligera* in the absence of zooplankton, produced a major shift from a cyanophycean community to one of diatom dominance, in terms of both abundance and biomass. There was also an increase in the mean contribution of the Euchlorophyceae to the mean total species diversity (34 to 61%), while the proportions of other classes either declined slightly or remained relatively constant throughout the experiment. However, the increase of the Euchlorophyceae in the zooplankton-enclosure was much smaller (31 to 40%).

Other authors (e.g., Porter 1973, 1975, 1977; Fott 1975; Gliwicz, 1975; Vyhnálek, 1983; Benndorf *et al.*, 1985) have also considered that selective herbivory was causal in similar shifts in phytoplankton community composition in non-humic systems.

Information pertaining to regulation of phytoplankton community structure in dystrophic lakes is scarce, but recent interest in artificially acidified lakes (by acid precipitation and mine-drainage) in North America and Europe has prompted several investigations involving selective herbivory, and the results are of some relevance, despite limitations imposed by differences in physico-chemical

TABLE 8/19 Mean number of species (%) within the GALD ⩽ 10 and 20 μm fractions of the phytoplankton on day 0 and day 13 in Lake Rotomanuka North, Experiment I (n = 3).

Day	Mean number of species in GALD ⩽ 10 μm fraction (%)	Mean number of species in GALD ⩽ 20 μm fraction (%)
Zooplankton-exclosure		
0	14.2 *	40.8 *
13	21.7	55.6
Zooplankton-enclosure		
0	12.3	40.9
13	10.0	34.1

* n = 9

TABLE 8/20 Mean number of species (%) within the GALD ⩽ 10 and ⩽ 20 μm fractions of the phytoplankton on day 0 and day 15 in Lake Maratoto, Experiment I.

Day	Mean number of species in GALD ⩽ 10 μm fraction (%)	Mean number of species in GALD ⩽ 20 μm fraction (%)
Zooplankton-exclosure (n = 9)		
0	4.4	27.0
15	1.8	24.8
Zooplankton-enclosure (n = 3)		
0	1.5	22.0
15	0.0	25.0

regimes. For example, an analysis of selective herbivory in Cheat Lake, West Virginia (Havens & DeCosta, 1985), showed that zooplankton exerted little grazing pressure on the phytoplankton community, and a removal of almost all zooplankton did not produce an increase in numbers of small, edible algae, a result remarkably similar to that obtained during the present study of Lake Maratoto.

8.7.2 Experiment I: Hypothesis II - that phytoplankton community biomass is not influenced by zooplankton grazing in Lakes Rotomanuka North and Maratoto.

Traditionally, it has been considered that zooplankton herbivory reduces phytoplankton biomass (Anderson *et al.*, 1955; Patten, 1969). However, it is now known that phytoplankton response to herbivory is variable and dependent upon many factors. Zooplankton may have at least two counteracting influences on phytoplankton populations: herbivory, which reduces biomass; and nutrient regeneration which can stimulate growth (Bergquist & Carpenter, 1986). Recent studies (e.g., Peer, 1986) have emphasised the complexity of the interactions. For example, zooplankton size distribution influences nutrient excretion rates (Peters & Rigler, 1973; Peters, 1975; Hall *et al.*, 1976; Bartell & Kitchell, 1978) and thus nutrient regeneration, a vital nutrient source for phytoplankton (Kitchell *et al.*, 1979; Lehman 1980a b, 1984; Axler *et al.*, 1981). Zooplankton selectivity and algal manageability and/or toxicity are other important factors. For example, some gelatinous, colonial, green algae are capable of increasing in numbers, despite experimental increases in grazer densities (Porter, 1973), because of their ability to remain intact and benefit from nutrient enrichment in the gut (Porter, 1976). Also, nutrients from zooplankton excretion and ejestion (Peters & Lean, 1973; Peters & Rigler, 1973; Peters, 1975) have been considered responsible for growth enhancement of both nutrient-limited, inedible algae (Lehman & Sandgren, 1985) and edible algae (Bergquist & Carpenter, 1986). Also, phytoplankters with significantly fast growth rates (e.g., *Coelastrum microporum*, *C. astroideum* and cryptomonads) have been known to increase in number despite heavy grazing pressure (Vyhnálek, 1983).

The reduction of grazing pressure markedly influenced phytoplankton biomass in Lake Rotomanuka North (Fig. 8/3). The slight

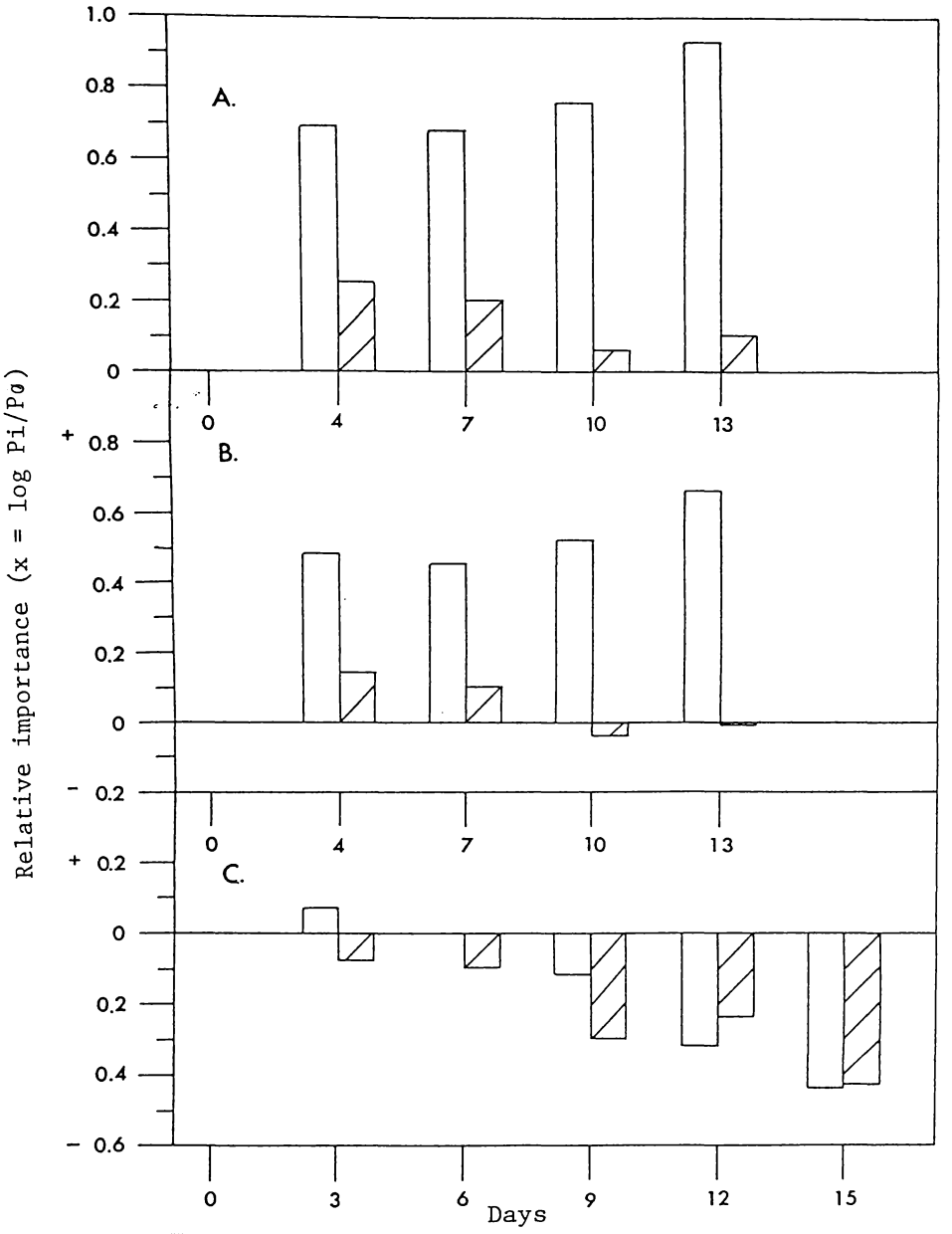
decline during the final three days of the experiment could be either a minor oscillation or an indication of nutrient limitation. In contrast, reduced herbivory had little impact on phytoplankton biomass in Lake Maratoto (Fig. 8/4). The marked increase which occurred in both treatments, (largely due to *Closterium acutum* var. *variable* [Fig. 8/2]), is noteworthy. It is possible that containment provided conditions especially suitable for this species thus promoting a rapid growth rate. For example, it may be assumed that a non-motile phytoplankter such as *C. a.* var. *variabile*, confined to the 0 to 1 m stratum, would experience a more favourable light regime than when randomly distributed within the water column of a humic lake.

The increases in relative importance of the contributions of the GALD $\leq$ 10 and 20 μm fractions to the total biomass in Lake Rotomanuka North but not Lake Maratoto (Fig. 8/13) also suggest that different factors regulated total phytoplankton biomass in these two contrasting lakes. If herbivory was regulating phytoplankton community structure in Lake Maratoto, the contribution of the edible size fraction would have presumably increased (because of lower mortality rates combined with their superior competitive abilities), when grazing pressure was reduced.

8.7.3 Experiment I: Bacterial Densities

Comparisons of bacterial densities from lakes of differing trophic status and allochthonous humic content are difficult to make because of the variety of enumeration techniques employed and the paucity of information about dystrophic lakes. Comparisons of dystrophic lakes are also problematical because frequently no secondary categorisation into eu-, meso- or oligotrophic types is available. However, despite widely ranging values among similar lake types, and also overlap between types, some generalisations have been made (e.g., Wetzel, 1975; Saunders, 1980; Gorlenko *et al.*, 1983), and these suggest that oligotrophic lakes have fewer bacteria than eutrophic lakes, while mesotrophic and dystrophic types occupy an intermediate position (Table 8/21). Thus, the initial mean concentrations of bacteria at the commencement of Experiment I conform to the expected values for meso-eutrophic and dystrophic systems, respectively.

Factors regulating populations of bacterioplankton have been the subject of much interest since the work of Henrici (1938). Variations



Key:

= Zooplankton - exclosure

= Zooplankton - enclosure

A. = Lake Rotomanuka North GALD < 10 µm fraction

B. = Lake Rotomanuka North GALD < 20 µm fraction

C. = Lake Maratoto GALD < 20 µm fraction

Fig. 8/13 Changes in relative importance of the contributions of the GALD < 10 and 20 µm fractions to the total phytoplankton biomass in the limnocorrals in Lake Rotomanuka North, and the GALD < 20 µm fraction to the total phytoplankton biomass in the limnocorrals in Lake Maratoto throughout Experiment I.

TABLE 8/21 A summary of the average and range of total numbers of bacteria in the surface waters of lakes of different trophic status.

Trophic Status	Average Total Number of Bacteria ($10^6.ml^{-1}$) After Saunders (1980)	Range in Total Number of Bacteria ($10^6.ml^{-1}$) After Gorlenko, Dubinina and Kuznetsov (1983)
Oligotrophic	0.5	0.06 - 1.3
Mesotrophic	1.0	1.0 - 2.2
Eutrophic	3.7	2.3 - 8.2
Dystrophic		(0.2) - 1.8 - 3.8

in numbers of bacterioplankton with depth have been significantly correlated with many environmental variables, particularly algal populations, temperature, oxygen concentrations and inorganic nutrients (Overbeck, 1968; Jones 1971, 1972), but temporal trends have frequently been more difficult to interpret (Gerletti & Melchiorri-Santolini, 1968; Jones, 1971, 1977), possibly because of long sampling intervals (Jones, 1973). However, a broad positive correlation has been found between phytoplankton primary productivity and bacterial abundance or microbial activity (Silvey & Wyatt, 1977; Cole, 1982). Generally, maximum numbers of bacterioplankton coincide with algal blooms or their death-phases (Jones 1972, 1976; Coveney *et al.*, 1977; Stráskrabová & Komárková, 1979).

Although numerous early studies demonstrated that zooplankton utilised cultured bacteria (McMahon & Rigler, 1965; Haney, 1973; Gophen *et al.*, 1974; Lampert, 1974) doubts existed concerning the extension of these findings to natural bacteria, owing to size differences (Peterson *et al.*, 1978; Porter *et al.*, 1979). Cultured laboratory strains frequently exceed 1 μm in length, and therefore are larger than natural bacterioplankton (range 0.1 to 1.0 μm) (Porter *et al.*, 1983). However, it has been shown recently that zooplankton (including the genera found in the two study lakes) can utilise small, bacterioplankton (Bogdan & Gilbert, 1984; DeMott & Kerfoot, 1982; Pedrós-Alió & Brock, 1983; Forsyth & James, 1984). Consequently, it is particularly significant that in the presence of zooplankton in Lake Maratoto, the number of bacterioplankton decreased throughout the experiment (56%), despite both a large increase in phytoplankton biomass and minimal environmental changes. This suggests that in the absence of small algae, zooplankton were forced to utilise bacteria to a marked degree. These results contrast markedly with those from the zooplankton-enclosure in Lake Rotomanuka North, where only a small decrease in bacterial density (12%) was recorded. The zooplankton-exclosures from Lake Maratoto and Lake Rotomanuka North, showed increases of 41 and 40%, respectively; the parallel pattern of change in phytoplankton biomass (Fig. 8/4) and bacterial numbers (Table 8/9) in Lake Maratoto is noteworthy.

8.7.4 Experiment II

The impacts of planktivorous fish on zooplankton abundance and

community composition are well-documented (e.g., Brooks & Dodson, 1965: Stenson *et al.*, 1978; Lynch, 1979; Zaret, 1980; Hulbert & Mulla, 1981; Cryer *et al.*, 1986; Vanni, 1987), and the suggestion that fish may be an indirect but major determinant of phytoplankton structure has also been emphasised (e.g., Loso & Hetesa, 1973; Gulati, 1975; Langeland & Reinersten, 1982; Reinersten *et al.*, 1986; Langeland *et al.*, 1987).

The results of Experiment II (Table 8/14) endorse those of Experiment I, and suggest that reduced zooplankton grazing pressure permitted a significant increase in mean phytoplankton species diversity in Lake Rotomanuka North. The highest level of species diversity coincided with the peak biomass (day 21), but was not maintained, presumably because of a dwindling nutrient pool and the concomitant competition for critical nutrients.

Also, as in Experiment I, the percentage contribution of the Euchlorophyceae to the total number of taxa increased dramatically (29 to 59%) when herbivory was reduced, whereas other classes declined slightly or remained relatively unaltered. By contrast, in the absence of fish, only a minor increase (32 to 37%) was recorded.

An alteration in species dominance also occurred. Initially, *Peridinium cinctum* (biovolume 28,742 μm^3) was the major biomass species in both LCs but, in the presence of fish, it declined in contrast with an increase by *Coelastrum microporum* (biovolume 4,190 μm^3) which replaced it as the dominant species (day 28) (Figs. 8/14 and 8/15). In comparison, the relative importance of both *Peridinium cinctum* and *Coelastrum microporum* in fish-enclosure 3 remained relatively stable, until the latter stages of the experiment. These replacements represent a shift from a large K- strategist to a fast-growing, smaller r- strategist, brought about by a reduction in nutrient regeneration by zooplankton. *Nephrocytium agardhianum* made the second largest contribution to the total biomass on day 39 in fish-enclosure 2, and the changes in relative importance which occurred in both LCs (Fig. 8/16), suggest that, despite its gelatinous sheath, this species was not successful under conditions of higher grazing pressure. By contrast, *Closterium acutum* var. *variable* was not disadvantaged by grazing (Fig. 8/17), and replaced *Peridinium cinctum* as the dominant species in fish-exclosure 3.

Fig. 8/14 Changes in relative importance of *Peridinium cinctum* in the limnocorrals throughout Experiment II.

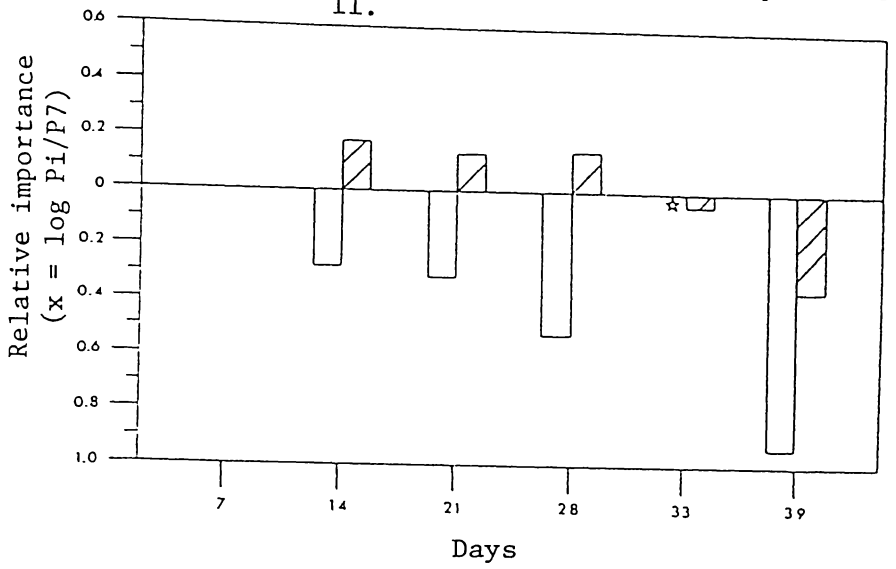
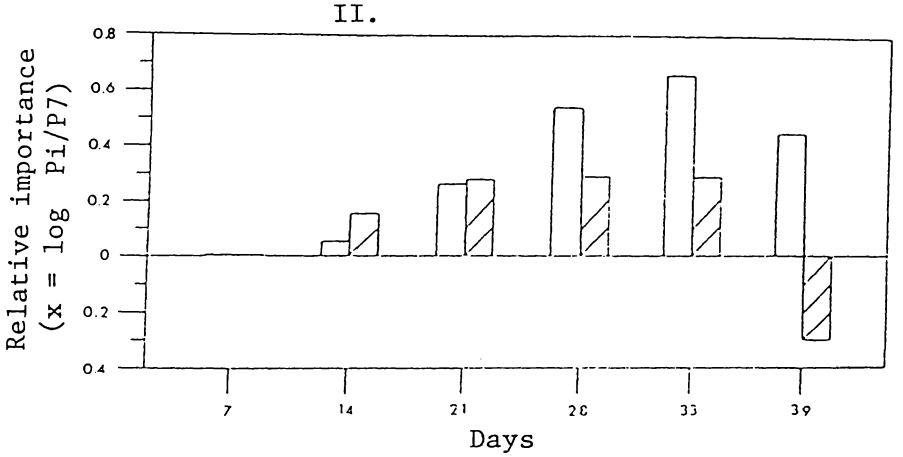


Fig. 8/15 Changes in relative importance of *Coelastrum microporum* in the limnocorrals throughout Experiment II.



Key:

☆ = missing value

□ = Fish-enclosure 2

▨ = Fish-exclosure 3

Fig. 8/16 Changes in relative importance of *Nephrocytium agardhianum* in the limnocorrals throughout Experiment II.

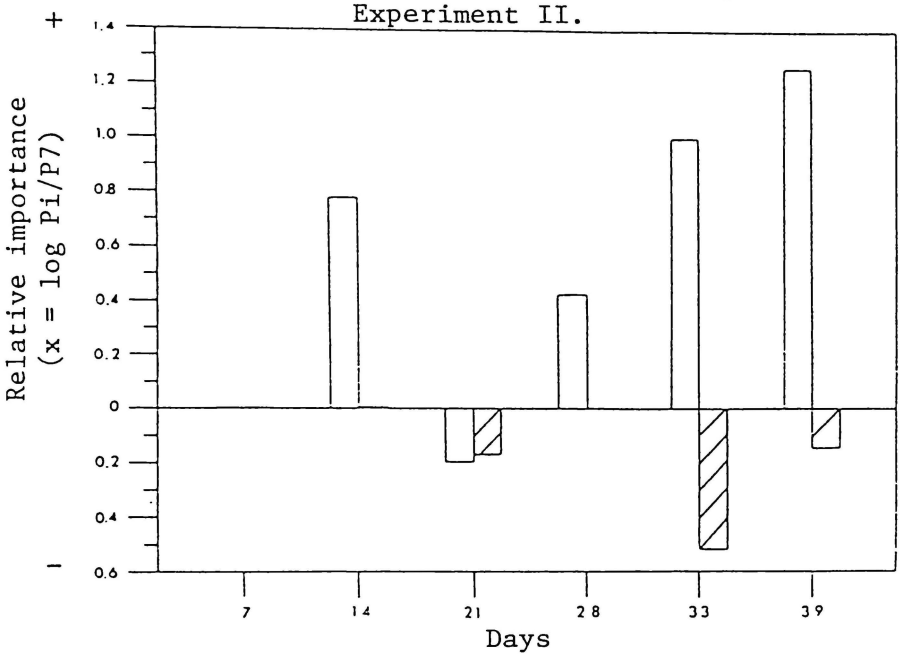
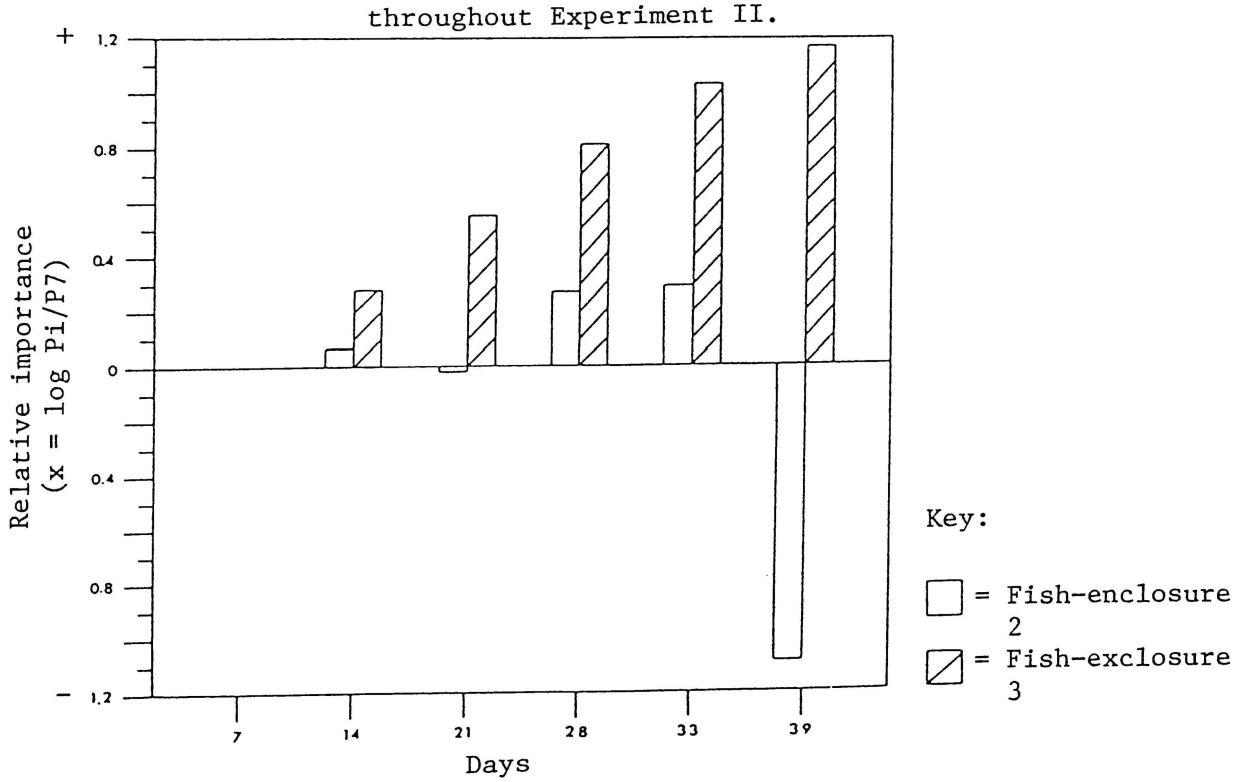


Fig. 8/17 Changes in relative importance of *Closterium acutum* var. *variabile* in the limnocorrals throughout Experiment II.



Thus, as in Experiment I, a reduction in zooplankton herbivory resulted in a shift in dominance from a large to a small species and suggests once more that zooplankton grazing was of major importance in regulating the phytoplankton community composition in Lake Rotomanuka North.

The changes in both the percentage contributions and relative importance of the GALD $\leq$ 10 and 20 μm fractions to the total biomass (Figs. 8/8 and 8/9, respectively), were also similar to those in Experiment I.

Besides the overall increase in zooplankton numbers in the absence of fish, there were also complex interactions occurring amongst the different zooplankton populations. *Ceriodaphnia* sp. was the superior competitor in this situation (Cryer, in press). In the absence of predation, both the cladocerans, but particularly *Ceriodaphnia* sp., increased in relative importance more markedly than the copepods (Figs. 8/10 and 8/11). Gut analyses showed that smelt exhibited a very strong positive electivity for cladocerans (Table 8/16), which may explain their rapid increase in importance in fish-exclosure 3. Similar results from gut analyses of smelt from Lake Rotomanuka North have also been obtained by Mennink (pers. comm.). The calanoid copepods, while appearing to compete less successfully with cladocerans than cyclopoids, were not as adversely affected by competition as rotifers. However, the decline in importance of rotifers in both LCs indicates that other factors as well as competition were determining their population numbers.

8.8 CONCLUSION

The results of Experiment I support the hypotheses that phytoplankton community composition and biomass were not influenced by zooplankton grazing in both study lakes. They suggest that herbivory played a major regulatory role in the almost clear Lake Rotomanuka North, but not in dystrophic Lake Maratoto. The paucity of small edible phytoplankton together with the absence of a marked response to reduced grazing pressure, suggests that the physico-chemical regime is probably the major determinant of phytoplankton community structure in dystrophic Lake Maratoto, which is more suited to large, slow-growing stress-tolerators (Chapter 6).

The Lake Maratoto zooplankton community, deprived of significant

quantities of autotrophic food resources must utilise alternative forms, and the rapid decrease in numbers of bacterioplankton in the presence of zooplankton, suggests that they may have been providing a valuable food supply. Further possiblities include detritus and/or its associated bacteria, heterotrophic microflagellates and dissolved organic material (DOM). Such a proposal is not new. Nauwerck (1963), after studies based on Lake Erken, suggested that zooplankton production could not be supported solely by primary production in all lakes. The importance within aquatic food chains of detritus, together with its associated bacterial community, has frequently been emphasised (Wetzel, 1975; Paerl, 1980; Schoenberg & Maccubin, 1985), and the role of DOM in such trophic systems has been an area of debate since early this century (Jørgensen, 1976). Recent evidence suggests that DOM is of particular significance to zooplankton in highly humic lakes as a direct food source and/or indirectly via heterotrophic microflagellates (Salonen & Hammar, 1986).

Finally, these results suggest that during the experiments the planktonic ecosystems within the two study lakes differed considerably. A phytoplankton-zooplankton trophic organisation (with fish an important regulator at the third trophic level), appeared to be operating in Lake Rotomanuka North, but not in Lake Maratoto. New concepts are required specifically for trophic interactions within dystrophic lakes. Although zooplankton and bacterial community dynamics were probably inextricably interrelated in Lake Maratoto, clarification of such a trophic system can only be gained from detailed investigations into many other related areas. For example, because of the temporal variability of zooplankton grazing, further studies are necessary to establish the influence of both seasonal periodicity and vertical migration of zooplankton on phytoplankton and bacterial communities, particularly in Lake Rotomanuka North where seasonality is important. Also, an investigation into numbers, distribution and relative importance of heterotrophic microflagellates, together with the precise role of DOM within the two types of food chains, would be highly informative. However, a more complete understanding of the trophic relationships and community regulators within these Waikato lakes demands similar analyses of others, particularly Lakes Mangahia and Mangakaware which, in terms of pH and water colouration (Table 3/10), occupy an intermediary position.

CHAPTER NINE

CONCLUDING SUMMARY

The present study shows that the nine study lakes (and by implication others in the area) form a unique group within New Zealand. Although located in relatively close proximity to one another, and of similar age and origin, they displayed a wide range of phytoplankton community structure and seasonal dynamics, largely caused by differences in: amounts of allochthonous DHM, which in turn varied upon the degree of catchment modification; exposure to wind, and thus stability of the water column; and morphometry, particularly mean depth.

Because of marked differences in pH, Secchi disc transparency, light absorbance (270 and 400 nm) and turbidity within the series, as well as various degrees of staining, the study lakes were separated into four groups. First, Lakes Maratoto and Mangahia were both dystrophic and characterised by low pH, darkly-stained waters, low Secchi disc transparencies, and very high light absorbance; secondly, Lakes Kainui and Mangakaware were both moderately stained with relatively high light absorbance and low mean Secchi disc transparencies, but their neutral median pHs (7.0 to 7.2, respectively) precluded a dystrophic classification; thirdly, Lakes Rotoroa, Rotokauri and Rotomanuka North were characterised by brown-green to almost clear water, high Secchi disc transparencies, low light absorbance, and neutral median pHs (range 7.6 to 7.9); and finally, Group IV lakes, Ngaroto and Rotomanuka South, were yellow-brown in colour, with high turbidities, conductivities and pHs, and low mean Secchi disc transparencies.

The majority of the study lakes were discontinuous, warm polymictic systems, a direct result of their generally shallow nature and exposure to prevailing winds. These lakes were further divided into two types. Lakes Maratoto, Kainui and Ngaroto were similar in that marked water column stability was apparent on only one brief occasion during summer. In Lakes Mangahia, Mangakaware, and Rotoroa, several periods of increasing stability developed throughout summer, but were frequently interrupted by complete vertical mixing. Lakes Rotokauri and Rotomanuka South were also polymictic, although both displayed more lengthy periods of marked summer stratification. 'Step

structuring' was apparent in the temperature profiles of many of the polymictic lakes, however, it always extended to the bottom waters, because frequent, complete mixing of their water columns precluded an establishment of 'older' basal water bodies.

Lake Rotomanuka North is the most sheltered of the nine study lakes, and also has the highest mean depth. Consequently, it was warm monomictic, with marked stratification during summer. It is the only study lake of this type, although this classification may well be appropriate for Lake Rotokauri in less windy years.

Despite fluctuating thermal regimes, oxygen saturations in both bottom and surface waters of the polymictic lakes were relatively low. Although several factors may have been responsible, the presence of DHM and high oxygen demands of the rich, organic sediments undoubtedly were key regulators, together with suspended particulate matter (itself resulting from the frequent mixing episodes). Such suspended particulate matter was of particular importance in Lakes Mangahia and Mangakaware, where high levels of turbidity were not coincident with high phytoplankton abundance.

The major differences which occurred in both phytoplankton community composition and seasonal dynamics can be interpreted in terms of these varying physico-chemical regimes. Phytoplankton community composition, in terms of both species diversity and the distribution of species within the major taxa, was markedly influenced by humic content. Species diversity was typically low in the two dystrophic lakes (Maratoto and Mangahia), and remarkably high in Lakes Rotokauri and Rotomanuka North, undoubtedly because of the approximately neutral pHs, relatively high Secchi disc transparencies, and stable thermal regimes of these latter two lakes. There were significant positive correlations between the mean number of species per sample, and both pH and mean Secchi disc transparency (when Group IV lakes were omitted from the analyses). Furthermore, numbers of euchlorophytes, and the proportions of cyanophytes, were also significantly correlated with pH. Such relationships are common in European humic lakes. In addition, the diatom floras of both dystrophic lakes were comprised largely of acidophilic, acidobiontic or indifferent species, which was not the case in other study lakes.

Floristically, the nine study lakes differed markedly from other groups of New Zealand lakes. Species diversity was extremely high (402) and yet undoubtedly, there are other species still to be found.

Eutrophic waters and rich organic sediments, together with a mix of both stratified and frequently mixed water columns, resulted in both relatively high euglenophyte species diversity and, at times, significant standing crops in terms of both density and biomass. These generally coincided with declines of major total phytoplankton biomass peaks. However, compared to many oligotrophic groups of lakes (e.g., some within the Rotorua Lake District), numbers of desmid species were relatively low, in contrast to the densities of some desmids (e.g., *Staurodesmus* spp.) which were remarkably higher. Compositional overlap between lakes at both generic and specific levels was low, with only 24 species being found in all nine lakes. Of these, however, 16 ranked as important species (ISI) in at least one lake, suggesting that the group contains a small core of ecologically versatile species; for example, *Closterium acutum* var. *variabile*, *Cryptomonas* spp., *Cyclotella stelligera*, *Monoraphidium contortum*, and *Trachelomonas volvocina*. Conversely, the study lakes were characterised by an extremely large 'hidden flora'; for example, 33% of all taxa were found in only one lake.

Most of the study lakes were highly productive, with mean total phytoplankton biomasses and densities ranging from 0.7 to 72.2 g m^3 and 0.4 to 11.6 pu ml^{-1}, respectively. These results indicate that some of the study lakes (Maratoto, Ngaroto and Rotomanuka South) are the most productive recorded in New Zealand to date. The majority of species (75%) which had one of the ten highest ISIs per study lake have either been recorded as 'dominant' in one or more eutrophic/meso-eutrophic New Zealand lakes, or are regarded as key indicators of such waters elsewhere.

Reduced annual temperature ranges in Lakes Rotomanuka North and Rotokauri resulted in unpredictable peaks of total phytoplankton biomass (and numbers) throughout the year, in marked contrast to the pronounced seasonal patterns found in warm monomictic Northern Hemisphere lakes. Such aseasonality must have important implications for zooplankton life cycles and strategies, and thus higher trophic levels, in lakes of both mixing patterns.

Hutchinson's (1967) provisional classification of phytoplankton types was appropriate for some of the associations: (1) Lakes Maratoto and Kainui were categorised as *Botryococcus braunii* and meso- or eutrophic desmid planktons, respectively; (2) Lakes Mangahia and

Mangakaware were, in general terms, diatom planktons; (3) Lakes Rotomanuka North and Rotoroa belonged to the dinoflagellate type; (4) and Lakes Ngaroto and Rotomanuka South were Myxophycean planktons. In addition, despite the relatively shallow nature and general instability of the water columns of most of the study lakes, several of Reynolds' (1980) species associations (in a strict phytosociological sense) were also identifiable.

Temporal patterns of community composition reflected the mixing patterns present during the study. Three types of seasonal dynamics were apparent. First, domination by one or two classes throughout the entire sampling year was found in those lakes with minimal water column stability throughout summer (Maratoto, Kainui, and Ngaroto). The species involved were usually overwhelmingly dominant, and were large K- strategists (*Botryococcus braunii*, *Staurodesmus* spp., and *Microcystis aeruginosa*). These study lakes were also characterised by relatively high mean PScs, and relatively low mean Shannon-Wiener indices and mean numbers of species per sample. Secondly, an unpredictable sequence of domination, one class replacing another after only a brief period of importance, occurred in lakes with frequent episodes of both temporarily stable and mixed water columns (Mangahia, Mangakaware and Rotoroa). The key species were generally r-strategists (e.g., *Asterionella formosa*, *Acanthoceras zachariasi*, or *Tetrastrum triangulare*) which are, as a result of their large surface area to volume ratios and potential for rapid density increases, favoured by allogenic changes. Predictably, the grand mean Shannon-Wiener index and mean number of species per sample were relatively high in these lakes. Finally, marked seasonal periodicity (including autogenic succession) occurred in Lake Rotomanuka North, with a shift from r- to K- selected species accompanying the changes in thermal stability from winter to summer/autumn.

The seasonal periodicity of Lake Rotokauri was slightly more complicated in that, despite the occurrence of lengthy periods of water column stability, species domination was episodic and unpredictable. Two factors may have been responsible, acting either alone or in concert: first, the influence of dense macrophyte beds, and their decomposition during the latter stages of the sampling programme; secondly, the lake may have mixed more frequently than the sampling programme revealed.

While the most fundamental changes in phytoplankton seasonal dynamics were directly related to morphometry and mixing patterns, experimental studies showed that zooplankton grazing was an important regulator of phytoplankton community structure in Lake Rotomanuka North, and by implication at least other Group III lakes, during summer. Reduced herbivory resulted in shifts, in terms of biomass, from communities dominated by large K- strategists (*Microcystis aeruginosa* [Experiment I] and *Peridinium cinctum* [Experiment II]) to smaller, fast growing species *Cyclotella stelligera* [Experiment I] and *Coelastrum microporum* [Experiment II]). Furthermore, minimal grazing pressure permitted increases in numbers of taxa and total biomass of smaller edible phytoplankton (GALDs $\leq$ 20 μm), as well as an increase in numbers of euchlorophyte species.

Such responses were not apparent in dystrophic Lake Maratoto, suggesting that zooplankton played little part in directly controlling its phytoplankton community structure and biomass (although it must have been indirectly important through nutrient recycling). Instead, the quantity of DHM, high nutrient levels, and polymixis are probably the key regulators.

However, as these experiments were carried out in summer only, repetitions during other seasons are a prerequisite for a detailed understanding of the role of herbivory in the regulation of both community composition and seasonal periodicity. This is particularly important in Lake Rotomanuka North, because of its pronounced seasonality. However, it is probably unlikely, in terms of the mixing pattern of Lake Maratoto, together with the overwhelming dominance of *Botryococcus braunii* throughout both the present study and 1979 (Etheredge, 1983), that repeats in this lake would produce different results. Nevertheless, if pH increases and the concomitant alterations in floristic composition continue, smaller species will undoubtedly become more important, and thus biological factors (particularly herbivory) will interact with the physical/chemical processes to determine annual periodicity. At present, however, it would appear that trophic organisation within the humic and almost clear water lakes differs considerably, with energy transfer in the former occurring largely through a heterotrophic-based food chain, shortened by a paucity of fish.

The present study prompts many questions. First, it is apparent

that experimental studies and analyses of phytoplankton communities from other darkly-stained lakes are necessary in order to establish the precise influences of DHM on these associations, as well as the role of herbivory as a community regulator in oligotrophic dystrophic lakes. Secondly, although in terms of Gleason's (1926) individualistic interpretation of 'succession', seasonal periodicity is a consequence of differential growth, reproductive and survival abilities of the various species, there is still remarkably little information about the life history strategies of abundant phytoplankters such as *Acanthoceras*, *Botryococcus*, *Monoraphidium*, *Tetrastrum* or *Vacuolaria*. Clearly there is an urgent need for long-term data sets from the study lakes to enable the formulation and testing of hypotheses regarding the autecology of their major species. At a more general level, further long-term monitoring would also permit estimations of inter-annual variability in the structure and biomass of the phytoplankton communities (which may be high in the less darkly-stained polymictic lakes) and, in turn, its influence on other organisms, particularly grazers, in these unique ecosystems.