The Role of Zooplankton Grazing
in the
Maintenance of Phytoplankton Species Richness

by

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ABSTRACT

The hypothesis that zooplankton grazing plays a major role in the maintenance of high phytoplankton species richness was tested over a two-year period using controlled field experiments at Heney Lake, Quebec. Reduction of grazing pressure in large volume polyethylene enclosures resulted in a significant decrease in the number of algal species considered inedible, whereas the diversity of the edible algae remained unaffected. Alteration of grazing pressure changed the structure of the inedible group, which became dominated by the diatom *Synedra*. The structure of the edible group did not appear affected by the manipulation, although there was an increase observed in the percent contribution of this group to total algal density. According to taxonomic affiliation the blue-green algae, especially *Chroococcus limneticus*, appear to rely heavily on the presence of zooplankton grazing for their existence in the community.

The effect of dilution on phytoplankton community structure was also examined. The major effects were to increase the importance of minor species in the edible group and to increase the domination of *Gloeotrichia echinulata* and *Synedra* in the inedible group. In enclosures which were initially diluted, the impact of lowering herbivore levels on phytoplankton community structure was reduced compared to the non-diluted conditions. Although the responses in species richness of the two groups were still in the same direction, the magnitude of change was reduced.

It is suggested that lowering the herbivore levels causes an intensification of exploitative competition among phytoplankton, which favours edible species and a few inedible algae like *Synedra* at the expense of many inedible species that are eliminated. In addition, possible changes in the role played by zooplankton in maintaining phytoplankton species richness as the nutrient status of lakes increases are discussed.

RÉSUMÉ

L'hypothèse que la prédation par le zooplancton joue un rôle majeur dans le maintien d'une grande diversité du phytoplancton fut testée pendant deux étés consécutifs, au Lac Heney, Québec. Une réduction des niveaux de zooplanctons dans des réservoirs de polyéthylène entraîna une diminution significative du nombre d'espèces non-comestibles de phytoplancton sans altérer le nombre d'espèces comestibles. La réduction de la pression prédative altéra la structure du groupe non-comestible dans lequel l'espèce Synedra devint dominante. La structure du groupe comestible ne fut pas affectée par ces manipulations, mais une augmentation de la densité relative de ce groupe parmi le phytoplancton total fut observée. Du point de vue taxonomique, les algues bleues, en particulier l'espèce Chroococcus limneticus, nécessitent la présence de la prédation par les zooplanctons pour se maintenir dans la communauté.

L'effet de la dilution sur la structure de la communauté phytoplanctonique a été également examiné. Les effets majeurs observés furent l'importance accrue d'espèces mineures comestibles et l'augmentation de Gloeotrichia echinulata et de Synedra dans le groupe non-comestible. Dans les réservoirs initialement dilués la réduction des niveaux du zooplancton sur la structure de la communauté phytoplanctonique eut un effet moindre que dans les conditions de non-dilution. Les changements dans le nombre d'espèces des groupes étaient toujours dans la même direction mais la magnitude du changement était réduite.

Il est suggéré que la réduction de la pression prédative intensifie la compétition exploitative entre les espèces du phytoplancton. Dans ce cas les espèces comestibles et quelques espèces non-comestibles comme Synedra sont favorisées aux dépens de nombreuses espèces non-comestibles qui sont éliminées. Le rôle joué par la prédation zooplanctonique dans le maintien d'une grande diversité phytoplanctonique est discuté pour le cas des lacs qui possèdent une plus grande concentration d'éléments minéraux.

INTRODUCTION

One of the major goals in ecology today is to gain an understanding of how natural communities are organized. A community can be defined as an association of interacting populations of all trophic positions, usually delimited by their interactions or by spatial occurrence (Pianka 1974). Two characteristics of communities are often examined to assess the role played by various factors in their organization (Caswell 1976). One is the number of species present or the species richness, and the second is the relative abundance of those species. These parameters are sometimes combined into a mathematical statement or index of community diversity (Pielou 1975). Frequently in utilizing these mathematical indices much information is lost, and as pointed out by May (1976), few indices reveal as much about the biological characteristics of a community as does simply the number of species present.

Several hypotheses have been put forward as factors controlling the species richness of communities. These differ mainly with respect to time scale (i.e. evolutionary or ecological), interactions involved (i.e. abiotic or biotic), and the scale of application (i.e. global or local), however they often overlap in their mechanism of action (Pianka 1966). Many hypotheses, especially those of a local nature, have been stimulated by the apparent contradiction between coexistence of species and the competitive exclusion principle (Hardin 1960). The principle simply states that at equilibrium complete competitors cannot coexist. Explanations have centered on the failure or success of achieving equilibrium in natural systems and on the amount of allowable overlap in the requirements of species before exclusion will occur.

Predation is one factor which has been implicated in allowing the coexistence of competing species ever since Darwin (1859) recorded the effect of mowing on grassland plant communities. Paine (1966) clearly formulated and tested the hypothesis that predation on dominant competitors could promote local coexistence of species in the intertidal community of rocky shores. Since then many workers have attempted to assess what characteristics of both the predator and prey are important in predicting when predation will enhance species richness. It is also of importance to predict the conditions under which the effect of predation on coexistence will be negative or negligible (Harper 1969; Caswell 1978). Although most applications of the predation hypothesis have been to explain local coexistence of species, Stanley (1973) has postulated that the evolution of herbivory in the Precambrian period could be responsible for the large increase in diversity of organisms observed at that time.

Depending on the intensity of predation, species richness can either be enhanced or reduced. If the intensity is severe, then the probability of local extinction of prey species would be increased, resulting in a lower number of species than was present without predation (Spight 1967; Paine & Vadas 1969; Lubchenco 1978). Further, intense predation pressure would decrease the rate of successful colonization of prey species entering the system therefore lowering species richness (Paine 1966). Competitive exclusion could be prevented under intermediate intensities of predation, which would maintain equilibrium densities of prey at a level lower than that required for exclusion (Cramer & May 1972; Addicott 1974; Lubchenco 1978). Under low predation pressure species would be able to reach levels high enough to bring about competitive exclusion thus reducing the number of coexisting species.

If the pattern of predation is intermittent or periodic, then its effect on prey coexistence will be determined by the relation between the time required to achieve equilibrium and the time between successive periods of predation (Caswell 1978). The temporary action of predation would generate potential for colonization. If the time period between disturbance is less than the time required to achieve equilibrium, then coexistence would be promoted (Hutchinson 1961). If however it is greater, then the action of intermittent predation should not affect the number of species present, but it may influence the qualitative composition of the prey community.

The mechanism of predation is also important in the coexistence of prey species. If the predator is selective, then predation on the dominant species can prevent the monopolization of resources, thereby promoting coexistence (Paine 1966, 1971; Cramer & May 1972; Lubchenco 1978). When the prefered prey is subordinate then the effect of predation would be to decrease species richness (Lubchenco 1978). For a switching predator which consumes the most abundant species preferentially, then species richness can be increased through increasing the maximum allowable niche overlap between prey (Roughgarden & Feldman 1975). If predation is indiscriminate or random then mild pressure will stabilize prey interactions if there is dominance expressed among the prey and thus promote coexistence (Yodzis 1976). All of the above statements contain the essential assumption that the prey species compete in the absence of predation. Yodzis (1977) has shown theoretically that if the prey are coexisting through resource partitioning then indiscriminant predation would be expected to decrease species richness in a randomly fluctuating environment. Therefore to make accurate predictions as to the role of predation in a community characteristics of both the predator and prey and also environmental considerations must be taken into account.

The community of interest here is that of the plankton, which consists of microscopic plants and animals found in the open water of lakes. The phytoplankton, or plant members of the plankton, constitute a closely related assemblage of species or guild (Root 1967). Throughout this work the phytoplankton is commonly referred to as a community simply because the terminology is firmly entrenched in the literature (Wetzel 1975) although it is recognized that it does not conform to the formal definition.

The major purpose of this thesis is to examine the role of predation by zooplankton in controlling phytoplankton community structure with emphasis on the maintenance of species richness. It is composed of three sections. The hypothesis that zooplankton grazing is important in the regulation of phytoplankton species richness is tested in the first section. The next section investigates how the role of predation may be altered by manipulating, through dilution, the degree of interaction between phytoplankton species. The last section examines the response of various phytoplankton species to reduced predation pressure under normal and diluted conditions.

Section I

The Role of Zooplankton Grazing in Maintaining Phytoplankton Richness and Community Structure

Several mechanisms have been proposed to explain the surprisingly high diversity found in lake phytoplankton communities. Hutchinson (1961) in presenting the "paradox of the plankton" put forward several hypotheses, including predation, as possible factors maintaining this high diversity. He suggested that with sufficient temporal variation in the environment coexistence would be possible due to the failure to achieve equilibrium and thereby competitive exclusion. This was supported by the model of Greeney _et al_. (1973) which allowed for coexistence by taking into account temporal variation in nutrients. Various workers (Moss 1969; Richerson _et al_. 1970, 1975; Reynolds 1976; Harris & Smith 1977) have illustrated through detailed sampling the possibility of spatial heterogeneity or patchiness in the phytoplankton, which could also account for the failure to achieve competitive equilibrium.

An alternate hypothesis, assuming equilibrium conditions, was proposed by Petersen (1975). Using a nutrient uptake model he predicted that coexistence is possible through the ability of phytoplankton species to partition resources. The model requires that species differ in their ability to obtain nutrients and that the growth of each species be controlled by a unique set of nutrients. Tilman (1976, 1977) has verified in laboratory experiments that resource partitioning can allow for coexistence in phytoplankton. Few workers however (Porter 1973, 1977; O'Brien 1974) have attempted to examine the possible role of predation by zooplankton in the maintenance of phytoplankton diversity.

The predation hypothesis was first formulated by Paine (1966) to explain local diversity patterns on rocky intertidal shores. He suggested that: "local species diversity is directly related to the efficiency with which predators prevent the monopolization of the major environmental requisites by one species". The presence of predation could act to alter the competitive outcome between prey in favour of coexistence. A large body of theoretical evidence has since accumulated to isolate the parameters affecting the operation of such a mechanism (Paine 1966; Spight 1967; Parrish & Saila 1970; Cramer & May 1972; Van Valen 1974; Roughgarden & Feldman 1975; Yodzis 1976, 1977; Caswell 1978). It is now clear that the characteristics of both predator and prey must be taken into account, and particularly the intensity, mechanism, pattern and mode of predation as well as the relative distribution of competitive abilities among prey and their correlation with intrinsic rate of increase (Addicott 1974). Perhaps, in addition, the nature of competition between the prey species (i.e. interference or exploitative) and also how the physical presence of the predator affects this interaction should be considered.

Most tests of the predation hypothesis, either experimental or descriptive, have been performed on communities where the primary requisite is space (Paine 1966, 1971, 1974; Harper 1969; Paine & Vadas 1969; Dayton 1971; Porter 1972, 1974; Lubchenco 1978). In many of these cases predation was shown to play an important role in regulating species richness. Few studies have tested the predation hypothesis in communities where the primary requisite is not space but nutrients. Addicott (1974) in studying protozoan communities of pitcher plants showed that predation was not important in regulating species numbers, although it did seem to control the evenness component. He concluded that the low degree of interaction present in the protozoan prey community, through either resource partitioning or temporal heterogeneity, was the primary reason for the invalidation of the hypothesis. However Brooks & Dodson (1965) and Hall _et_ _al_. (1970) found that predation by fish was important in maintaining diversity in zooplankton communities.

Several characteristics have been shown for both phytoplankton and zooplankton which suggest that predation could be of importance in maintaining high algal diversity. Hutchinson (1961) stated that because of the similar requirements of phytoplankton and the severe nutrient depletion which occurs in lakes during summer months, competition could be expected to be intense. In addition phytoplankton species differ in their abilities to utilize nutrients (Dugdale 1967; Eppley _et_ _al_. 1969; Carpenter & Guillard 1971; Lewis 1976, 1977; Friebele _et_ _al_. 1978), which suggests an uneven distribution of competitive abilities. There is also extensive evidence from both laboratory (Burns 1968a, 1968b; Arnold 1971) and field experiments (Gliwicz 1969, 1975; Porter 1973; Weers & Zaret 1975; Nadin-Hurley & Duncan 1976), that zooplankton feed selectively on the basis of size, taste, and morphology of their prey items.

The major purpose of this study was to test, using controlled field experiments, if predation is important in the maintenance of high diversity in phytoplankton. The experiments described below were de-signed to test the prediction that a reduction of zooplankton grazing pressure would cause a decrease in the number of phytoplankton species.

MATERIALS & METHODS

Field experiments were performed over a two year period in Heney Lake, Quebec (46°02'N, 75°55'W) which is located approximately 96 km north of Ottawa, Ontario. Heney Lake is a hard-water lake of low nutrient status attaining a maximum depth of 25 m. A relatively sheltered bay of uniform depth 10 m located at the northern end of the lake was chosen as the site for the experiments.

Experiments involved the use of polyethylene enclosures or tubes to isolate a column of water with its associated biota. The enclosures are cylindrical with a diameter of 1 m and are 10 m in length (approximate volume = 8000 l). They are sealed at the bottom and are open at the top to allow for gaseous exchange. The enclosures were launched by sinking the collapsed container, then, after return to calm conditions, drawing it up through the water column. They were then filled to capacity using a gas powered water pump.

In 1976 preliminary experiments were conducted on a long-term basis from June 17 to November 10. In an attempt to generate appreciable differences in predator/prey ratios the following manipulations were carried out. Two enclosures were enriched weekly with nitrogen (NO_3^-) and phosphorous (PO_4^{3-}) in concentration of 100 μgN/l and 10 μgP/l respectively. The other two were left unenriched. Further, in two containers - one from each set - the adult stages of crustacean zooplankton were removed once weekly by passing a net of 135 μm aperture and 0.75 m diameter through the water column.

Sampling for both phytoplankton and zooplankton was conducted weekly prior to manipulation. Samples were taken at four depths: subsurface, 3, 6, and 9 m using a 2 l Van Dorn bottle. They were then filtered to concentrate (100 ml) using a 35 μm mesh filter and immediately preserved with Lugol's solution. To assess the possible modification of the physical environment in enclosures, oxygen and temperature profiles were recorded weekly using a YSI model 54 meter in both the lake and the enclosures.

Phytoplankton samples were analysed for both species composition and abundance using a Zeiss inverted microscope following the technique described by Lund et al. (1958). Usually a 5 ml aliquot was examined and one strip enumerated. Species identification was made using keys provided in Irénée-Marie (1939), Prescott (1961), and Bourrelly (1966). The number of species recorded in the count was taken to represent species richness. Phytoplankton data were expressed in terms of both density (ind./l) and volume (μm^3/l). Estimates of phytoplankton volume were made by first calculating the volume for each species following Kovala and Larrance (1966) and then extrapolating using concentration values. Zooplankton samples were enumerated using a Wild M-7 stereomicroscope. Usually a 20 ml aliquot was examined and a minimum of 200 individuals counted. Zooplankton species were identified using keys in Pennak (1953) and Edmondson (1965).

The following year several improvements to the experimental procedures were implemented. In 1977 the experiments involved six enclosures and lasted six weeks from July 15 to August 19. In three enclosures the levels of zooplankton were altered by passing the 135μm mesh net through the water column twice weekly after biological sampling was completed. The manipulation was performed twice to induce a greater reduction of zooplankton stocks than had been achieved in the previous year. Three enclosures remained untouched and acted as controls.

Phytoplankton sampling was modified in that this time the samples were combined prior to filtration then concentrated to 100 ml. Furthermore to improve the degree of accuracy, two strips were enumerated and usually a minimum of 800 individuals counted. Zooplankton sampling was by vertical net haul using a 110μm mesh net of diameter 0.28 m. The samples were concentrated to 100 ml and preserved in Lugol's solution. A 20 ml aliquot was enumerated after preliminary statistical analysis had established that this volume ensured an accuracy greater that 90% ($p < 0.05$) on the estimates of zooplankton abundance.

In analysing the data the following criteria were adopted on the basis of experimental evidence cited in the introduction. Phytoplankton considered inedible are all blue-green algae irrespective of size and all other algae greater than 50μm in maximum dimension. Phytoplankton which are edible are all those less than 50μm and including *Asterionella formosa* which can be broken down easily and ingested by herbivores (Nadin-Hurley & Duncan 1976). Some taxa were excluded from the analysis due to questionable status. These include species of *Dinobryon* (Tappa 1965), *Sphaerocystis* and *Elakotothrix* (Porter 1975, 1976), and *Fragilaria* and *Tabellaria* (Porter, pers. comm.).

Species of zooplankton considered to be herbivores included the cladocerans *Chydorus sphaericus*, *Bosmina longirostris*, *Daphnia galeata*, *D. longiremis*, *D. retrocurva*, *Diaphanosoma leuchtenbirgianum*, *Ceriodaphnia reticulata*, and *Holopedium gibberum*, and two copepod species of the genus *Diaptomus*. In addition, the immature stages of both calanoid and cyclopoid copepods were included as herbivores.

RESULTS

Experiments 1976

The physical data collected (Table 1) suggest that enclosures do not modify to any extent temperature or oxygen regimes. The effect of reduced predation was actually tested in only two enclosures. Those were the unfertilized ones that registered a significant difference (Wilcoxon matched-pairs signed-ranks test, $p < 0.025$) in herbivore levels from June 23 to September 1 (see Table 2). Surprisingly a larger concentration of grazers was found in the manipulated container than in the control. The level of the rotifer population was not observed to be affected by the manipulation (Table 3).

The response of the phytoplankton to reduced grazing pressure is shown in Fig. 1. In the enclosure containing less herbivores total species richness appears slightly reduced (Fig. 1a). This is due to the significant reduction (Wilcoxon test, $p < 0.025$) in the inedible group (Fig. 1c), which counteracts the intermittent increase observed in the edible group (Fig. 1b).

Experiments 1977

The levels of herbivorous zooplankton recorded in each enclosure are indicated in Table 4. One of the control enclosures was damaged in a storm during the course of the experiment and thus was discarded from the analysis. Following an initial decline in zooplankton abundance in

Table 1 Examples of oxygen (ppm.) and temperature (°C) profiles recorded from inside enclosures and from the lake during 1976.

TABLE 1

	Oxygen (ppm)		Temperature (°C)		Temperature (°C)	
	July 13		July 13		August 2	
Depth (m)	Enclosure	Lake	Enclosure	Lake	Enclosure	Lake
subsurface	8.4	8.2	20.8	20.8	20.2	20.2
1	8.4	8.2	20.5	20.5	20.2	20.2
2	8.4	8.3	20.2	20.2	20.2	20.2
3	8.5	8.2	20.0	20.0	20.2	20.2
4	8.6	8.2	19.0	19.0	20.2	20.2
5	8.0	7.9	17.1	17.0	20.2	20.2
6	7.6	7.4	16.0	16.0	20.2	20.2
7	7.2	7.2	15.2	15.5	20.2	20.0
8	7.1	6.8	13.8	14.3	20.1	20.0
9	6.7	6.5	13.0	12.5	20.1	20.0

Table 2 Densities (No./10 litres) of herbivorous zooplankton recorded in the four enclosures used in 1976.

TABLE 2

	Density			
	Unenriched		Enriched	
Date	Control	Manipulated	Control	Manipulated
June 23	570	1,057.5	1,970	607.5
July 6	307	1,625	3,845	1,732.5
July 13	457.5	1,262.5	3,125	1,395.0
July 27	587.5	757.5	---	---
August 3	937	1,550	6,157	2,520
August 10	325	1,487.5	7,695	6,432
August 17	287.5	995	11,482.5	7,232
August 24	607	2,137.5	10,875	8087.5
August 31	1,050	4,550	6,845	3,775
September 7	2,675	3,162	6,037.5	1,957
September 14	3,375	2,337.5	3,000	3,775
September 21	3,900	1,025	507.5	837.5
September 28	632.5	1,445	657.5	375
October 5	832.5	1,725	637.5	407.5
October 12	920	695	570	570
October 19	2,100	862.5	682.5	445
October 25	857	875	907.5	662.5

Table 3 Densities (No./10 litres) of rotifers recorded in the unenriched enclosures used in 1976.

TABLE 3

	Density	
	Unenriched	
Date	Control	Manipulated
June 23	3,957	11,845
July 6	3,920	2,975
July 13	2,625	6,100
July 27	3,770	3,095
August 3	820	5,132
August 10	2,045	3,437
August 17	5,555	5,400
August 24	5,622	5,962
August 31	2,455	6,487
September 7	3,337	4,050
September 14	3,082	3,325
September 21	3,732	4,045
September 28	2,720	5,387
October 5	4,145	6,995
October 12	3,095	5,662
October 19	4,087	4,495
October 25	2,787	4,032

Fig. 1 1976 Test: Species richness of (A) the entire phytoplankton community, (B) the edible group, and (C) the inedible group under low (open circles) and significantly higher grazing pressure (solid circles).

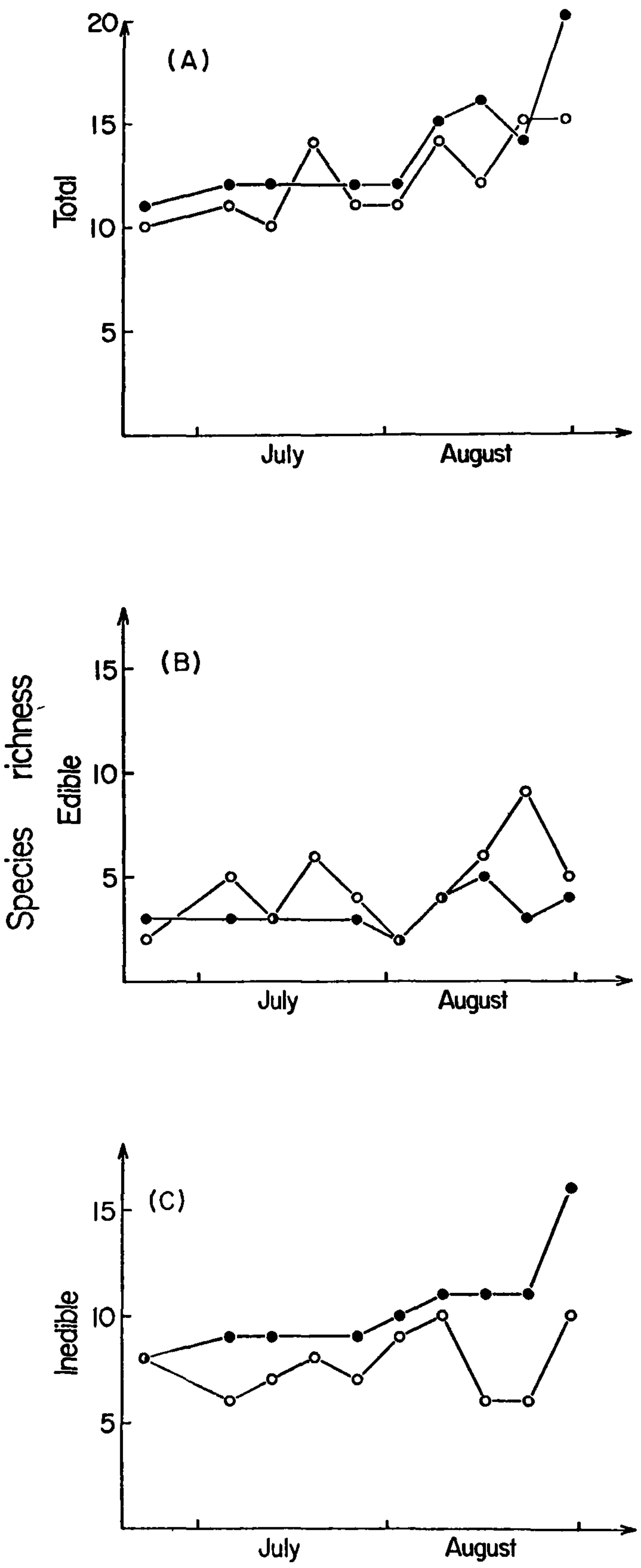

(A)
Total
20
15
10
5
July
August
(B)
Species richness
Edible
15
10
5
July
August
(C)
Inedible
15
10
5
July
August

Table 4 Densities (No./10 litres) of herbivorous zooplankton recorded in the two control and three manipulated enclosures from the 1977 test.

TABLE 4

	Density				
	Control		Manipulated		
Date	A	B	C	D	E
July 22	93.7	116.9	130.0	56.6	25.6
July 29	129.5	202.1	19.9	98.0	113.1
August 5	426.2	380.17	155.7	205.0	167.5
August 12	391.5	315.5	135.2	151.1	190.6
August 19	1,025.7	745.5	92.6	159.7	98.8

all containers during the first week of experimentation one observes thereafter a significant reduction of herbivore levels in the manipulated enclosures (Friedman two-way analysis of variance, $p < 0.01$), which extends to six-fold at some points.

The reduction of grazing pressure achieved from July 22 to August 19 resulted in a decline in total phytoplankton species richness that became very pronounced at the end of the experiment (Fig. 2). Unfortunately, due to the loss of one of the control enclosures, the number of replicates does not allow for testing statistically differences at one point in time. The inedible group registers a significant reduction (Friedman test, $p < 0.05$) of species richness under reduced predation (Fig. 3), whereas the number of edible species appears generally unaffected (Fig. 4). This result is consistent for both years of experiments and provides evidence that the observed response was due to reduced predation and not simply to the effect of manipulation on the system.

The relative contribution of each group to total algal volume and density is presented in Table 5. While the relative volume of both groups appears unaffected by the manipulation, the relative density of the edible species increased with reduced herbivore levels.

Figures 5 and 6 illustrate for each group the effect of reduced grazing pressure on the relative volume of their major species. Only those species contributing more than 10% to the total algal volume are labelled. They are listed in Table 6. The structure of the inedible

Fig. 2 1977 Test: Total algal species richness in control (solid symbols) and manipulated enclosures (open symbols). Significant differences in grazing pressure occur between enclosures from July 29 to August 19.

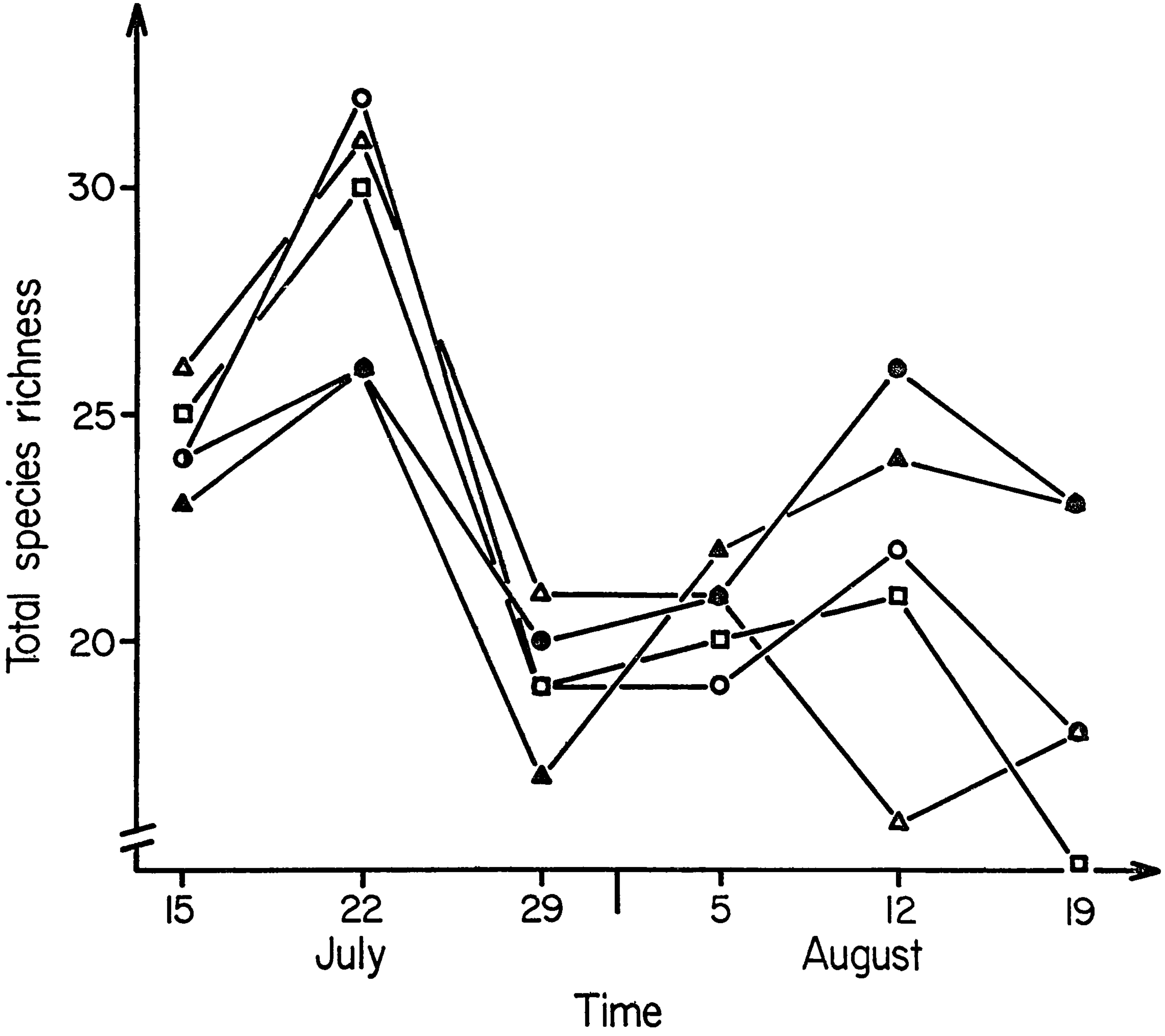

Total species richness
30
25
20
15
22
29
5
12
19
July
August
Time

Fig. 3 1977 Test: Species richness of inedible algae in control (solid symbols) and manipulated enclosures (open symbols). From July 29 to August 19 significant differences in both the level of herbivores and also the number of inedible species occur between enclosures.

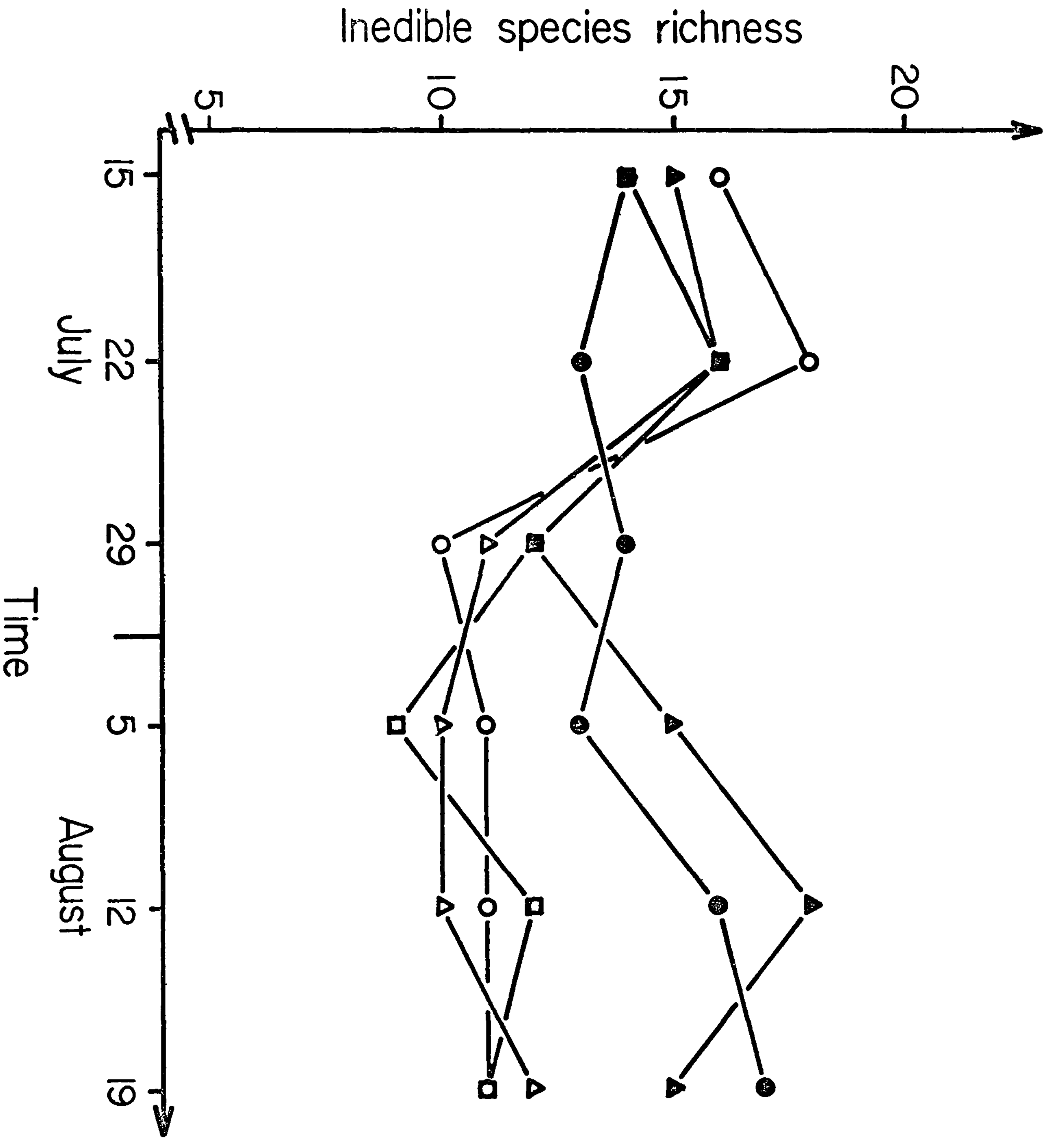

Inedible species richness
5
10
15
20
15
22
29
5
12
19
July
August
Time

Fig. 4 1977 Test: Species richness of edible algae in control (solid symbols) and manipulated enclosures (open symbols). During the period in which significant differences in grazing pressure exist between enclosures (July 29 - August 19) there is no significant difference in the number of edible species.

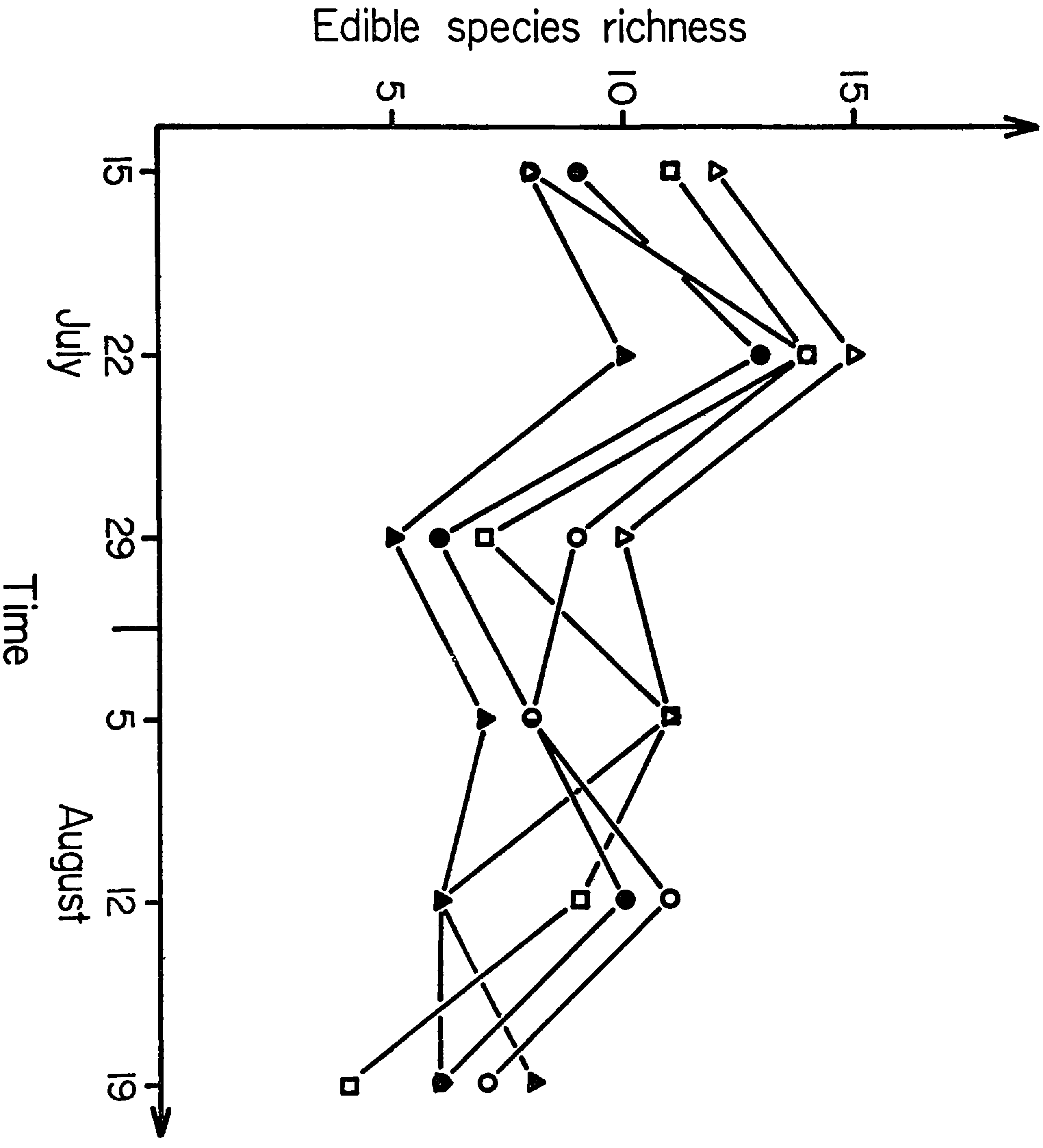

Edible species richness
5
10
15
15
22
July
29
Time
5
12
August
19

Table 5 Relative percent contribution of the edible and inedible group to total phytoplankton volume and density during the period of significant reduction in the level of herbivores (1977).

TABLE 5

		Date				
		July 22	July 29	August 5	August 12	August 19
1) Volume						
Inedible Control	A	96.5	92.2	84.1	96.3	98.3
	B	95.1	87.2	92.0	97.0	97.5
Manipulated	C	97.1	92.9	92.5	92.2	94.4
	D	96.5	91.2	87.7	94.0	96.9
	E	84.7	92.5	83.0	97.4	99.5
Edible Control	A	3.5	7.8	15.9	3.7	1.7
	B	4.9	12.8	8.0	3.0	2.5
Manipulated	C	2.9	7.1	7.5	7.8	5.6
	D	3.5	8.8	12.3	6.0	3.1
	E	15.3	7.5	17.0	2.6	0.5

TABLE 5 (Cont'd)

		Date				
		July 22	July 29	August 5	August 12	August 19
2) Density						
Inedible Control	A	95.9	96.0	89.4	94.5	97.4
	B	96.5	94.7	85.8	92.1	96.4
Manipulated	C	96.0	92.2	89.0	89.2	92.5
	D	93.9	90.1	83.1	82.4	94.2
	E	89.5	86.5	71.9	88.3	95.8
Edible Control	A	4.1	4.0	10.6	5.5	2.6
	B	3.5	5.3	14.2	7.9	3.6
Manipulated	C	4.0	7.8	11.0	10.8	7.5
	D	6.1	9.9	16.9	17.6	5.8
	E	10.6	13.5	29.1	11.7	4.2

group (Fig. 5) varies greatly between the control and manipulated enclosures. With reduced herbivore levels this group becomes dominated by the diatom Synedra, whereas blue-green and green algae dominate the control situation. The structure of the edible group (Fig. 6) appears less affected by changes in the degree of predation. Under reduced grazing pressure one observes a decline in the dominance of Asterionella formosa and a larger contribution by species that are of minor importance in the control situation.

Table 6 List of species contributing volume in excess of 10% to their respective groups (edible or inedible) during the 1977 experiments.

TABLE 6

Code	Species
1	*Anabaena* sp.
2	*Anabaena spiroides*
3	*Aphanizomenon flos-aquae*
4	*Ceratium hirundinella*
5	*Gleoetrichia echinulata*
6	*Lyngbia Birgei*
7	Inedible pennate diatoms
8	*Peridinium* sp.
9	*Staurastrum paradoxum*
10	*Synedra* sp.
11	*Ankistrodesmus falcatus*
12	*Asterionella formosa*
13	*Chlamydomonas* sp.
14	*Cryptomonas erosa*
15	*Euglena* sp.
16	Edible pennate diatoms
17	*Scenedesmus obliquus*
18	*Stephanodiscus* sp.

Fig. 5 Structure of the inedible group on the basis of volume for the time period in which significant differences in grazing pressure existed between control and manipulated enclosures (1977 test). Species contributing volume in excess of 10% to the group are labelled with a numerical code and presented in Table 6.

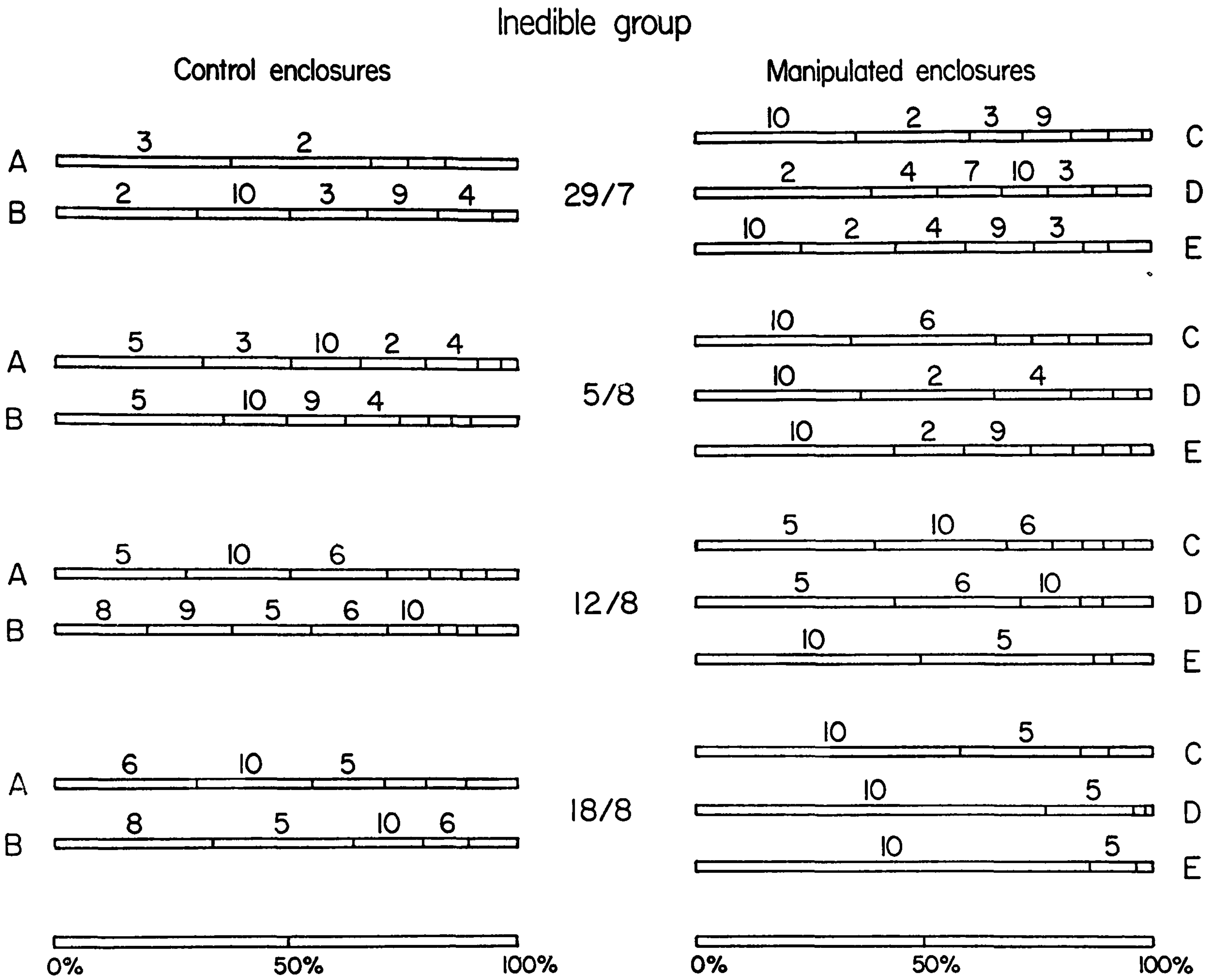
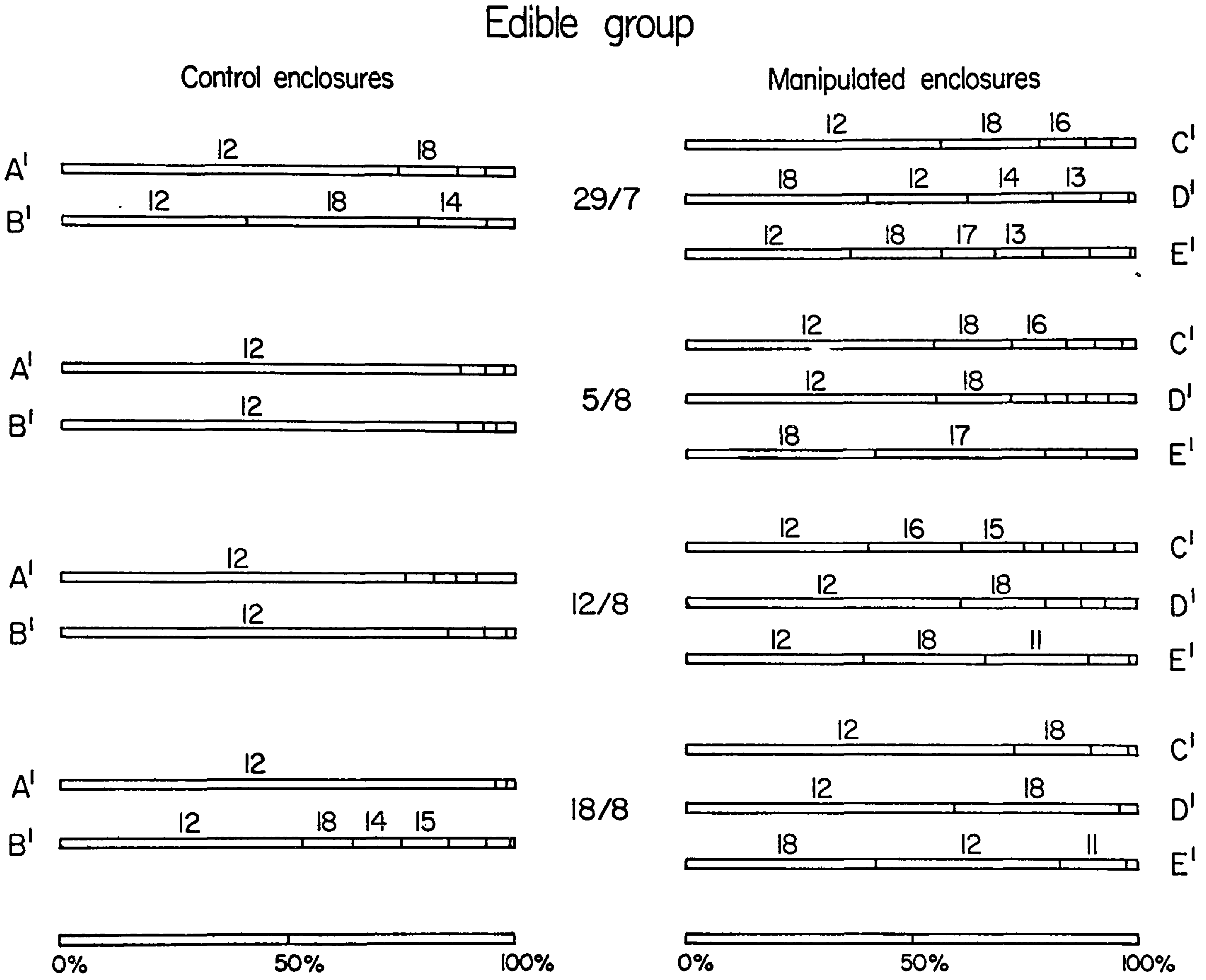

Inedible group
Control enclosures
Manipulated enclosures
A 3 2
B 2 10 3 9 4
29/7
C 10 2 3 9
D 2 4 7 10 3
E 10 2 4 9 3
A 5 3 10 2 4
B 5 10 9 4
5/8
C 10 6
D 10 2 4
E 10 2 9
A 5 10 6
B 8 9 5 6 10
12/8
C 5 10 6
D 5 6 10
E 10 5
A 6 10 5
B 8 5 10 6
18/8
C 10 5
D 10 5
E 10 5
0%
50%
100%
0%
50%
100%

Fig. 6 Structure of the edible group on the basis of volume for the time period in which significant differences in grazing pressure existed between control and manipulated enclosures (1977 test). Species contributing volume in excess of 10% to the group are labelled with a numerical code and presented in Table 6.


Edible group

DISCUSSION

The results of the field experiments lend additional support to the predation hypothesis since reduced grazing pressure resulted in an appreciable reduction of phytoplankton species richness. This implies that the prey widely differ in their competitive abilities (Paine 1966). Indeed the differential response of the edible and inedible species to the manipulations suggests that the former are better competitors than the latter, and that coexistence is mediated by predation.

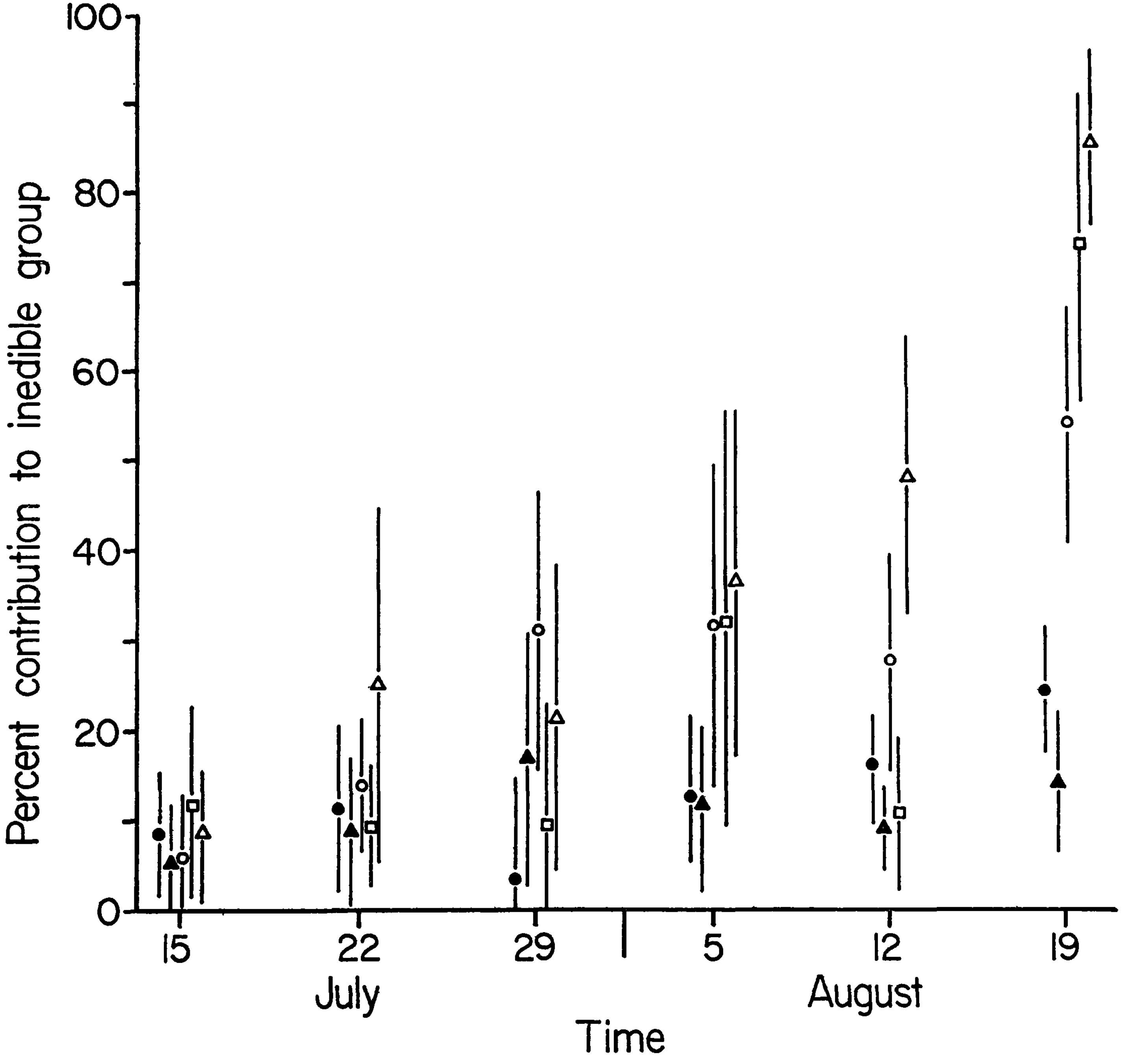
The basis for such a mechanism may be provided by differential nutrient uptake that is related to the size and shape of the cell (Dugdale 1967; Eppley *et al*. 1969; Carpenter & Guillard 1971; Lewis 1976, 1977; Friebele *et al*. 1978). As reviewed by Porter (1977) the smaller species or the species with the higher surface/volume ratios are generally favoured at low nutrient concentrations. Small size is also a criterion of edibility, therefore the edible species may well have the ability to out-compete some inedible species when their density is no longer limited by grazers. This was the case here: as predicted in our cybernetic model (Briand & McCauley 1978), decreasing the herbivore levels allowed the density of the edible group to increase appreciably (see Table 5).

As a result a few inedible species, that were rare to begin with, may have been eliminated. However the extent of this increase in density was probably insufficient to cause the rapid reduction of as many as a third of all inedible species, particularly since the increase in the relative volume of the edible algae was negligible due to their much smaller size. In other words the reduction observed in the number of inedible species under reduced grazing pressure cannot be accounted for by only intensified competition between edible and inedible species. Perhaps the changes in herbivore levels resulted in new nutrient ratios that were less beneficial to the inedible than to the edible species. It is possible that increased competition within the inedible group for nutrients provides an additional mechanism to explain the disproportionate decrease in the number of inedible species. The specific hypothesis to be tested is that under reduced grazing pressure the density of certain inedible algae reaches levels high enough to cause the competitive exclusion of other inedible species.

This study provides evidence that supports this hypothesis: suffice to notice the spectacular rise of the population of the inedible diatom _Synedra_ in the three manipulated enclosures (Fig. 7). This is in agreement with the findings of Hurlbert _et al_. (1972) who recorded a similar shift in some experimental ponds where zooplankton stocks had been reduced following the application of an insecticide.

Since it is inedible _Synedra_ is not directly limited by grazers, therefore why does this species become dominant only when herbivore levels are decreased? Grazers regenerate nutrients and also prevent some nutrients from being consumed by certain species. Therefore reducing herbivory rate may affect both the absolute quantities and the

Fig. 7 Relative contribution of *Synedra* to the volume of the inedible group, expressed as a percentage, in control (solid symbols) and manipulated enclosures (open symbols) during the 1977 test. Vertical bars indicate error estimates in the enumeration of samples as determined from Lund *et al*. (1958).


Percent contribution to inedible group
100
80
60
40
20
0
15
22
July
29
5
12
August
19
Time

relative proportions of available nutrients. Since diatoms are particularly sensitive to changes in phosphorous: silicon ratio (Tilman 1976, 1977), it could be that Synedra became dominant as a response to such a shift. Another possibility is that under normal conditions Synedra is prevented from dominating the community because of its susceptibility to the growth inhibitors secreted by some members of the inedible group, in particular certain blue-green algae (see Keating 1977, 1978). Only under grazing pressure, when the density of those toxic species is reduced by exploitative competition with edible algae, would Synedra be able to reach high enough levels to bring them to extinction.

The results indicate that predation is important in preventing the smaller more efficient species from monopolizing resources and also in indirectly altering the competitive outcome among certain inedible species. Whether this is a general case in the phytoplankton needs to be examined further. The experimental lake used in this study is of relatively low nutrient status. Perhaps in lakes with different regimes and trophic structures the importance of predation in controlling community structure may be altered.

In order to make predictions as to the role of predation as one moves from nutrient-poor lakes to those of rich status, changes in the characteristics of both herbivores and prey must be examined. In lakes with a very rich supply of nutrients the competitive advantage provided nannoplankters by their small size may be reduced. This would make the relative distribution of competitive abilities among phytoplankton more even, subsequently increasing the time for exclusion. Exclusion time is an important factor in determining the competitive outcome among prey. Knowing its relation to environmental change one can generate predictions as to coexistence of species (Hutchinson 1961). By increasing the time for exclusion, coexistence is more likely due to the failure to achieve competitive equilibrium, thereby decreasing the necessity of predator mediated coexistence.

It is also necessary to consider possible changes in the nature of competition and resource utilization among phytoplankton as the nutrient status changes. Case and Gilpin (1974) have suggested that along resource gradients, the interference competitor will dominate in the region of high resource availability, whereas the exploitative competitor is favoured at the low end. In nutrient-rich lakes, algal standing stock can reach high levels. Under these conditions the ability of species to utilize light efficiently becomes increasingly important (Talling 1971). Thus species capable of regulating their position in the water column so as to optimize light utilization are at a definite advantage (Fogg & Walsby 1971; Reynolds 1972, 1975). Shading, a form of interference competition, where one species interferes with the ability of another to obtain light, should occur more often. In addition the high density of algae facilitates the use of allelopathic mechanisms of interference, since the concentration of extracellular products is important for their impact (Keating 1978). The algal community of nutrient rich lakes is usually dominated by species which are particularly suspect of using allelopathic mechanisms such as the blue-green algae. Thus there is a shift in the nature of competition from a dominance of exploitation in nutrient poor waters to that of interference in nutrient rich lakes.

Predation can mediate coexistence through its ability to prevent the dominant competitors from monopolizing resources. However because of the shift in the nature of competition as the nutrient status of lakes increase and the subsequent dominance of phytoplankton species considered inedible, this role must be questioned. It is hypothesized here that the role of predation in promoting coexistence among phytoplankton should decrease as the nutrient status of lakes increases. There is some evidence to support this hypothesis. A common observation is that lakes rich in nutrients are less diverse than lakes of low nutrient status (Margalef 1964) possibly reflecting the decreased importance of predation in mediating coexistence. Gliwicz (1969) in examining zooplankton feeding found an increased importance of bacteria and a reduction of phytoplankton in the diet of grazers as the nutrient status of lakes is increased, indicating alteration of the trophic structure.

The hypothesis as to the role of predation could be tested by performing experiments similar to that described in this section in a variety of lakes with different nutrient regimes. The specific prediction to be tested is that a reduction in zooplankton grazing pressure would not cause a significant decrease in phytoplankton species richness in nutrient-rich lakes as opposed to that found here in a nutrient-poor lake.

Porter (1977) in discussing this reduction in diversity as nutrient status increases, suggested that in oligotrophic waters "low densities of algae presumably reduce the intensity of biological interactions that would lead to exclusion of algal species". However the intensity of the biological interaction depends less on the absolute abundance of species than on the relative availability of resources shared in common. Therefore this does not appear to be a plausible explaination for the observed trend in diversity.

Menge and Sutherland (1976) hypothesized that predation will be of more importance in maintaining diversity at lower trophic levels and in trophically complex communities whereas competition is more important at higher trophic levels and in trophically simple communities (Dobzansky 1950; Pianka 1966). The results of this study and that of Addicott (1974) support this hypothesis, however it is not clear whether it is resource partitioning or temporal heterogeneity which is responsible for the maintenance of diversity in Addicott's work. In their formulation, Menge and Sutherland relied heavily on observations from the intertidal zone where space is the resource in demand. The availability of space depends on both biological factors and physical disturbance for its renewal (Connell 1975). In aquatic communities nutrient availability depends not only on the turnover time but also on the input and output of the system. Therefore this variable must also be taken into account in postulating the closeness of organisms to their carrying capacity and thus the degree of interaction.

In concluding it is suggested that zooplankton predation allows the coexistence of a large number of phytoplankton species by preventing the competitive exclusion of many inedible algae which would otherwise occur as a result of intensified exploitative competition in the absence of grazing. In addition, the role of predation in maintaining phytoplankton richness is postulated to decrease as the nutrient status of lakes increases. The diverse array of phytoplankton communities found in nature offer the possibility of testing the various hypotheses concerning diversity and community organization. These hypotheses are not mutually exclusive, therefore the demonstration of one mechanism does not preclude the operation of another. Indeed much valuable information about a community can be gained through understanding how the various mechanisms interact and under what conditions one would be expected to predominate.

Section II

The Effect of Dilution
on
Phytoplankton Richness and Community Structure
and in
Altering the Role of Predation

Whether predation is important in maintaining species richness has been shown to depend on a variety of factors, including characteristics of both the predator and prey. In considering the prey, the relative distribution of competitive abilities as well as the correlation with intrinsic rate of increase are important (Addicott 1974). The degree of interaction between prey species will depend not only on their biological characteristics but on environmental considerations as well. As mentioned earlier factors such as the time for exclusion are of considerable importance in determining the competitive outcome among prey species. Predation is likely to mediate coexistence when the degree of interaction between species in intense. It may act to increase the time for exclusion to a length such that exclusion is an unlikely event (Caswell 1978).

In the phytoplankton community, the degree of interaction between coexisting species will depend on a variety of factors such as availability of resources, level or abundance of species, similarity of their requirements, and the amount of spatial and temporal heterogeneity.

Since the requirements of the phytoplankton have been shown to be very similar (Provasoli 1958) one would expect the degree of interaction to be intense. Besides the elements which all species require such as nitrogen, phosphorus and carbon, other micronutrients and several vitamins are considered essential for growth. Although several authors (Moss 1969; Richerson _et al_. 1970, 1975; Harris & Smith 1977) have demonstrated the ability of phytoplankton to partition temporally and spatially their environment, Wall and Briand (in prep.) found surprisingly high overlap values in Heney Lake during the summer months. This would also suggest a high degree of interaction between phytoplankton species because of the low amount of partitioning in either space or time.

The experimental examination of how the intensity of interaction between prey species affects the role of predation in promoting coexistence is a difficult task. Both the level of interaction between prey and the intensity of predation have to be altered simultaneously. In Section I, reduction of predation pressure was achieved by removing herbivorous zooplankton from enclosures. To manipulate the prey interaction it is necessary to concentrate on the relationship between resource availability and species abundance. There are several ways to alter this relationship thereby changing the degree of interaction between phytoplankton species on a short-term basis. By increasing the level of nutrients or alternately decreasing the level of species, the intensity of interaction could be lessened. Both manipulations would act to decrease the immediate demand for resources by increasing the difference between the population densities and the carrying capacity of the environment. Conversely the intensity of interaction could be increased by either removing resources or increasing the demand through addition of phytoplankton.

Several studies have examined the effect of nutrient enrichment on systems. Some authors (Rosensweig 1971, 1972; Riebesell 1974) argue that enrichment can lead to instability, potentially causing the extinction of species which were initially intended to be enhanced by the treatment. McAllister et al. (1972) have demonstrated experimentally that enrichment can produce beneficial effects from a managerial point of view and need not lead to instability of the system. In their experiments involving nutrient enrichment of an oligotrophic lake the desired effects of increasing fish stocks were obtained without causing eutrophy of the lake, that is, phytoplankton stocks remained unaltered. However Schindler et al. (1971, 1973) found that nutrient enrichment of an experimental lake did produce significant increases in phytoplankton standing stocks by nearly two orders of magnitude and observed a shift from a community dominated by cryptomonads and golden-brown algae to one dominated by blue-green and green algae.

The major goals of enrichment studies in lakes have been either to identify the major limiting nutrients involved in phytoplankton growth or to increase ecosystem productivity directed at the level of fish stocks. However the addition of bulk nutrients into a system may affect other components, leading to unexpected results. O'Brien and de Noyelles (1972) pointed out that increased photosynthetic activity by phytoplankton caused by addition of nutrients could drastically alter the pH of the medium and cause significant zooplankton mortality. Talling (1976) also observed in natural waters that phytoplankton could cause severe depletion in CO_2 availability, and by altering pH could affect the growth of various phytoplankton species. It is also difficult when performing enrichment experiments to decide in what ratio the major nutrients should be added. The relative importance of the various elements is presently a matter of strong debate (King 1970; Kuentzel 1971; Schindler *et al*. 1971; Goldman *et al*. 1972, 1974; Talling 1976).

Perhaps an alternate method to that of nutrient enrichment is community dilution. If one reduces phytoplankton levels by either increasing their mortality and/or physically reducing their density, this should decrease the degree of interaction on a short-term basis. Increased phytoplankton mortality could be accomplished through addition of zooplankton stocks to the community. However predation is a selective force affecting primarily one group of phytoplankton. Dilution on the other hand may be a feasible method to alter the level of interaction between phytoplankton species.

The purpose of this study is 1) to examine the effect of dilution on phytoplankton species richness and community structure and 2) to examine the effects of reduced predation under diluted conditions using controlled field experiments.

MATERIALS AND METHODS

The dilution experiments were carried out at Heney Lake concurrent with the 1977 experiments described in Part I. They involved six enclosures and were initiated on July 14, 1977. The enclosures used were of the same type employed in the first set of experiments. In order to dilute the community they were launched however in a different manner. The containers were drawn through the water column with a ring of diameter 0.70 m as opposed to that of 1 m normally used. This reduced diameter was selected because it describes a right circular cylinder of volume one-half that of the normal enclosure. After launching with this smaller ring the container was equiped with a ring of 1 m diameter and filled to capacity. Water from the lake was added to the enclosure using a 3 h.p. gas powered pump linked to a Carborundum filtering apparatus (model WYFT18). The Honeycomb filter tubes (W19R10A) used removed particles greater than 10 μm.

In three of the six diluted enclosures an attempt was made to reduce the levels of herbivores in the manner described precedently (see Part I). Sampling and enumeration of phytoplankton and zooplankton were carried out similarly as before with one exception. In the enumeration of phytoplankton samples from the diluted enclosures four strips instead of two were counted to obtain the same level of accuracy as in the non-diluted enclosures.

In order to assess the effect of dilution the two non-manipulated enclosures from the first set of experiments acted as controls for this study.

RESULTS

Of the six enclosures in which an attempt was made to dilute the community only two appeared to differ in total phytoplankton cell volume from the control situations (Fig. 8). One of these was an enclosure in which zooplankton levels were being manipulated (G) and one was not (F). Enclosure F attained a dilution of over 50% with enclosure G being diluted by 33%. Therefore to assess the effect of dilution, enclosures A and B from the first section were compared with enclosure F and to assess the effect of reduced predation intensity under diluted conditions, enclosure F was compared to G. Unfortunately the phytoplankton samples for enclosures F and G from August 19 are not available due to a laboratory accident.

The remaining four non-diluted enclosures were treated as a supplemental test of the predictions from the first section, the results of which are presented in Appendix 1.

I] The Effect of Dilution

Dilution did not alter the level of herbivorous zooplankton throughout the course of the experiment (see Table 7).

Total species richness (Fig. 9) appears to be reduced in the diluted enclosure. A very sharp initial decline in species richness (July 22) was followed by a sharp peak (August 5) and a subsequent de-

Fig. 8 Comparison of total algal volume (μm^3/l) between control enclosures (A and B) and those in which an attempt to dilute (F to K) was made. Vertical bars represent estimation of counting error as determined from Lund *et al*. (1958).

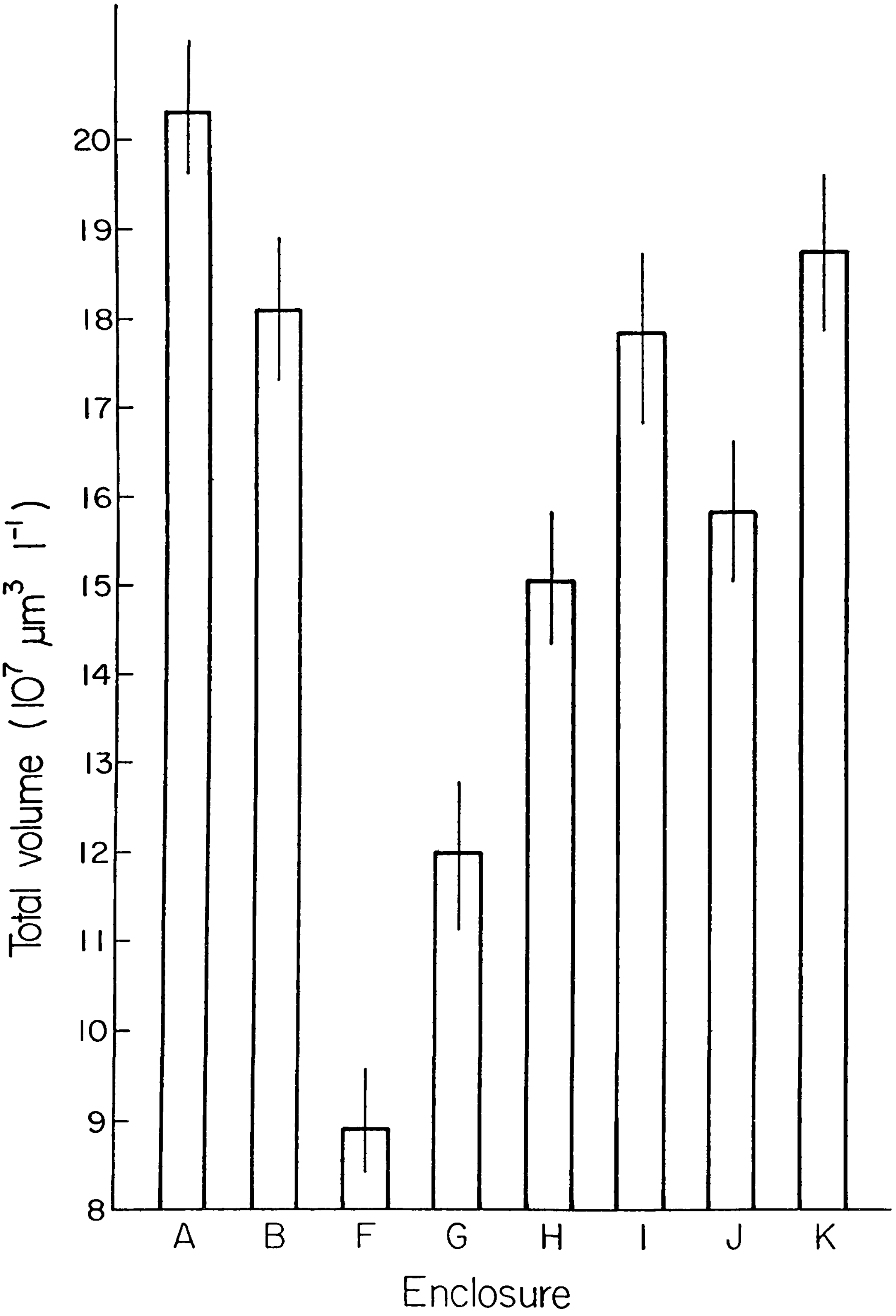

Total volume (10^7 µm^3 l^{-1})
20
19
18
17
16
15
14
13
12
11
10
9
8
A
B
F
G
H
I
J
K
Enclosure

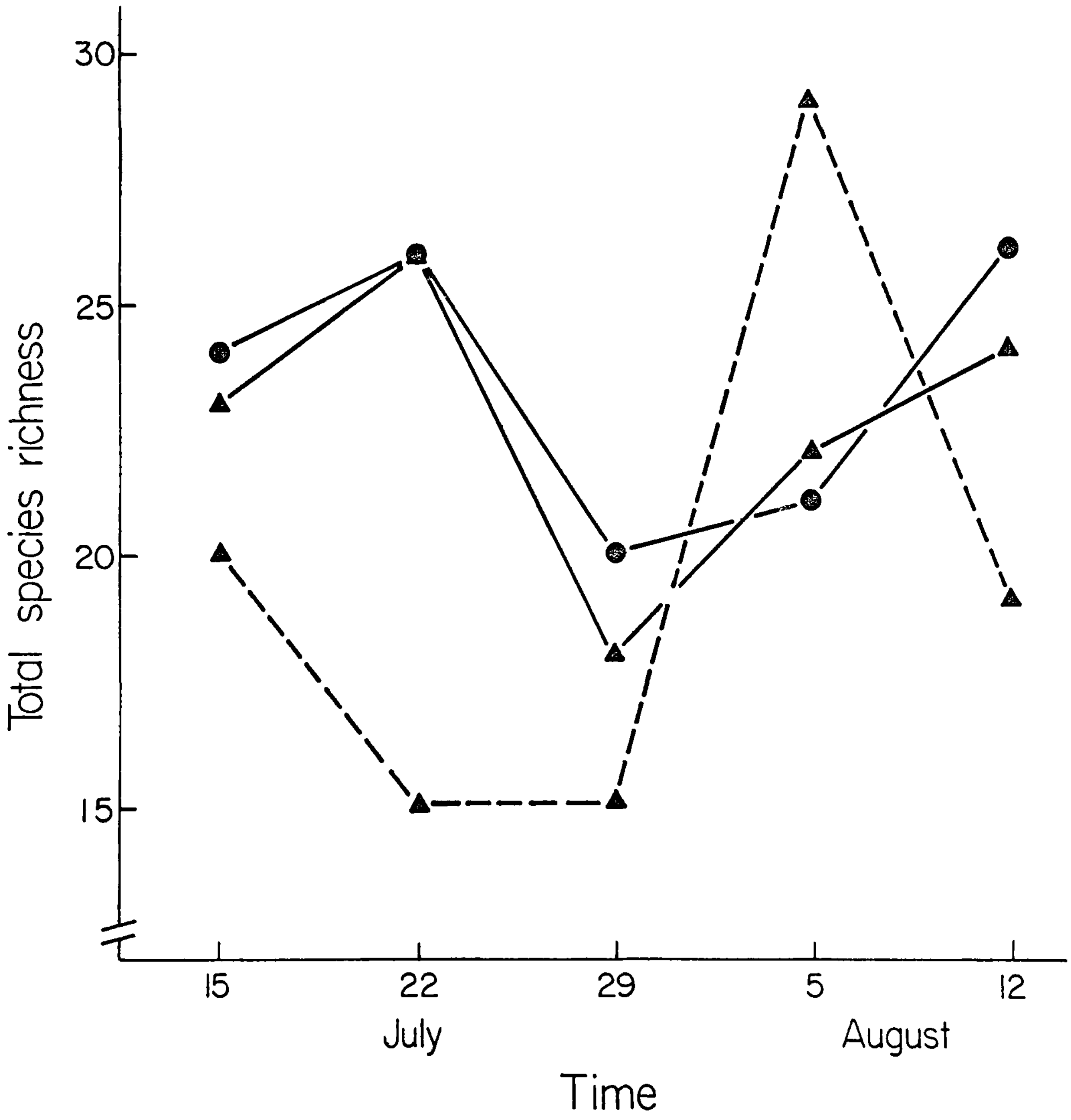
Table 7 Densities (No./10 litres) of herbivorous zooplankton recorded in the control (A and B) and diluted (F) enclosures.

TABLE 7

Density

	Control		Diluted
Date	A	B	F
July 22	93.7	116.9	121.0
July 29	129.5	202.1	331.9
August 5	462.2	380.2	526.17
August 12	391.5	315.5	387.59
August 19	1,025.7	745.5	562.03

Fig. 9 The effect of dilution on total algal species richness. Control enclosures are designated by solid lines, the diluted enclosures by a dashed line.


30
25
20
15
Total species richness
15
22
29
5
12
July
August
Time

cline. The variation in species richness of the edible group (Fig. 10) reflects very strongly the observed changes in total species richness in the diluted enclosure. The species richness of the inedible group (Fig. 11) appears to be lower in the diluted case and also follows a similar pattern as total species richness.

The relative contributions of each group in terms of volume and density are presented in Table 8. Dilution did not affect the relative density of each group between the control and diluted enclosures. However in terms of volume, at the end of the experiment the inedible group was relatively larger in the diluted than in the control situations.

The structure of both the edible and inedible groups was altered by dilution. The number of inedible species (Fig. 12) contributing more than 10% of the total volume is reduced. The group becomes dominated by the blue-green *Gloeotrichia echinulata* and the diatom *Synedra* sp.. The structure of the edible group (Fig. 13) responds in the opposite manner. More species such as *Cryptomonas erosa*, *Stephanodiscus* sp., and *Cosmarium* sp. contribute a greater percentage of volume in the diluted container.

II] The Effect of Reduced Predation Intensity Under Diluted Conditions

The levels of herbivorous zooplankton in both the control (F) and manipulated (G) enclosures are presented in Table 9. Differences in the levels of herbivores were recorded from July 22 to August 12. At

Fig. 10 The variation in species richness of the edible group between control (solid lines) and diluted (dashed line) enclosures.

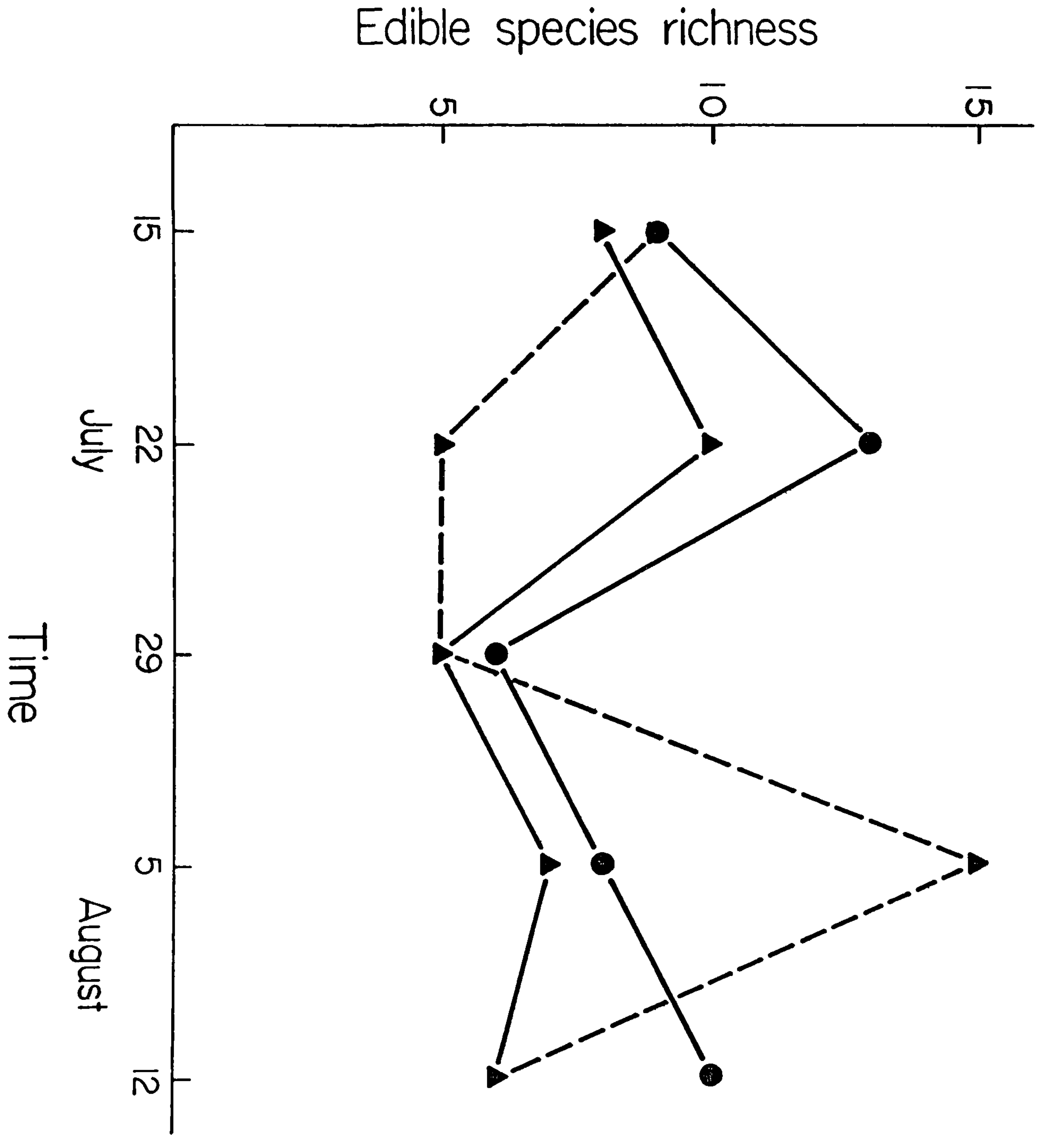

Edible species richness
5
10
15
15
22
29
5
12
July
August
Time

Fig. 11 The variation in species richness of the inedible algal group between control (solid lines) and diluted (dashed line) enclosures.

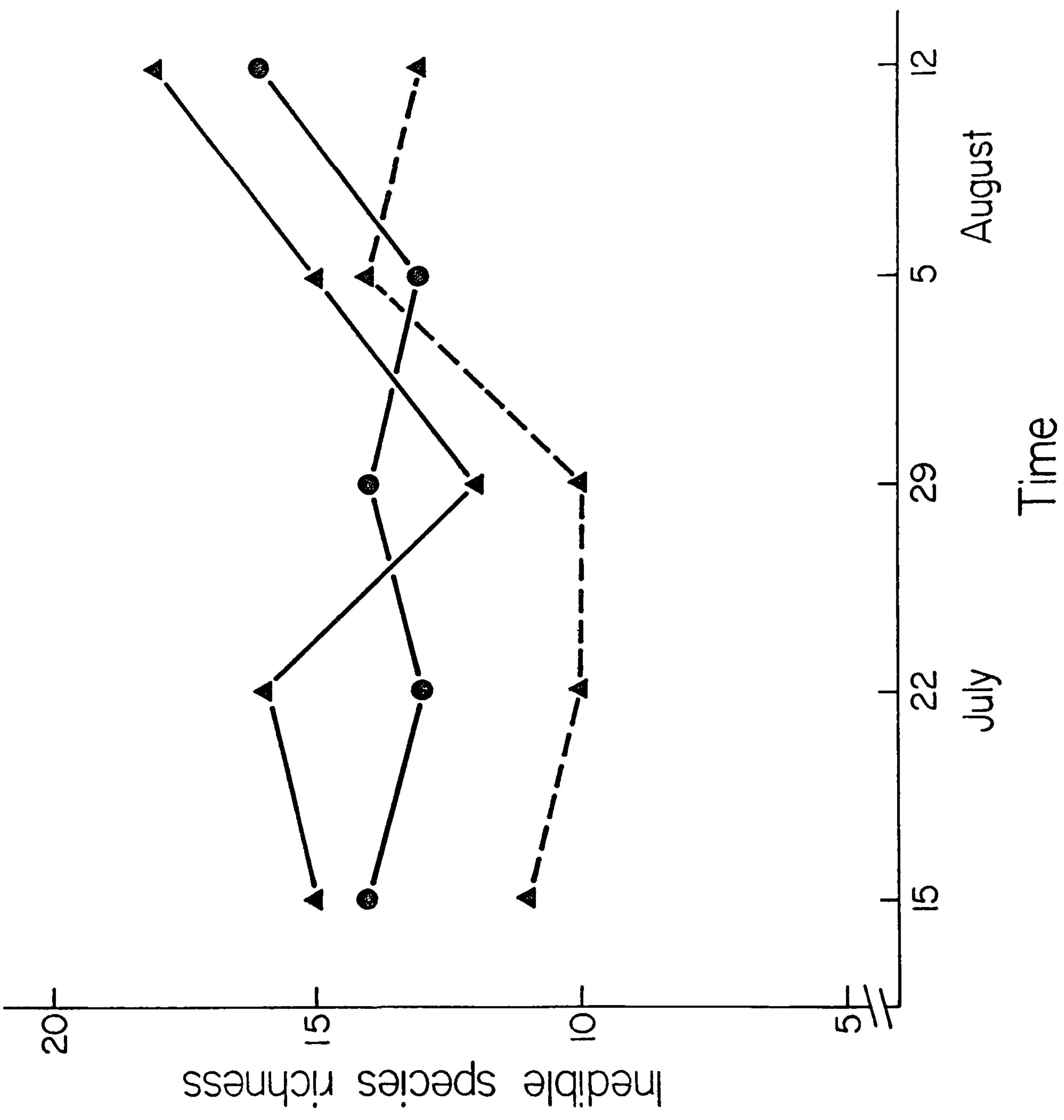

Inedible species richness
20
15
10
5
Time
15
22
29
5
12
July
August

Table 8 Relative percent contribution of the edible and inedible group to total phytoplankton volume and density between the control (A and B) and diluted (F) enclosures.

TABLE 8

			Date			
			July 22	July 29	August 5	August 12
1) Volume						
Inedible	Control	A	96.5	92.2	84.1	96.3
		B	95.1	87.2	92.0	97.5
	Diluted	F	97.9	96.1	93.3	98.8
Edible	Control	A	3.5	7.8	15.4	3.7
		B	4.9	12.8	8.0	3.0
	Diluted	F	2.1	3.9	6.7	1.2
2) Density						
Inedible	Control	A	95.9	96.0	89.4	94.5
		B	96.5	94.7	85.8	92.1
	Diluted	F	95.3	95.5	94.7	95.5
Edible	Control	A	4.1	4.0	10.6	5.5
		B	3.5	5.3	14.2	7.9
	Diluted	F	4.7	4.5	5.3	4.5

Fig. 12 The effect of dilution on and the response to reduced predation pressure under diluted conditions of the structure of the inedible group. To ascertain the dilution effect, compare enclosures A and B with F. To examine the response of the group to reduced predation pressure under diluted conditions compare enclosures F and G. Species contributing volume in excess of 10% to the group are labelled with a numerical code and presented in Table 6.

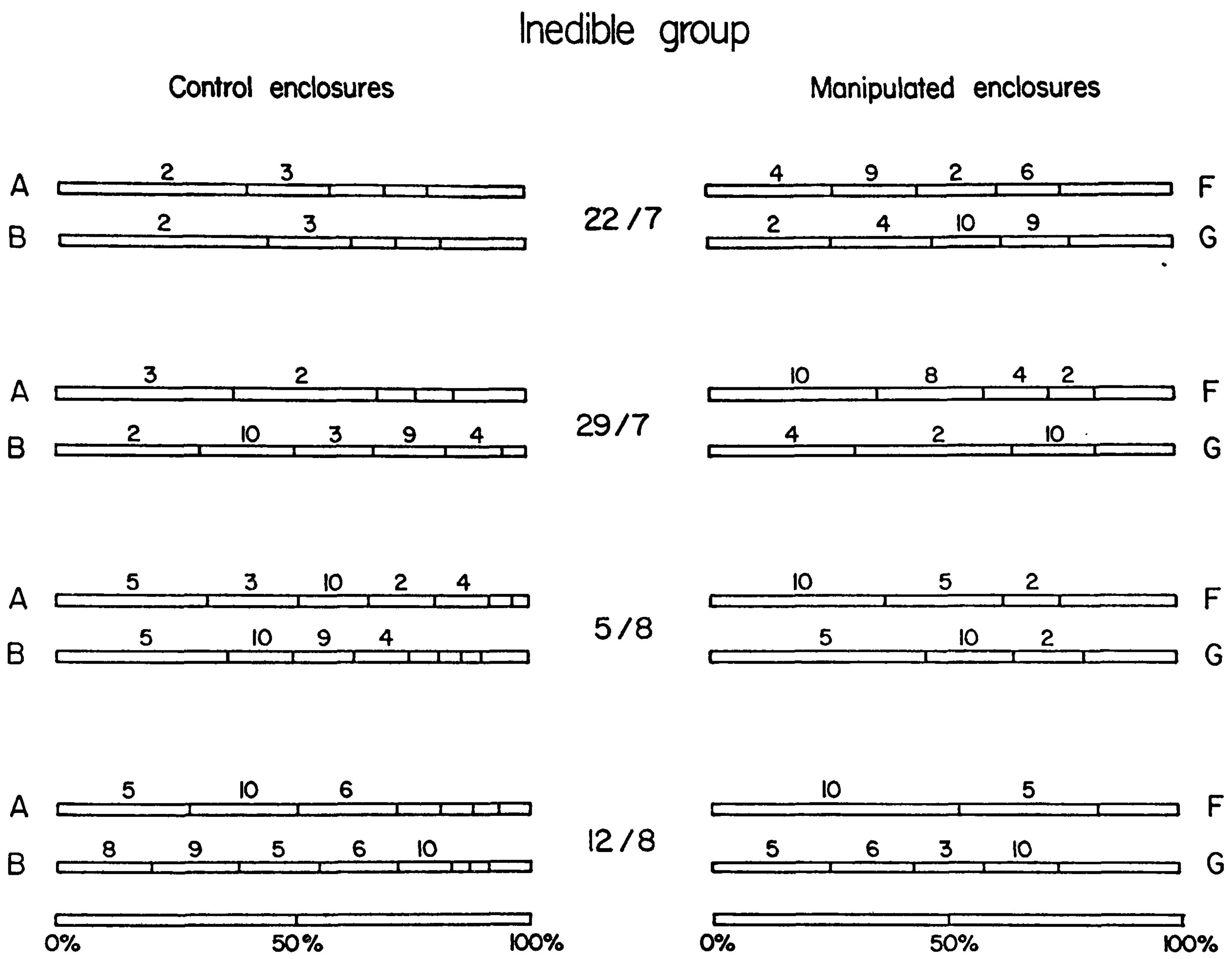

Inedible group
Control enclosures
Manipulated enclosures
A
2 3
B
2 3
22/7
4 9 2 6
F
2 4 10 9
G
A
3 2
B
2 10 3 9 4
29/7
10 8 4 2
F
4 2 10
G
A
5 3 10 2 4
B
5 10 9 4
5/8
10 5 2
F
5 10 2
G
A
5 10 6
B
8 9 5 6 10
12/8
10 5
F
5 6 3 10
G
0%
50%
100%
0%
50%
100%

Fig. 13 The effect of dilution and the response to reduced predation pressure under diluted conditions on the structure of the edible group. To ascertain the dilution effect compare enclosures A and B with F. To examine the response of the group to reduced predation pressure under diluted conditions compare enclosures F and G. Species contributing volume in excess of 10% are labelled with a numerical code and presented in Table 6.

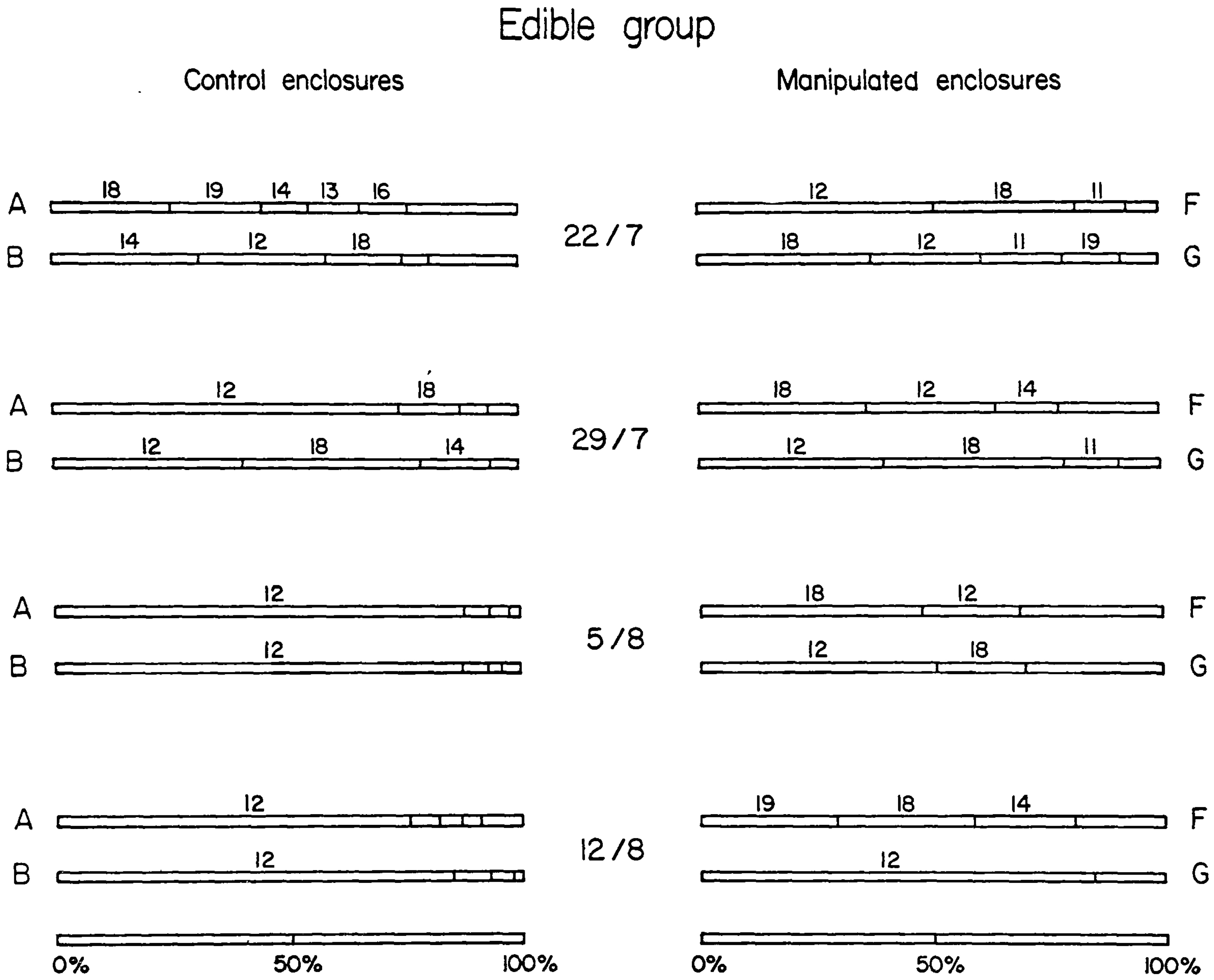

Edible group
Control enclosures
Manipulated enclosures
A
18
19
14
13
16
B
14
12
18
22 / 7
12
18
11
F
18
12
11
19
G
A
12
18
B
12
18
14
29 / 7
18
12
14
F
12
18
11
G
A
12
B
12
5 / 8
18
12
F
12
18
G
A
12
B
12
12 / 8
19
18
14
F
12
G
0%
50%
100%
0%
50%
100%

Table 9 Densities (No./10 litres) of herbivorous zooplankton under diluted conditions between control (F) and grazer reduced (G) enclosures.

TABLE 9

Date	Density Diluted Control (F)	 Diluted Manipulated (G)
July 22	121.0	19.7
July 29	331.9	96.8
August 5	526.17	41.5
August 12	387.59	61.27
August 19	562.03	116.49

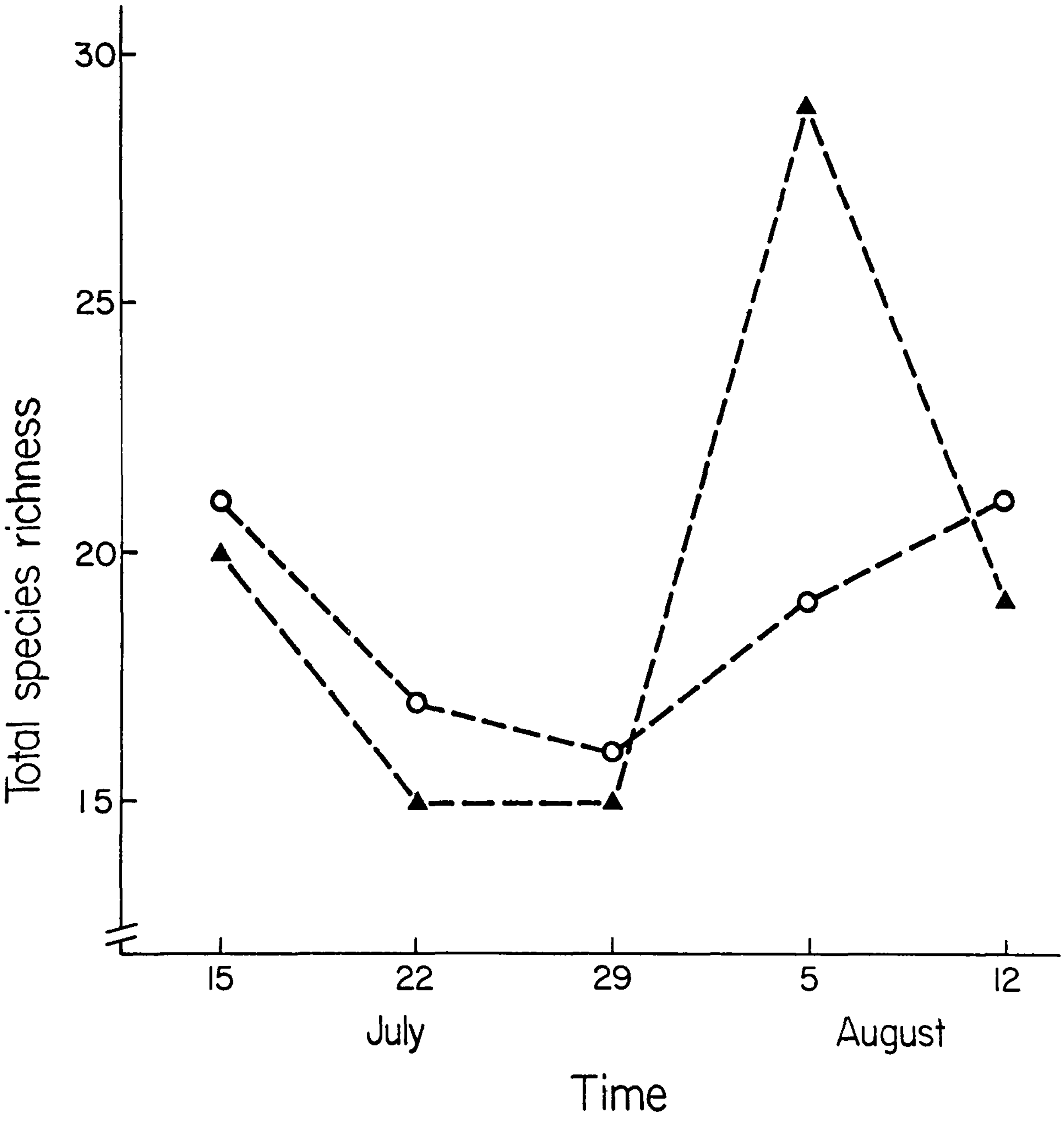
some points (e.g. July 29 and August 5) there is almost a ten-fold difference in the number of herbivores between the control and manipulated enclosure.

There does not appear to be any difference in total species richness between enclosures (Fig. 14) except on August 5. On this date the control enclosure had a much greater species richness than the manipulated enclosure. On the remaining days total species richness is slightly higher in the enclosure with reduced levels of herbivores. The species richness of the edible group (Fig. 15) does not appear to differ greatly between enclosures, being slightly higher in the manipulated enclosure on July 29 and August 12 and being quite lower on August 5. A slight reduction in the species richness of the inedible group was observed for the last three weeks of the experiment in the manipulated enclosure (Fig. 16).

The relative contribution of each group to total volume and density is presented in Table 10. There is no difference between the control and manipulated enclosure in the contribution of volume or density of either the edible or inedible groups throughout the course of the experiment.

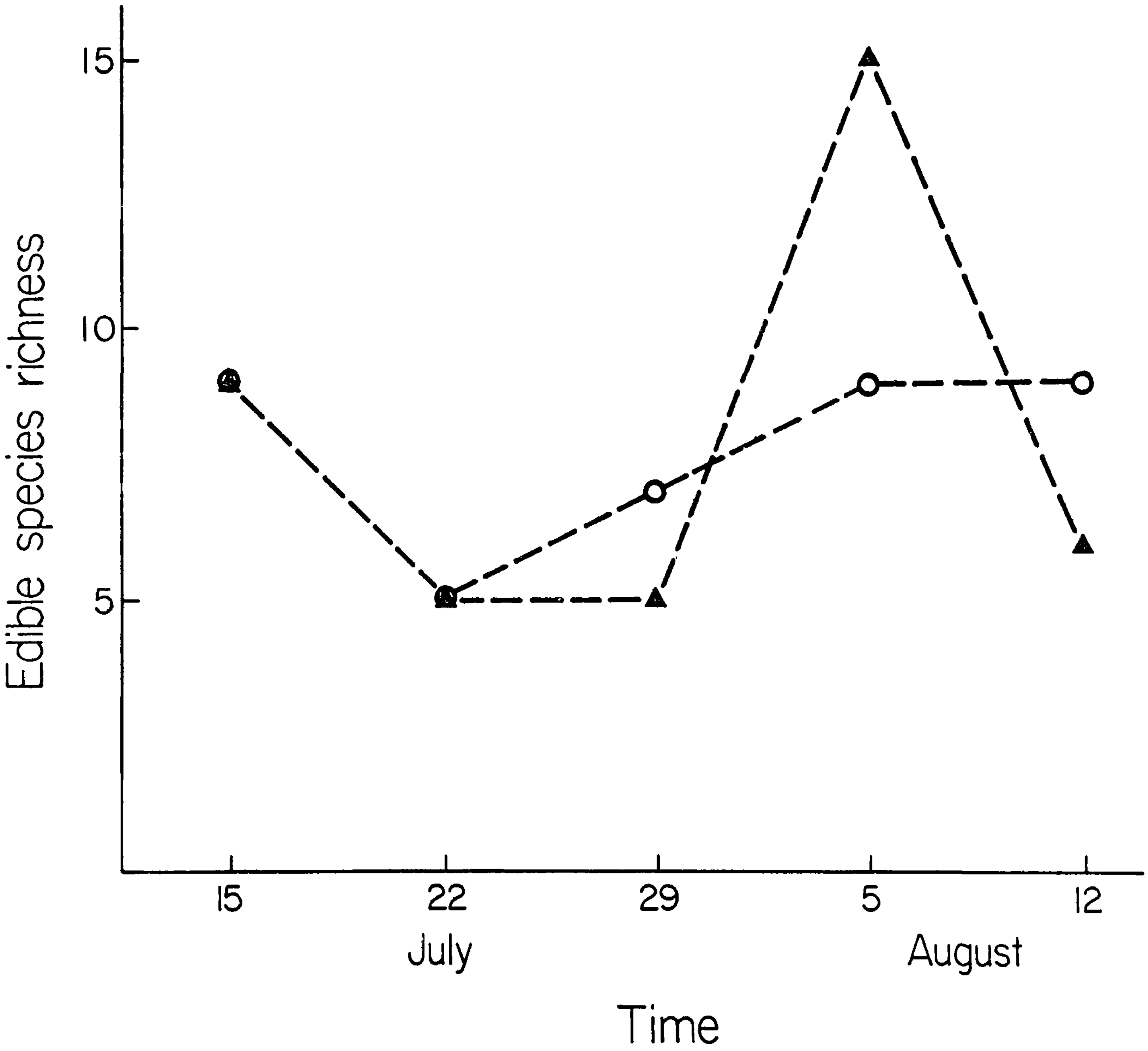
The structure of the edible (Fig. 13) and inedible (Fig. 12) groups appear to be very similar in both the control (F) and manipulated (G) enclosures with the exception of the last week of the experiment. During this week in the enclosure with reduced levels of herbivores, the edible group is dominated to a great extent by the diatom

Fig. 14 The effect of reduced grazing pressure on total phytoplankton species richness under diluted conditions. Solid symbols represent the control enclosure, open symbols the enclosure in which the level of herbivores was reduced.


30
25
20
15
Total species richness
15
22
29
5
12
July
August
Time

3 ,

Fig. 15 The effect of reduced grazing pressure on the species richness of the edible group under diluted conditions. Solid symbols represent the control enclosure, open symbols the enclosure in which the level of herbivores was reduced.



Edible species richness
15
10
5
15
22
29
5
12
July
August
Time

Fig. 16 The effect of reduced grazing pressure on the species richness of the inedible group under diluted conditions. The control is represented by solid symbols, the manipulated enclosure by open symbols.

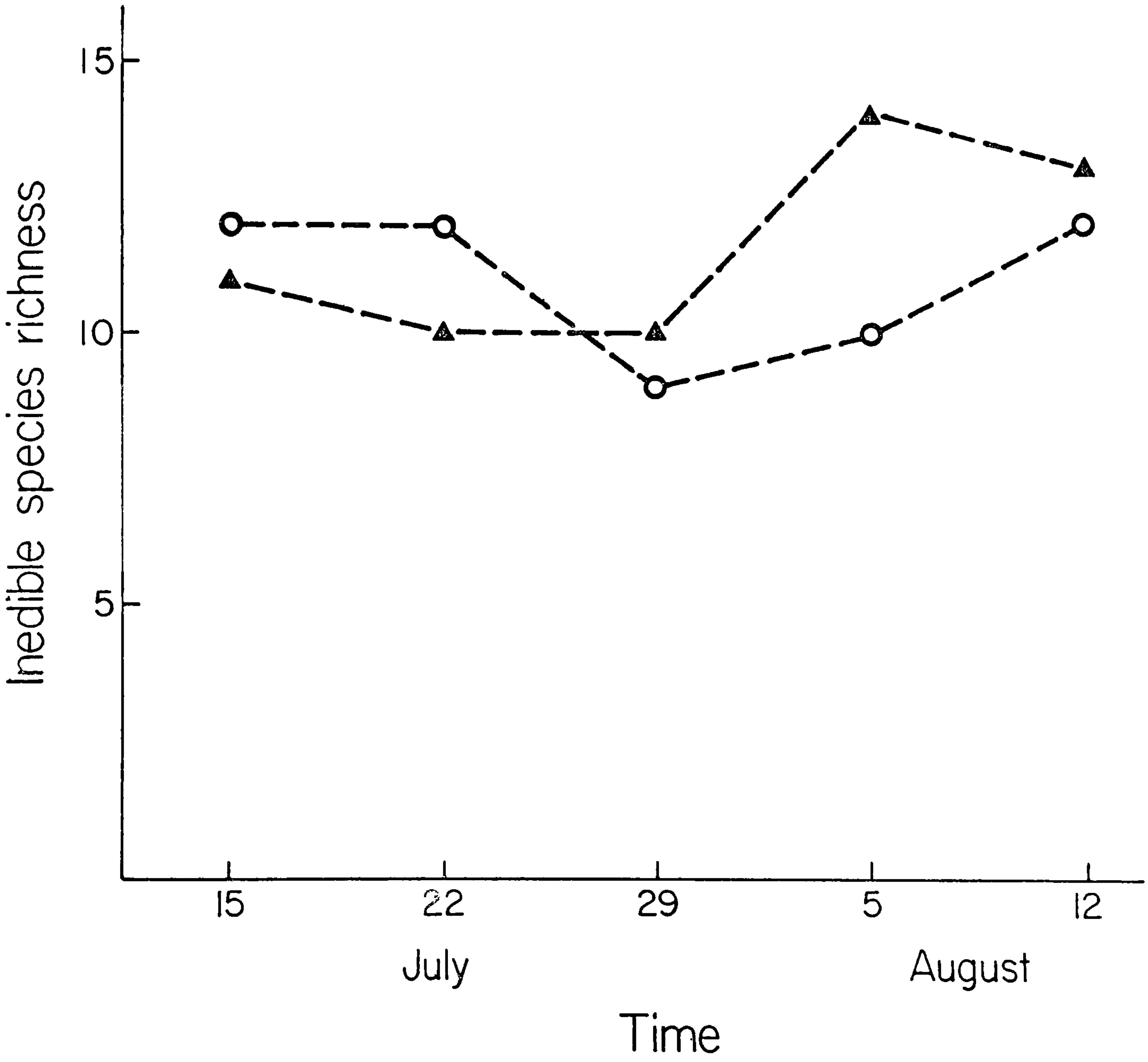

Inedible species richness
15
10
5
15
22
29
5
12
July
August
Time

Table 10 Relative percent contribution of the edible and inedible group to total phytoplankton volume and density under diluted conditions between control (F) and grazer reduced (G) enclosures.

TABLE 10

			Date			
			July 22	July 29	August 5	August 12
1) Volume						
Inedible	Diluted Control	F	97.5	96.1	93.3	98.8
	Diluted Manipulated	G	96.1	96.4	95.4	90.3
Edible	Diluted Control	F	2.1	3.9	6.7	1.2
	Diluted Manipulated	G	3.9	3.6	4.6	9.7
2) Density						
Inedible	Diluted Control	F	95.3	95.5	94.7	95.5
	Diluted Manipulated	G	95.1	94.6	92.7	92.7
Edible	Diluted Control	F	4.7	4.5	5.3	4.5
	Diluted Manipulated	G	4.9	5.4	7.3	7.3

Asterionella formosa, whereas in the control enclosure the group is co-dominated by *Cosmarium* sp., *Stephanodiscus* sp., and *Cryptomonas erosa*. On August 12, in the inedible group more species contribute volume in excess of 10% in the enclosure with reduced levels of herbivores. The control enclosure on this date is dominated by the diatom *Synedra* sp. and the blue-green *Gloeotrichia echinulata*.

DISCUSSION

Dilution had a considerable effect on the phytoplankton community: not only was total species richness reduced but also the pattern of change differed markedly. Since the manipulation was an unique event in time it is possible that it represented a type of perturbation or disturbance to the system in which nutrients and/or space became more available. In this instance phytoplankton species which are capable of rapid growth or expansion of their population would be favoured. This may be analogous to a colonization situation where a patch was created through disturbance and species not considered to be dominant competitors gain access to nutrients (Levin & Paine 1975). The initial decline observed in species richness could be a result of the colonization process.

Peterson (1977) suggested, using a neutral model analysis, that any perturbation resulting in species mortality would cause a decline in diversity. The model assumes no interaction between species and therefore, explanation of the result excludes the possible role of biotic factors such as competition or predation. As the results of this study support the prediction of Peterson's model, interactions between species need not necessarily be invoked to explain the decline observed. However the model cannot predict the long-term response of the system to perturbation. It is possible that the long-term response or recovery of the community will rely on factors such as competition and predation.

The distinct oscillation in the number of species caused by dilution was primarily due to the fluctuation in the number of edible species. Members of the edible group, because of their small size and nutrient uptake abilities, would be expected to benefit most from the manipulation. However an increase in the level of this group was not recorded. It is possible that the expected increase was buffered or prevented from occuring by zooplankton grazing. If this is true then an increase in zooplankton stocks should be observed due to the increased food supply. This was in fact recorded (see Table 7, July 29). In addition it appears that the available nutrients, both from the manipulation and presumably from nutrient regeneration, were picked up by the inedible group as they were observed to increase.

Rosensweig (1971) predicted that enrichment of predator-prey systems may result in the extinction of both the exploiter and victim in a two-species system. In this study, although species richness decreased, no conclusions can be made as to possible extinctions. However the perturbation did result in a form of oscillation which may be interpreted as possible destabilization of the system (Rosensweig 1972b). In criticizing Rosensweig's predictions McAllister _et al_. (1972) presented results of their enrichment experiments performed on an oligotrophic lake. Destabilization of their system was not observed and the desired increase in fish stocks was achieved. A possible explanation to account for this discrepancy between the theoretical and experimental results is that the impact of increased fish stocks was not registered in the experimental system. Mature fish were allowed to migrate out of the lake and therefore increased predation pressure and nutrient regeneration which could ultimately have drastic effects on other components were not felt. In the theoretical analysis the system was considered closed, with neither emigration nor immigration occurring. Schindler _et_ _al_. (1973) in performing similar field experiments using a closed system found that the phytoplankton community shifted from edible species to those considered to be inedible. Thus in this system enrichment did lead to unfavourable conditions which can be interpreted as a form of destabilization.

The response of the phytoplankton community to reduced levels of herbivores is different than was observed in the first study (see Part I). Although there was a reduction in the number of inedible species, total species richness was not reduced. In addition community structure was not altered to as great a degree. These observations suggest that, while predation appears important in maintaining diversity, its role is reduced under diluted conditions. It is possible that dilution reduced the degree of interaction among prey species, as a reduction in grazing pressure did not cause this time a significant decrease in the total number of species.

It was suggested above that the response of the edible group to dilution was restricted by the action of zooplankton. Therefore in the diluted enclosure where grazing pressure was reduced the edible group should register a significant increase. However this was not observed, perhaps because of the nature of the manipulations. Dilution was a unique event and was achieved immediately. Reduction of zooplankton stocks, on the other hand, required two weeks before significant results were obtained. Therefore during the time that the phytoplankton community was responding to dilution, zooplankton stocks were similar in both enclosures. Perhaps a superior method would be to install enclosures with a pumping system, similar to that of a laboratory chemostat, in the lake. In this manner filtered lake water could be added to enclosures and the phytoplankton community cropped by pumping unfiltered water out at identical rates. Manipulation of zooplankton levels could then be carried out. The major drawback with this system is the large amount of mixing caused by the addition and removal of water. This factor would tend to favour certain species and may lead to problems in interpreting the results.

Although both manipulations favour species of the edible group, it is possible that species enhanced by reduced predation are not the same as those enhanced by dilution. Perhaps this is the reason that no overall increase in the edible group was observed under conditions of reduced predation.

It appears that dilution, in changing the species present in a community, can alter the role of predation in mediating coexistence. If dilution is regarded as a disturbance, then the results suggest that in communities where disturbance occurs, predation will be of minor importance in maintaining diversity. This however does not exclude predation as a possible force in driving algal succession (Porter 1973) or initiating blooms of certain species (O'Brien 1974). Rather it supports the contention that factors controlling the number of species form an interacting set, the predominance of one another being dictated by the conditions at hand (Addicott 1974). This interdependence is amply indicated by the high degree of overlap in the mechanism of action of the various hypotheses involved (Pianka 1966).

Section III

The Response of Phytoplankton Species
to
Reduced Predation and Dilution

Experiments performed in the laboratory using individual species can provide valuable information concerning their responses or characteristics. Indeed microcosms, where combinations of species or miniature communities are reproduced, may closely represent the organization of larger communities (Neill 1975) and provide excellent experimental systems. However these approaches are limited in their interpretation simply because they require extrapolation from the laboratory to nature. Thus there is no reason to assume that the specific response to a perturbation recorded in isolation will be repeated in nature or that it actually reflects the normal response of the species. Clearly a species response not only reflects its biological characteristics but also the influence of other species and the physical environment.

Although experimentation in nature on individual species is an exceedingly difficult task (Connell 1975), much valuable information can be gained in monitoring the response of species to a variety of perturbations in nature, where all factors influencing its reaction are present. The role of chemical influence (Keating 1977), shading (Talling 1960), sinking rates (Tilman & Kilham 1976), or nutrient regeneration (Porter 1976) in altering the outcome of competitive interactions for nutrients illustrates the importance of performing experiments in situ and if possible with all components of the system intact. Another approach to obtain information about species is to examine statistically how they vary along known environmental gradients (Whittaker

1975). Lewis (1976, 1977) has applied this analysis to the phytoplankton in assessing their abilities to take up nutrients and also in community ordination.

By combining observations derived from field experiments with more precisely controlled and manipulatable laboratory systems many questions can be generated concerning the biology of a particular species. The previous sections have dealt primarily with the organization of communities. This section reports on the response of the various phytoplankton species to the different perturbations, with the purpose of suggesting possible areas of investigation. In addition several predictions derived from hypotheses presented earlier are now pursued at the species level.

MATERIALS AND METHODS

From the set of data previously collected, the response of individual species to the various perturbations was compared between control and manipulated enclosures. In addition the data were reorganized or reclassified according to the classical framework, grouping species on the basis of taxonomic affiliation instead of edibility. The response of these groups was then examined in terms of species richness and volume for the three manipulations.

RESULTS

I] Response to Reduced Grazing Pressure

The variation in the number of species for each group - Cyanophyceae (blue-green), Chlorophyta (green), Chrysophyceae (golden-brown), Bacillariophyceae (diatoms), Cryptophyceae (cryptomonads) and the Pyrrophyta (dinoflagellates) - is presented in Table 11. Species richness remained constant for the Bacillariophyceae, Cryptophyceae, Chrysophyceae and Pyrrophyta throughout the course of the experiment. However the number of blue-green species decreased in the enclosures with reduced levels of herbivores (e.g. August 12 and 19). Further the number of green algal species was initially higher in the manipulated enclosures, but by the end of the experiment their numbers were similar.

The relative contribution of cell volume for each group is presented in Table 12. The only difference appears to be in the contribution of diatoms, which were notably increased in the manipulated enclosures. Consequently the contribution of blue-green algae was lessened.

There were five algal species negatively affected by the manipulation (Table 13). These include the blue-green algae _Chroococcus_ _limneticus_ and _Dactylococcopsis_ _accicularis_, the green algae _Gloeocystis_ _ampla_ and _Staurastrum_ _paradoxum_, and the dinoflagellate _Peridinium_ sp.. There were also five algal species positively affected (Table 13).

Table 11 Species richness recorded for each taxonomic group between control (A and B) and grazer reduced (C to E) enclosures.

TABLE 11

Number of Species

		Date				
		July 22	July 29	August 5	August 12	August 19
1) Cyanophyceae						
Control	A	9	9	9	10	10
	B	9	9	9	11	9
Manipulated	C	9	7	9	8	7
	D	10	7	7	8	8
	E	9	6	7	7	8
2) Chlorophyta						
Control	A	9	6	7	9	7
	B	7	4	6	6	6
Manipulated	C	13	8	5	8	3
	D	12	5	4	9	4
	E	13	11	8	4	5

TABLE 11 (Cont'd)

Number of Species

		Date				
		July 22	July 29	August 5	August 12	August 19
3) Chrysophyceae						
Control	A	0	1	1	0	0
	B	1	1	1	0	0
Manipulated	C	2	1	1	1	1
	D	1	1	2	1	0
	E	2	1	1	1	1
4) Bacillariophyceae						
Control	A	7	6	5	7	4
	B	8	5	7	6	7
Manipulated	C	8	6	6	6	7
	D	7	7	7	7	5
	E	8	4	7	6	6

TABLE 11 (Cont'd)

Number of Species

		Date				
		July 22	July 29	August 5	August 12	August 19
5) Cryptophyceae						
Control	A	2	0	2	2	1
	B	2	1	2	2	1
Manipulated	C	2	0	0	1	1
	D	2	1	1	0	0
	E	2	1	1	0	1
6) Pyrrophyta						
Control	A	1	1	1	1	2
	B	1	1	1	2	2
Manipulated	C	2	1	1	1	1
	D	1	1	1	1	1
	E	1	1	1	1	0

Table 12 Relative percent contribution of the major taxonomic groups to total phytoplankton volume in the control (A and B) and grazer reduced (C to E) enclosures.

TABLE 12

Percent Contribution of Volume

			Date			
		July 22	July 29	August 5	August 12	August 19
1) Bacillariophyceae						
Control	A	17.3	21.3	32.5	21.6	29.6
	B	19.1	32.2	28.7	18.5	18.7
Manipulated	C	25.3	44.0	45.4	35.4	30.8
	D	20.3	33.1	55.3	22.6	79.4
	E	38.8	28.0	56.9	54.0	84.2
2) Cyanophyceae						
Control	A	76.2	74.5	61.4	48.2	59.9
	B	73.0	46.6	47.8	42.5	17.2
Manipulated	C	47.3	44.4	43.6	62.1	36.0
	D	64.8	52.2	40.7	66.3	17.2
	E	48.8	41.1	36.4	40.7	12.4

TABLE 12 (Cont'd)

Percent Contribution of Volume

		Date				
		July 22	July 29	August 5	August 12	August 19
3) Chlorophyta						
Control	A	4.61	2.4	1.3	4.0	3.2
	B	3.09	13.7	17.7	19.2	1.4
Manipulated	C	9.06	10.5	3.5	0.9	1.4
	D	10.27	3.2	2.1	5.5	0.3
	E	9.67	19.2	5.3	0.9	0.1
4) Other						
Control	A	1.8	1.8	4.9	26.1	7.2
	B	4.8	7.5	5.8	19.6	19.9
Manipulated	C	18.3	1.0	7.8	1.5	31.7
	D	4.5	11.5	1.9	6.6	3.0
	E	2.7	11.6	1.4	3.3	3.3

Table 13 Algal species affected by reduced levels of herbivores during the 1977 test. Species levels are expressed as percent contribution of volume to their respective group (edible or inedible).

TABLE 13

Percent Contribution of Volume

		Date				
		July 22	July 29	August 5	August 12	August 19
1) Species Negatively Affected:						
a) Chroococcus limneticus						
Control	A	0.08	0.25	0.18	0.04	0.15
	B	0.22	0.10	0.16	0.05	0.03
Manipulated	C	0.03	---	0.15	---	0.03
	D	0.05	---	---	---	0.03
	E	4.09	---	---	---	0.07
b) Dactylococcopsis accicularis						
Control	A	0.06	0.28	0.12	---	---
	B	0.05	0.10	0.09	0.04	0.04
Manipulated	C	0.03	---	---	---	---
	D	0.04	0.25	---	---	---
	E	0.23	---	---	---	---

TABLE 13 (Cont'd)

		Percent Contribution of Volume				
				Date		
		July 22	July 29	August 5	August 12	August 19
c) *Gloeocystis ampla*						
Control	A	---	---	0.41	0.09	0.05
	B	0.68	---	---	1.69	0.60
Manipulated	C	0.32	---	---	---	---
	D	---	---	---	---	---
	E	2.49	0.41	---	---	---
d) *Staurastrum parodoxum*						
Control	A	---	---	---	3.39	2.63
	B	---	14.93	11.4	17.7	---
Manipulated	C	4.53	9.56	---	---	---
	D	5.4	---	---	---	---
	E	---	15.1	---	---	---

TABLE 13 (Cont'd)

		Percent Contribution of Volume				
		Date				
		July 22	July 29	August 5	August 12	August 19
e) *Peridinium* sp.						
Control	A	---	---	---	---	8.6
	B	---	---	---	19.34	33.7
Manipulated	C	14.8	---	---	---	---
	D	---	---	---	---	---
	E	---	---	---	---	---
2) Species Positively Affected:						
a) *Ankistrodesmus falcatus*						
Control	A	2.5	2.9	---	---	---
	B	2.3	2.5	0.89	---	7.55
Manipulated	C	2.9	5.08	5.9	3.4	0.97
	D	5.2	6.97	3.8	2.98	2.12
	E	5.3	9.4	0.88	21.88	9.72

TABLE 13 (Cont'd)

Percent Contribution of Volume

		Date				
		July 22	July 29	August 5	August 12	August 19
b) *Chlamydomonas* sp.						
Control	A	3.0	2.4	0.15	0.6	0.53
	B	3.6	3.1	1.82	1.17	1.71
Manipulated	C	3.0	3.69	5.96	4.68	0.4
	D	2.5	9.8	3.87	4.05	2.02
	E	12.2	10.22	2.04	8.9	2.64
c) *Scenedesmus obliquus*						
Control	A	1.5	6.59	0.11	---	---
	B	---	---	---	---	---
Manipulated	C	1.0	---	1.12	2.89	---
	D	1.15	1.3	2.66	2.08	---
	E	6.3	11.84	37.75	1.75	4.08

TABLE 13 (Cont'd)

		Percent Contribution of Volume				
		Date				
		July 22	July 29	August 5	August 12	August 19
d) *Stephanodiscus* sp.						
Control	A	13.2	12.69	4.89	4.75	--
	B	12.6	38.19	3.86	---	10.85
Manipulated	C	16.5	21.91	17.18	---	16.77
	D	9.0	40.09	16.37	19.26	36.54
	E	15.0	20.25	41.71	26.96	41.9
e) *Synedra* sp.						
Control	A	11.14	3.81	15.3	16.91	25.2
	B	8.73	19.92	13.13	9.66	14.8
Manipulated	C	13.93	33.58	34.37	29.03	57.6
	D	9.34	10.25	36.6	11.64	77.15
	E	25.1	23.3	44.14	49.97	86.68

These were the green algae Ankistrodesmus falcatus, Chlamydomonas sp. and Scenedesmus obliquus, and the diatoms Stephanodiscus sp., and Synedra sp..

II] Response to Dilution

The dilution manipulation did not affect overall the number of species in any of the groups (Table 14). Although the number of blue-green algal species in the diluted enclosure appeared slightly depressed at first, it was similar to the controls toward the end of the experiment.

The only difference registered in the relative contribution of each group (Table 15) is that the diluted enclosure possessed a higher proportion of diatoms than the controls.

Three species (Table 16) were favoured by dilution: Ankistrodesmus falcatus, Stephanodiscus sp., and Synedra sp.. In addition two species were negatively affected (Table 16) by the manipulation: Aphanizomenon flos-aquae (Cyanophyceae) and Asterionella formosa (Bacillariophyceae).

III] Response to Dilution and Reduced Grazing Pressure

Species richness remained constant for all groups, except for the blue-green algae (Table 17). The number of blue-green algal species was lower in the enclosure that was diluted and had herbivore levels reduced.

Table 14 Species richness recorded for each taxonomic group between control (A and B) and diluted (F) enclosures.

TABLE 14

		Number of Species			
		Date			
		July 22	July 29	August 5	August 12
1) *Cyanophyceae*					
Control	A	9	9	9	10
	B	9	9	9	11
Diluted	F	6	8	10	10
2) *Chlorophyta*					
Control	A	9	6	7	9
	B	7	4	6	6
Diluted	F	8	5	12	8
3) *Chrysophyceae*					
Control	A	0	1	1	0
	B	1	1	1	0
Diluted	F	0	1	1	1

TABLE 14 (Cont'd)

		Number of Species			
		Date			
		July 22	July 29	August 5	August 12
4) Bacillariophyceae					
Control	A	7	6	5	7
	B	8	5	7	6
Diluted	F	6	6	8	6
5) Cryptophyceae					
Control	A	2	0	2	2
	B	2	1	2	2
Diluted	F	0	2	2	2
6) Pyrrophyta					
Control	A	1	1	1	1
	B	1	1	1	2
Diluted	F	1	2	1	1

Table 15 Relative percent contribution of the major taxonomic groups to total phytoplankton volume between control (A and B) and diluted enclosures.

TABLE 15

Percent Contribution of Volume

		Date			
		July 22	July 29	August 5	August 12
1) Bacillariophyceae					
Control	A	17.3	21.3	32.5	21.6
	B	19.1	32.2	28.7	18.5
Diluted	F	21.1	53.4	51.8	55.1
2) Cyanophyceae					
Control	A	76.2	74.5	61.4	48.2
	B	73.0	46.6	47.8	42.6
Diluted	F	42.3	23.2	44.3	41.7
3) Chlorophyta					
Control	A	4.6	2.4	1.3	4.0
	B	3.1	13.7	17.7	19.2
Diluted	F	18.6	0.6	3.5	2.4
4) Other					
Control	A	1.8	1.8	4.9	26.1
	B	4.8	7.5	5.8	19.6
Diluted	F	17.9	22.6	0.4	0.8

Table 16 Phytoplankton species affected by dilution. Species levels are expressed as percent contribution of volume to their respective group (edible or inedible).

TABLE 16

Percent Contribution of Volume					
		Date			
		July 22	July 29	August 5	August 12
1) Species Negatively Affected:					
a) *Aphanizomenon flos-aquae*					
Control	A	19.6	37.6	17.66	7.19
	B	17.4	16.57	5.31	2.67
Diluted	F	15.67	5.54	5.65	0.54
b) *Asterionella formosa*					
Control	A	30.6	74.2	87.9	75.6
	B	60.5	40.8	88.8	85.9
Diluted	F	51.8	24.4	21.75	3.5
2) Species Positively Affected:					
a) *Ankistrodesmus falcatus*					
Control	A	2.5	2.9	---	---
	B	2.3	2.5	0.89	---
Diluted	F	9.87	13.0	2.33	7.55

TABLE 16 (Cont'd)

Percent Contribution of Volume		Date			
		July 22	July 29	August 5	August 12
b) *Stephanodiscus* sp.					
Control	A	12.5	12.7	4.9	4.8
	B	11.7	38.2	3.9	---
Diluted	F	31.9	37.6	48.9	32.6
c) *Synedra* sp.					
Control	A	11.1	3.8	15.3	16.9
	B	8.7	19.9	13.1	9.7
Diluted	F	7.1	36.8	38.0	54.5

Table 17 Species richness recorded for each taxonomic group under diluted conditions, between control (F) and grazer reduced (G) enclosures.

TABLE 17

		Number of Species			
		Date			
		July 22	July 29	August 5	August 12
1) Cyanophyceae					
Diluted Control	F	6	8	10	10
Diluted Manipulated	G	8	6	7	9
2) Chlorophyta					
Diluted Control	F	8	5	12	8
Diluted Manipulated	G	8	7	7	8
3) Chrysophyceae					
Diluted Control	F	1	1	1	1
Diluted Manipulated	G	1	1	1	0
4) Bacillariophyceae					
Diluted Control	F	6	6	8	6
Diluted Manipulated	G	6	5	8	7

TABLE 17 (Cont'd)

		Number of Species			
				Date	
		July 22	July 29	August 5	August 12
5) Cryptophyceae					
Diluted Control	F	0	2	2	2
Diluted Manipulated	G	0	1	2	2
6) Pyrrophyta					
Diluted Control	F	1	2	1	1
Diluted Manipulated	G	1	1	1	1

The relative contribution of each group is presented in Table 18. Initially, the relative volume of green algae was higher in the enclosure with reduced herbivore levels whereas that of diatoms was lower.

When interpreting the response of species to reduced grazing pressure, the direction of change recorded for the dilution manipulation was considered. Therefore a species was deemed affected if its level differed from both the controls (A and B) and also the control diluted enclosure. Using this criteria two species were found negatively affected in the enclosure with reduced levels of herbivores. Both species, *Chroococcus limneticus* and *Microcystis* sp., are members of the blue-green algae (Table 19). No species was found to be positively affected by the manipulation.

Table 18 Relative percent contribution of the major taxonomic groups to total phytoplankton volume under diluted conditions between control (F) and grazer reduced (G) enclosures.

TABLE 18

Percent Contribution of Volume		Date			
		July 22	July 29	August 5	August 12
1) Bacillariophyceae					
Diluted Control	F	21.1	53.4	51.7	55.1
Diluted Manipulated	G	23.6	30.9	26.7	26.6
2) Cyanophyceae					
Diluted Control	F	42.4	23.2	44.3	41.7
Diluted Manipulated	G	41.9	40.5	67.1	67.2
3) Chlorophyta					
Diluted Control	F	18.6	0.6	3.5	2.4
Diluted Manipulated	G	27.3	0.9	4.8	5.5
4) Other					
Diluted Control	F	17.9	22.6	0.4	0.7
Diluted Manipulated	G	7.1	27.7	2.7	0.6

Table 19 Phytoplankton species affected by reduced levels of herbivores under diluted conditions. Species levels are expressed as percent contribution of volume to their respective group (edible or inedible).

TABLE 19

		Percent Contribution of Volume			
		Date			
		July 22	July 29	August 5	August 12
1) Species Negatively Affected:					
a) *Chroococcus limneticus*					
Diluted Control	F	---	0.53	0.09	0.03
Diluted Manipulated	G	0.07	---	---	---
b) *Microcystis* sp.					
Diluted Control	F	---	1.0	0.32	2.6
Diluted Manipulated	G	0.51	---	---	0.6

DISCUSSION

All the species negatively affected by reduced predation were considered members of the inedible group. The direction of response suggests that these species are relatively "poor" competitors for nutrients and that their existence in the community depends largely on the presence of herbivores. The negatively affected species all possess characteristics which are not considered favourable for uptake of nutrients at low concentrations. Three species have mucilaginous sheaths which, although important in buoyancy regulation, tend to retard the movement of nutrients into the organism. The other two species negatively affected are of large size and possess low surface/volume ratios. Upon reduction of zooplankton levels, these species are first to be eliminated by the intensified demand for resources. Whether the herbivores favour them by lowering the level of the smaller more efficient species or through control of nutrient levels by regeneration remains to be tested. The latter mechanism may particularly apply to the species Gloeocystis ampla. Porter (1976) has shown that a closely related species, Sphaerocystis shroteri, is enhanced by grazing due to viable gut passage which allows the alga to pick up nutrients. Perhaps this is the case for Gloeocystis ampla, although there is some question as to whether it can be ingested by herbivores due to its size.

Of the five species that were enhanced by reduced levels of herbivores, four are considered edible and easily digested by zooplankton (Porter 1973). These species appear to be "good" competitors for nutrients and in the absence of grazers would be expected to dominate. The terms "good" and "poor" competitors must always be used in a relative sense, as it is important to clearly state the environmental conditions under which the species responses are predictable. All four species are of small size and presumably capable of rapid reproduction as compared with the larger algae. In Heney Lake, which is a relatively low nutrient status lake and also seasonally variable, these characteristics are of definite advantage. That these species do not dominate and are replaced by the larger slower growing algae illustrates the key importance of predation in dictating the species composition of the phytoplankton community.

Since only a few species of the edible group were enhanced on a long-term basis this possibly suggests an uneven distribution of competitive abilities within the group. However because the number of species was not reduced to a significant degree, the relative dispersion in abilities must be rather small. Perhaps if herbivores were absent a more significant response would have been recorded. The only inedible species to be favoured by reduced levels of herbivores was Synedra. Possible hypotheses to explain this response have been discussed in Part I.

It is difficult to determine with the dilution manipulation whether the species response was due to the immediate availability of nutrients or to the subsequent alteration of the nutrient regime. As mentioned above, several of the species characteristics are advantageous for both rapid growth and competition for nutrients. For example, small size allows for high division rates of cells and also implies a high surface/volume ratio which facilitates the uptake of nutrients when they are low. It would be of great interest to determine using finely controlled experiments, what characteristics are involved for each strategy. The relationship between intrinsic rate of increase and competitive ability could then be specified for the phytoplankton.

To interpret the direction of species change under conditions of both reduced predation and dilution, the direction of response in the dilution treatment also had to be considered. This problem was not encountered in Section II because the changes in species richness were in the same direction.

In comparing both sets of predation experiments, dilution did appear to alter the response of species. The number of species negatively affected by reduced grazing pressure is lower under diluted conditions. This indicates that the degree of interaction between species was lessened. Both species negatively affected in the diluted, grazer reduced case were considered inedible. One species <u>Chroococcus limneticus</u> was negatively affected in each experimental reduction of herbivore levels and therefore should be considered as being very sensitive to changes in predation pressure. Unfortunately no species of the edible group was affected which prevents the hypothesis concerning the differential response of species in this group, mentioned in Section II, to be tested. Obviously, experiments involving a larger number of replicates should be performed before definitive conclusions can be reached regarding the effect of both dilution and reduced predation intensity at the species level.

Of the taxonomic groups assessed only two were shown to be affected by the manipulations. The enhancement of diatoms by dilution possibly illustrates the opportunistic nature of the group. They were capable of rapidly converting available nutrients into growth and reproduction as compared with the larger slower growing species. This is an important strategy if the environment is unpredictable or undergoes severe fluctuations in nutrient supply. Blue-green algae were affected by reduced grazing pressure in both sets of experiments. This was reflected by species richness and volume changes. In evolving mechanisms to prevent significant losses in mortality due to grazing, this group has sacrificed certain aspects of competitive ability. Large size, formation of colonies, and enclosure in mucilaginous sheaths are some mechanisms to prevent ingestion by herbivores, however they are disadvantageous in the uptake of nutrients. It is not surprising therefore to find an increase in domination of blue-green algae in nutrient rich lakes where the importance of exploitative competition is reduced. This study indicates that in low nutrient status lakes zooplankton are important for blue-greens as they lower the levels of other phytoplankton species which are competitively superior in obtaining nutrients.

Comparing the results yielded by both functional and taxonomic analyses, reveals that the former is more sensitive in detecting changes when predation intensity is altered. It has often been demonstrated that species responses span taxonomic lines so that one should not neglect the functional classification of closely related species.

In order to make accurate predictions as to the response of natural systems to various perturbations knowledge of the factors controlling community structure and composition must be well understood. In addition information concerning the relative importance of species in the community and how they react to different conditions is important. With this knowledge perhaps communities can be manipulated to achieve desirable effects or to reverse current changes in natural communities imposed by the activity of man.

CONCLUSIONS

The results of this study indicate that zooplankton grazing plays an important role in the maintenance of phytoplankton species richness and community structure in low nutrient status lakes. The presence of herbivory on edible algae is especially important for mediating coexistence within the phytoplankton group considered to be inedible. That the role of zooplankton is altered by an unique disturbance such as dilution indicates that this role may vary in importance seasonally. By examination of characteristics of both phytoplankton and zooplankton, it is suggested that the role of herbivory in the maintenance of phytoplankton community structure should decrease as the nutrient status of lakes increases.

APPENDIX I

The four enclosures in which dilution was unsuccessful were considered as supplemental tests of the prediction from the first section. It is believed that dilution was not achieved because of a malfunctioning within the Carborundum filtering apparatus. These enclosures were considered separate because of possible modification of the phytoplankton community brought about by filling one-half of the enclosure by volume with lake water passed through the gas-powered pump. In analysing the data the enclosures were paired - one control and one manipulated - according to the initial total algal volume recorded (Fig. 8). Thus enclosures H (control) and J (manipulated) were considered as one pair, as were enclosures I (control) and K (manipulated). The specific prediction tested was that a reduction of zooplankton grazing pressure would cause a decrease in the number of phytoplankton species.

The levels of zooplankton in each of the enclosures is presented in Table 20. Differences in grazing pressure between enclosures are registered from July 29 until the termination of the experiment. The variation in the number of algal species appears to be very similar to that observed in Section I. Total species richness for the paired enclosures (Figures 17 and 20) is reduced in the enclosures with lower herbivore levels. There was a distinct reduction in the number of inedible species (Figures 18 and 21) while the species richness of the edible group (Figures 19 and 22) was generally not affected.

The response of each group (edible and inedible) to reduced herbivore levels appears to be a reproducible event, since the same trends were observed here as in Section I. The results of these experiments provide additional support for the hypothesis that predation plays an important role in the regulation of phytoplankton species richness.

Table 20 Densities (No./10 litres) of herbivorous zooplankton recorded in control (H and I) and manipulated (J and K) enclosures during 1977.

TABLE 20

	Density			
Date	Control (H)	Manipulated (J)	Control (I)	Manipulated (K)
July 22	166.7	43.9	54.5	59.1
July 29	93.9	84.9	248.5	116.7
August 5	---	90.9	324.2	124.2
August 12	1,045.5	159.1	772.7	174.2
August 19	439.4	197.0	894.0	197.0

Fig. 17 The effect of reduced grazing pressure on total algal species richness (1977 supplemental test). The control enclosure is designated by solid symbols, the manipulated enclosure by open symbols.

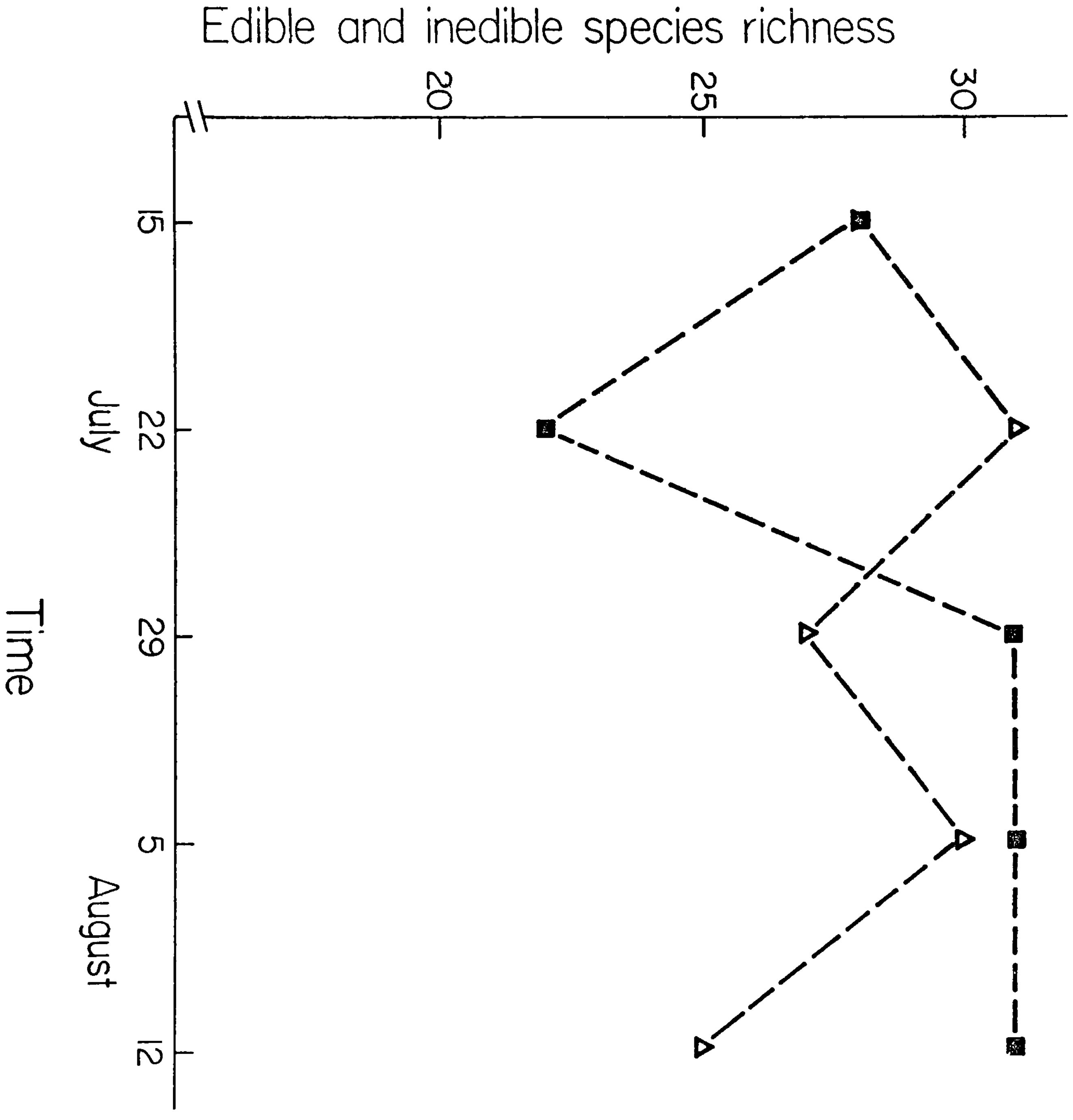

Edible and inedible species richness
20
25
30
15
22
29
5
12
July
August
Time

Fig. 18 The effect of reduced grazing pressure on the species richness of the inedible group (1977 supplemental test). The control enclosure is designated by solid symbols, the manipulated enclosure by open symbols.

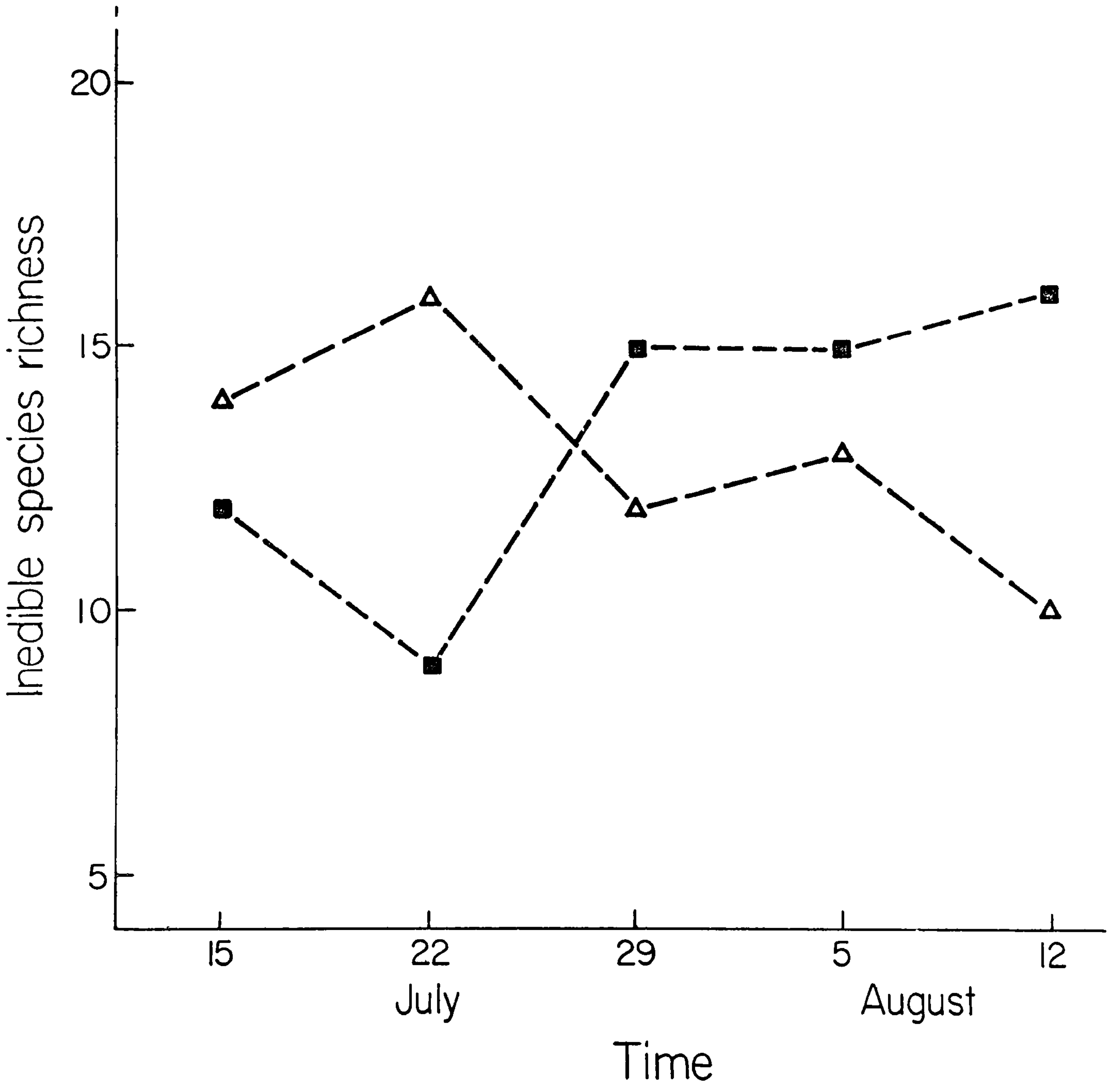

Inedible species richness
20
15
10
5
15
22
29
5
12
July
August
Time

Fig. 19 The effect of reduced grazing pressure on the species richness of the edible group (1977 supplemental test). The control enclosure is designated by solid symbols, the manipulated enclosure by open symbols.

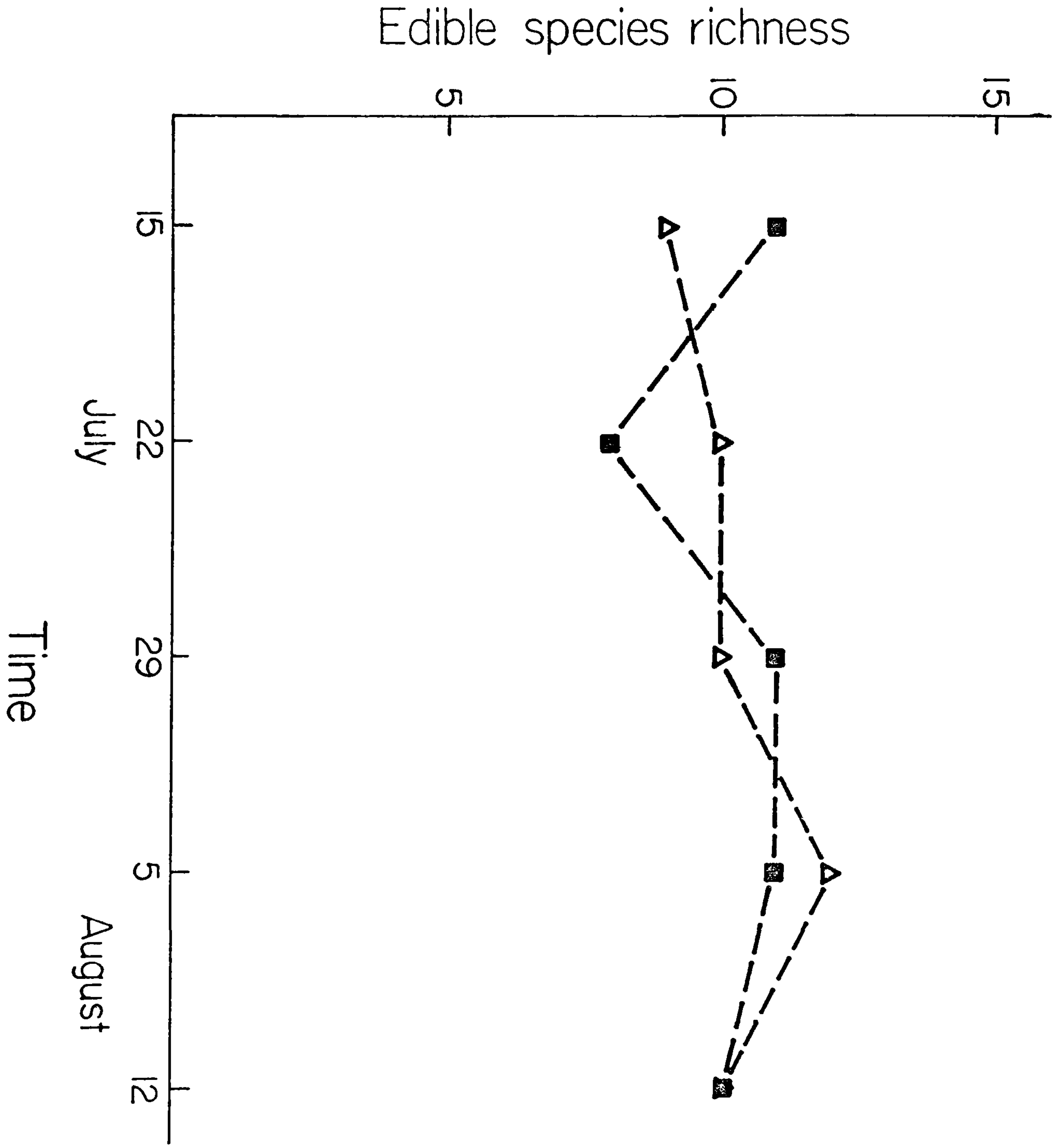

Edible species richness
5
10
15
15
22
29
5
12
July
August
Time

Fig. 20 The effect of reduced grazing pressure on total algal species richness (1977 supplemental test). The control enclosure is designated by solid symbols, the manipulated enclosure by open symbols.

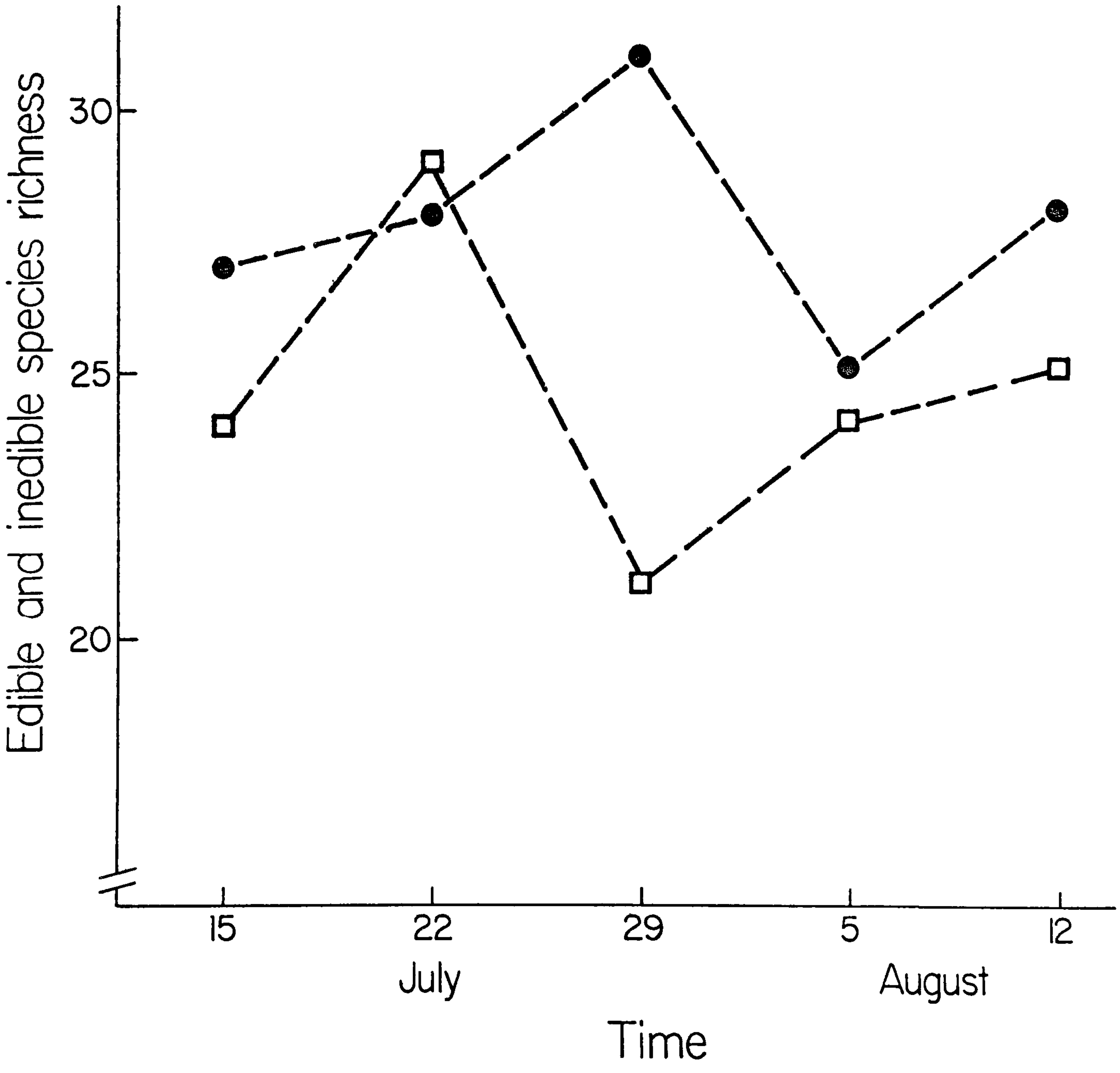

Edible and inedible species richness
30
25
20
15
22
29
5
12
July
August
Time

Fig. 21 The effect of reduced grazing pressure on the species richness of the inedible group (1977 supplemental test). The control enclosure is designated by solid symbols, the manipulated enclosure by open symbols.

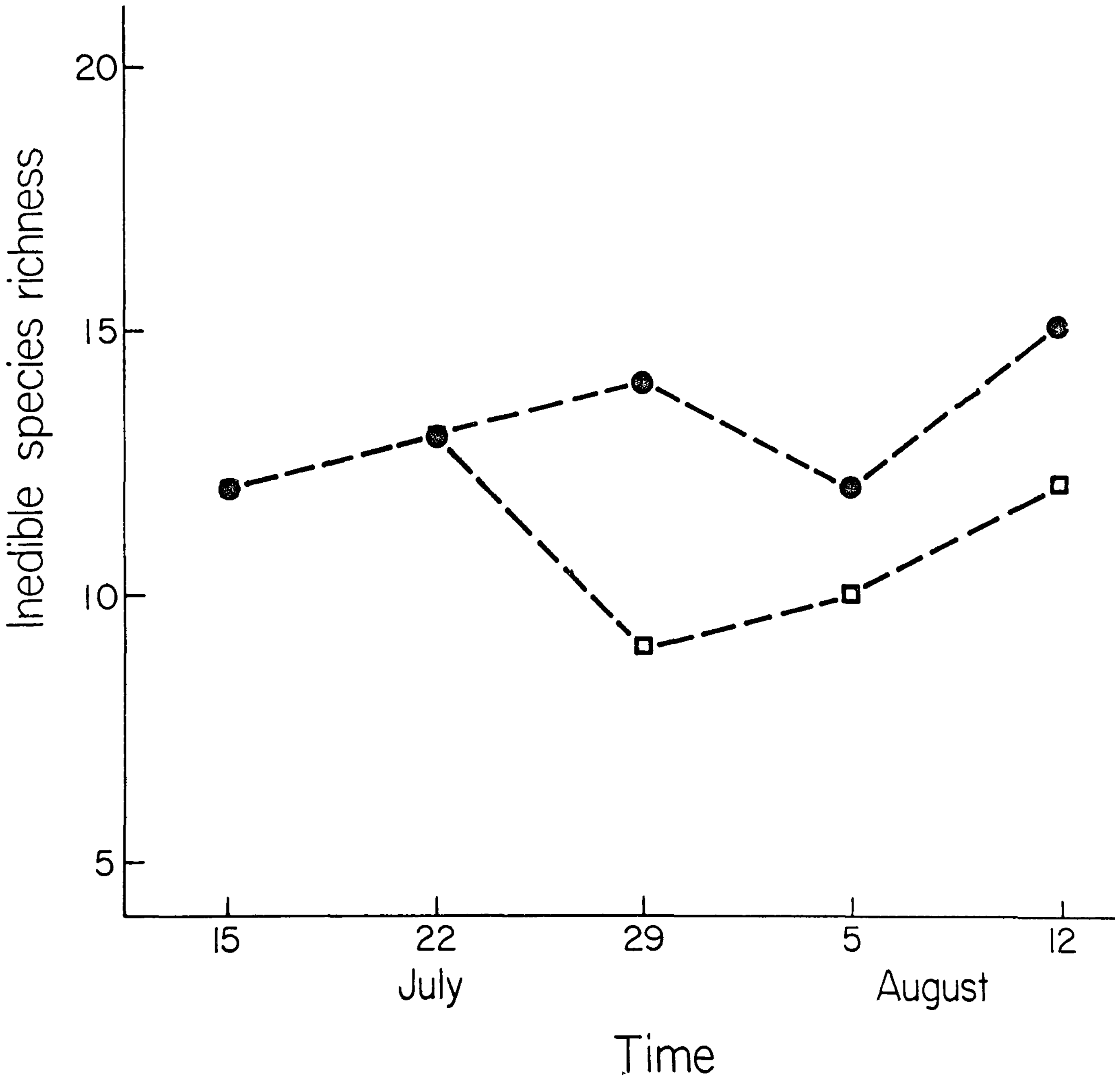
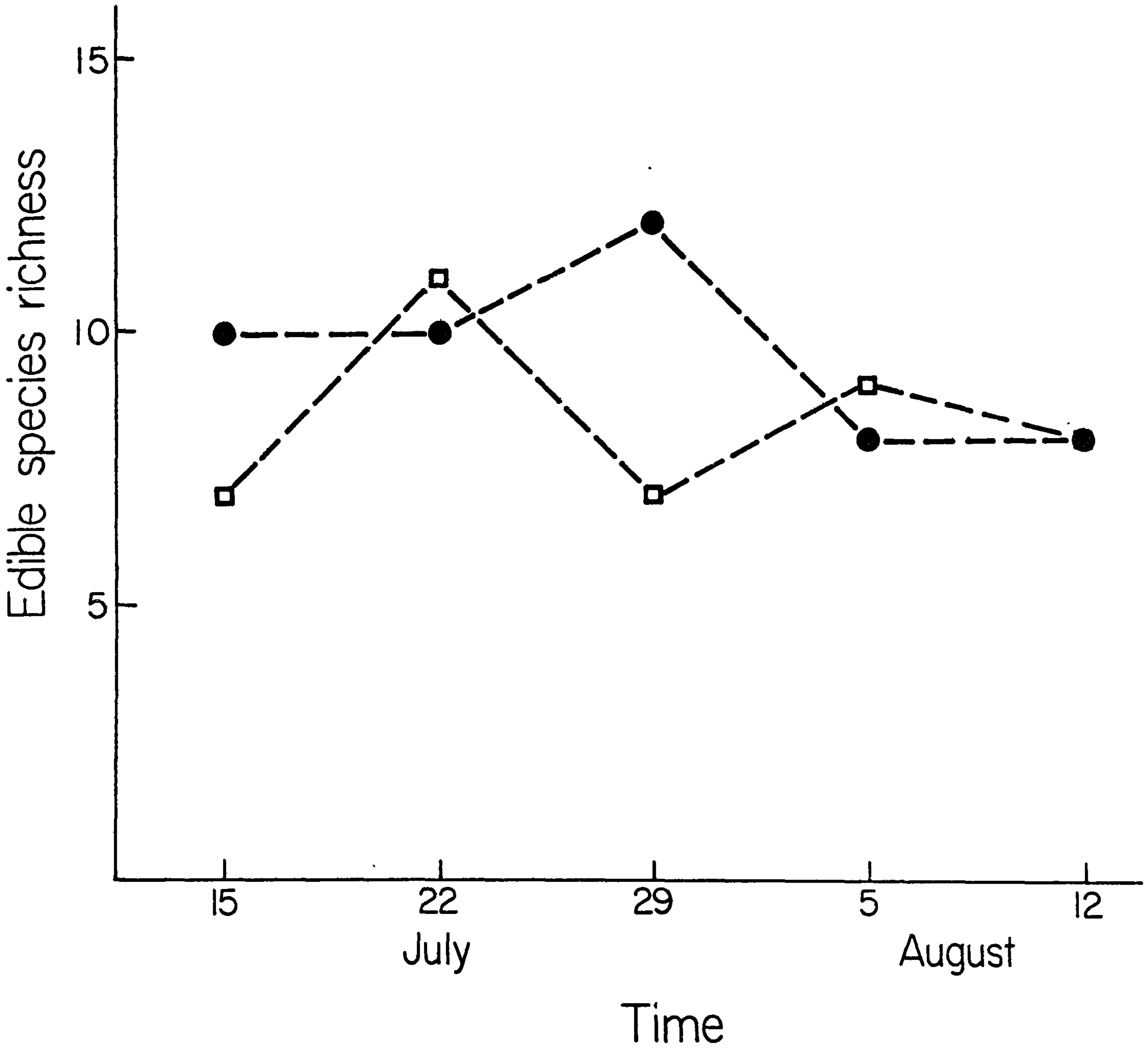

Inedible species richness
20
15
10
5
15
22
29
5
12
July
August
Time

Fig. 22 The effect of reduced grazing pressure on the species richness of the edible group (1977 supplemental test). The control enclosure is designated by solid symbols, the manipulated enclosure by open symbols.


Edible species richness
15
10
5
15
22
29
5
12
July
August
Time

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