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Bottom-up effects of bream (*Abramis brama* L.) in Lake Balaton

I. Tátrai, G. Tóth, J. E. Ponyi, J. Zlinskzky & V. Istvánovics
Balaton Limnological Research Institute, H-8237 Tihany, Hungary

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Abstract

Enclosures (17 m^3) were used in the mesotrophic area of Lake Balaton to determine the impact of benthivorous bream (*Abramis brama* L.) on the lower trophic levels during summers of 1984–86. In enclosures with a fish biomass similar to the biomass in the eutrophic area of the lake, the number of phytoplankton species was highest. In enclosures with a low fish biomass the phytoplankton was dominated by the greens. A high biomass of bream in the mesotrophic basin caused bacterial production corresponding to that of the eutrophic part of the lake. Crustaceans were dominated by copepods and were unable to control phytoplankton peaks. Bottom-up effects of bream were more obvious than top-down effects and seem to be more important in the possible control of water quality.

Introduction

The trophic state of a lake is not determined only by the external nutrient load but also by the structure of food chain. A number of studies show the effect of food web manipulation as a measure for water quality management (Shapiro *et al.*, 1982; Benndorf *et al.*, 1984; Carpenter *et al.*, 1985; McQueen & Post, 1988). However, it is uncertain if water quality will also improve in lakes with high nutrient load and with fish fauna dominated by benthivores. In the case of both high external (Benndorf *et al.*, 1988) and internal phosphorus load (Lammens, 1988) not all the desired improvements in water quality were achieved.

There is hardly any experience of food web manipulations in eutrophic, shallow, unstratified large lakes with high internal nutrient load from sediments dominated by cyanobacteria, benthivorous bream and carp (see Meijer *et al.*, 1990).

The most common approaches to reverse or stop the eutrophication process are reducing the nutrient load and enlarging the grazing on phytoplankton by manipulation of zooplankton-phytoplankton interactions. Our study was designed to investigate the effect of the fish-zooplankton-phytoplankton interactions in a large eutrophic shallow lake where the zooplankton is dominated by copepods (up to 90%) and the fish by benthivores.

Materials and methods

The enclosure experiments were carried out in the mesotrophic area of Lake Balaton during the summers of 1984–86. The enclosures (diameter 3 m, 210 cm deep) were open to the sediments and the atmosphere. Details of construction are given in Tátrai & Istvánovics (1986). One enclosure served as a control (CE) while the others were stocked with a varying biomass of bream (*Abramis brama* L.) (FE) corresponding to biomasses in the different basins of Lake Balaton (Table 1).

The initial size and biomass of introduced fish

Table 1. The number and size of bream (*Abramis brama* L.) used for the experiments.

Date of the experiments	Average water temp. °C	Number and biomass of fish, g m^{-2}	Average weight (g) of fish, (range)	Total increment in weight %
01.06–11.09	18.7	9	47.9	82.8
1984		60.7	(10.0–106.5)	
21.06–18.07	19.0	6	94.3	49.6
1985		79.7	(8.0–158.0)	
04.07–11.09	21.9	4	82.4	21.4
1986		46.4	(69.0–107.0)	

to the enclosures was the highest in 1985 and the lowest in 1986 corresponding approximately to the biomasses in the eutrophic and mesotrophic basins of lake Balaton (LB), respectively. During the study periods the fish weight increased 20–80%.

Water samples for physical, chemical and biological analyses were taken every 2–5 days from the two enclosures and LB nearby the enclosures with a surface-mud tube sampler 12 cm in diameter. In 1985 and 1986, mixed unfiltered samples were used to measure bacterial production (after Fuhrman & Azam, 1982) based on the incorporation of thymidine, labelled with tritium (3HT) into DNA of bacteria.

Phytoplankton samples were lumped and preserved with Lugol's solution and enumerated using the method of Utermöhl (1958). The wet weight of each algal species was calculated from cell volume. Primary production was measured from unfiltered samples using ^{14}C-method. The radioactivity was determined with Rack-Beta-2 liquid scintillation counter.

Crustaceans were sampled filtering minimally 10 l of water through a 50 μm net. Cladocerans and copepods were sized and counted using microscopes.

Results

Temperature

The water temperature of Lake Balaton occasionally was 3–6 °C cooler in 1984 than in 1985–86. However, thermostratification has never developed (Fig. 1).

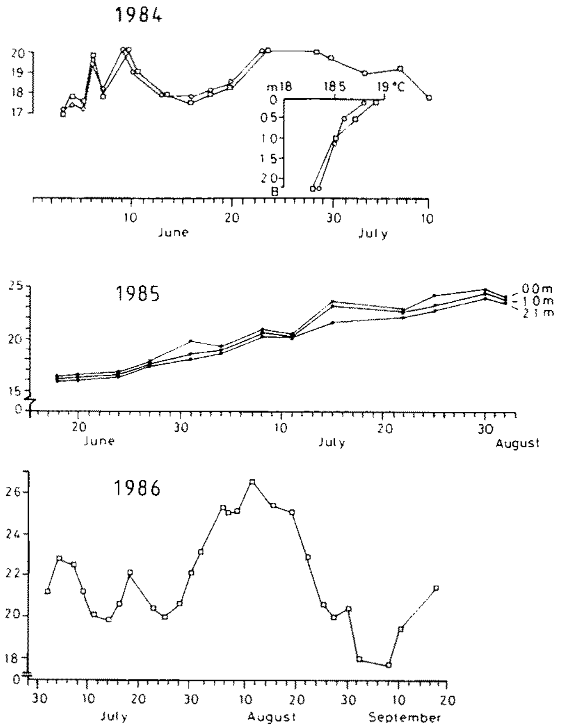

Fig. 1. Seasonal temperatures and depth profiles in lake Balaton (□), in the fish (●) and control (○) enclosures.

Bacteria

In 1985 and 1986 the production of the bacterioplankton was highest in the presence of fish (Fig. 2). Surprisingly in 1985 the bacterial production in FE was very close to that measured in the eutrophic basin of the lake.

Phytoplankton

The species composition of phytoplankton communities as well as the species number varied between enclosures, lake and years. In 1985 72 algal species were found in LB, almost the same number in CE(71) and 83 in FE. At the beginning of the study mainly diatoms (*Cyclotella ocellata* and *C. bodanica*) dominated at all sampling points (Fig. 3). In FE, however, the diatoms were replaced by filamentous cyanobacteria (*Aphanizomenon flos-aquae* and *A. issachenkoi*). The number of filaments doubled within 4–5 days and amounted more than 90% of the total biomass at the end of the experiments (Fig. 3). Cyano bacteria appeared in CE and LB as well but their biomass was only 20% of that found in FE (Fig. 3). In CE the biomass of phytoplankton, apart from the small fluctuations, decreased throughout the study.

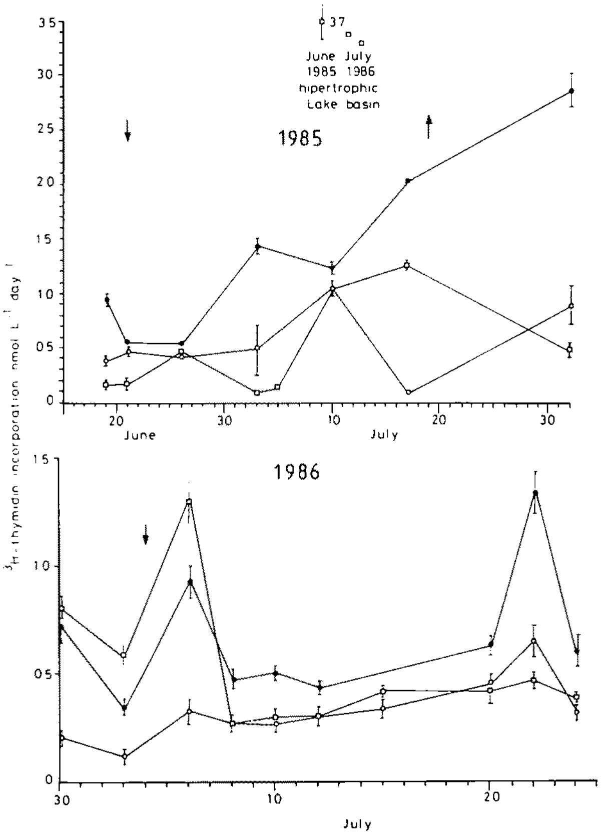

Fig. 2. The activities of bacterioplankton in the fish (●) and fish free(○) enclosures and in Lake Balaton (□).

In 1986 the number of phytoplankton species was lower but the biomass higher than in 1985 (Fig. 3). At the beginning again mainly diatoms (*Cyclotella* sp., *Cymatopleura* sp.) dominated in the enclosures as well as in the lake. In FE diatoms were replaced by the filamentous cyanobacteria (*Aphanizomenon* species) in July. In the next month again remarkable changes in algal structure occurred at the presence of fish: cyanobacteria were replaced by greens (*Closterium* species) increasing in biomass up to more than 10 mg l^{-1} at the end of the study and contributing 78% to the total biomass. Phytoplankton community biomass was many times lower in CE and LB than in FE and were dominated by cyano bacteria.

Primary production was lower at higher fish biomass in 1984 and always coincided with the peaks in algal biomass. However, the trend in primary production was very similar in both years (Fig. 4).

Crustaceans

Copepods, predominantly *Eudiaptomus gracilis*, were more numerous than cladocerans (except the last week in 1985) in any study area in all three years (Figs 5, 6, 7). The density of crustaceans did not decrease even at the very high fish biomass. On the contrary there was a tendency for copepods in 1984 and for cladocerans in 1985 to increase in number at the presence of fish. Neither cladocerans nor copepods were affected essentially by bream through predation. Moreover, a high fish biomass seems to stimulate reproduction of some species of crustaceans. For example the relatively large *Eudiaptomus* was not eliminated by fish and occurred in high densities in FE. The density of cladocerans was much lower at any study area in all years and dominated by small bodies *Bosmina longirostris* in 1984 and *Diaphano-*

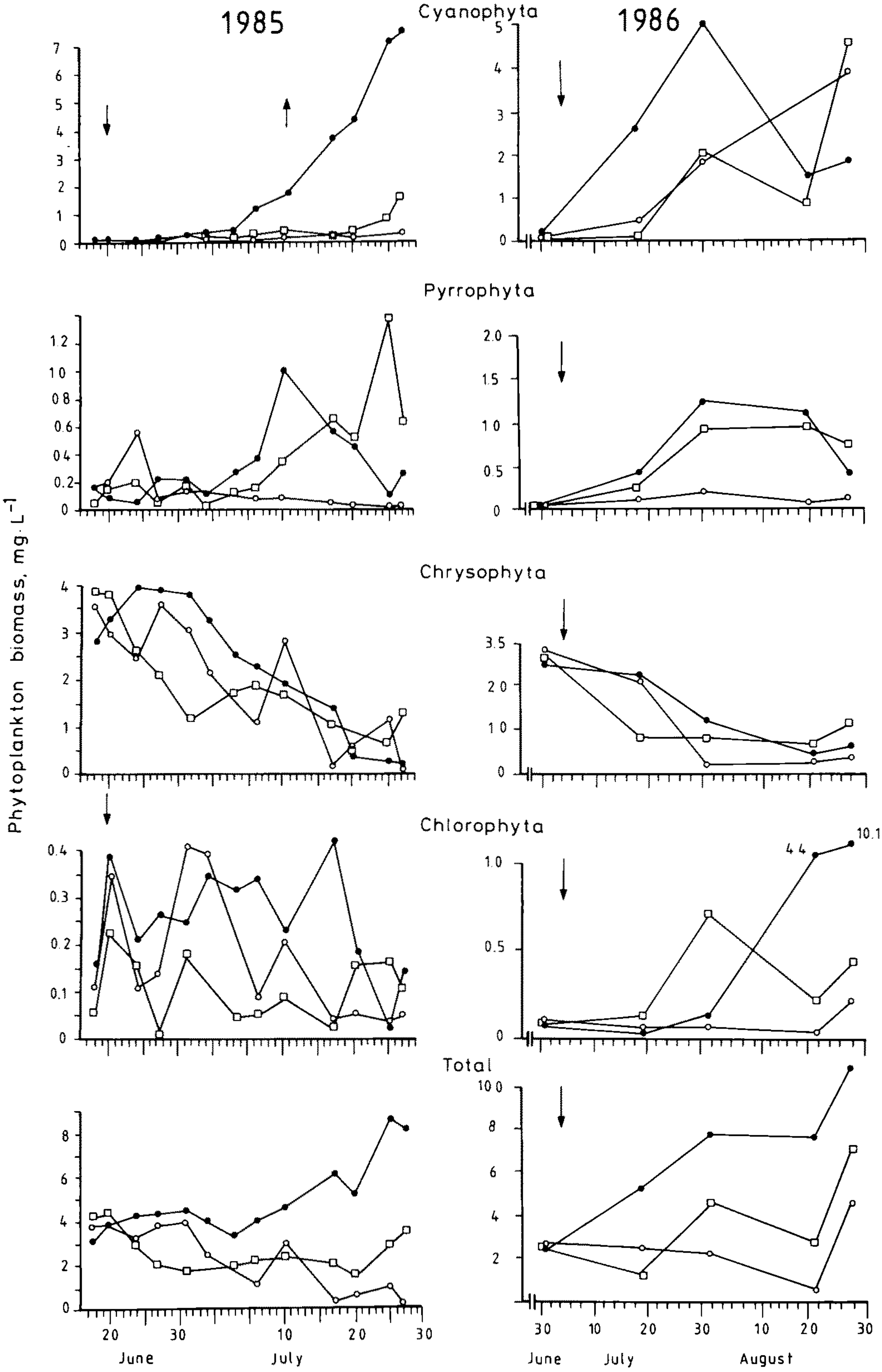

Fig. 3. Changes in biomass of different genera of phytoplankton in the enclosures and in the lake (symbols as in Fig. 2).

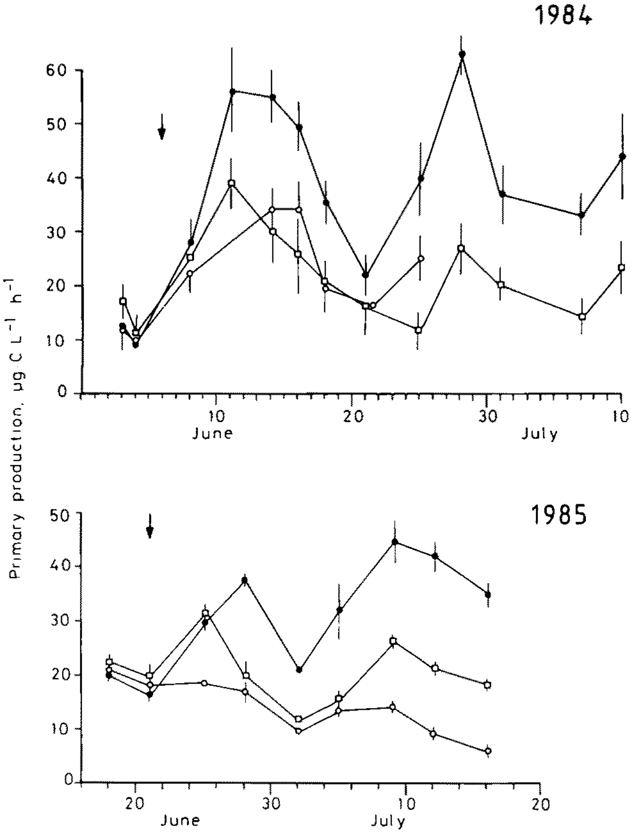

Fig. 4. The rates of primary production in the enclosures and for the lake in 1984 and 1985 (symbols as in Fig. 2).

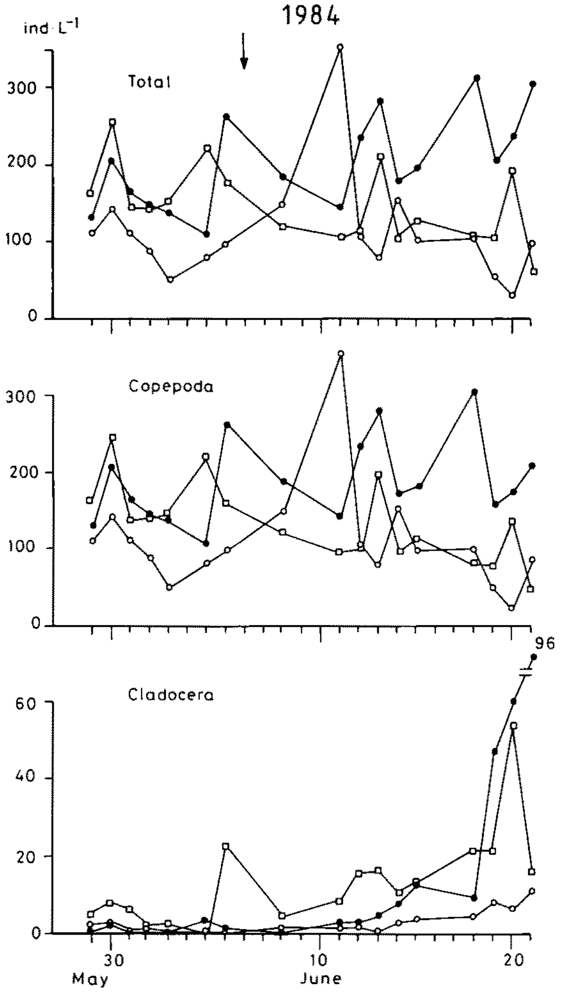

Fig. 5. Crustacean abundance for the enclosures and for the lake in 1984 (symbols as in Fig. 2).

soma branchyurum in 1985–86. CE showed similar taxonomic composition with the same dominating species. Surprisingly *Daphnia cucullata* occurred only in the lake but in a low density.

In summary, the enclosures containing fish did not develope 'classical' crustacean communities characterized by smaller filter-feeding cladocerans but developed communities with the dominance of large bodied filter-feeding copepods.

The size of the cladocerans and the species composition of the crustaceans did not differ significantly (t-test, $p > 0.05$) between treatments or between different years (Fig. 8). Large species (above 1 mm) were absent from both FE and CE. Large sized *D. cucullata* never exceeded 20 ind l^{-1}. Size selection of *D. brachiurum* in FE was only obvious in one occasion at the end of August in 1986.

Interactions

Regressions of crustacean abundance against the totel phytoplankton biomass in FE show significantly positive relationships for cladocerans in 1985 and negative ones for copepods only in 1985 (Table 2, Fig. 9). The same relationship in CE proved to be negative for cladecerans in 1985 and positive for copepods in 1986. Positive correlation in FE in 1985 suggests that large sized (mainly females more than 0.8 mm) *D. brachyurum* might also contribute to changes in algal biomass. A similar type of relationship existed in CE in 1986 for copepods as well.

Table 2. Analysis of variance of simple regression of phytoplankton biomass on crustaceans' abundance for the enclosure experiments in 1985–86.
CE = Control Enclosure, FE = Fish Enclosure, LB = Lake Balaton

Independent variables	df	MS	F	r	P
1985					
Cladocera					
CE	9	2.1	12.36	- 0.87	0.0053*
FE	10	3.14	16.20	0.96	0.0027*
LB	10	0.78	0.74	- 0.26	0.4092
Copepoda					
CE	9	1.34	1.48	0.37	0.2542
FE	11	1.54	10.93	- 0.71	0.0069*
LB	10	0.83	0.07	- 0.08	0.7952
1986					
Cladocera					
CE	10	0.72	2.91	- 0.47	0.1185
FE	10	10.14	1.11	- 0.32	0.3167
LB	11	3.88	0.4E–4	- 1.9E–3	0.9949
Copepoda					
CE	10	0.44	11.06	0.72	0.0076*
FE	10	8.13	3.85	- 0.53	0.0779
LB	11	3.49	1.25	0.31	0.2877

* = relationships are significant at $P < 0.05$ level.

Discussion

Biomanipulation theory (Shapiro *et al.*, 1982) and cascading trophic interaction theory (Carpenter *et al.*, 1985) suggest that a reduction in planktivorous fish abundance can lead to an increase in large cladocerans and a subsequent increase in phytoplankton grazing. Many experimental studies (see McQueen *et al.*, 1986) showed that this top-down effect of fish varies considerably depending on the trophic state of the lake.

The results of our enclosure experiments contradict in some points with the data in the literature. It seems that the top-down effects, due to the low stockings of the planktivorous fish populations, are much less important in Lake Balaton than in other lakes. In Lake Michigan for example top-down manipulations of food web can impose strong controls on the phytoplankton community and overwhelm even nutrient effects especially at summer conditions (Dorazio *et al.*, 1987).

In the review paper McQueen *et al.* (1986) showed that top-down effects are only obvious in less eutrophic lakes and very limited in hypertrophic lakes. In our experiments top-down effects were observed as well but were limited only to copepods. Copepods dominate the zooplankton of Lake Balaton during summer. Because their filtering capacity is much lower than that of cladocerans (Zánkai & Ponyi, 1986), they are not able to control effectively the algal production especially at its peaks. Because copepods are smaller targets than big daphnia species for visually orienting fish, they are less susceptible to fish predation (Winfield & Towsend, 1988). Instead of increase in number of filter-feeding large sized copepods it seems that top-down manipulation of the Lake Balaton's food web has little effect on grazers' during summer.

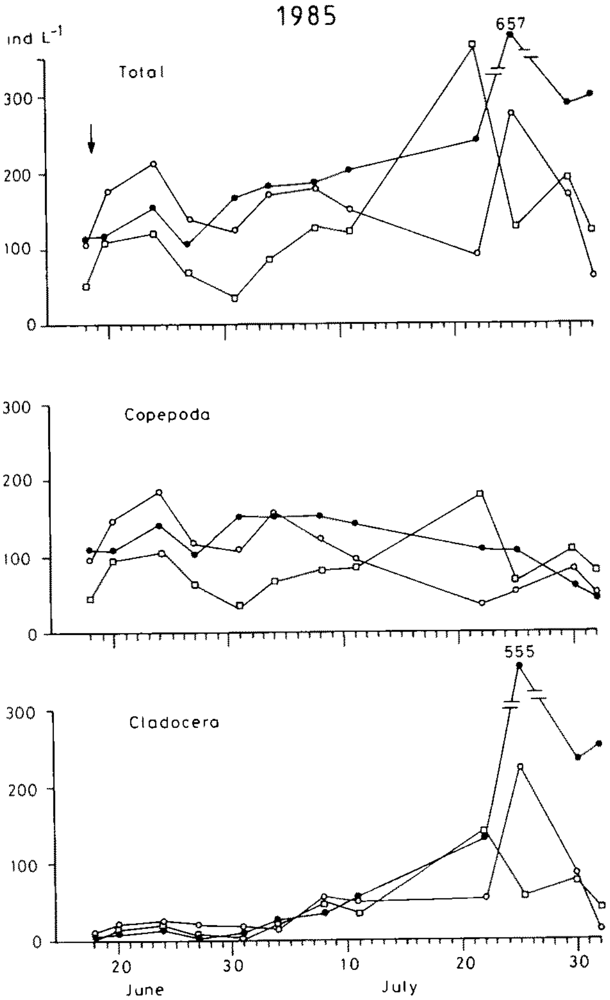

Fig. 6. Crustacean abundance for the enclosures and for the lake in 1985 (symbols as in Fig. 2).

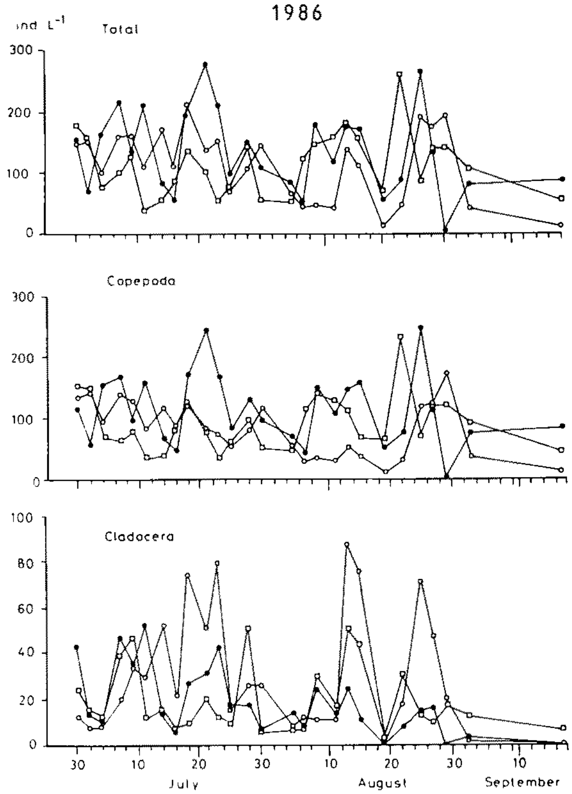

Fig. 7. Crusteans abundance for the enclosures and for the lake in 1986 (symbols as in Fig. 2).

The intensity of 3H-thymidine incorporation by bacteria has pointed out the growing organic substrate in the fish enclosures which can be the result of egestion and bioturbation effect (Lammens, 1988) of benthivorous fish. Subsequent organic matter (e.g. detritus) and bacteria, particularly heterocystic cyanobacteria spores (Gorzó, 1985) might have been released from the sediments by bream when searching for food (Table 3).

Our observations in the enclosures are consistent with those in whole lake (Lake Tjeukemeer) biomanipulation studies in Holland (Lammens, 1988) where similarly the bottom-up effects proved to be the more important due to the dominance of benthivorous fish species. But in contrast to the Lammens's (1988) conclusion we, however, believe that bream removal will probably decrease the nutrient effects (Tátrai *et al.*, in press) and thus change the phytoplankton dynamics in Lake Balaton. The various indirect effects and feedback mechanisms change the nutrient metabolism of lakes. Since the 'loading threshold' of nutrients (Benndorf, 1989) is restricted only to the eutrophic basin of Lake Balaton, improvement in water quality of the mesotrophic basin might be achieved by food-web manipulation.

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Table 3. Abundance of macroinvertebrates in the enclosures and in Lake Balaton on the day of fish introduction into one of the enclosures (4th July 1985) and two weeks later (16th July 1985). (Estimates are based on 3 Ekmans on each sampling point)

Group of Animals (ind m^{-2})		Control enclosure		Fish enclosure		Lake Balaton	
	Date:	04/07	16/07	04/07	16/07	04/07	16/07
Chironomidae		1,554	2,309	1,266	356	1,199	1,678
Oligochaeta		2,531	3,641	3,419	2,975	1,642	746
Nematoda		355	0	266	355	266	222
Mollusca		9,457	6,660	9,546	7,992	12,432	9,003
Others (Ephem. Coleop)		0	0	44	0	89	44
Total		13,894	12,610	14,541	11,678	15,628	11,693

enclosures, to the Diver's Club Amphora for the installation, and to T. F. Klein for technical assistance. Many thanks to the two anonymous reviewers for constructive criticism and useful comments on an earlier version of this manuscript. Research was supported partly by the MTA-AKA grant form the Hungarian Academy of Sciences.

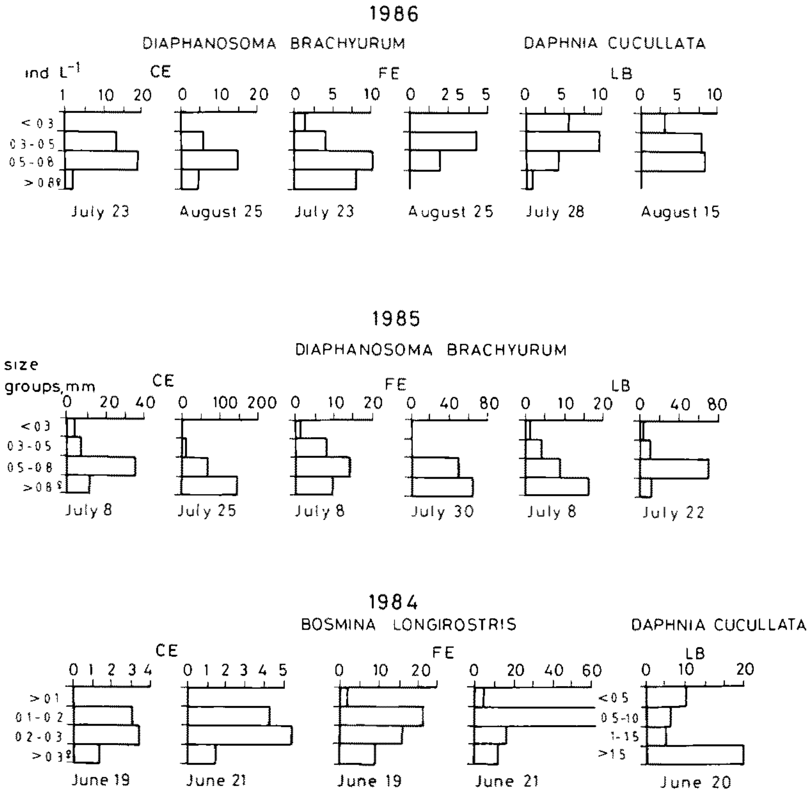

Fig. 8. Length frequency changes in dominant cladocerans for the enclosures and for the lake in different years (FE = Fish Enclosure, CE = Control Enclosure, LB = Lake Balaton) (symbols as in Fig. 2).

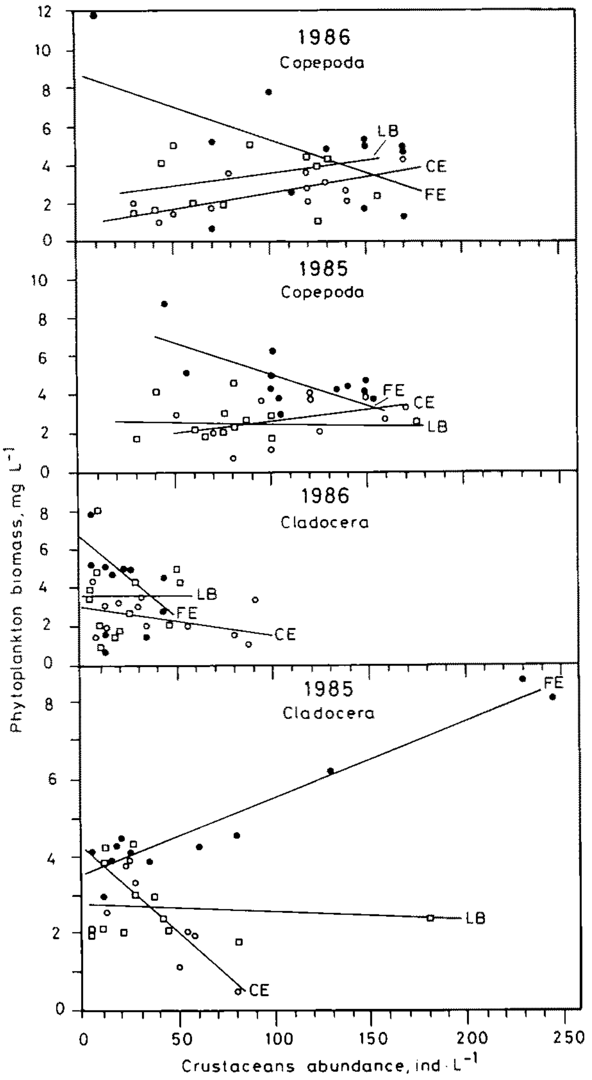

Fig. 9. The relationship between crustacean abundance and phytoplankton biomass for the enclosures and the lake (FE = Fish Encloures, CE = Control Enclosure, FB = Lake Balaton) (symbols as in Fig. 2).

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