

Fish impact on rotifer community structure

J. A. E. Stenson

Department of Zoology, University of Göteborg, Box 25059, S-400 31 Göteborg, Sweden

Keywords: fish, invertebrate predators, phytoplankton structure, rotifers, community structure, feedback, field experiment

Abstract

Larger species, e.g. *Asplanchna priodonta* and *Conochilus unicornis*, and grasping species, e.g. *Gastropus stylifer* and *Ascomorpha* spp., became more abundant, while smaller filter feeders, e.g. *Keratella cochlearis*, decreased after an experimental reduction of the fish population. This development is probably caused by changes in basic regulating factors. The change to invertebrate predator dominance may affect smaller species (e.g. *Keratella cochlearis*) more than others, the increase of net phytoplankton (e.g. peridineans) will favour grasping species, and the change in seasonal occurrence of certain crucial food species may affect the competitive balance between certain rotifers (e.g. *Polyarthra* spp.).

Introduction

What specific influence does a fish population have on the rotifer community in a lake? This may seem to be quite an ambitious question, but nevertheless it is a logical question to ask. During the last two decades much work has been done on the relations between fish and zooplankton. Most investigations, however, have concentrated upon crustacean zooplankton, which according to many reports is regulated by a strong selective predation by fish. Intense predation will reduce mean size and change species composition towards dominance of smaller species, i.e. the whole zooplankton community is affected (e.g. Hrbacek 1962; Brooks & Dodson 1965; Stenson 1972).

Invertebrate zooplankton predators, another important functional group in fresh water ecosystems, have also been shown to be selective and able to reduce abundance of their prey organisms in the smaller size intervals (McQueen 1969; Confer 1971; Dodson 1972). Most invertebrate plankton predators are themselves susceptible to predation and their abundance and predatory influence may

therefore be regulated by the fish population (Stenson 1976; Lane 1979).

It has recently been shown that changes in the fish population will produce certain effects even on the primary production level (Andersson *et al.* 1978; Stenson *et al.* 1978). Lakes heavily stocked with fish will have a predominant development of smaller algae (Hrbacek *et al.* 1961) while a reduction of the fish density will enhance the development of large net-phytoplankton species (Stenson *et al.* 1978). The ability of fish to regulate mean body size and species composition of zooplankton thereby influencing grazing pressure and turnover rates of nutrients, points to one possible way of interaction between fish and the primary producers (Henrikson *et al.* 1980).

This knowledge about interactions between the top levels and the lower trophic levels in the lake ecosystem makes it possible to suggest some probable pathways for fish influence on rotifer populations.

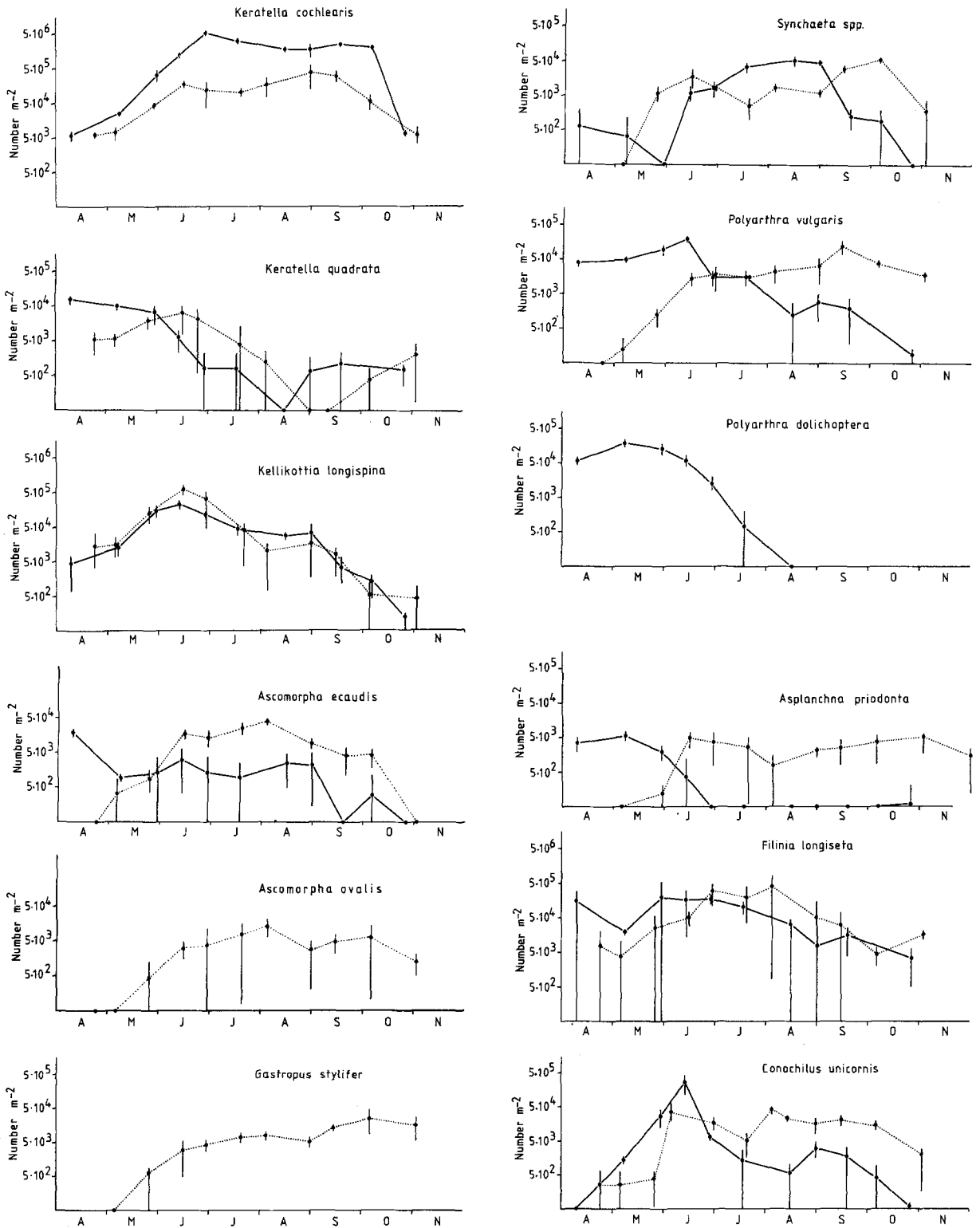


Fig. 1. Number of rotifers per m², 1973 (solid line) and 1977. Y-axis is logarithmic, which also gives asymmetrical confidence intervals.

Mode of interaction

a) *Direct predation from fish*: Rotifers are in general too small to be affected. There may, however, be some exceptions. The population density of large species like *Asplanchna priodonta* and the colony-living *Conochilus unicornis* may be negatively influenced by fish predation.

b) *Invertebrate predation*: Invertebrate predators may reduce population density of smaller rotifers. This effect may, however, be balanced by fish predation.

c) *Phytoplankton composition*: The possibilities for fish to change the species composition of phytoplankton through feedback mechanisms indicate a third possible way of influence, i.e. via the food base.

The purpose of this paper is to present a field study in which the validity of the above hypothetical modes of interaction can be tested. The main questions were the following: does an experimental elimination of the fish population result in an increase in the number of large rotifers, an intensification of invertebrate predation pressure and thereby a decline in the number of susceptible prey species, and changes in the rotifer species composition due to a change in the phytoplankton structure?

Experimental design and methods

The experiment and observations were made in Lake Lilla Stockelidsvatten in southwest Sweden (area 1 ha; max depth 8 m). The lake originally had a dense fish population dominated by roach (*Rutilus rutilus* (L.)). Other species present were pike (*Esox lucius* L.), tench (*Tinca tinca* L.) and eel (*Anguilla anguilla* L.). All fish species except eel reproduced every year, which resulted in the production of large schools of fry. The fish population was eliminated by means of rotenone in November 1973. A more detailed description of the experiment and the fish population is given elsewhere (Stenson 1972, 1979; Stenson *et al.* 1978).

Rotifers were sampled with a net (mesh 25 μm ; mouth area 200 cm^2 ; length 50 cm) at six randomly selected places in the pelagic zone. The net was vertically retrieved from the bottom to the surface at a constant speed of 0.5 m s^{-1} . All samples were fixed in 4% formalin. Counts were carried out on sub-

samples. Species identification was made according to Voigt (1957) and Ruttner-Kollisko (1972).

Results

After the elimination of the fish population, the rotifer community changed in several respects, including abundance of different species, temporal development of population density, biomass and numeric relations between different functional groups.

I consider that real changes between the years exist where there is no overlap between the confidence intervals (C.I.). The size of the C.I. depends on the distribution of the animals within the water mass. Thus species with a patchy distribution pattern will have larger C.I. *Filinia longiseta*, for example, with high densities below the thermocline, is very sparse in samples from the shallow sites, which results in wide C.I.

Keratella cochlearis and *Polyarthra dolichoptera* have decreased in number, the latter species to an undetectable level (Fig. 1). *Conochilus unicornis*, *Gastropus stylifer*, *Ascomorpha ecaudis*, *A. ovalis* and *Asplanchna priodonta* became more frequent after the elimination of the fish population. *Gastropus stylifer* and *Ascomorpha ovalis* were not found at all before the elimination (Fig. 1). *Polyarthra vulgaris*, finally, shows a changed seasonal development after the elimination. After an abundance maximum in June 1973 there was a drop throughout the summer. In 1977 the peak came in September after a spring with low densities.

Furthermore the rotifer biovolume was altered (Fig. 2). After a biomass maximum early in May

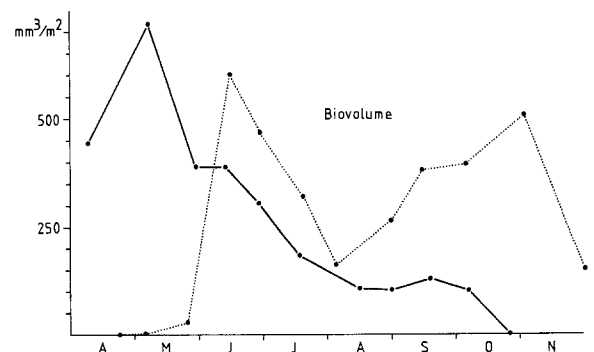


Fig. 2. Total biomass of rotifers in mm^3 per m^2 , 1973 (solid line) and 1977 in Lake Lilla Stockelidsvatten.

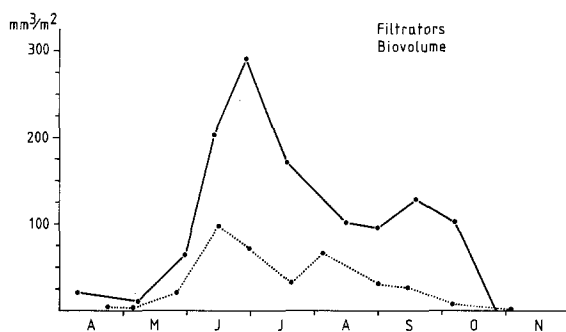


Fig. 3. Biomass of filtering rotifers in mm^3 per m^2 , 1973 (solid line) and 1977 in Lake Lilla Stockelidsvatten.

1973, there was a continuous drop throughout the summer. After the elimination of the fish population, the building up of maximum biomass progressed slowly. The peak occurring in the middle of June was followed by a second peak, almost as high as the first one, in the beginning of November. There was a net biomass increase and also a drop in the total number of organisms, two facts which together indicate an increase in the mean body size among the rotifers.

There were also significant changes in the balance between certain functional groups. Filter-feeding species became less abundant, while grasping species increased (Fig. 3).

Discussion

In the interpretation of the results the question whether the rotenone treatment *per se* can produce the effects must be considered.

Organisms other than fish are also sensitive to rotenone. The direct effects on the crustaceans were severe, while rotifers seemed to be less affected. The chances of restoring the populations, however, are good, due to the occurrence of resting eggs and the ability to escape the poison within the vegetation and along sediment surfaces (Kiser *et al.* 1963; Anderson 1970; Stenson 1972). Every rotifer species found before the treatment was thus found again the following year, a fact which indicates the short duration of the effect of rotenone.

The elimination of the fish population probably is responsible for the large biological changes. Small-sized forms, e.g. *Bosmina longirostris*, were replaced by large calanoids, e.g. *Eudiaptomus*

gracilis, among the herbivorans and their biomass increased. The abundance of *Chaoborus* larvae, one very important invertebrate zooplankton predator, increased dramatically (Stenson *et al.* 1978; Stenson 1978). How could these changes possibly influence the rotifers?

The first problem to deal with is the reason for the population increase of the two largest species, *Asplanchna priodonta* and *Conochilus unicornis*. In 1973 the population of *A. priodonta* exhibited a peak in the spring and a rapid decrease in June to an undetectable level where it stayed until October when a slight recovery occurred. *Asplanchna priodonta* is a polyphagous species with a strong preference for animal food, especially *Keratella cochlearis* (e.g. Pejler 1965; Gliwicz 1969; Dumont 1972). Sorokin (1968) showed that animal food was more easily assimilated than algal food. Esjmont-Karabin (1974) calculated Ivlev's index of electivity and found low values (near zero) for algal food, while it reached high values for animal food. This information may suggest that a decrease in suitable prey is responsible for the reduction in the abundance of *Asplanchna*. This is probably not the case, as *Keratella cochlearis*, probably the main prey, remains abundant (see Fig. 1). *Asplanchna* is big enough to be a suitable prey for fish. The decline of *Asplanchna* in 1973 was in fact correlated with increasing predation activities of fish, especially fish fry, which probably reduced the abundance of *Asplanchna*. This very marked summer reduction in number did not occur when the fish population was eliminated. The presence of eggs and embryos may increase the visible size, which in turn may increase the predation pressure on gravid females of *Asplanchna*.

Conochilus unicornis is also big enough to be preyed upon by fish. The decline in 1973 did coincide with the increase in the predation pressure from fish (Stenson 1979). However, this decline may be partly caused by competition. This is difficult to prove, but the fact that *Keratella cochlearis*, one probable competitor, which according to Pourriot (1977) is microphagous and detritus-eating just like *Conochilus*, continued to increase even after the maximum of *Conochilus* and then stayed at high densities may support the competition theory.

Although *Asplanchna priodonta* and *Conochilus unicornis* both occurred in fish stomachs (Sten-

son 1979) it is very difficult to obtain quantitative information about the importance of fish predation. Both species have soft body structures which seem to be easily destroyed in the stomachs. However, the fact that they occur in the fish stomachs indicate that they may be preyed upon by a visually-dependent predator, which selects prey, in a size-dependent manner from a zooplankton community where *Asplanchna* (0.3–1.0 mm) and *Conochilus* colonies (0.5–1.3 mm) are both well above the mean size of the crustaceans (mean length: 0.33 mm; SD: 0.09, in June).

Among the filter-feeding species, *Keratella cochlearis* is the one that has probably been most affected by the change to invertebrate predation on zooplankton. Both *Chaoborus* larvae, especially the younger instars and *Asplanchna priodonta* prey on *K. cochlearis* (Comita 1972; Lewis 1977; Pourriot 1977), and may thus be responsible for a significant reduction of the *K. cochlearis* population density. *Keratella cochlearis* was the most common animal prey noted in the stomachs of *Asplanchna*. Another factor which also may contribute to the reduction is an increasing competition for suitable food. Again, this is difficult to prove, but there are two facts that may support this presumption. Species like *Kellikottia longispina*, *Conochilus unicornis* and *Eudiaptomus gracilis*, which according to Edmondson (1965), Pourriot (1977) and McNaught (1975) are potential competitors for the smaller fraction among the nanoplankton, have become abundant, while their food base, small nanoplankton, have probably decreased (Henrikson *et al.* 1980; Larsson, in prep.).

The change to invertebrate predation probably has less direct effects on the other filter-feeding or detritus-eating species. The presence of long spines in e.g. *Kellikottia longispina* and *Filinia longiseta*, the latter occupying a less favourable habitat (below the thermocline water with low oxygen content), makes them less susceptible to invertebrate predation. Moreover, the *Conochilus unicornis* colonies may be too large in size to be significantly preyed upon by invertebrate predators.

As mentioned above, there have been changes in the phytoplankton, which may be caused by the elimination of the fish population as follows: the larger biomass of large herbivorans can maintain a

harder grazing pressure on the edible part of phytoplankton, i.e. the smaller size fraction. The reduction of these smaller algae may create better nutrient conditions for the perhaps less competitive larger net phytoplankton species. The mean body size increase among the grazers may not only improve the effectiveness of grazing but also influence the turnover rate of nutrients in a negative way. According to several authors, smaller species have higher turnover rates and are therefore more effective in recycling nutrients than are larger species (e.g. Peters & Rigler 1973; Peters 1975). The elimination of the fish population also resulted in a decreased import to the pelagic zone of nutrients from areas outside this zone. This set of biotic changes is probably important for the development of the new phytoplankton community characterized by larger mean cell size and lower productivity (Henrikson *et al.* 1980). Figure 4 shows the increase of net phytoplankton biomass. According to Larsson (in prep.) there is an increase of mainly dinoflagellates, e.g. *Peridinium* spp. and *Ceratium hirundinella*, but also other species like *Mallomonas caudata* and *Rizosolenia longiseta*. This changed phytoplankton composition has obviously been beneficial for three rotifer species in particular. *Gastopus stylifer* has, according to Ruttner-Kollisko (1972), a preference for peridineans and also *Mallomonas* sp. (Pejler 1965). The increase of the two *Ascomorpha* species is obviously also a result of the improved food situation. Both species subsist on dinoflagellates; *A. ovalis* has a strong preference for *Ceratium* (Pourriot 1977).

The next problem to deal with is the disappearance of *Polyarthra dolichoptera*. Before fish elimination, the species exhibited a population maximum during the spring and a decline during the summer. According to other studies (e.g. Pejler 1956, Nauwerck 1963), it is considered to be a cold steno-thermal, winter and spring form. Pejler (1956) showed that *P. dolichoptera*, in contrast to *P. vulgaris*, is tolerant to water with low oxygen content. Guiset (1977) showed that *P. vulgaris-dolichoptera* belonged to those rotifers that are frequently eaten by *Asplanchna priodonta*. Gilbert & Williamson (1978) on the other hand reported that *Asplanchna* only rarely captured *Polyarthra*. (In their study they used *A. girodi*.) Finally, the two *Polyarthra* species are considered to have similar

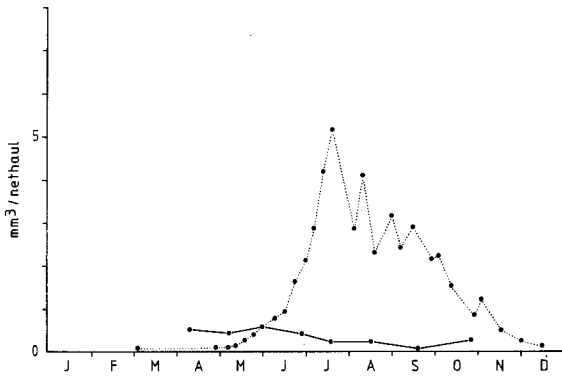


Fig. 4. Net phytoplankton biomass in mm³ per net haul, 1973 (solid line) and 1977 in Lake Lilla Stockelidsvatten. (Modified from Larsson, in prep.).

rather narrow food niches including e.g. Cryptomonadales and Crysomonadales (Pejler 1957; Edmondson 1965; Pourriot 1977). *Dinobryon* spp. was an important food source according to Buikema *et al.* (1978).

There is no such change in the oxygen situation over the years that could possibly explain the decline of *Polyarthra dolichoptera*. Furthermore the population of *Asplanchna priodonta*, one possible predator, is weak in the spring. *Chaoborus* larvae, also presumptive predators, are in the fourth instar stage during spring and then prey mainly on crustaceans. In summary, predation is not the most probable cause for *P. dolichoptera* disappearance. If the two *Polyarthra* species really have very similar feeding niches, competition should be severe if mechanisms have not evolved that obviate competition. The different seasonal occurrence and the difference in tolerance to low oxygen content may be such mechanisms. One important prerequisite for existence, however, is

the availability of a proper food resource. Table 1 shows the occurrence of probable food groups during the critical spring and early summer period. There are obvious differences between the years. Food was present earlier in 1973, when the water was still cold. Water of low temperature and with appropriate food are important to make *P. dolichoptera* competitive if Pejler's (1956) presumption is correct. These conditions did not exist in 1977. No food was present this year during the period with low water temperature, i.e. during the period when *P. dolichoptera* may have competitive advantages over *P. vulgaris*.

Final remarks

Many of the changes shown in this study concern species which are reported to be sensitive to trophic changes of lakes. *Kellikottia longispina* and *Ascomorpha* spp. decrease in eutrophicated lakes according to Pejler (1957) and Dumont (1968). Pejler (1965) considered *Ascomorpha ovalis* to prefer nutrient poor conditions. *Keratella cochlearis* on the other hand is known to increase in eutrophicated lakes (Dumont 1977). *K. cochlearis* shows an increase also when the lake turnover is increased as a result of fish stocking, according to Hillbricht-Ilkowska & Weglénska (1973). These species mentioned showed an opposite development in this study, which may indicate a change of the lake in an oligotrophic direction. This is in fact supported by changes in the same direction of several abiotic factors, e.g. pH, transparency, nutrient content, etc., which are commonly used as trophic criteria. These changes have taken place without changes in the external nutrient loading (Henrikson *et al.* 1980). The manipulation at the

Table 1. Occurrence of significant food species for *Polyarthra vulgaris* and *P. dolichoptera* in Lake Lilla Stockelidsvatten.

	1973					1977						
	9/4	7/5	29/5	28/6	17/7	2/3	27/4	5/5	11/5	8/6	15/6	12/7
<i>Dinobryon bavaricum</i>	+	+	+						+	+	+	+
<i>D. cylindricum</i>	+	+	+	+	+			+	+	+	+	+
<i>D. divergens</i>	+	+	+								+	+
<i>D. pediforme</i>					+							
<i>D. sertularia</i>	+	+		+								
<i>D. crenulatum</i>				+	+				+	+		
<i>Cryptomonas</i> spp.		+							+	+		

top of the ecosystem thus resulted in changes of the entire biotic feedback system including interrelations between predators and prey, grazers and algae, and biotic nutrient recirculation, all of which are significant for the development of the new rotifer community.

Acknowledgements

This investigation was financially supported by grants from the National Swedish Environment Protection Board, the National Research Council of Sweden and the Fishery Board of Sweden. I am grateful to Dr. Bruno Berzins, who helped me with species identification.

References

- Anderson, R. S., 1970. Effects of rotenone on zooplankton and a study of their recovery patterns in two mountain lakes in Alberta. *J. Fish. Res. Bd. Can.* 27: 1335-1356.
- Andersson, G., Berggren, H., Cronberg, G. & Gelin, C., 1978. Effects of planktivorous and benthivorous fish organisms and water chemistry in eutrophic lakes. *Hydrobiologia* 59: 9-15.
- Brooks, J. L. & Dodson, S. I., 1965. Predation, body size, and composition of plankton. *Science* 150: 28-35.
- Buikema, A. L. Jr., Miller, J. D. & Yongue, W. H. Jr., 1978. Effects of algae and protozoans on the dynamics of *Polyarthra vulgaris*. *Verh. int. Verein. Limnol.* 20: 2395-2399.
- Comita, G. W., 1972. The seasonal zooplankton cycles, production, and transformations of energy in Severson lake, Minnesota. *Archs. Hydrobiol.* 70: 14-66.
- Confer, J. L., 1971. Intra-zooplankton predation by *Mesocyclops edax* at natural prey densities. *Limnol. Oceanogr.* 14: 693-700.
- Dodson, S. I., 1972. Mortality in a population of *Daphnia rosea*. *Ecology* 53: 1011-1023.
- Dumont, H. J., 1968. Rotatoria en *Gatrottricha* uit Plankton en Periphyton van het Donk meer in Oost-Vlaanderen met voorlopige nota over de trofische en faunistische evolutie van het milieu. *Biol. Jb. Dodonaea* 36: 139-149.
- Dumont, H. J., 1977. Biotic factors in the population dynamics of rotifers. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 8: 98-122.
- Edmondson, W. T., 1965. Reproductive rate of planktonic rotifers as related to food and temperature in nature. *Ecol. Monogr.* 35: 61-111.
- Ejsmont-Karabin, J., 1974. Research on the feeding of plankton polyphagous rotifer *Asplanchna priodonta* Gosse. *Ekol. Polska* 22: 311-317.
- Gilbert, J. J. & Williamson, C. E., 1978. Predator-prey behavior and its effects on rotifer survival in associations of *Mesocyclops edax*, *Asplanchna girodi*, *Polyarthra vulgaris* and *Keratella cochlearis*. *Oecologia* 17: 13-22.
- Gliwicz, Z. M., 1969. Studies on the feeding of pelagic zooplankton in lakes with varying trophicity. *Ekol. pol., Ser. A*, 17: 663-707.
- Henrikson, L., Nyman, H. G., Oscarson, H. G. & Stenson, J. A. E., 1980. Trophic changes, without changes in the external nutrient loading. *Hydrobiologia* 68: 257-263.
- Hillbricht-Ilkowska, A. & Weglenska, T., 1973. Experimentally increased fish stock in the pond type lake Warniak VII. Number, biomass and production of zooplankton. *Ekol. Pol.* 21: 533-552.
- Hrbacek, J., 1962. Species composition and the amount of zooplankton in relation to the fish stock. *Rozprawy Ceskoslovenske Akademie Ved* 72: 1-116.
- Hrbacek, J., Dvorakova, M., Korinek, V. & Procházková, L., 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. *Verh. int. Verein. Limnol.* 14: 192-195.
- Kiser, R. W., Donaldson, J. R. & Olson, P. R., 1963. The effects of rotenone on zooplankton populations in freshwater lakes. *Trans. Am. Fish. Soc.* 92: 17-24.
- Lane, P., 1979. Vertebrate and invertebrate predation intensity on freshwater zooplankton communities. *Nature* 280: 391-393.
- Lewis, W. M. Jr., 1977. Feeding selectivity of a tropical *Chaoborus* population. *Freshwat. Biol.* 7: 311-325.
- McNaught, D. C., 1975. A hypothesis to explain the succession from calanoids to cladocerans during eutrophication. *Verh. int. Verein. Limnol.* 19: 724-731.
- McQueen, D. J., 1969. Reduction of zooplankton standing stock by predaceous *Cyclops bicuspidatus thomasi* in Marion lake, British Columbia. *J. Fish. Res. Bd. Can.* 26: 1605-1618.
- Nauwerck, A., 1963. Die Beziehungen zwischen Zooplankton und Phytoplankton im See Erken. *Symb. bot. upsaliens.* 17: 1-163.
- Pejler, B., 1956. Introgression in planktonic rotatoria with some points of view on its causes and conceivable results. *Evolution* 10: 246-261.
- Pejler, B., 1957. Taxonomical and ecological studies on planktonic Rotatoria from northern Swedish Lapland. *K. Svenska Vetensk. Akad. Handl. ser. 4, 6, 5*.
- Pejler, B., 1965. Regional-ecological studies of Swedish freshwater zooplankton. *Zool. Bid. Uppsala* 36: 407-515.
- Peters, R. H., 1975. Phosphorus regeneration by natural populations of limnetic zooplankton. *Verh. int. Verein. Limnol.* 19: 273-279.
- Peters, R. H. & Rigler, F. H., 1973. Phosphorus release by *Daphnia*. *Limnol. Oceanogr.* 18: 821-829.
- Pourriot, R., 1977. Food and feeding habits of Rotifera. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 8: 243-260.
- Ruttner-Kolisko, A., 1972. Rotatoria. Das Zooplankton der Binnengewässer. I. Teil. In: *Die Binnengewässer* 26: 99-234.
- Sorokin, Ju. I., 1968. The use of ^{14}C in the study of nutrition of aquatic animals. *Mitt. Int. Verein. Limnol.* 16: 41 pp.
- Stenson, J. A. E., 1972. Fish predation effects on the species composition of the zooplankton community in eight small forest lakes. *Rep. Inst. Freshw. Res. Drottningholm* 52: 132-148.
- Stenson, J. A. E., 1976. Significance of predator influence on composition of *Bosmina* spp. populations. *Limnol. Oceanogr.* 21: 814-823.

- Stenson, J. A. E., 1978. Differential predation by fish on two species of *Chaoborus* (Diptera, Chaoboridae). *Oikos* 31: 98-101.
- Stenson, J. A. E., 1979. Predator-prey relations between fish and invertebrate prey in some forest lakes. *Rep. Inst. Freshw. Res. Drottningholm* 58: 166-183.
- Stenson, J. A. E., Bohlin, T., Henrikson, L., Nilsson, B. I., Nyman, H. G., Oscarson, H. G. & Larsson, P., 1978. Effects of fish removal from a small lake. *Verh. int. Verein. Limnol.* 20: 794-801.
- Voigt, M., 1957. *Rotatoria. Die Rädertiere Mitteleuropas* Berlin, 508 pp.

Received 19 Januari 1981.