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TROPHIC CHANGES, WITHOUT CHANGES IN THE EXTERNAL NUTRIENT LOADING

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Abstract

The impact of the fish population on trophic properties of lake water, was experimentally studied in an oligotrophic Swedish forest lake. Biotic changes following fish removal resulted in a development in oligotrophic direction as shown by the drop in limnetic primary production, pH, total phosphorus, total nitrogen and the increased transparency.

Introduction

The trophic level of lakes has been considered to be a direct function of input of nutrients from external sources (Vollenweider, 1968; 1976; Shannon & Brezonik, 1972). Models which deal mainly with the influx of nutrients have been used in the field of lake management in order to predict effects and recovery times of specific external loadings (e.g. Vollenweider, 1976; Sonzogni *et al.*, 1976). In most cases these models give satisfactory predictions and are therefore valuable. One obvious problem, however, when working with these models, is the estimation of the importance of biotic factors for the internal flux of nutrients and the role of biota in the trophic degree regulation.

From many studies it is evident that activities on the uppermost level in an ecosystem also influence, via feedback mechanisms, other organisms and processes within other trophic levels. For example, it is well known that through selective predation fish are capable of reducing mean body size and changing species composition in the zooplankton community (e.g. Hrbacek, 1962; Brooks & Dodson, 1965; Stenson, 1976). Changes on the grazer level will most likely affect the food level (Porter, 1977), i. e. the phytoplankton and their production, which in turn may affect even abiotic properties of the water.

The purpose of the present work is to check the importance of these feedback systems and the hypothesis that biotic interactions within the system influence factors which are commonly used as trophic criteria.

Study strategy

The influence of biotic feedbacks on abiotic factors may be studied in an experiment where major changes of the properties of e.g. the limnetic community are made, with other influencial environmental factors under control. By manipulating the predation pressure from fish on the grazers it may be possible to change the structure of the grazer community and thereby its impact on the primary producers. This sequence of changes may, according to the hypothesis, result in an alterred production level and physical and chemical changes.

Experimental design

The study was carried out in lake Lilla Stockelidsvatten, a small forest lake in the middle of Bohuslän, SW Sweden. Some basic data are shown in Table 1. Until November 1973, the lake had a fish population dominated by roach (*Rutilus rutilus* (L.)). The fish population was eliminated by means of rotenone in November 1973. Data were gathered in order to follow the changes after the elimination of fish. In order to be able to relate changes to the

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	Lake LS	Lake SS
Drainage area (ha)	15	7
Lake area (ha)	1	2
Lake volume (m^3)	35,000	40,000
Renewal time (year)	0.6	1.4

Table 1. Some basic environmental data for the experimental lake, lake Lilla Stockelidsvatten (LS) and the control lake, lake Stora Stockelidsvatten (SS).

experiment *per se* and not to any large scale changes in the whole area, some reference data were checked in lake Stora Stockelidsvatten another lake in the same drainage area with basic similarities concerning physical and chemical properties.

Methods

Transparency was measured with a standard 25 cm Secchi disc. Water for chemical analyses was sampled at five levels in the limnetic zone. In situ ^{14}C fixation, using $NaH^{14}CO_3$ was measured in 60 ml pyrex glass bottles placed at the same five levels. Uptake was measured over a 3 hour period between 10.30 and 13.30 hrs. Phytoplankton and zooplankton were sampled with nets (mesh 25 µm and 63 µm) at six randomly selected places in the limnetic zone.

Results

The zooplankton has changed from a community with a predominance of small cladocerans (e. g. *Bosmina longirostris* (O. F. Müller)) into a community dominated by larger copepods (e.g. *Eudiaptomus gracilis* G. O. Sars) (Fig. 1). The crustacean biomass has also changed. After the elimination of fish, the peak in biomass occurred later in the summer. Furthermore, the biomass of netphytoplankton (> 25 µm) increased and there was also a change to a dominance of larger species. Before removal of the fish population, the most common species was *Peridinium aciculiferum* (~ *30* µm), while *Ceratium hirundinella* (~

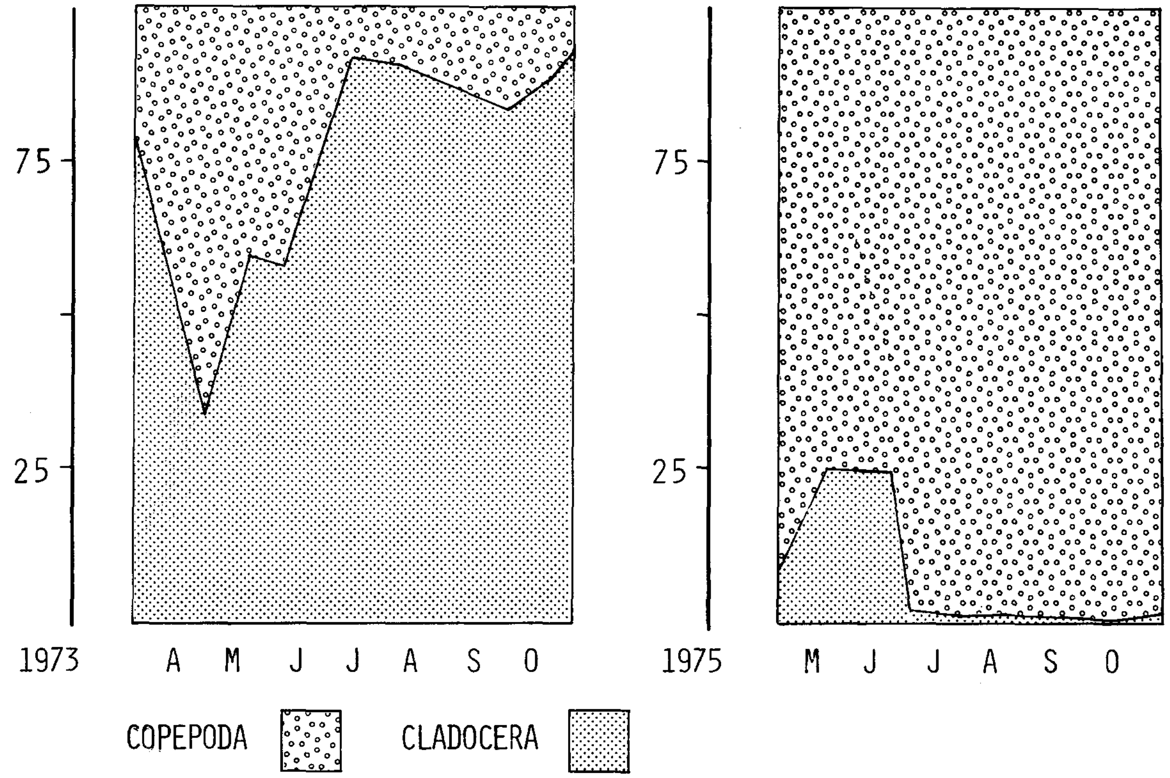

Fig. 1. Percentage composition of the crustacean zooplankton in lake Lilla Stockelidsvatten before (1973) and after the elimination of the fish population.

300 µm) seems to have replaced it after removal (Larsson, in prep.) Moreover the increase in transparency indicates, a decrease in nannoplankton abundance. The limnetic primary production is lowered by approximatly 90% after the fish reduction (Fig. 2). The new phytoplankton communty is obviously less productive than the old one.

There are apparent changes also concerning certain abiotic factors. Transparency has increased as mentioned above (Fig. 3), while pH, total phosphorus and total nitrogen declined when the fish population was eliminated (Fig. 4, 5).

Discussion

In the interpretation of the results three sets of questions must be considered: a) can the rotenone treatment *per se* produce the effects, b) are there any environmental changes in the drainage area that are responsible and c) is the elimination of predation from the fish population responsible for the observed changes?

Organisms other than fish are also sensitive to rotenone. The effects on the crustacean zooplankton are severe, while rotifers seem 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 vegetation and along sediment surfaces (e.g.

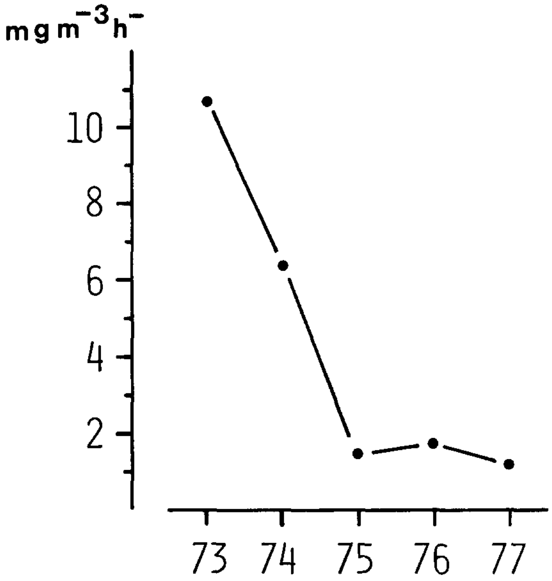

Fig. 2. Limnetic primary production. Mean mid-day values. Each point represents a mean value based upon the same order of measurements during the ice-free season.

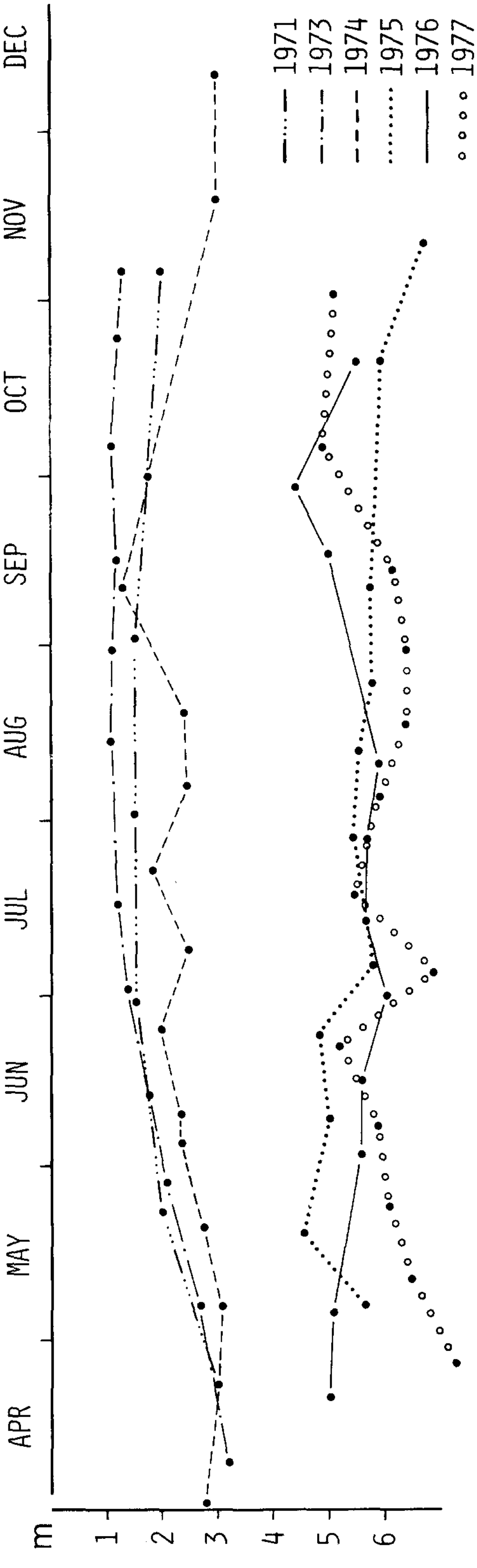

Fig. 3. Transparency in lake Lilla Stockelidsvatten. The figure shows two years before and four years after the elimination of the fish population.

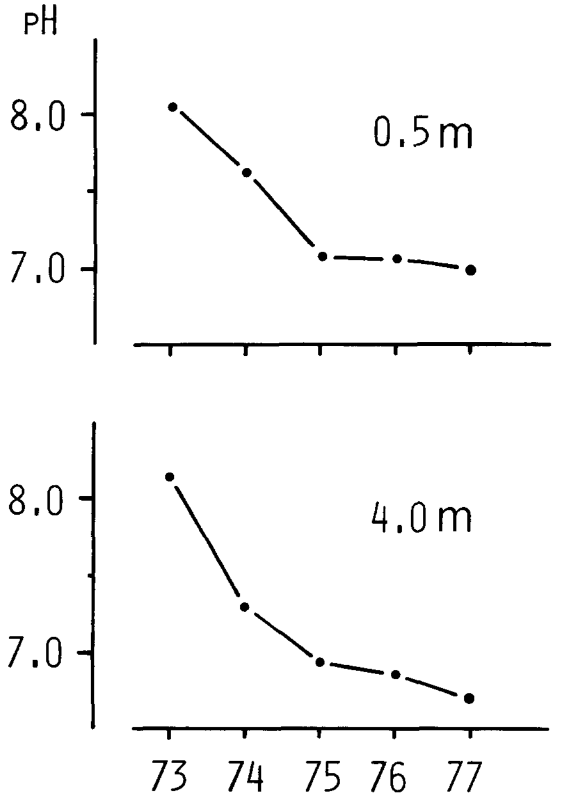

Fig. 4. The pH development at two depths in lake Lilla Stockelidsvatten. (See text to Fig. 2).

Berzins, 1958; Almquist, 1959; Kiser *et al.,* 1963; Anderson, 1970). According to Anderson (op. cit.) phytoplankton is almost unaffected.

The relatively stable situation in the control lake as shown in Fig. 6, 7, indicates that there is no reason to suspect that large scale environmental changes are responsible for the developement in the experimental lake.

Since selective predation from fish has been shown to reduce the mean body size in crustacean plankton communities, it is evident that removal of fish may cause increased mean size and a changed structure of the zooplankton community. This is also what has happened. However, the fact that the predation pressure from fish ceased does not alone explain the dramatic decline of smaller cladocerans. One other possible reason for this may be a changed predation pressure from invertebrate plankton feeders. Stenson (1978) showed that *Chaoborus flavicans* (Meig.) as well as *C. obscuripes* (Van der Wulp) became abundant in the lake as a result of the fish removal. *Chaoborus* spp. larvae are very potent plankton predators, which may cause significant mortality in popu-

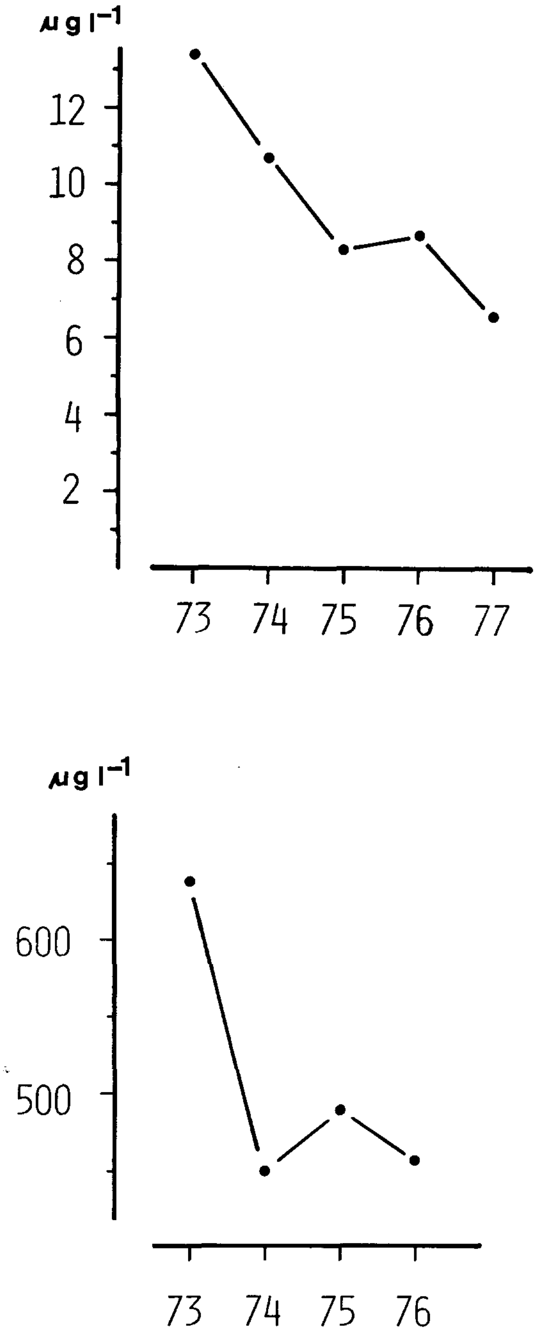

Fig. 5. Total phosphorus (above) and total nitrogen development during the experimental period in lake Lilla Stockelidsvatten. (See text to Fig. 2).

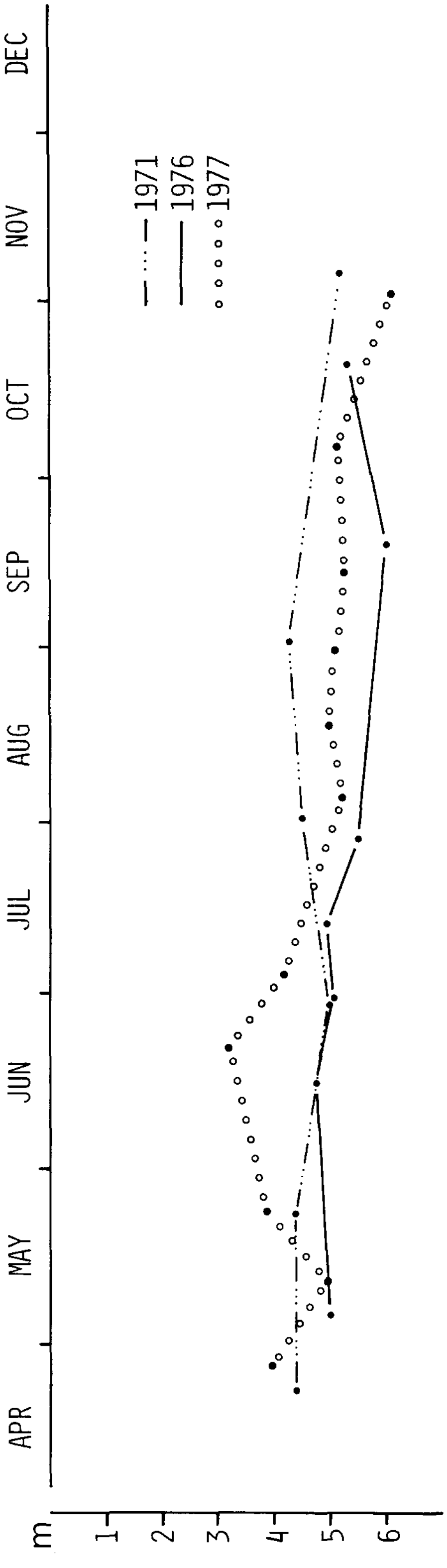

Fig. 6. Transparency in lake Stora Stockelidsvatten, the referrence lake.

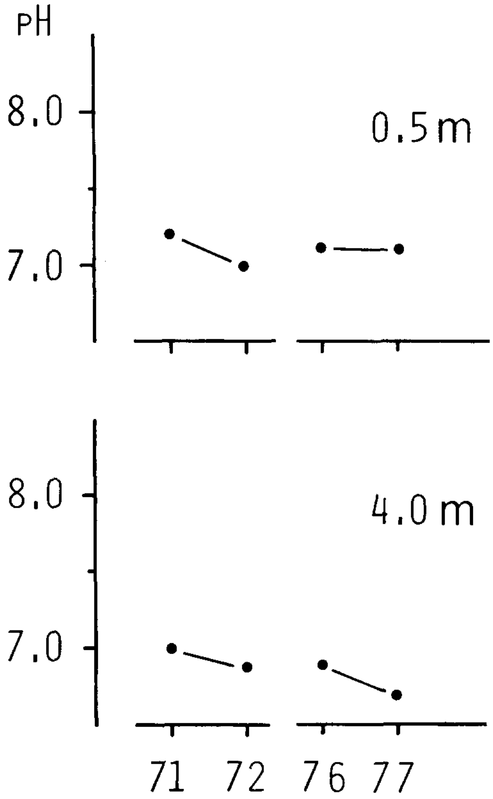

Fig. 7. The pH at two depths in lake Stora Stockelidsvatten. (See text to Fig. 2).

lations of small zooplankton species (Dodson, 1972; 1974; Fedorenko, 1975; Lewis, 1977).

The most remarkable change during the experimental period was the drop in the limnetic primary production. The production seems to have stabilized on a level almost 90% lower than before the elimination of fish. How can this be explained? The first problem to deal with is the lowered productivity in the new phytoplankton community. As described above, we now have a community with a larger share of larger net-phytoplankton species and probably fewer nannoplankton, i.e. a change towards a community with a higher mean cell size. Cell size seems to be crucial for productivity. Stull *et al.* (1973) reported that small cells with a low carbon content tend to have shorter renewal times compared to larger cells with high cell carbon content. This was on the whole confirmed by Desortova (1976), who found a negative relationship between the cell volume of different algal species and their photosynthetic activity.

The next important question is why a new structure within the phytoplankton community has occurred. There are, of course, many reasons, of which only a few important ones will be mentioned. The larger biomass of large herbivorans can maintain a harder grazing pressure on the edible part of the phytoplankton (nannoplankton–smaller net plankton). The reduction in abundance of these smaller species may create better nutrient conditions for the large net species, which also may be less competitive than the smaller species. The reduced competition may therefore promote the development towards a larger mean cell size in the phytoplankton.

The mean body size increase in the grazer community may not only enhance the effectiveness of grazing but also influence the flux of nutrients. According to several authors, the body size is important for the regeneration rate of nutrients. Smaller species have higher turnover rates and are therefore more effective in recycling e.g. phosphorus and nitrogen than are larger species (e.g. Peters & Rigler, 1973; Peters, 1975). Nutrients from the zooplankton probably is the most important source for the producers, at least during stagnant conditions (Rigler, 1973). There are, however, also other sources. Fish activities in the sediment probably contribute to the need for nutrients for the pelagial production. This may be more important in smaller and more shallow lakes (for example our experimental lake), where only minor parts of the bottom are closed to fish because of e.g. oxygen deficit. In summary: increased grazing pressure from larger herbivors on the smaller phytoplankton size interval, lowered rate of mineralization via zooplankton, and decreased import of nutrients from areas outside the pelagial zone are some changes occurring after fish removal. These changes are probably important for the development of the new producer community characterized by larger mean cell size and lower productivity.

Finally, the major abiotic changes, are perhaps more easily explained. The pH, in this weakly buffered lake as in most fresh waters, is mainly a function of H^+ ion dissociation of carbonic acid and OH^- ions from the hydrolysis of bicarbonate ions. Changes in the carbon dioxide content influence the equilibrium reactions between the components resulting in pH changes. The decrease in photosynthesis activity implies reduced consumption of carbon dioxide which damps the pH fluctuations resulting in a lower pH level. The transparency-increase shows the decrease of particulate matter, mainly of organic orgin. The drop in the abundance of these organic particles is also indicated by the decrease of both total phosphorus and total nitrogen.

The experimental lake show very apparent changes in oligotrophic direction after the removal of fish. Our attempt to explain this development does not cover all the mechanisms involved, but it is our opinion that we have treated some of the most important ones. That our interpretations may be realistic is supported by the results of some other studies. Hrbacek *et al.* (1961) showed that, when large shallow ponds were stocked heavily with cyprinid fish there was a decrease in transparency with the predominant development of smaller algae. Andersson *et al.* (1978) more recently reported that the productivity as well as physical and chemical factors within experimental enclosures were closely correlated with the density of the fish populations. Thus, enclosures with dense fish populations had high productivity and pH and very turbid water with low transparency.

Final remarks

Both Hrbacek & Andersson *et al.* worked in eutrophic lakes, whereas our study was carried out in an oligotrophic lake. The differences in trophic level between the lakes studied apparently have little significance for the results. The mechanisms are the same and the reactions following fish manipulations are consistent, irrespective of the trophic level of the experimental water. It is now even more evident that fish, through selective predation, is a key factor not only for size and species composition within the prey populations but also via feedback mechanisms on phytoplankton productivity, nutrient regeneration and physical and chemical properties of the water i.e. factors used as trophic criteria. According to this, the practical management of lakes must be based on knowledge not only about loading figures but also about the structure and functions of the biotic feedback systems. Much work is, however, still needed to make this knowledge a precise tool in lake management.

Acknowledgements

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References

Almquist, E. 1959. Observations on the effect of rotenone emulsives on fish food organisms. Rep. Inst. Freshw. Res. Drottningholm 40: 146-160.

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(8): 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.

Berzins, B. 1958. Om fiskevård med rotenon. S. Sveriges Fisk. Fören., Årsskr. 1957: 41-57. (In swedish).

Brooks, J. L. & Dodson, S. I. 1965. Predation, body size, and compostion of plankton. Science 150: 28-35.

Desortova, B. 1976. Productivity of individual algal species in natural phytoplankton assemblage determined by means of autoradiography. Arch. Hydrobiol./Suppl. 49: 415-449.

Dodson, S. I. 1972. Mortality in a population of Daphnia rosea. Ecology 53: 1011-1023.

Fedorenko, A. Y. 1975. Feeding characteristics and predation impact of Chaoborus (Diptera, Chaoboridae) larvae in a small lake. Limnol. Oceanogr. 20: 250-258.

Hrbácek, J., Dvorakova, M., Korinek, V. & Procházkóva, 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. Internat. Verein. Limnol. 14: 192-195.

Hrbácek, J. 1962. Species composition and the amount of zooplankton in relation to the fish stock. Rozpravy Ceskoslovenske Akademie Ved 72: 1-116.

Kiser, R. W., Donaldson, J. R. & Olson, P. R. 1963. The effects of rotenone on zooplankton populations in freshwater lakes. Trans. Amer. Fish. Soc. 92: 17-24.

Lewis, W. M. Jr. 1977. Feeding selectivity of a tropical Chaoborus population. Freshwat. Biol. 7: 311-325.

Peters, R. H. 1975. Phosphorus regeneration by natural populations of limnetic zooplankton. Verh. Internat. Verein. Limnol. 19: 273-279.

Peters, R. H. & Rigler, F. H. 1973. Phosphorus release by Daphnia. Limnol. Oceanogr. 18: 821-839.

Porter, K. G. 1977. The plant animal interface in freshwater ecosystems. Amer. Scientist 65: 159-170.

Rigler, F. H. 1973. A dynamic view of the phosphorus cycle in lakes. In: E. J. Griffiths et al. (eds), Environmental Phosphorus handbook, 539-572. Wiley and Sons, New York.

Shannon, E. E. & Brezonik, P. L. 1972. Relationships between lake trophic state and nitrogen and phosphorus loading rates. Environ. Sci. & Technology 6: 719-725.

Sonzogni, P. C., Uttormark, P. C. & Lee, G. F. 1976. A phosphorus residence model: theory and application. Water Research 10: 429-435.

Stenson, J. A. E. 1976. Significance of predator influence on composition of Bosmina spp. populations. Limnol. Oceanogr. 21: 814-822.

Stenson, J. A. E. 1978. Differential predation by fish on two species of Chaoborus (Diptera, Chaoboridae). Oikos 31: 98-101.

Stull, E. A., Amazaga, E. de, & Goldman, C. R. 1973. The contribution of individual species of algae to primary productivity of Castle lake, California. Verh. Internat. Verein. Limnol. 18: 1776-1783.

Vollenweider, R. A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to phosphoras and nitrogen as factors in eutrophication. OECD Technical Report DAS/CSI/ 68.27, 159 pp. Revised 1971.

Vollenweider, R. A. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. Mem. Ist. Ital. Idrobiol. 33: 53-83.