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Volume 7

Biomanipulation in Lakes and Reservoirs Management

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Biomanipulation in Lakes and Reservoirs Management

Editors:

R. De Bernardi and G. Giussani

International Lake Environment Committee
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International Lake Environment Committee Foundation
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Shiga 525, Japan

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FOREWORD

Tatuo Kira

Lake ecosystems and island ecosystems seem to be homologous with respect to their intolerance to the invasion of alien species of plants and animals, probably because both ecosystems consist of the limited biota which could migrate by chance across the surrounding barriers of land or water and may therefore be less firmly organized as compared with those in the ocean or on the continent.

Due to the ever-increasing inter-continental communication and transportation, more and more alien species are being introduced either intentionally or by chance to a number of lakes, where they often propagate explosively, resulting in severe damage to native species. In certain extreme cases, the introduction of a single fish species may completely alter the structure of a whole lake ecosystem. This is a serious threat to the biodiversity of certain geologically old lakes in which many indigenous taxa were born through hundreds of thousands of years.

On the other hand, such variability of lake ecosystems may also indicate the possibility of effectively controlling their structure and thereby changing aquatic environments by artificial intervention in the biological processes within lakes - the so-called biomanipulation. Its practice is not new; people have long been trying to introduce various new organisms into their home lakes in order to increase fishery production, to remove unfavourable plants and animal species, etc.. However, systematic studies on biomanipulation have started rather recently. A lot of papers dealing with the subject are appearing in scientific journals, but it is still difficult for non-specialists to understand what has so far been achieved by those studies and how their results can be applied in the practical management of lake resources and environments.

This volume of the ILEC/UNEP guideline book series is expected to fill the need by offering a general introduction to the role of biomanipulation in lake management with emphasis on the control of excessive algal growth in lakes suffering from eutrophication. We hope that this new approach may give stimulative suggestions to lake environment managers worldwide.

The ILEC Foundation would like to sincerely thank the editors Dr. R. de Bernardi and Dr. Giussani and the other contributors for their efforts in preparing this useful and unprecedented book. The continued support to the serial publication by the United Nations Environment Programme is also heartily acknowledged.

ILEC Foundation
Kusatsu, Shiga, Japan

FOREWORD

Jorge Illueca

Eutrophication is surely the most important process affecting lakes and reservoirs worldwide. An important consequence of this process is the general reduction of the possibilities for water use, so that the importance of lakes and reservoirs as primary resources for socio-economic development can be seriously compromised. On the other hand, biological processes in eutrophic environments increase productivity, including fish yield and this process can be regarded positively as a source of protein in developing countries. It is well-known that eutrophication involves increasing nutrient inputs resulting from human activities. Historically, the way to prevent this process from eroding the quality of the environment and to rehabilitate freshwater environments once eutrophied, was engineering for the control and reduction of nutrient inputs. This costly process is unquestionably necessary in many cases, but it does not necessarily produce the expected improvement in a reasonable time, due to the resistance of the ecosystem itself.

For this reason several in-lake ecotechnologies have been proposed, developed and tested on a natural scale. These ecotechnologies have to be considered as an alternative to the engineer's reduction of nutrient loads. Among them, one of the most promising is the biomanipulation of the aquatic food chains.

Biomanipulation began in the late fifties as an approach to the study of ecosystem function. Since then many real scale experiments have proved that biomanipulation can ameliorate eutrophic water bodies. It is now clear that the principles of biomanipulation can be utilized to manage the ecosystem on a scientifically sound basis. This technique is still largely empirical and needs a more profound scientific basis. Nevertheless, biomanipulation holds great promise for the management of lake and reservoir quality. It is also important to stress that biomanipulation is not limited to remediating eutrophic lakes, but can also help improve fisheries in terms of both quality and quantity of products.

This booklet, the 7th in the Guidelines of Lake Management series, explains the scientific bases of biomanipulation in detail, illustrating the techniques with case studies of successful lake recovery. Some chapters also illustrate how appropriate biomanipulation can help enhance fisheries.

Assistant Executive Director
Environmental Management Division
UNEP

AUTHORS

Riccardo de Bernardi
Istituto Italiano di Idrobiologia
Consiglio Nazionale delle Ricerche
Pallanza (NO), Italia

Gianluigi Giussani
Istituto Italiano di Idrobiologia
Consiglio Nazionale delle Ricerche
Pallanza (NO), Italia

Peter Kasprzak
Institute of Freshwater Ecology and Inland Fisheries
Department of Limnology of Stratified Lakes
Heuglobsow, Germany

Moshe Gophen
Israel Oceanographic and Limnological Research Ltd.
Tiberias, Israel

Ramesh Gulati
Netherlands Institute of Ecology
Centre for Limnology
Nieuwersluis, The Netherlands

Péter Bíró
Balaton Limnological Research Institute
Hungarian Academy of Sciences
Tihany, Hungary

Brian Moss
The University of Liverpool
Department of Envrionmental and Evolutionary Biology
Liverpool, England

S. E. Jφrgensen
Royal Danish School of Pharmacy
Copenhagen, Denmark

Gaetano Galanti
Istituto Italiano di Idrobiologia
Consiglio Nazionale delle Ricerche
Pallanza (NO), Italia

István Tátrai
Balaton Limnological Research Institute
Hungarian Academy of Sciences
Tihany, Hungary

Akira Kurata
International Lake Environment Committee
Kusatsu, Shiga, Japan

C. H. D. Magadza
University Lake Kariba Research Station
University of Zimbabwe

CONTENTS

CHAPTER 1

BIOMANIPULATION: BASES FOR A TOP-DOWN CONTROL

Riccardo De Bernardi and Gianluigi Giussani

At the beginning of the 60s, Hrbácek and co-workers (Hrbácek *et al.* 1961) drew attention to the existence of a top-down control of the food chain, of equal importance to bottom-up control.

On the basis of an analysis of data referring to the relationship between phosphorus and chlorophyll suggested by Dillon and Rigler (1974), Hrbácek (Hrbácek *et al.* 1978) again showed how cases of extreme deviation from this relationship could be explained convincingly by the intensity of top-down control.

These results sparked off a series of studies undertaken to identify the mechanisms responsible for this kind of control and the consequences of its existence at a structural and functional level, not only in aquatic communities but also in lake ecosystems as a whole.

It was thus clear that this biological control process was able to account for much of the resilience seen in the variations in communities which accompany the lake eutrophication process, and still more the oligotrophication process which take place as a consequence of treatment operations aimed at reducing the nutrient load and therefore the bottom-up control of biological productivity (de Bernardi 1981, 1983).

It is widely accepted that lake ecosystems may be divided into two components, the biotic and the abiotic, which interact through reciprocal feed-back mechanisms. Consequently changes in one component will induce corresponding changes in the other. A second basic ecological concept is that biological communities are structured along trophic hierarchies-food chains which direct energy-flow within the ecosystem (Lindeman 1942) and thus influence virtually every aspect of ecosystem function. However, since each species has its own biological and ecological characteristics, food chains of different structure or species composition will accomplish their function in different ways and with different efficiencies. These simple beliefs have fostered much of the great interest in the structure of biological communities and in the response of community structures to environmental changes.

Lake ecosystems can be subdivided into a series of well defined but highly interacting sub-systems. Among these, the pelagic environment is the most peculiar. Most environments display complex geometries scored by sharp physical gradients and discontinuities; the open water of lakes contains a relatively simple vertical gradient in light, temperature and chemistry with the result to be one of the most uniform of all environments.

A further peculiarity of the pelagic environment is that its primary producers (unicellular or colonial algae) are very small relative to the size of the planktonic herbivores. These herbivores, in turn, are much smaller than many of their own predators. Thus, because pelagic predators are often much larger than their prey, the prey are completely open to predator attack. In addition, despite differences in the mechanisms of food gathering (Hrbácek, 1977) all planktonic herbivores compete for food particles in the same size range (about 1 to 15 mm) (Brooks & Dodson 1965). Thus, in the pelagic environment, the biotic interactions of competition and predation may rank among the most important factors determining and regulating community structure.

That eutrophication is, without any doubt, the most important reason for lacustrine environment deterioration is widely accepted. Similar consensus exists on the fact that causes of eutrophication must be recognized in an increased availability of nutrients (mainly P) for algae growth.

The eutrophication and oligotrophication of a lacustrine environment do not proceed according to a linear relationship between nutrient load and vegetal biomass, but display rather a sigmoid trend with delay. Biological systems show a marked resistance to variation, both when there is an increase in nutrient load and when it is reduced. This phenomenon is analyzed in de Bernardi (1989), Hosper (1989), Sas (1989). Moreover, this non-linearity of response is much more accentuated in smaller and shallow environments, on account of the considerable importance that internal loads may have in them. It would appear, however, that there exist threshold values in nutrient loading, for both increase and decrease, which cause rapid changes in the state of the system (Vollenweider 1968, 1976; Hosper 1989) (Fig. 1.1). But while for the process of nutrient enrichment these values

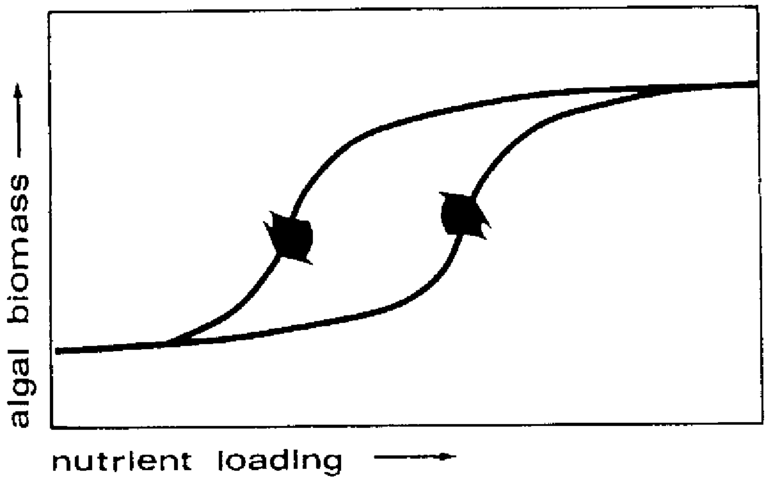

Fig. 1.1 Changes in algal biomass with increasing and decreasing nutrient loading: a lake under restoration may have more algal biomass than before restoration. The area within the two curves represents the field of action of biomanipulation (from Hosper, 1989, redrawn).

have been statistically identified as in-lake average P concentration of 10 (for the passage from oligotrophy to mesotrophy) and 40 mg P l^{-1} for the passage from mesotrophy to eutrophy) (Vollenweider, 1976), no realistic estimate has yet been made for the reduction processes.

A eutrophic lake produces much more plant material than can be used by the herbivores. This surplus accumulates in the lake until decomposed by bacteria. This leads to a progressive decline in dissolved oxygen in the deeper strata and, in extreme cases, to anoxia and accumulation of nutrients released from the sediments to these deep layers. In the surface water, an increase in pH is observed following the consumption of CO_2 by photosynthesis. These variations in the chemical environment provoke modifications in the biological community. Stenotypic fish species such as salmonids and coregonids are gradually replaced by more tolerant cyprinids; in the phytoplankton, green algae are supplanted by blue-greens which gain more advantage in competition for CO_2 and nutrients at higher pH values. The zooplankton populations also undergo a profound structural change passing from a dominance of calanoid copepods to small cladocera and rotifers. More generally speaking, at this level of the food chain a gradual shifting to smaller species is observed. This represents a very important point for the energy budget in the lake environment. As smaller-sized species are less efficient in utilizing the available food particles, the eutrophication determines a larger gap between primary production and algae biomass utilization by herbivorous zooplankton.

There are two main reasons for the shift toward smaller herbivores in the planktonic community of eutrophic lakes: first a variation in the fish community with a dominance of planktophagous species, selectively preying upon larger zooplankters; and, second, the reduced possibility presented by the latter to avoid clogging of the filtering apparatus by filamentous and colonial algae that progressively dominate phytoplankton communities. It must be noted in this respect that formation of filamentous or large colonies by planktonic algae has been interpreted as an evolutive strategy to avoid grazing by filter-feeders.

The result of the eutrophication process is thus a decrease of the efficiency of energy transfer along the pelagic food chain with more important losses to the detritus chain (Fig. 1.2).

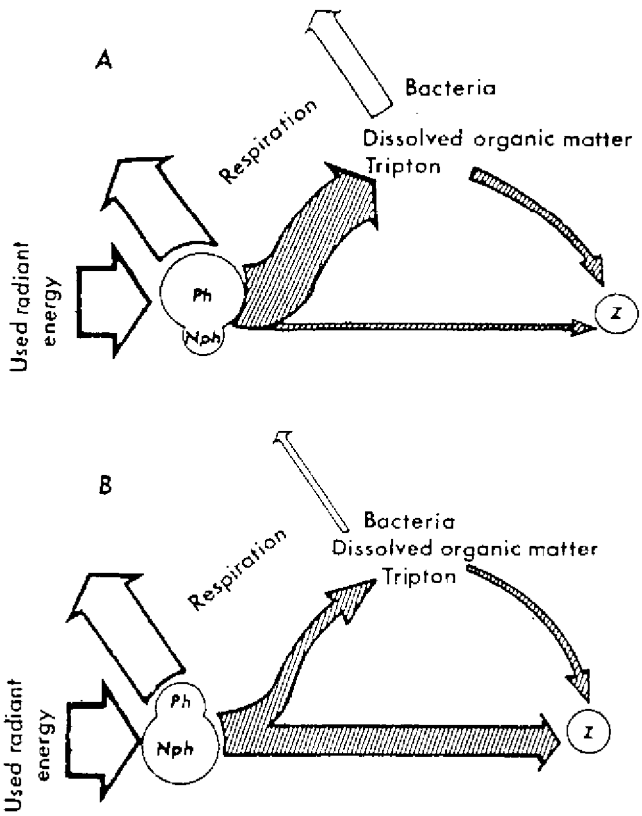

Fig. 1.2 The schematic diagram of main path of energy flow between the producers and consumers level in the pelagial of eutrophic (A) and oligotrophic (B) lakes. As the trophic level of a lake increases a contemporaneous increase of energy flowing directly to bacteria is observed. Ph = phytoplankton; Nph = nannophytoplankton; z = zooplankton (from Gliwicz, 1969, redrawn).

A typical eutrophic community tends to maintain its identity by counteracting attempts at purification. In such cases, manipulation of the food chain could prove a useful and efficient mechanism for reducing the most obvious drawbacks in eutrophy.

In effect, such biomanipulation consists of a shift in controlling factors from that shown as "type A", to that of "type B" (Tab. 1.1). A type A community is that usually found in lacustrine environments. The phytoplankton is limited by the availability of algal nutrients, but the second level, the zooplankton, is not limited by food availability, but by predation from still higher trophic levels represented by the fish. The fish are in turn limited by food availability. One appropriate intervention in a "type A" eutrophic lake would induce control of the algal community by grazers rather than nutrients. This could be achieved by reducing the population of planktivorous fish (Shapiro 1978) for example by removing all fish from the lake, or by selective poisoning of planktivores, or by introduction of large fish which prey upon the planktivores and by other mechanisms as well (Gammon & Hasler 1965; Schmitz & Hetfeld 1965).

Tab. 1.1 Most important limiting factors of major components of the limnetic community under two different systems of management (from de Bernardi 1981).

Link	Limiting factor A	 B
Phytoplankton	Nutrients (P and N)	Grazing
Zooplankton	Predation	Food availability
Planktophagous fish	Food availability	Predation

Therefore, it appears evident that there exist in lacustrine environments internal processes in the structural organization of the ecosystem, which exercise a role of equal importance to that played by external processes of eutrophication control.

Some examples may give a more complete picture of such theoretical considerations. Figure 1.3 shows biomass values and percentage composition of phytoplankton populations in plastic bags with and without fish placed in the eutrophic Swedish lakes Trummen and Bisjon (Andersson *et al.* 1978). It appears from this figure that the bags with fish present all the elements that characterize the algal communities of eutrophic environment, that is, high biomass values and the dominance of blue-green algae, together with high pH values and low water transparency. On the other hand, in the bags without fish, despite the similar

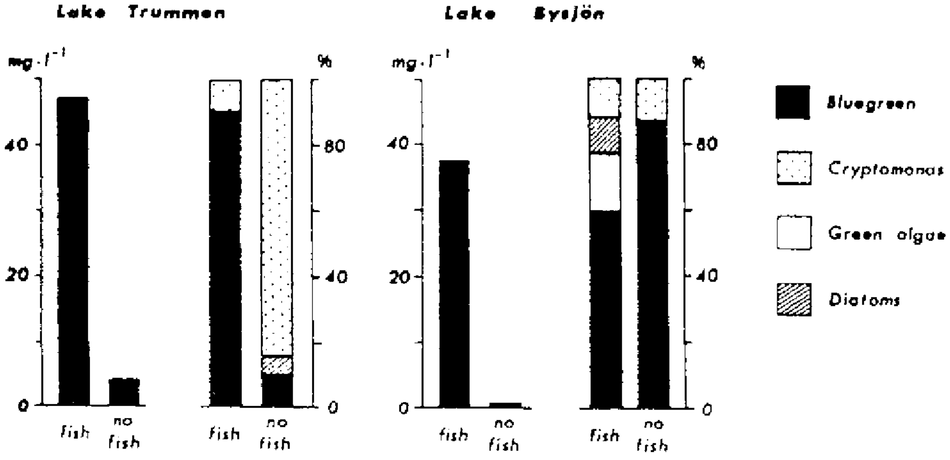

Fig. 1.3 Biomass (mg fresh weight/litre) and percent composition of phytoplankton in plastic bags with and without fish in two Swedish lakes: Lake Trummen and Lake Bysjon. The presence of fish resulted in an increase in phytoplankton and, in Lake Trummen, dominance by blue-green algae (from Anderson *et al.,* 1978).

initial level of nutrients, algae are less abundant, pH values are "normal" and transparency is high.

Ever clearer evidence may be drawn from Figure 1.4 which reports the results of experiments by Lynch (1975) in the USA. In this case also the presence of an increasing number of fish, in environments with a comparable nutrient content, is strictly correlated with a reduction in water transparency and with an increase in algae density. In both the above examples, the relationship between fish and algae is mediated by the zooplankton community, which, in the absence or low density of fish, may constitute a dominant factor for phytoplankton control.

After their initial phase in semi-natural environments, these studies have been later transferred to natural environments.

Among the increasing number of real scale biomanipulation treatments of natural environments two examples are those of Andersson (Andersson *et al.* 1978) on some Swedish lakes, and of Shapiro on American lakes (Shapiro 1978).

The results obtained by Henrikson (Henrikson *et al.* 1980) in the Swedish lake Lilla Stockelidsvatten, which has undergone biomanipulation treatment, are very indicative. In this lake the whole fish population had been removed by poisoning in 1973.

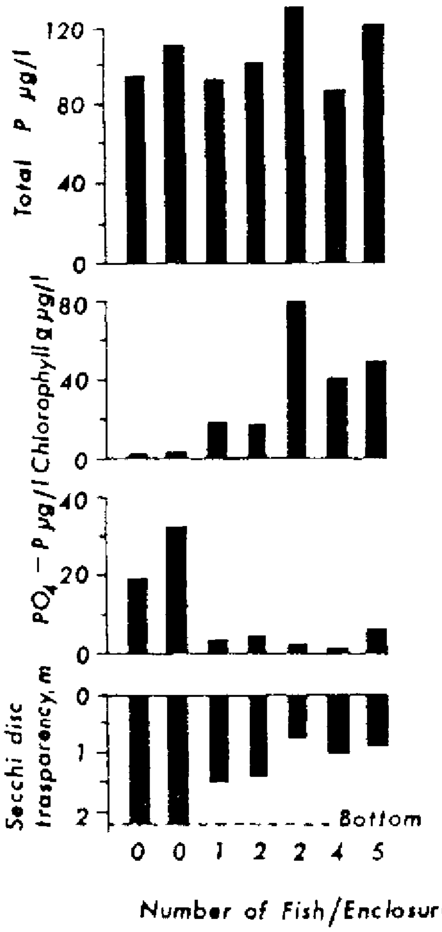

Fig. 1.4 The effect of increasing fish stock on water transparency, chlorophyll-*a* and phosphate concentrations in plastic bags containing similar concentrations of total P. The evidence for eutrophy is most marked when more fish are present (from Lynch, 1975, redrawn).

Figures 1.5 and 1.6 show that the results obtained in experiments using plastic bags are also repeated on real scale, thus confirming the effectiveness of biomanipulation techniques.

The results emerging from this “disruptive” experiment, similar to those of other experiments in which the same “all or nothing” technique was applied, must be regarded as highly significant from an experimental point of view, and corroborate the basic theory. However, the great limitations of these experiments are that they are hardly applicable in general terms, and that, in particular, the results obtained are not stable. In fact, it is difficult to envisage keeping a lake completely without its fish fauna, and it is still very uncertain whether it is possible to build up, from

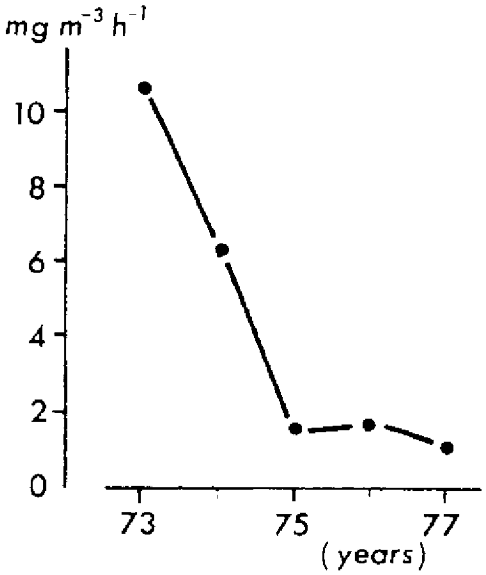

Fig. 1.5 Lake Lilla Stockelidsvatten; limnetic primary production. Mean mid-day values. The removal of fish by rotenone in November 1973, determine a decrease in primary production, (from Henrikson *et al.*, 1980, redrawn).

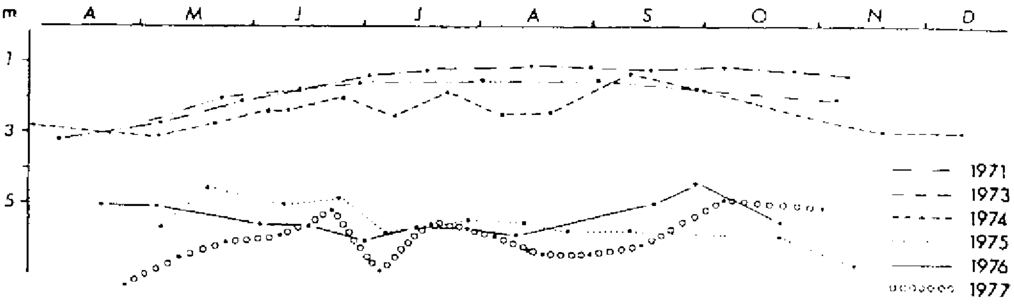

Fig. 1.6 Lake Lilla Stockelidsvatten:Secchi disk transparency before and after the treatment with rotenone in November 1973 (from Henrikson *et al.*, 1980, redrawn).

scratch, an artificial fish community with the conditions of stability which are indispensable.

Again, the complete disappearance of planktivorous fish would indeed bring about a reduction in predation pressure on the large herbivores, but at the same time would also reduce invertebrate predators such as *Leptodora* and *Chaoborus*. These last would consequently take the place of the planktivorous fish in controlling the herbivores and would restrict their expansion (de Bernardi 1974; de Bernardi & Giussani 1975).

In the last few years, many experiments have been carried on applying biomanipulation techniques gradually, following a step-by-step procedure, to produce a less stressing effect and to have the possibility to modify at any moment the intensity and the direction of the intervention. So, plans of gradual reduction of planktivorous fish by increasing fishing efforts, restocking or improving the stocks of predatory fish, introducing or harvesting acquatic macrophytes have been used as tools to produce the desired improvements in eutrophic lake environments. With this approach, there have been several cases which have yielded positive results, useful in defining a multifaceted management strategy (see case studies in the following pages).

Then, biomanipulation does not appear as a cure for all the ills afflicting lakes, or that it can always and in every case offer an alternative intervention to those which are now usual. The field of action, the characteristics of environments in which intervention is possible and the already emphasized need for an in-depth ecological knowledge, of necessity limit the field of these techniques. Nevertheless, once the above conditions are satisfied, the correct application of biomanipulation techniques can be a useful supplement to (and in certain specific cases a substitute) the usual technological interventions for the recovery of the quality of lacrustrine waters.

This is particularly important each time the internal loading is sufficient, without further external loading, to maintain the eutrophication level or, again, to speed up the recovery in environments previously subjected to the control of external loading through conventional treatment plants. This observation has led to the development of two parallel and complementary strategies for controlling lake eutrophication:

- control of external factors through the control of nutrient loads;
- control of processes within the ecosystem.

A combination of these strategies undoubtedly produces more advantageous results in terms of cost benefit in operations of control and reduction of eutrophication (Benndorf 1988) (Fig. 1.7).

The complexity and delicacy of the ecological processes in which we have to intervene mean that at the moment an indiscriminate application of these biological control techniques would be unthinkable. The applicability of the techniques must

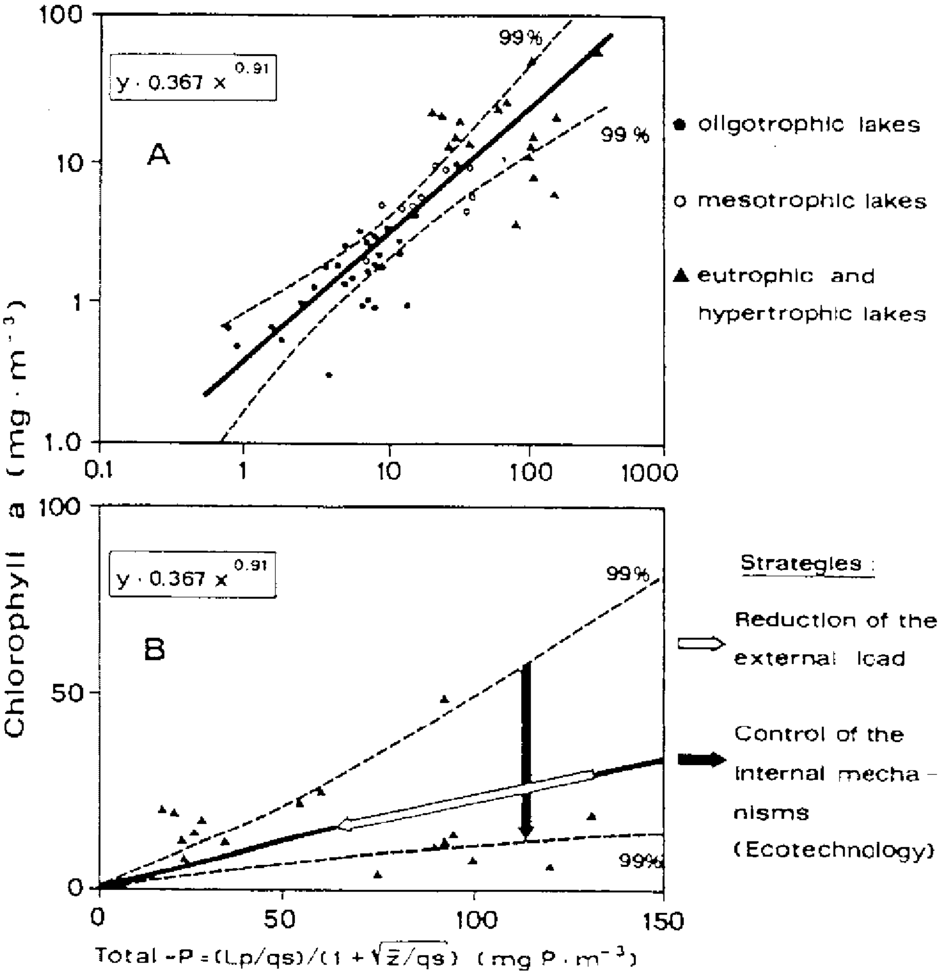

Fig. 1.7 The relationship between total phosphorus and chlorophyll-*a* in the epilimnion of lakes in North America, (a) according to Vollenweider (1976), (b) transformation in a linear scale. The area between the 99 % confidence limits represents the control space which can be used by strategy (1) (white arrow) and strategy (2) (black arrow) from Benndorf, 1988, redrawn).
Lp = areal P-load (mg TP. m^{-2}. year^{-1}); qs = hydraulic load (m. year^{-1}); Z = mean depth of lake (m)

be verified through experiment, each case being taken on its own merits, and must undergo rigorous scientific testing, so that they may be adjusted to fit the individual environment to be biomanipulated .

Several problems still require satisfactory scientific elucidation. The following research topics in particular would seem to be high on the list of priorities (Benndorf 1988).

- Development of undesirable species of algae, that is, analysis of the conditions which make it possible for blue-greens to maintain their dominance of the phytoplankton community.

- Reciprocal relationships between interactions such as those of prey-predator and those of competition within the pelagic trophic network, their relative weight and the effects of the importance of one of the two on the weight assumed by the other form of interaction.

- Effects of the lack of spatial homogeneity of the chemical and physical parameters on the dynamics of the communities and the interactions within them.

- Threshold limits higher than the internal and external nutrient loads which must not be exceeded if biomanipulation interventions are to be successful.

- How best to effect planktivore control so as to achieve environmental conditions which are stable in time.

However, leaving aside these problems of considerable importance which still await a satisfactory solution, it is clear that techniques of integrated biomanipulation show good prospects for managing eutrophic aquatic environments with a view to the ultimate recovery of their quality.

These techniques should not be seen, however, as an alternative to nutrient control which can be effected by "conventional" means (that is, by reducing nutrient loads conveyed to lakes from their watersheds), which must remain the primary objective of any intervention directed towards the restoration of a waterbody. They should be regarded rather as supporting operations which can facilitate and accelerate the recovery process by intervening in those mechanisms that are responsible for the powerful processes of environmental resilience which arise and persist within the ecosystem.

The most important advantages deriving from the application of these techniques, which may be compared with the integrated biological control used in agriculture, may be summarized as follows:

- the possibility of recovering eutrophic environments when the nutrient load derives from non-point sources which are not easy to control;

- the possibility of improving the environmental characteristics of waterbodies in which the eutrophication process is caused essentially by excessive internal loads of nutrients;

- integrated ecological management of waterbodies in relation to the use they are to be put to, carried out on a scientific basis;

- relatively low implementation costs.

It should be stressed that if it is to be possible to improve the quality of waterbodies by implementing these management techniques, there must be a detailed knowledge of environmental characteristics and of certain important processes essential to the functioning of the ecosystem, and the following fundamental conditions must be satisfied:

- knowledge of the principal trophic relationships between the species present;

- assessment of the variations to which the population to be controlled will be subjected;

- assessment of the extent and the trend of the response of the different populations to the interventions;

- assessment of the environmental role of the key species making up the trophic network;

- knowledge of the nutrient cycle and the processes controlling nutrient production and use.

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CHAPTER 2

OBJECTIVES OF BIOMANIPULATION

Peter Kasprzak

2.1 BIOMANIPULATION - A HISTORY OF SUCCESS AND DISAPPOINTMENT

Since Vollenweider's (1968) investigations regarding the influence of nutrients on water quality, the discussion of eutrophication management has been concerned with nutrient loading and nutrient concentrations. However, it was also thought at about the same time that the structure of the food-web had a decisive influence on the quality of ponds, lakes and reservoirs (Hrbácek *et al.* 961; Brooks & Dodson 1965; Reif & Tappa 1966; Wells 1970; Warshaw 1970; Stenson 1973).

Shapiro (1975) and his co-workers understood the importance of these findings concerning the management of eutrophication in lakes. They used the term "biomanipulation" to define a broad spectrum of possibilities for controlling the water quality of lakes and reservoirs, and none of the manipulations involved nutrients directly (Shapiro *et al.* 1982). However, for different reasons (both practical and scientific), the prevailing measure which is currently used is the manipulation of herbivorous zooplankton by manipulating their predators.

There are different definitions of the objectives of biomanipulation. All of them concentrate more or less on quality management aspects. Probably the best of them is suggested by Moss *et al.* (1991): "Biomanipulation is a kind of biological engineering which attempts to reconstruct the ecosystem by using biological as well as, or instead of, nutrient reduction to reduce the algal crops."

At the beginning there was great enthusiasm for the promising possibilities of biomanipulation in the field of water quality management. The hope to possess a simple and cheap solution for the complicated and expensive pollution problem of eutrophication was certainly one of the reasons for the tremendous increase in biomanipulation research during the last fifteen years (Northcote 1987). However, already in the earliest papers some typical problems of water quality management through biomanipulation became obvious (blue-green algae, long-term stability)

Tab. 2.1 Example of biomanipulation experiments; abreviations: piscv - piscivores, plankty - planktivores, zoop - zooplankton, graz - zooplankton grazing, zoob - zoobenthos, phyt - phytoplankton, primprod - planktonic primary production, macroph - macrophytes, nutr - nutrients, transp - water transparency; "scientific" - basically devoted to research, applied - basically devoted to lake restoration by biomanipulation; trophic state - nutrient concentration according to very different sources, therefore not further specified.

No	Site Description	Trophic State, Stratification Pattern	WholeLake/ Enclosure Experiment	Aim of Investigation	Manipulation Measures	Observed Trophic Levels	Duration of Observations	Source
1	L. Trummen, Sweden, mean depth 1.1 m, area 1 km^2	eutrophic, 250 mgSRP m^{-3} polymictic	enclosure, 15 m^3, whole-lake	scientific, applied	introduction of different numbers of planktivores into the enclosures, manual fish removal	plankty, zoopl, phyt, primprod, nutr, zoob, pH, transp	5 month, 4 years	ANDERSSON *et al.* 1978, BENGTSSON *et al.* 1975, ANDERSSON 1988
2	L. Bysjoen, Sweden, mean depth 3.6 m, maximum depth 8.6 m area 0.12 km^2	eutrophic, 400 mgTP m^{-3} stratified	enclosure, 15 m^3	scientific	introduction of different numbers of planktivores into the enclosures	zoop, phyt, primprod, nutr, zoob, pH, transp	5 month	ANDERSSON *et al.* 1978, COVENEY *et al* 1977
3	Americana Reservoir, Brazil, mean depth 9.2 m, area 11.5 km^2	eutrophic, 190 mgTP m^{-3} polymictic	enclosure, 2.5 m^3	scientific, applied	introduction of different numbers of planktivores into the enclosures	plankty, zoopl, phyt, nutr, transp	4 weeks	ARCIFA *et al.* 1986
4	L. Greifensee, Switzerland	highly eutrophic stratified (?)	enclosure, 2.5 m^3	scientific	manipulation of zooplankton	zoopl, phyt, nutr, transp	2 weeks	BUERGI *et al.* 1979
5	Velky Palenec, Fish Pond, Czech Republic, mean depth 1.4 m, area 0.31 km^2	eutrophic polymictic	whole-lake	scientific, applied	different stocks of planktivores	zoopl, phyt, primprod, transp	2 years	FOTT *et al.* 1980
6	Experimental Ponds, California, USA, mean depth 0.5 m, area 0.000024 km^2	eutrophic (?) polymictic	whole-lake	scientific	introduction of different numbers of planktivores into the ponds	zoop, phyt, pH, O_2, zoob.	8 month	HURLBERT & MULLA 1981
7	Habo Pond 1, Sweden, maximum depth 5.5 m, area 0.0025 km^2	highly eutrophic, 250-545 mgTP m^{-3}	whole-lake	scientific	introduction of planktivores	zoop, phyt, nutr, transp	7 years	ANDERSSON & CRONBERG 1984

8	Lake St. George. Ontario. Canada. maximum depth 15.0 m	eutrophic. 80-100 mgTP m^{-3} stratified	enclosure. 750 m^3	scientific	introduction of different numbers of planktivores into the enclosures	planktv. zoop. phyt. nutr. transp	18 month	McQueen & Post 1988a. McQueen *et al.* 1986. McQueen & Post 1988a. McQueen *et al.* 1992
9	Cornell Experimental Ponds. Ithaca. USA. mean depth 1.3 m. area 0.0007 km^2	eutrophic (?) polymictic	whole-lake	scientific	introduction of different numbers of planktivores into the enclosures	zoop	2 years	Murtaugh 1989
10	L. Zwelmlust. The Netherlands. mean depth 1.5 m. area0.015 km^2	highly eutrophic. 500-1.700 mgTP m^{-3}. polymictic	whole-lake	applied	intoduction of piscivores. manual removal of planktivores	zoop. graz. phyt. macroph. primprod. nutr	2 years	Van Donk *et al.* 1989. Gulati 1989. Ozimek *et al.* 1990.
11	L. Frederiksborg Slotsoe. Denmark. mean depth 3.1 m. area 2.1 km^2	highly eutrophic 113-447 mgSRP m^{-3} temporarily stratified	whole-lake	applied	intoduction of piscivores. manual removal of planktivores	planktv. zoop. phyt. nutr. transp	2 years	Riemann *et al.* 1990. Riemann 1985
12	L. Michigan	stratified	whole-lake	scientific. applied	manipulation of piscivores	zoop. phyt. transp	several years	Wells 1979. Scavia & Fahnenstiel 1988
13	8 Forrest Lakes. Sweden		whole-lake	scientific	poisoning of total fish community	zoop	2 yeras	Stenson 1973
14	Dynamite Lake. Illinois. USA. maximum depth 2.5 m. area 0.06 km^2	mesotrophic. 5-25 mgTP m^{-3} polymictic	enclosure. 1 m^3	scientific	introduction of different numbers of planktivores into the enclosures	zoop. phyt. O_2	1 month	Vanni 1986. Vanni 1987
15	L. Wononskopomuc. Connecticut. USA. maximum depth 31 m. area 1.48 km^2	stratified	whole-lake	scientific	planktivores die-off. (natural" biomanipulation)	zoop	2 years	Warshaw 1972
16	Bautzen Reservior. Germany. mean depth 7.4 m. area 5.33 km^2	highly eutrophic. 500-700 mgTP m^{-3} stratified	whole-lake	scientific. applied	introduction of piscivores	piscv. planktv. zoop. phyt. nutr. transp	8 years	Benndorf 1978 Benndorf *et al.* 1988.

17	Crystal Lake, Connecticut, USA		whole-lake	scientific	change in plantivores ("natural" biomanipulation)	zoop	2 years	Brooks & Dodson 1965
18	Paul L., Tuesday L., Michigan, USA, maximum depth 12.2 - 18.5 m, area 0.12 - 0.079 km^2	stratified	whole-lake	scientific	reciprocal exchange of fish communities	zoop, phyt, primprod	2 years	Carpenter *et al.* 1987, Elser & Carpenter, 1988
19	L. Helgetjern, Norway, maximum depth 3.5 m, area 0.12 km^2	eutrophic, 200 mgTP m^{-3} stratified	whole-lake	applied	poisoning of total fish community	zoop, phyt, nutr, transp	4 years	Faafeng & Brabrand 1990
20	L. Gjersjoen, Norway, maximum depth 63.0 m, area 2.7 km^2	mesotrophic - eutrophic stratified	enclosure, 7 m^3	scientific, applied	introduction of different numbers of planktivores into the enclosures	zoop, phyt, nutr	4 weeks	Faafeng *et al.* 1990
21	Green Lake, Seattle, Washington, USA, mean depth 3.4 m, maximum depth 8.8 m	eutrophic stratified	enclosure, 12 m^3	applied	introduction of different numbers of planktivores into the enclosures	zoop, phyt	2 weeks	Goad 1984
22	Back Waters, Czech Republick, mean depth 1.9-2.7 m, area 0.0015 km^2	eutrophic, 125 mgTP m^{-3} stratified	whole-lake	scientific, applied	poisoning of total fish community	zoop, phyt, nutr, transp	2 years	Hrbacek *et al.* 1961
23	Hubenov Reservoir, Czech Republic, mean depth 8.9 m, area 0.92 km^2	eutrophic, 25 - 40 mgTP m^{-3} stratified	whole-lake	applied	introduction of piscivores	zoop, phyt, nutr, transp	2 years	Hrbacek *et al.* 1978
24	Graefenhain Quarry, Germany, mean depth 7.0 m, 0.0044 km^2	mesotrophic, 3-10 mgSRP m^{-3} stratified	whole-lake	scientific	introduction of piscivores	zoop, phyt, nutr, transp	5 years	Benndorf *et al.* 1984, Koehler *et al.* 1989
25	L. Lilla Stockelidsvatten, Sweden, mean depth 3.5 m, area 0.01 km^2	oligotrophic - mesotrophic	whole-lake	scientific	poisoning of total fish community	zoop, phyt, primprod, transp, pH, nutr	3 years	Stenson *et al.* 1978, Henrikson *et al.* 1980

26	Broads at Brundall, Norfolk Broadland, U. K. depth 1-2 m, area 0.015-0.025 km^2	hypertrophic, 1.000 mgTP m^{-3} polymictic	whole-lake	scientific	unplaned biomanipulation by cormorant predation (?)	zoop, phyt, macroph, zoob, nutr, transp, pH	2 Years	Leah *et al.* 1980
27	L. Bleiswijkse Zoom, The Netherlands, mean depth 1.1 m, area 0.14 km^2	highly eutrophic, 400 mg TP m^{-3}	whole-lake	applied	manual removal of planktivores	planktiv, zoop, phyt, macroph, zoob, nutr, transp	1 year	Meijer *et al.* 1989
28	Hoveton Great Broad, Ranworth Broad, Norfolk Broad Land U.K., depth 1.0-1.3 m, area 0.26-0.31 km^2	highly eutrophic, 200 mg TP m^{-3} polymictic	enclosure, 5 m^3	scientific	introduction of different numbers of planktivores into the enclosures	zoop, phyt	6 month	Moss *et al.* 1991
29	Round Lake, Minnesota, USA, mean dept 2.9 m, maximum depth 10.5 m	eutrophic 20-70 mgTP m^{-3} polymictic	whole-lake	applied	poisoning of total fish community	zoop, phyt, nutr	2 years	Shapiro & Wright 1984
30	L. Emily, St.Paul, Minnesota, USA	eutrophic, 250 mgTP m^{-3} polymictic	enclosure	scientific, applied	introduction of different numbers of planktivores into the enclosures	zoop, phyt, nutr	3 month	Shapiro *et al.* 1975
31	L. Haugatjern, Norway, mean depth 7.6 m, area 9.1 ha	eutrophic, 40 mgTP m^{-3}	whole-lake	applied	poisoning of total fish community	zoop, phyt, primprod, pH, transp.	2 years	Reinertsen & Olsen 1984, Reinertsen *et al.* 1989
32	L.Haussee, Germany mean depth 6.6 m, area 1.35 km^2	highly eutrophic, spring maximum 1.300 mgTP m^{-3} stratified	whole-lake	scientific, applied	introduction of piscivores, manual removal of planktivores	piscv, planktv, zoopl, phytopl, primprod, nutr, pH, transp	9 years	Koschel *et al.* 1990, Kasprzak *et al.* 1993
33	L. Candia, Italy, mean depth 3.8 m, area 1.7 km^2	eutrophic, annual average 30-40 mgTP m^{-3} stratified	whole-lake	scientific, applied	planktivores reduction by netting, hydrophytes harvesting	phytopl, zoopl, nutr, transp	6 years	Giussani & Galanti 1992

indicating that things were not as simple as was originally thought (Shapiro *et al.* 1975; Stenson *et al.* 1978; Edmondson & Litt 1982; Benndorf *et al.* 1984). Subsequently, interest in basic research has increased, to evaluate what different processes are involved in biomanipulation (food-web manipulation, trophic-cascading interactions, top-down forces; e.g. Carpenter & Kitchell 1985, McQueen *et al.* 1986, Benndorf 1988, Kasprzak *et al.* 1988, Lyche 1989, Shapiro 1990, Benndorf 1990, De Melo *et al.* 1992).

To see whether biomanipulation was successful or not, 34 examples were selected from the literature (Tab. 2.1) and the characteristic changes of the food-web were assessed with respect to water quality management (Tab. 2.2). For that purpose the method of De Melo *et al.* (1992) was adapted.

Tab. 2.2 Success and disappointment of biomanipulation experiments with respect to water quality management derived from the examples in table 2.1, + = successful, − = disappointing, 0 = ambiguous; numbers in [%] of total observations.

Characteristics	Number of Observations	+	0	
Piscivores	3	33	33	33
Planktivores	4	75	25	0
Zooplankton Biomass	21	52	43	5
Zooplankton Structure	29	83	14	3
Zooplankton Grazing	2	100	0	0
Zoobenthos	5	100	0	0
Invertebrate Predators	3	0	100	0
Phytoplankton Biomass	25	64	28	8
Phytoplankton Structure	18	44	28	28
Primary Production	5	100	0	0
Macrophytes	3	100	0	0
Phosphorus (TP)	15	40	33	27
Phosphorus (SRP)	9	22	44	44
Oxygen	1	100	0	0
pH	6	100	0	0
Transparency	21	67	30	0

2. 2 SUCCESS OF BIOMANIPULATION

Even in the light of the problems which have been identified, there is undoubtedly success in biomanipulation research and in the application of biomanipulation as a lake management strategy.

It was found that the basic assumptions of the biomanipulation concept have general validity in all types of standing waters, although experiments in small and shallow lakes are more likely to be successful (McQueen 1990). Moreover, our kowledge about the functioning of the pelagic food-chain and the whole lake ecosystem increased tremendously (McQueen *et al.* 1986; Lyche 1989; Shapiro 1990; Benndorf 1990; De Melo *et al.* 1992). The most important positive results are:

- enhancement in standing stocks of piscivorous fish (Hrbácek *et al.* 1978; Benndorf & Horn 1985; van Densen & Grimm 1988; Köhler *et al.* 1989);

- decrease in the standing stocks of planktivorous fish (Henrikson *et al.* 1980; Benndorf *et al.* 1984; van Donk 1989; Reinertsen *et al.* 1989; Riemann *et al.* 1990);

- increase in suspension-feeding zooplankton, especially of *Daphnia,* and the increase in mean size of zooplankton (Hrbácek *et al.* 1978; Leah *et al.* 1980; Reinertsen & Olsen 1984; Elser *et al.* 1988; Lyche *et al.* 1990);

- increase in zooplankton grazing (Riemann *et al.* 1985; Gulati 1989);

- improved development of macrozoobenthos (Van Donk 1989; Meijer *et al.* 1989);

- decrease in phytoplankton biomass (Hrbácek *et al.* 1961; Stenson *et al.* 1978; Leah *et al.* 1980; Shapiro & Wright 1984; Meijer *et al.* 1989, van Donk 1989; Reinertsen *et al.* 1990);

- change in phytoplankton structure (van Donk *et al.* 1989; Scavia & Fahnenstiel 1988; Vanni 1986);

- reduction in planktonic primary production (Stenson *et al.* 1978, Hrbácek *et al.* 1986; Carpenter *et al.* 1987; Faafeng *et al.* 1990);

- increase of macrophyte standing stocks in shallow lakes (Ozimek *et al.* 1990; Leah *et al.* 1980; Meijer *et al.* 1989);

- increase in water transpareny (Fott *et al.* 1980; Andersson & Cronberg 1984; Faafeng & Brabrand 1990);

- reduction of total phosphorus concentration (Henrikson *et al.* 1980; Wright & Shapiro 1984; Meijer *et al.* 1989; Reinertsen *et al.* 1989; Koschel *et al.* 1993);

- restrainment of diurnal rhythm of O_2-concentration (Hulbert & Mulla 1981);

- restrainment of diurnal rhythm of pH (Hrbácek *et al.* 1961; Stenson *et al.* 1978; Reinertsen & Olsen 1984; Andersson *et al.* 1978).

2.3 DISAPPOINTING RESULTS AND PROBLEMS IN BIOMANIPULATION

Nevertheless, success and disappointment are not widely separated, because every top-down mechanism is accompanied by a counteracting bottom-up effect, creating a complex system of structures and non-linear processes which is difficult to control (Miller & Kerfoot 1987). The most important problems are as follows:

- The creation and stabilization of a strong population of piscivorous fish is difficult and time-consuming (Barthelmes 1988; Benndorf 1988; van Densen 1988; van Donk 1989);

- The population of planktivorous fish is sometimes difficult to control and tends to re-establish high standing stocks (Vijverberg 1984; Mills *et al.* 1987; Shapiro 1990; Koschel *et al.* 1993);

- except for poisoning the fish community, the food-web impulse established by manual removal of zooplanktivorous fish and/or introduction of piscivorous fish is sometimes too weak to evoke strong reactions (Riemann *et al.* 1990; De Melo *et al.* 1992).

- The extent to which planktivorous fish have to be removed depends considerably on the species and size composition of the fish community (Barthelmes 1988; Benndorf 1988; Benndorf 1990; Shapiro 1990);

- *Daphnia*-populations are difficult to stabilize; i.e. on the one hand they are threatened by planktivorous fish and on the other they can suffer from food shortage in response to "over"-biomanipulation (Mills *et al.* 1987);

- Bottom-up and top-down mechanisms are sometimes difficult to separate (McQueen 1990);

- The coupling within the food-web is strongly damped, stochastically disturbed, and influenced by seasonal changes (Cryer *et al.* 1986; Faafeng *et al.* 1990; McQueeen 1990; McQueen *et al.* 1992).

- Due to very different turnover times of the organisms a new and stable equilibrium may require several years to develop (Cryer *et al.* 1986; McQueen *et al.* 1986; Miller & Kerfoot 1987);

- Phytoplankton is usually treated as a homogeneous group. Differences are only considered with respect to the nutritional value for suspension-feeding zooplankton (Köhler *et al.* 1989; Riemann *et al.* 1990; Moss *et al.* 1991; Kasprzak *et al.* 1993);

- As the grazing pressure increases, the phytoplankton community tends to develop several defence mechanisms (non-ingestible, Gliwicz & Siedlar 1980; Kasprzak *et al.* 1993; undigestable, Porter 1973, toxic, Benndorf & Henning 1989; high growth rate, Fott 1980);

- With increasing phosphorus concentration, the probability for successful biomanipulation decreases (Benndorf 1987);

- The role of proto-zooplankton and bacteria is seldom considered (Riemann 1985).

2.4 FUTURE DEVELOPMENT

Comparing the encouraging results with the disappointing ones, it sometimes seems that biomanipulation as a lake management concept is lost before it matures (Benndorf 1987; McQueen 1990; De Melo *et al.* 1992). From the limnological point of view this may be especially disappointing because biomanipulation gained its attraction, among other things, from the fact that it was truly a limnological endeavor (at least during its early development chemists, physicists and engineers played only a minor role; Shapiro *et al.* 1975; Shapiro *et al.* 1982). Moreover, from an ecological point of view it is a careful method (except for rotenone poisoning) and it needs little additional energy to function, because sunlight is the main driving force.

What can be done to prevent biomanipulation being lost as a lake management concept ?

The only way to reach this aim may be the reunification of the loading and the biomanipulation concept and the integration of indirect mechanisms (Benndorf 1987; van Donk 1989; Benndorf 1990; Riemann *et al.* 1990:Carpenter & Kitchell 1992).

It is not completely clear why both approaches developed more or less independently over such a long time frame. One reason may become obvious if we look into the history of the subject. Welch (1952) noted in his textbook of limnology: "While various reciprocal relations exist between the plankton and the non-plankton animals there is reason to believe, that if all the non-plankton animals were removed from a lake and kept out, the plankton, with possibly some minor modification, would continue to exist". Some years later Hrbácek *et al.* (1961) concluded that their "investigations...indicate that the biocenotic relations between the fish stock and the plankton...are at least as important as the influence of the physical and chemical...factors for the formation of the plankton association...".

Obviously, opinions about the processes most responsible for the fuctioning of lake ecosystems at that time were completely different, and if we also take into account the paper of Dillon & Rigler (1974), with its close relationship between phosphorus and chlorophyll concentrations in lakes, there was obviously thought to be no need for more biology in lake restoration techniques. This situation lingered on until the beginning of the eighties.

However, at present we have first to realize that biomanipulation is neither a simple nor a cheap method to solve a complicated and expensive environmental problem. This hope has not been fulfilled. On the contrary, it became clear that biomanipulation experiments are very complicated interventions into the whole ecosystem and are far from being a routine method of water quality management in lakes (Carpenter *et al.* 1987; Kerfoot & Sih 1987; Benndorf 1988; Gulati *et al.*

1990). If they should not be compared to a "black box", their development must be followed very carefully by a team of experienced scientists who will need well equipped laboratories and field sampling devices. Moreover, because the process of re-oligotrophication can take several years (especially in highly eutrophic stratified lakes), the efforts often have to be carried out for a longer time period with corresponding costs. Therefore, biomanipulation can no longer be regared as a cheap method of lake restoration (Koschel 1990). In short - the costs of environmental deterioration have to be paid for even in the case of eutrophication. The most promising way to reduce the financial needs is perhaps through the combination of load reduction and biomanipulation (Lyche 1989; Benndorf 1990; Brabrand *et al.* 1990; Carpenter & Kittchell 1992). These conclusions must be explained to the decision makers in the water authorities, as well as to the public.

2.5 INDIRECT EFFECTS

During the development of the biomanipulation approach, we experienced a remarkable change in opinions about the supposedly most important processes involved. In the early years we believed that direct top-down effects were of special importance (Hrbácek *et al.* 1961; Shapiro *et al.* 1975; Shapiro *et al.* 1982; Benndorf *et al.* 1984). In fact, biomanipulation means nothing without the cascading trophic interactions moving down the food chain (Carpenter *et al.* 1985). Nevertheless, to reach stable results the indirect mechanisms became more and more noticeable because they lower the nutrient concentration and/or the nutrient turnover (Leah *et al.* 1980; Lammens 1988, Kőhler *et al.* 1989; Lyche *et al.* 1990; Reinertsen *et al.* 1990). Without them the same things would always happen again: sometimes we would be successful, but mostly not (De Melo *et al.* 1992). However, given a lake with a restored catchment, suffering only from internal nutrient load, biomanipulation can help to improve its self-purification performance and to increase the velocity of re-oligotrophication (Koschel *et al.* 1990; Koschel *et al.* 1993). For that reason we have to address the indirect mechanisms in such a way that top-down and bottom-up mechanisms can work together to lower the trophic state of standing waters. If it is necessary, support by technical measures such as destratification or deep-water aeration is possible (Oskam 1978). This approach to integrated lake restoration may be especially important for the future application of biomanipulation in the field of water quality management.

Important indirect effects involved in biomanipulation that can possibly be better addressed by careful control of direct mechanisms are as follows:

- development of macrophyte communities (Leah *et al.* 1980; Meijer *et al.* 1989; van Donk *et al.* 1989);
- increased nutrient sedimentation in response to zooplankton grazing (Ferrante 1976; Wright & Shapiro 1984);
- increased nutrient sedimentation by calcite precipitation in hardwater lakes (Koschel *et al.* 1985; Koschel *et al.* 1990);
- decreased phosphorus remobilization as a consequence of decreased pH in littoral sediments (Reinertsen *et al.* 1990);
- increase of N/P-ratios (Kasprzak *et al.* 1993);
- higher consumption rate of phytoplankton by suspension-feeding zooplankton in the epilimnion, leading to a lower oxygen deficit in hypolimnion and decreased phosphorus remobilization in profundal sediments (Köhler *et al.* 1989; Reinertsen *et al.* 1990);
- inhibited phosphorus recycling due to lower sediment redistribution and excretion by benthivorous fish (Horppila & Kairesalo 1990; Keto *et al.* 1992; Lamarra 1975; Shapiro *et al.* 1982; Lammens 1988);
- decreased phytoplankton biomass yield per unit phosphorus (Lyche 1990);
- improved development of zoobenthos and periphyton (Leah *et al.* 1980; van Donk *et al.* 1989);
- creation of refuges for big-sized crustaceans (Shapiro 1990; McQueen & Post 1988).

2.6 CONCLUSIONS

The basic assumptions of the biomanipulation concept were found to be generally valid, although quantitatively hard to predict. Nevertheless, biomanipulation can be used as an additional or exclusive measure to improve the quality of stagnant waters.

There exist a number of disappointing results and open problems in biomanipulation research relevant to the application of biomanipulation as a lake management strategy. Most of them concern the stabilization of the non-equilibrium structure of the manipulated food-chain and the damped top-down interactions.

The future application of biomanipulation as a part of an integrated lake restoration approach (load reduction, indirect effects, technical measures) may be of special importance.

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CHAPTER 3

FOOD WEB ALTERATIONS BY PHYSICAL CHANGES: EUTROPHICATION AND SELECTIVE FISHERIES

Moshe Gophen

3.1 INTRODUCTION

Human utilization of freshwater is vital and primarily aimed at drinking, agricultural irrigation, fishery, recreation (tourism), industry and inland transportation. Nevertheless, only 0.014% of the earth's water (0.001% in the atmosphere, biota and rivers; 0.008% in lakes and 0.005% in the soil) is biospheric freshwaters and an additional of 1.97% is ice and 0.61% ground waters, while the rest (97.406%) is saline waters (la Riviere 1989). The meagre 2.594% of earth's biospheric waters has a large significance on human societies. Human life is directly dependent on fresh water availability i.e., the global distribution of human population is strongly related to freshwater supply from lakes, rivers, underground and desalination resources. About 90% of the world's inland surface water supply comes from large (>500 km^2) lakes and 10% from small lakes and other sources (Herdendorf 1990). Consequently, water quality and limnological processes dynamics in large and small lakes are a major concern of human society. The food web structure and dynamics has a large significance for ecosystem stability and prevention of water quality deterioration.

Food web alterations are defined in different ways. One of them is eutrophication, which is an enrichment of organic content in the water, with wide varieties of consequent environmental modifications. The level of importance we give to eutrophication is mostly due to water utilization. If a lake (or reservoir) is part of a water supply system where quality protection is top priority in management design, minor change of algal densities (i.e., organic content) could be crucial. On the other hand, if a water-body is utilized for recreation, algal densities become deleterious at a higher level. Moreover, when a water body is utilized for drinking water supply under certain quality standard levels, respective algal densities are acceptable. Nevertheless, if the standards are changed to be more rigorous, the previously accepted level of algal density might be classified as more eutrophic and unacceptable under the new tougher formulated levels. Keeping in mind that scientific definitions and quantifications of eutrophication process rate are considered differently for practical engineering operations.

The eutrophication process is also caused by a very wide spectrum of factors like development and management modifications in the catchment area, nutrient loads and internal dynamics, fisheries management, climatological conditions, and others. Nevertheless, in most cases of advanced eutrophication, combined alterations of internal dynamics of nutrient, biotic community structure and population dynamics and more, are followed. Therefore, it is not so easy to evaluate causative reasons of observed effects and distinguish between primary, secondary and tertiary factors. In this chapter I will discuss several aspects of food web alterations. This chapter addresses the potential effects of physical conditions, fisheries management and eutrophication on food web alterations in lakes. These effects are complicated and have different significances in large and small lakes and reservoirs.

3.2 CLIMATOLOGICAL EFFECTS

Global changes in climatic conditions are significant for aquatic ecosystems in general, particularly in lakes. Not less significant are the local microclimate changes in certain locations. The global change that will be considered here is "warming". Nevertheless, air loading capacity of nutrients (mostly P and N) and acidity also has large significance for lakes, especially in highly industrialized continents.

3.3 GLOBAL WARMING

There is an international consensus about global warming and one of the major concerns is that due to the greenhouse warming effects, precipitation and evaporation will increase (Schneider 1992) and some regions of our planet will become wetter and others drier, accompanied by shifting of the global distribution of rivers, lakes and wetlands (Waggoner 1990). Rind *et al.* (1989 a, b) indicated a possible decrease of variability of temperature and the diurnal range, while increasing the variability of precipitation. If global warming of 2-4℃ occurs, changes in runoffs over the next century are predicted (Carpenter *et al.* 1992). An expansion of the land-water interface and contract with fluctuations in the water supply in the zone of intense biogeochemical activity is also anticipated

(Wetzel 1990). This trend of changes in interface is especially important in small lakes because of their large shore line to volume ratio. Global warming followed by precipitation changes will likely alter biomass, productivity and species composition of vegetation in the catchment and consequently the input (quantitative and qualitative) regime of nutrients into the lakes. Global warming will probably enhance eutrophication mostly in small-shallow lakes. Physical changes in eutrophicated lakes might have feed-back influence on riparian environments. Two case studies will be discussed: Lake Victoria in East Africa and North American lakes.

3.4 LAKE VICTORIA

Eutrophication was indicated in Lake Victoria (East Africa) during the 1980s. The effect of two major ecoforces was indicated in enhancing these limnological modifications: a) top down effect by exotic invading piscivore Nile perch (*Lates niloticus*) who devastated the biodiversity of the native and endemic haplochromine fish fauna; b) changes of nutrient loads and internal dynamic (Tab. 3.1). Fish and fishery effects will be discussed later. The changes in loads and internal dynamics were caused by human activity in the drainage basin of the lake: increase of human population (one of the highest rates known in the world) and livestock, deforestation, intensive agricultural fertilization, urbanization and industrialization (Kaufman 1992; Hecky 1993). As a result of enhanced industrialization in the catchment area and in adjacent countries, P concentration in rainfall (85% of inflows) (Tab. 3.1) on and around the lake area increased by *ca* 3-fold compared to the 1960s (Hecky 1993). Major (85%) inflows of Lake Victoria water budget is direct precipitation. Therefore, increase of atmospheric nutrient loadings enhanced eutrophication. Air pollution and atmospheric conditions initiated pollution in the second largest (by area) lake in the world. Consequently, the phytoplankton biomass and productivity increased and a shift from diatom to blue-green occurred. Anoxia was enhanced in the hypolimnion and fish kills became more frequent. The lake ecosystem was split into two chains with low algal grazing capacity in the epilimnion and increased densities of prawns in the deoxygenated hypolimnion (Gophen *et al.* 1994; Goldschmidt *et al.* 1993). Similar effects of air pollution caused acidification of lakes in North America and Europe.

Tab. 3.1 Comparative data from the offshore zone of Lake Victoria: 1960-Uganda-(Talling 1966); 1990-Uganda-(Hecky 1993); 1990-Kenya-(Gophen *et al.* 1994). *

	UGANDA		KENYA
	1960	1990	1990
N-NH_4 (ppm), Epil.		0.028	0.008-0.013
N-NH_4 (ppm), Hypol.		0.056-0.12	0.021-0.152
N-NO_3 (ppm)	0.00-0.01	0.011-0.084	0.01-0.030
SRP (ppm)	0.091-0.50	0.012-0.043	0.004-0.073
Total-P (ppm)		0.062-0.124	0.07-0.103
Total-N (ppm)		0.336-0.448	0.44-1.16
TN/TP (Wt/Wt)		3.2-9.0	4.7-18.5
Upper depth of 4.0 ppm DO isopleth	45 m	23 m	23 m
Silica (ppm)	4.2-8.4	0.01-2.5	
Chlorophyll ($\mu g\ l^{-1}$)	2-4	11-23	
Dominant alga	Diatoms	Cyan.	Cyan.
P. Prod. ($mgO_2\ m^2$)	100-130	180-600	
Secchi Depth		1.2 m	1.8 m
Euphotic Zone	0-15 m	0-7.5 m	

* Source: Gophen *et al.* 1994.

3.5 NORTH AMERICAN LAKES

As in Lake Victoria, eutrophication was indicated in North American lakes where both fish communities and climatological conditions were changed. Weather condition anomalies caused by El-Nino and the Southern Oscillation (ENSO) with several year frequencies were documented by Enfield (1989). Lakes response to these climatic effects were studied in North America (Melack 1983; Ragotzkie 1978; Barry 1985). Small to moderate sized lakes are affected mostly by local climatological conditions while large lakes response to global or large scale atmospheric changes is manifested (Melack 1992). Robertson (1989) formulated an index of combined data of local weather in Lake Mendota, Wisconsin, and ENSO's frequency and demonstrated the association between warmer winters, less snowfall, shorter ice cover duration and ENSOs. Further implications of these climatological effects go through runoff regime, nutrient loads, stratification and destratification durations, internal dynamics and interactions between nutrients and food web effects (Kitchell & Carpenter 1992). Schindler *et al.* (1990) described lacustrine responses of northwestern Ontario lakes, to 2℃ increase in air temperatures where duration of the ice-free season became 3 weeks longer. Moreover, residence time of lake water increased due to consequent higher evaporation and lower precipitation accompanied by more frequent forest fires, increasing tree exposed areas and higher wind speeds, higher mixing in lake water which caused deeper thermocline and cold water habitat (for lake trout) volume was reduced.

3.6 LOCAL CLIMATOLOGICAL EFFECTS

Greenhouse effect on global warming and in turn, its effect on lakes, has become an international concern. Nonetheless, local effect of temporal changes of climatological conditions on lake dynamics can not be easily analyzed mostly because of the lack of accurate and methodologically unified long-term records. Paleolimnological data collected from cores can partly replace long term research.

3.7 THE KINNERET CASE

During the last 25 years, Lake Kinneret waters have cooled by 2.5℃ (Hambright *et al.* 1994). Water temperature in the offshore zone (deeper than 10 m; the mean depth of the lake is 26 m) of the lake declined from 20.2 to 17.5℃. During 1969-1992 the thermocline mean depths became shallower at an average rate of 0.13 m per year (3.0 m during 23 years) (Hambright *et al.* 1994). The absolute and relative (to the epilimnion) volume of the hypolimnion significantly increased. The consequent implication on the food web is enhancing nutrient fluxes from the anoxic hypolimnion to algal production in the epilimnion. Stanhill (1993) demonstrated decline of solar radiation during the last 25 years in the Kinneret area. He suggested that lake water cooling was accompanied by decline of evaporation and the heat budget was changed respectively (Stanhill 1993). He also suggested that the decline of solar radiation was caused by increase of aerosols fluxes from the Israeli coastal plan and south-eastern Europe to the atmosphere. Temperature decrease of epilimnic water has a significant effect on the dynamics of the biological constituents of the food web, such as photosynthesis, respiration and nutrient uptake by phytoplankton; respiration, reproduction, ingestion and growth rates of zooplankton, fish, and others.

Hawkins & Griffiths (1993) documented a case where artificial destratification (by aeration) in small tropical reservoirs reduced chlorophyll content in the epilimnion and shifted species composition from cyanophytes (stratified) to diatoms (destratified).

3.8 PHYSICAL FACTORS

Physical factors such as in-and outflows have a significant effect on lake dynamics. Changes in the water budget of a lake are natural (floods or droughts) and/or man made (water removal by pump or diversion). Diversion can be done directly from the lake or in the catchment before coming into the lake. There are differences in lake response to water budget changes. Changes in water budget are respectively accompanied by water levels fluctuations and consequently in thermal structure, nutrient and food web dynamic. In subtropical stratified lakes with high values of Relative Thermal Resistance (RTR) (Wetzel 1983), and long-term decline of solar radiation (Stanhill 1993), reductions of inflows, intensified pumping or water removal with consequent severe lowering of lake water level can cause cooling of the hypolimnion, shallower thermocline, delay of turnover (i.e. longer stratification period) and increase of RTR values. As a result of higher stabilization of stratification, reduction of exchange between the hypolimnion and epilimnion can be predicted. On the other hand, in lakes with internal seiche and high amplitude movements of the thermocline these exchanges might be intensified. As a result of lower volume of the epilimnion, the nutrient concentrations and phytoplankton densities in it will increase. Increasing densities of suspensoids (phytoplankton, detritus, inorganic particles) in the euphotic zone might also enhance light back-scattering (Hambright *et al.* 1994; Mazumder *et al.* 1990) resulting in an additional cooling effect of the epilimnion and shallower thermocline. It should be noted that back scattering of light is positively correlated with the number of particles suspended per volume unit. Therefore, phytoplankton species composition is important: small sized cells with high density is more effective than large cells or colonies even with higher biomass concentrations (Mazumder *et al.* 1990). Another scenario of the same system could be changes in water budget with respective water level lowering but stable climatic conditions. In such a case the volume of the epilimnion will stay unchanged (i.e. unchanged thermocline depth-distance between water level and the thermocline-but lower altitude of the thermocline) and the hypolimnion volume will decline. The activity of the biota in the epilimnion will stay the same (qualitatively and quantitatively) as before but suspended matter will sink into a hypolimnion with smaller volume. Soluble nutrients released from bottom sediments and/or degraded products from decomposed organic matter will be dissolved in a smaller hypolimnic volume. Consequently, the concentrations will increase followed by higher reduction capacity (E_h values more negative), lower pH and higher concentrations of sulfides, ammonia or methane are predicted if carbon supply from organic decomposition will be sufficiently available (Wetzel 1983). Volohonsky *et al.* (1992) calculated the effects of water budget changes (inflows diversion) in Lake Kinneret (Israel) and the results indicated that reductions of 12% and 18% of the inflows will cause an increase of 24% and 40% of phosphorous mass content in lake water, respectively.

3.9 THE LAKE SEVAN (ARMENIA) CASE (Ostrovsky 1989; Parparova 1989)

Lake Sevan is an oligotrophic, high altitude large lake. During the period of 1938-1978 water was removed from the lake through man made canals for irrigation of agricultural crops in the Ararat Valley. Water outflow was consistently higher than inflow during almost 40 years and a 19 m drop in water level was recorded. It was accompanied by introduction of exotic fish. The lake has undergone severe changes aimed at eutrophication: blue-greens became dominant, primary production and algal densities increased, Secchi depths became shallower by 80%, endemic fishes became extinct and fishery of native species abruptly declined. Following increased levels of primary production the flux of organic matter to the bottom was enhanced and a sixfold increase of benthic biomass was recorded. This is a clear case where man made modifications of water budget caused eutrophication.

Man made modifications are mostly relevant to moderate or small natural lakes, but play a major role in reservoirs of all sizes. In man-made reservoirs the water budget is mostly under human control whereas in natural lakes the control depends on headwater discharges. Table 3.2 shows three water budgets: 85% of Lake Victoria inflows are direct rain while in Lake Kinneret and Lake Mendota 8% and 24% respectively. In Lakes Mendota and Kinneret man made modifications have a significant effect on the ecosystem structure (Lathrop 1992; Volohonsky *et al.* 1992), while the effect of natural fluctuations of precipitations in the drainage basin and consequent inflow discharges depends upon the amplitude of the change, the time span and the lake size (volume). The higher and longer the fluctuation is, the more severe are the effects on the ecosystem. In riverine lakes and reservoirs where residence time (RT) span is weeks or months, the effect of water budget on the food web structure is different from water-bodies with longer (years) RT period. Nutrient flushing rates in short RT riverine lakes is measured in weeks or months and therefore the impact of internal chemical process is lower (Kennedy & Walker 1990). De Angelis (1980) analyzed ecosystem resilience. He suggested that the shorter the time a unit of material resides in an ecosystem, the more

Tab. 3.2 Water budget of three lakes: Victoria (East Africa) (HEST 1988), Kinneret (Israel) (Mero 1978), and Mendota (Wisconsin, USA) (Lathrop 1992); % of total inflow are given.

	Victoria	Kinneret	Mendota
Inflow			
Direct Rain (10^9m^3)	100 (8.5 %)	0.07 (8 %)	0.03 (27 %)
Runoff (10^9m^3)	18 (15 %)	0.70 (81 %)	0.07 (64 %)
Sublacustrine or groundwater (10^9m^3)	negligible	0.09 (11 %)	0.01 (9 %)
Outflow			
Evaporation (10^9m^3)	100 (85 %)	0.30 (35 %)	0.04 (36 %)
Overflow (10^9m^3)	18 (15 %)	0.56 (65 %)	0.07 (64 %)
Total Inflow (10^9m^3)	118	0.86	0.11
Lake Volume (10^9m^3)	2760	4	0.51
Lake Area (km^2)	69000	170	40
Residence time (y)	23.4	4.7	4.6

resilient the ecosystem will be to perturbations of that material.

When epilimnion volume becomes smaller and the thermocline is shallower there is less potential refuge for zooplankton to avoid fish predation during day time. It is because of a smaller volume of epilimnion and increasing encounter probabilities between predators and prey as well as higher light intensity close to metalimnion (Lampert 1993).

3.10 EUTROPHICATION AND NUTRIENT COMPOSITION EFFECTS

The major known factor which enhances eutrophication is increase of nutrient loads and vice versa: lake restoration by nutrients removal (Lathrop 1990; Edmondson & Abella 1988; Calderoni *et al.* 1993). As shown before, nutrient mass increase in a lake might be a result also of a shorter water residence time (Volohonsky *et al.* 1992). Nutrient enhancement is not only driven by a shorter cycle of water exchange but also by lower water levels. The final result of these different mechanisms is higher nutrient availabilities to algal production and increasing level of organics in the water. Consequent processes are higher levels of oxygen consumption by decomposition of organic matter, enhanced anoxia and changes of species composition of biota. Higher densities of species adapted to low oxygen conditions, like small rotifers or certain species of crustaceans are predicted. Gophen *et al.* (1994) indicated high densities of the prawn *Caridina nilotica* in

Lake Victoria more than was previously known in the hypolimnion of Lake Victoria (East Africa) (Goldschmidt *et al.* 1993). Nevertheless, change in food-web structure can be observed even before eutrophication symptoms are indicated. A slight increase of P fluxes in non-eutrophicated Lake Kinneret during the 1980s enhanced chlorophytes biomass which slightly deteriorated water quality (see Gophen, L. Kinneret, this volume).

An important effect which accompanies increasing algal biomass concentrations is higher dissolved oxygen content in the epilimnion. Hecky (1993), Hecky *et al.* (1994) and Gophen *et al.* (1994) documented such a case in Lake Victoria during the early 1990s where high algal biomass enhanced DO concentration in the euphotic zone to an oversaturated level during daytime. Talling (1966) measured concentrations of DO below saturation at similar depths during the 1960s. It should be taken into account that the complete diurnal cycle is crucial and oversaturation during daytime is probably followed by low DO levels during night due to respiration.

The significance of eutrophication to the food web is not only through increasing algal biomass and lowering levels of DO content. Quite often eutrophication also causes change of algal species composition and this factor has a large impact on grazer communities which in turn affect higher trophic levels like pelagic fish and/or benthos. These sequences are complicated and highly integrated to each other (Crowder *et al.* 1988). In general we call them "food web" and their impact on each other are food web interactions. Alterations, fluctuations or dynamic changes between food web components as a result of eutrophication can not be indicated without a thorough understanding of the ecosystem complexity (Carpenter 1988). Efficiency of ecosystem manipulation depends on its structure and function. Vanni *et al.* (1992) demonstrated the viability of management strategy for reducing the severity of summer algal blooms by food web manipulation (reduction of planktivory) in eutrophicated Lake Mendota. Nevertheless, Kitchell & Carpenter (1992) rejected the hypothesis that food web interactions alone regulate algal community structure in Lake Mendota (see also De Melo *et al.* 1992). The cases of Lake Kinneret (see Gophen this volume) and Lake Victoria (Gophen *et al.* 1994; Hecky 1993) also supported the hypothesis that food-web alterations in phytoplankton production and species composition is regulated by both food web interactions (Vanni *et al.* 1992) and nutrients (Lathrop 1990). Moreover, nutrient and food web interact, alternate in importance and operate in different time and spatial scales (Kitchell & Carpenter 1992).

Vanni *et al.* (1992) used a simulation model of the interactions among nutrients phytoplankton and zooplankton for Lake Mendota. They (1992) demonstrated that food web manipulation is a viable management strategy for reducing the severity of summer algal bloom and reduction in planktivory led to reduced phytoplankton biomass in the summer.

Eutrophication is not only enhanced by load quantities, but also by their relative abundance. Hecky *et al.* (1993) analyzed the impact of particulate C, N, and P contents in 51 lakes and their basins covering a very high geographical distribution. The elemental ratios (C:N, C:P, and N:P) occurred in shield lakes with long residence times were high and originated from in-lake processes and not from streamborn or atmospherically deposited particles (Hecky *et al.* 1993). In lakes there is a very wide variety of N and P deficiency and sufficiency (Sommer 1989a). Throughout this wide spectrum of N/P ratio (Hecky *et al.* 1993) the phytoplankton response vary as well: from P and N enriched waters with high chlorophytes densities to low N (N limitation) predominated by blue-greens. The more the ecosystem is oligotrophic, the more it is susceptible to nutrient effects. Increasing nutrient inputs in nutrient-limited ecosystems enhance eutrophication at a higher rate than similar loadings in meso- or eutrophic lakes. The elemental ratios in the loadings affect algal species composition. In Lake Victoria, Hecky (1993) suggested that increasing level of P inputs by precipitations and through runoffs enhanced dominant diatom production, and silica therefore declined. Silica decline together with low N/P ratio in loadings enhanced blue greens which are presently dominant (Hecky 1993). Sterner *et al.* (1993) examined influence of nutrient limitation on the nutritional quality of *Scenedesmus* as food for *Daphnia.* Nutrient limitation greatly influences the rate at which *Daphnia* converts *Scenedesmus* into body biomass. The N and P contents and ratio in *Scenedesmus* fluctuated when limited while in *Daphnia* N content and to a lesser extent also P content was less variable with essential constant N/P ratio in body tissues (Sterner *et al.* 1993). Sterner (1989) suggested a particular pattern of N and P recycling by *Daphnia* in ecosystems with different nutrient concentrations: when feeding on P-limited algae with N/P higher than in the *Daphnia* the zooplankter must assimilate a greater fraction of P than N. Therefore, a greater fraction of ingested N is not assimilated and recycled N is higher than P return to the environment. This process by itself has an impact on nutrient dynamics. Urabe and Watanabe (1992) suggested that particulate elemental ratios (C:N:P) may have an effect on zooplankton community structure. They (1992) documented different threshold N:C and P:C ratios for *Daphnia galeata* and for *Bosmina longirostris.* The effect of food availability (grazed seston) on zooplankton community structure is not only through particle concentration but also by elemental composition on the feeding and production rates and consequently, on the density as well as on competitive interaction between species. Hessen (1992) described similar effects on zooplankton community structure. Lehman & Naumosky (1985) documented P content variation in *Daphnia* at only 1.6-fold when fed on algae with P variations of 2.3-2.7 fold. Variations of quantities and elemental ratios of the loadings can initiate changes of seston (algae, detritus) composition and density and consequently alterations of zooplankton community structure. When N is in excess, zooplankton regulated by stoichiometry, release higher N content than in the food ingested (Sterner 1989). In other words, N:P ratio needed for metabolism and in N:P ingested determine the N:P released. Zooplankton feed on P-limited algae at suboptical concentration will enhance P-limitation because of lower P content in the excretions. The same for N: mild N limitation would become severe N limitation (Sterner 1989). Urabe (1993) demonstrated a case of N limited food for zooplankton and the animals net clearance rate was therefore higher for N than for P and C, indicating that limited nutrient is removed (assimilated) with a higher efficiency than nonlimited elements. He (1993) showed how zooplankton keep their body elemental composition constant when N:P ratio in the food supply varies. Sterner (1993) represented further results which indicate that the logarithm of *Daphnia's* biomass is well predicted by the logarithm of algal growth rate. The algal growth rate is related to their elemental (P, N) composition and quality. The P limitation for *Daphnia* growth when feeding on low P content algal cells was concluded (Sterner 1993). Thus, feedback interactions between zooplankton and phytoplankton indicate potential alterations in nutrient limitations for algae caused by grazers. Elser & George (1993) determined stoichiometric ratios of C:N, C:P and N:P in dissolved, seston and zooplankton pools in Castle Lake, California. They suggested that changes in zooplankton biomass and community structure may produce significant shifts in nutrient storage among pelagic pools. They concluded that zooplankton potentially enhanced P limitation of phytoplankton. One of the most described alteration caused by eutrophication is the shift from large zooplankters (*Daphnia* type) to small bodied organisms (*Bosmina* type). Such a shift is followed by decline of clearance rate and therefore grazing capacity of the population is lower, and algal densities are enhanced (Dawidowicz 1990).

3.11 SELECTIVE FISHERIES AND FISH INTRODUCTIONS

Selective fisheries and fish introductions in a wide sense is similar to food web manipulation or biomanipulation. Most food web manipulations include fish as manipulated component with two major options: 1) introduction of desired species and b) selective removal of unwanted species. The rational is successive modifications in the food web structure initiated by higher trophic level organisms (fishes) towards lower trophic level components (zooplankton and phytoplankton) aimed at water quality improvement.

The literature on food web manipulation indicate a difference in lake response between large-deep and small-shallow water bodies (Fig. 3.1) (Carpenter 1988; Gulati *et al.* 1990; Kitchell 1992; Sommer 1989b). If a significant change follows fish manipulation in small lakes, the new structure might be stable for a short period. If man-made manipulation or natural event like fish mortality are not repeated, a reversible process is predicted. This is probably the sequence observed in Lake Mendota (Kitchell 1992) or in small Danish lakes (Jeppesen *et al.* 1990). In larger and deeper lakes fish manipulation can cause lower scale, less stable and change over longer periods (Fig. 3.1). The most important factor in this comparative consideration is the manipulated fish population stability. If the manipulated fish population structure is stable during long periods the new food web structure is stable as well. In Lake Round, after two years reversible changes were observed as before the rotenone fish removal (Shapiro & Wright 1984). Fish mortality in

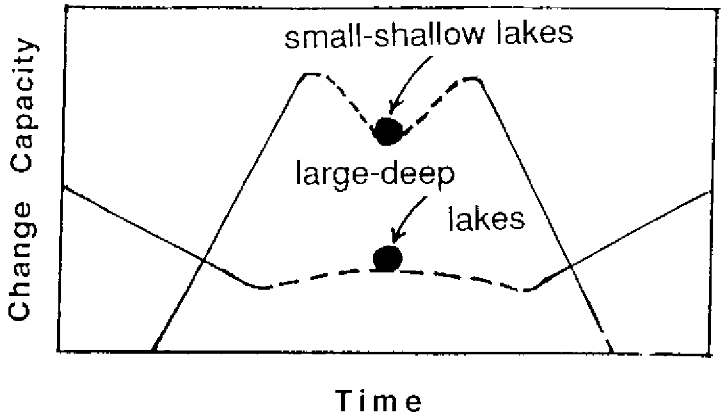

Fig. 3.1 A diagram of lake (small-shallow; large-deep) stability (●) as responded to manipulated (-----) and unmanipulated (——) changes. In large-deep lakes, manipulated alterations are less stable, with lower capacity and longer duration, while unmanipulated changes has longer span and higher stability; in small-shallow lakes its conversely expressed.

Lake Mendota (Vanni *et al.* 1990) was consequently accompanied by increase of zooplankton body size, increasing grazing pressure and longer spring clear water phase and lower biomass of phytoplankton in summer, but reversible changes were observed later. Similar effects were demonstrated by Sanni & Waerragen (1990). A different example is the invasion of the piscivore Nile Perch in Lake Victoria which produced a new and unchangeable food web structure, but an unstable ecosystem and long-term fluctuations are predicted. Vadas (1989) in his reply to Fretwell & Oksanen suggested that compensatory mechanisms are usually strong enough to overcome temporal changes in consumer abundance. This is probably relevant to lakes Kinneret and Mendota but not to Lake Victoria. The different response of large-deep and small-shallow lakes to food web manipulation is also due to stratification. In deep stratified lakes the manipulated populations are in the epilimnion while the hypolimnion is indirectly affected. Therefore the significance of the manipulation is higher in shallow lakes where manipulated populations occupy the whole volume.

The classical approach to biomanipulation as phytoplankton biomass suppression by fish-induced shift towards larger zooplankton with increased community grazing rate is given in Hrbáček *et al.* (1961), Brooks and Dodson (1965), Lynch and Shapiro (1981), Shapiro and Wright (1984), Carpenter and Kitchell (1988), Oksanen (1988), Leucke *et al.* (1992) and others.

None of the cases presented in these studies existed over a long period of several years. Nevertheless, the effectiveness of large bodied zooplankton, particularly *Daphnia,* is not unlimited (Dawidowicz 1990). Moreover, relations between large zooplankters (particularly *Daphnia*) grazing rates and phytoplankton, depend on algal species. Ingestion of blue-greens (unicell or filamentous) is positively related to algal concentration up to a certain limit (Gliwicz 1990; de Bernardi & Giussani 1990). Lampert (1988) quantified zooplankton biomass needed for seston concentration control with findings that showed 1.5-4.0 mg dry weight per m^2 are needed for clear water phase. He documented a grazing rate value of 200% per day by zooplankton in mesotrophic lakes. Most of classical biomanipulation studies of fish effects on the whole community structure were carried out in small and shallow lakes, ponds, mesocosms (tanks or tubs) or enclosures. In most studies only few parameters and treatment combinations were tested. For example: when fish zooplanktivory was studied - a predator fish with or without not more than 1 or 2 other fish species were also present while in nature many more exist (see papers in Gulati *et al.* 1990 and in Kerfoot & Sih 1987). Very few studies on whole natural lakes with long term records were carried out, such as Lake Mendota (Kitchell 1992); or Lake Kinneret (see, Gophen, this volume). Small scale experiments can give indications only for partial boxes of the food web structure. For the whole ecosystem analysis of nutrients and food web manipulation effects, both factors must be simultaneously studied. In several documented whole lake cases, such as Victoria (East Africa), (Hecky 1990; Gophen *et al.* 1994), Kinneret (Israel) (see Gophen this volume) and Mendota (Wisconsin, USA) (Kitchell 1992) changes in the ecosystem were controlled by nutrients and food web manipulations simultaneously. It is probably impossible to quantify the relative role (effect) of each ecoforce. Nevertheless, it is evident that both are involved as driven forces of the ecosystem alterations. Changes of nutrient dynamics and loadings were altered as well as fish communities, and the two ecoforces alternated in importance but simultaneously affected the systems. In each one of these three lakes the alterations are differently scaled but clearly documented.

Lammens *et al.* (1990) summarized recent studies on fish and zooplankton effects. In their review they presented a synthesis of studies done in whole lakes and mesocosms where manipulated fishes were phytoplanktivorous, planktivorous, benthivorous and piscivorous, and their effects were recorded. They also included several studies where nutrients were involved. Lammens *et al.* (1990) indicated that the most dramatic effects of food web manipulations were observed in shallow and eutrophic lakes. Lampert (1988) indicated a higher grazing rate in oligotrophic conditions, but demonstrated that a high rate does not necessarily mean a high rate of particle elimination. Zooplanktivory declined and zooplankton biomass was enhanced with consequent intensification of grazing capacity resulting in lower algal biomass, deeper secchi depths, higher light penetration and macrophyte enhancement (Lammens *et al.* 1990). The positive (improving water quality) response of shallow small lakes to fish manipulation was more successful when TP concentration was $<50\ \mu g\ l^{-1}$. Therefore selective fishery and removal of benthivorous fish is important to extend successful zooplanktivory manipulation. Removal of benthivorous fish reduce P release from the sediments (Meijer *et al.* 1990).

The top-down effect from piscivorous fish through zooplanktivory to algal control in most cases caused dominance of small bodied zooplankton assemblages. Small bodied zooplankters have lower clearance rate as was shown in many studies (Dawidowicz 1990; Sterner 1989). These conditions can be described as a paradox with dense zooplankton assemblages dominated by small species having lower grazing capacity of the entire community than ones dominated by large species. The size structure of the grazers strongly influence total herbivore biomass. Dominance of larger species have higher biomass than populations dominated by small species (Sterner 1989). This is the major reason for the abrupt and significant decline of algal biomass when zooplanktivory decline and large zooplankters are more abundant. Zooplankton communities dominated by *Daphnia* have higher grazing capacity. It happens when fish zooplanktivory allows *Daphnia* population biomass density to become high. Shapiro and Wright (1984) documented higher grazing rates in seasons when *Daphnia* dominated and lower grazing rates when *Bosmina* dominated. Gulati (1984) presented data on the eutrophic Loosdrech Lake where small species (*Bosmina, Chydorus,* rotifers) dominated and the grazing rate was low.

Arnott & Vanni (1993) presented results of experimental manipulations with large bodied *Daphnia* and invertebrate predators and concluded that predation is more important than competition (between *Daphnia* and small zooplankton) in restricting distribution of small zooplankters in big lakes. They found that pH also inhibits successful invasion of small organisms. They (1993) concluded that invertebrate predators and abiotic conditions (pH) are important factors determining zooplankton community structure.

3.12 THE KINNERET CASE (see also Gophen, Lake Kinneret, this volume)

In Lake Kinneret fish introduction and selective fishery occurred simultaneously with nutrient changes. Zooplanktivorous bleak populations were enhanced in the lake and together with exotic and other introduced fish species, zooplanktivory was intensified. As a result, zooplankton biomass density declined and small bodied zooplankters became more abundant. The community grazing rate declined during the last 20 years. Independently, P increased, N declined and nanoplankton (mostly chlorophytes) was enhanced but zooplankton biomass was too low to control the algal biomass. Zooplankton was predation limited and nanoplankton was therefore nutrient limited.

3.13 LAKE VICTORIA CASE

During the 1950s the piscivore Nile Perch was introduced to the lake. During the 1960s and 1970s the Perch invaded the entire lake, and increased in the early 1980s. The Nile Perch preyed on a major part of the native and endemic haplochromine fishes. More than 50% of their biomass were seston feeders. By eliminating seston consumers organics content was enhanced and its decomposition lowered oxygen content in deep layers. Increase of nutrients (mostly P) inputs started during the 1950s and simultaneously continued with the Nile Perch piscivory. The outcome is advanced eutrophication. The major changes in the ecosystem were: shift from diatoms to cyanophytes dominance, increased algal biomass and primary production, higher fluxes of P and N and decline of silica concentrations (Gophen *et al.* 1994; Hecky 1993).

De Melo *et al.* (1992) reviewed studies on food web manipulation effects on the ecosystem structure. They found that in many cases experimental studies in enclosures, ponds and lakes did not give the predicted results partly because of the compounded effects of other factors not included in treatment combinations. Nevertheless, studies presented in Gulati *et al.* (1990) which were carried out in small and shallow lakes did give predicted results. There is a controversy whether selective fishery or stocking is sufficiently effective to maintain long term changes in lakes. It can be concluded that man induced food web alterations by fish can last a relatively long time if manipulated populations are kept constantly at their modified compositions and densities. The effectiveness of the change is different between large-deep and small-shallow lakes. It is more effective in small water bodies. The effectiveness of the change also depends on nutrient conditions since these two group of factors are combined and integrated.

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CHAPTER 4

MANIPULATION OF FISH POPULATION FOR LAKE RECOVERY FROM EUTROPHICATION IN THE TEMPERATE REGION

Ramesh D. Gulati

4.1 INTRODUCTION

4.1.1 Food-chain, fish and phosphorus

Eutrophication is the primary cause of persistent algal blooms and deterioration of underwater light climate in lakes. Most efforts to alleviate the detrimental and undesirable effects of eutrophication on aquatic systems addressed the problem of nutrient reduction, especially of phosphorus in the inflows (Edmondson & Lehman 1981). Nevertheless, pioneering studies on the role of fish stock and species composition of zooplankton by Hrbácek *et al.* (1961), and subsequently the "size-efficiency" hypothesis based on such works drew attention to the role of fish on size-structuring zooplankton. There is now overwhelming evidence, especially from fresh water lakes, that fish can greatly influence the plankton community structure. Basic research has shown that fish are size-selective zooplankton predators (see in Gophen 1990). The planktivorous fish thus suppress the populations of large-bodied zooplankters by visually foraging on them (Zaret 1980; Lazzaro 1987). Consequently, the small zooplankton species become abundant with an accompanying increase in the phytoplankton populations. When the planktivorous fish are rare, e. g. if predation by piscivorous fish is high, the zooplankton community shifts to larger zooplankton species and small densities of small species are markedly reduced (Brooks & Dodson 1965).

The role of fish in the lake ecosystems can be considered as important in three aspects: a) predation on zooplankton; b) contribution to the nutrient dynamics; and c) resuspension of the bottom sediments. First, through their size-selective predation the planktivorous fish cause greater size-selective mortality of large-bodied grazers which leads to an increase in the smaller-bodied crustaceans and rotifers (Gulati 1990) the grazing of which is restricted to relatively smaller-sized seston particles only so that the grazing pressure on the algae is markedly reduced. This results in the development of increased algal mass. Second, as regards the importance of fish in a lake's nutrient dynamics and thus also in the eutrophication process, the fish metabolism, feeding activities and mortality are important factors. The fish standing crop will, of course, determine the extent of P regeneration by fish, both via the digestive activity and excretion (see in Lazzaro 1987). Data from about 30 lakes >10 ha in Sweden and Denmark show that total-P in these lake systems increases sharply up to 0.1 mg P l^{-1} as the proportion of planktivorous fish (>10 cm) in the total fish (>10 cm) reaches about 80% and the total-P even reaches 1 mg P l^{-1}, or more, if the proportion increases to about 100% (Jeppesen *et al.* 1990a). A multidisciplinary study of the Lake Loosdrecht during its restoration (Van Liere & Gulati 1992) demonstrated two important points. About *ca* 50% of the total particulate-P (≫300 mg P m^{-2}) in different trophic levels is "locked" in fish. The fish daily regenerated 1.4 mg P m^{-2}, which is 140% of the external P-loading (see also in VanLiere & Janse 1992). Meijer *et al.* (1994a) report that reduction of 150 kg ha^{-1} of fish in lake Wolderwijd, as a biomanipulation measure, led to a reduction of P-loading via fish, which was equivalent to 60% of the external loading. Third, the benthivorous fish also directly contribute to nutrient (P) availability for phytoplankton due to their browsing activity in the lake bottom, e.g. bream (*Abramis brama*) in most shallow lakes, by which sediments may get resuspended. Though difficult to quantify, one would expect that the resuspension will bring the mineralized P from the sediments into suspension as well as promote aerobic mineralization of P in open water.

Therefore, the efforts at reducing algal mass in lakes should primarily address the need to control planktivorous fish. In the light of a direct relationship between total-P and planktivorous fish, reduction of the stocks of planktivorous fish is imperative. By contributing to P-flux, fish apparently retard the pace of restoration. So, any steps to reduce phytoplankton abundance in lakes and reservoirs for improving under-water light climate in these waters should be aimed at reducing the stocks of planktivorous fish: firstly, to stimulate development of large-bodied zooplankton, e.g. *Daphnia* spp, to stimulate grazing-induced mortality on a wider size range of phytoplankton (Gulati 1990; Gulati *et al.* 1990) and, secondly, to reduce nutrient inputs via the fish. Such an approach to restore or rehabilitate lakes has been called biomanipulation. In this paper I describe the 'state of art' in the field of lake eutrophication and restoration in the lakes of temperate region particularly in relationships with fish management and fish manipulation in Europe and North America.

4.1.2 Biomanipulation: a lake restoration strategy

The term biomanipulation implies "biological control in lake restoration or improvement in which relatively small changes in biological relations produce favourable changes in a lake" (see e.g. in Edmondson 1991: pages 281-282). Thus, the changes brought in the food web enable the natural processes to take over and help bring about the desired improvements in the water quality. This implies decrease in the rates of primary production and consequently increase in light penetration to deeper water layers. This method is, however, not considered as an alternative to direct reduction of nutrient inputs from the external or internal sources but is a complementary technique. If applied in conjunction with other control measures it will hasten the process of rehabilitation or recovery.

There are perhaps a whole realm of organisms, from bacteria, fungi and algae to fish, manipulation (introduction, reduction or removal) of which can be cited as examples of biomanipulation. Here the biomanipulation concept to lake recovery is restricted to fish management/manipulation measures. The strategy mainly consists of reducing and regulating the impact of planktivorous fish, respectively, through their reduction or removal and introduction of piscivorous fish. The trophic-level response of the lakes to such measures is called top-down or cascading effect within the food-chain (Carpenter *et al.* 1985). The response, triggered by manipulating these fishes, trickles down through zooplankton to the autotrophs, the phytoplankton. Besides, it is perceptible as changes in the nutrient dynamics and the underwater light climate. However, in the food-chain these top-down effects may gradually weaken in the lower trophic levels (McQueen *et al.* 1986). Also, discrepancies arise since fish species, being size-structured, switch from planktivory to benthivory as they grow, e.g. in bream in many Dutch lakes (Lammens *et al.* 1990).

Lake rehabilitation studies are generally primarily aimed at reducing nutrients that cause high rates of phytoplankton primary production (see in Van Liere & Gulati 1992). They, therefore, also imply reducing the production of higher trophic levels, for example, of the planktivorous fish. However, nutrient reductions do not necessarily lead to recovery from eutrophication nor are they necessarily accompanied by quick reductions in fish stocks. The fishes affect both the nutrient dynamics and food web relationships. By contributing to P-flux, they apparently retard the pace of restoration. The planktivorous fish have received more attention than the benthivorous fish, although in shallow lakes the latter are the predominant fish community. Thus, there are two mechanisms by which the fishes affect the ecosystem dynamics. First, the pelagic fish will play a more important role in decimating the population of the larger zooplankton species, especially the large-bodied *Daphnia* species. Also, as mentioned, benthivorous fish, bream (20-30 cm) in shallow eutrophic waters, are known to switch to planktivorous feeding behaviour and may derive a part of their food in this manner. The daphnids are both the most preferred food of fish and most effective grazers of seston. Since they are the most important grazers of the pelagic seston (phytoplankton and detritus), their densities inversely affect the seston concentrations. Secondly, in contrast to the pelagic fish, the benthivorous fish, e.g. bream, are known to continuously stir up the bottom sediments during their foraging activity. They, thus, bring as well the sedimented seston as the nutrients in to resuspension, causing deterioration of the under-water light climate. In this respect, these fish probably play an even more vital role than the pelagic fish in retarding the recovery process. In the temperate regions, there are no known phytoplanktivorous fish which can reduce the seston in suspension, as in the tropical waters (Gophen 1990), and thus improve light climate.

Background information on the status of fisheries, fish-stocks and fish composition is an essential prelude to the decision making for the feasibility of fish manipulation as a restoration measure.

4.2 TEMPERATE FISH COMMUNITIES AND THEIR TROPHIC RELATIONS

Fish communities in the lakes of different geographical areas can be classified on the basis of the frequency of distribution of the more common species. Ryder & Kerr (1990) examined the fish communities in over 2300 lakes in the Ontario region (Canada) and divided them broadly in to: 1) percid community, inhabiting the so-called walleye lakes; and 2) salmonid community with lake trout (*Salvelinus*). However, the species common to the two groups are considered to play a critical role in the process of 'harmonising'. The salmonids inhabit oligotrophic lakes while the percids occupy mesotrophic waterbodies. The trophic difference, though generally reflected in the production rates, is expressed as mean concentration of the limiting nutrient, for example total-P. A P-level of $<10\text{-}20$ mg l^{-1} characterizes oligotrophic lakes that are inhabited by salmonids. But a P-level exceeding this range is found in eutrophic lakes with percids as the predominant community. However, several species are common to both the communities: white sucker (*Catostomus commersoni*), yellow perch (*Perca flavescens*) and, to some extent northern pike (Ryder & Kerr 1990). Such species are likely to have more generalized niches and to be more successful over a wide range of environments.

Lake morphometry and water temperature generally contribute to trophic separation of the fish communities: the oligotrophic lakes are generally deeper and relatively colder than the mesotrophic ones. Some of the large, deep oligotrophic lakes (having salmonids as the main community) with shallow and sheltered bays also provide suitable habitats for percid communities (Ryder 1968). Nevertheless, the fish communities in very large lakes such as the Laurentian Great Lakes and marine ecosystems may be difficult to generalize. This is mainly due to complexities related to the greater openness and lack of barriers to migration/movement in these large lakes, or because of the inherent greater diversity in marine systems.

The fishery resources of inland waters both in Europe and North America are over exploited (Van Densen *et al.* 1990), especially in large productive lakes because of the unrestricted access to commercial fishing. The various fish species are, however, valued differently in the different geographical areas, because of taste and thus in commercial value. The salmonids are preferred to cyprinids fish in northern Europe, but the cyprinids are preferred in central Europe. Also in the countries of the Mediterranean area, in the absence of salmonids, the cyprinids are a preferred fish. A pragmatic management measure for inland fisheries until recently was restocking, to retain harvestable pool of fishes in balance, a dynamic equilibrium between the predator and their prey (Ryder & Kerr 1990). Such a harmony between the relative biomass of the species will be generally reflected in ecosystem stability. However, a balance between the terminal predators, e.g. walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*) as in North American lakes or pike or pikeperch (*Stizostedion lucioperca*) or perch (*Perca fluviatilis*) and their cyprinid prey (bream or other white fish), as in many European lakes, may be difficult to realize, except in the simplified farm ponds or manipulated small waterbodies.

4.3 FISHERY MANAGEMENT AND EUTROPHICATION CONTROL

4.3.1 Influencing factors and strategies

Detailed management plans are necessary in ecosystems in which fishery is either overexploited or the system needs to be rehabilitated from eutrophication, especially to eradicate the undesirable symptoms, usually the persistent algal blooms. The fishery management becomes all the more important if the nutrient reduction or removal has not produced the desired results. Though retaining the natural fish communities may be a very germane approach, it may be rendered unfeasible by the prevailing abiotic conditions or by the exotic fish. Moreover, there may be a clash of interests among the fishery managers, the ecosystem restorers and water quality managers. Fish management for improving the water quality and eutrophication control necessitates implementing several other corrective measures that lie essentially outside the domain of the water-body in question. For example, water level fluctuations, both seasonal and due to draw-downs for power generation, for irrigation and potable water-supplies, especially during the spawning period of fish, will adversely affect the fish stocks. Similarly, the lake morphometry influences: 1) the extent of the lake littoral area as well as its vegetation, and 2) the water temperature and level of oxygen in the pelagial zone and their vertical heterogeneity. These factors will in turn have profound effects on both the fish growth and distribution. Through the fish there will be a cascade effect on the other biotic elements in the food chain. Therefore, inlake corrective measures should always consider the external constraints with regard to the different functions assigned to the system under restoration. Besides, there may be sociopolitical restraints. In short, both the type of fish introduced and production goals envisaged will put demands on the system. These will be reflected in food web interactions encompassing both competition and predation. In addition, food-chain effects which may be adverse for trophic levels other than the fish, will manifest themselves in an increase or a decrease of certain species to undesired levels. Therefore, corrective measures to be taken must consider these factors concurrently.

4.3.2 Food web manipulations: progress, perspectives, types of lake responses

In the last one decade fish and fisheries of several lakes have been manipulated to improve water quality, invariably in conjunction with reduction in nutrient loading (papers in Benndorf 1988; review by Gophen 1990; and papers in Gulati *et al.* 1990). Such studies have contributed to our understanding of the cascading food web effects and their application in lake-recovery.

The assertion of food web biomanipulation, either directly through the management of planktivorous fish-stocks or indirectly through the piscivore addition, is that the effects cascade through the pelagic community to significantly affect the algal standing-stock. Support for the theory comes mainly from the works of Carpenter *et al.* (1985, 1987), Lynch & Shapiro (1980), Shapiro (1980) and the works cited in Gulati *et al.* (1990). Several long-term studies, however, do not show correlations between the planktivore biomass and chlorophyll-*a* (Benndorf *et al.* 1984, 1988), Lehman (1988), McQueen *et al.* (1989) and De Melo *et al.* (1992). Some of these works cast doubts on the statistical relationship between decrease in the abundance of planktivore fish and improvement in light climate since a few extreme lakes, oligotrophic lakes, may considerably influence the general relationships. The analyses done by McQueen and associates are based on stratifiying, north temperate lakes in which order of magnitude changes in planktivore biomass may alter underwater light climate, but long-term changes in phytoplankton biomass, computed from chlorophyll-*a* data, are unlikely. Also several studies on shallow Dutch lakes (Meijer *et al.* 1994 a, b) have indicated that the crux of the problem lies with not only reducing the planktivorous biomass to low levels but also of the benthivorous fish and of sustaining these low levels. Besides, since in these shallow lakes the nutrients are in constant circulation due to mixing, the development of littoral vegetation is crucial to limit nutrient availability to the phytoplankton.

McQueen & Post (1988) derived statistical relationships between total P, chlorophyll and planktivorous fish and piscivorous fish in order to determine the relative importance of nutrient control and food-chain manipultion. They suggested that role of bottom-up effects - relationships between total-P and chlorophyll and between chlorophyll and zooplankton - is strongest near the bottom of the food-chain and weakens at higher trophic levels. In contrast, top-down interactions are strongest at higher levels: piscivorous-fish/planktivorous-fish and planktivorous-fish/zooplankton and that the effects weaken down in the food-chain. From predictions based on the model of McQueen *et al.* (1989) it can be deduced that in the more eutrophic lakes top-down measures become relatively less effectual than the bottom up measures. In such lakes chlorophyll cannot be effectively reduced because larger-sized *Daphnia* populations are inadequately developed. This is because these daphnids do not have refuges against planktivorous fish, predation by which is generally high.

In several cases the failure of the steps was clearly related to a rise in planktivore biomass. The more recent polemics on the efficacy of biomanipulation approach (De Melo *et al.* 1992); Carpenter & Kitchell 1992) has come as note of caution for those planning or engaged in biomanipulation research to examine the prospects more critically. One has to define: 1) the goals more critically; and 2) apply biomanipulation measures in concert with the reduction of nutrients in the lake and in external loadings.

4.3.3 Wholelake Experiments

Shapiro (1990: Tab. 1) summarised some 50 manipulation works on fish in whole waterbodies, all of them in the temperate region, along with the methods used and the effects produced. All these studies were carried out since the classic studies of Hrbăcek *et al.* (1961) on the Elbe back-waters. Also, Benndorf (Benndorf 1988, 1990 and Benndorf *et al.* 1988) cites more than two-dozen studies on the European reservoirs and lakes in Bautzen Reservoir. These are among the classical attempts to restore water-bodies using a food web manipulation approach, in the so-called whole-lake experiments. However, not all the cases of manipulation summaized had the primary aim of improving water quality nor were they all successful. Virtually all cases involved manipulation of fish stock and fish composition. Effects produced in most cases were favourable. The studies provide insight into the role of fish in ecosystem functioning and mechanism causing improved water quality. Benndorf (1990) divides the fish manipulation studies in to four types, which are discussed below with remarks on the relative stability in course of time.

4.3.3.1 Unintentional or natural changes in fish stocks

The changes in fish stocks relate to natural fish kill, and subsequent alterations which may be unstable as in Lake Sobygärd (Jeppeson *et al.* 1988) or changes involving natural, two-year periodicity in roach (*Rutilus rutilus*) recruitment as in Alderfen Broads (Cryer et al 1986). In another case, the changes following the fish kills or high mortality lasted for 1-2 years, e.g. in Lago di Annone (De Bernardi & Giussani 1978). However, in the Queen Elizabeth II reservoir (Duncan 1975) the effect was prolonged over a period of five years as reflected in its low algal biomass and high water transparency which is considered by Duncan (1990) as a general feature of these storage reservoirs. Besides the effect of increased mixing depth of the reservoirs to increase light limitation and to reduce algal growth, the algal growth in spring is curtailed by the grazing impact of large-bodied daphnid populations (*Daphnia magna, D. pulicara & D. hyalina*), especially at concentration >0.2 mg C l^{-1}. The existence of the larger-bodied zooplankters in the reservoirs is supported by the low levels of predation by fish since the late sixties. Based on the populations of ruffe, roach and perch from the littoral area (depth <4 m), the fish density of reservoir is estimated to be around 0.33 fish m^{-2}, assuming absence of the fish in the pelagic part. The fish situation in the Queen Elizabeth II reservoir appears to have had three phases in a 20-year period (1968-1988): 1) 'fish kills' of mainly large-bodied perch in many of the reservoirs during 1966 and 1967 due to a viral epidemic that caused dermal necrosis of the fish; 2) an increasing recruitment of roach and increasing proportion of roach in the fish fauna during 1974-1981; and 3) a mass escape from the cages in to the reservoir of a new predatory fish, the rainbow trout during 1984-1988. Although this was an unintended change in fish fauna, the effect cascaded through the trophic levels and was manifest as increased numbers of daphnids and increased grazing on planktonic algae. Such episodes are quite instructional and add to our knowledge about the importance of fish which can be used in the more deliberate attempts of lake rehabilitation.

4.3.3.2 Manipulation related to fish-stock management

The goals of sport fishery and professional fishery differ. For the former, the aim of active fish-stock management is to enlarge the body-size of the fish, to both maximize and sustain the yield. For example, the ending of commercial gill-net fishery in Lake Tjeukemeer (The Netherlands) in 1977 resulted in marked positive effects on the body size and standing crop of pikeperch - the most important piscivorous predator in the lake (Vijverberg & Van Densen 1984). Before 1977, the pikeperch population consisted of only a few year-classes. But after the catch restrictions in 1977, the reproductive part of the population grew markedly, enhanced by the abundance of O^{+} smelt which served as an ideal food for the pikeperch. In 1982, five years after the measure, the pikeperch had reached a standing stock of about 100 kg ha^{-1}. Such a development would certainly cascade down to the planktivorous fish and contribute positively to subdue their predation intensity on zooplankton. This was revealed by the presence in moderate to large numbers in Lake Tjeukemeer of the large-bodied *Daphnia galeata.* However, no specific follow-up data in this regard exist in Lake Tjeukemeer to corroborate these convictions. The catch restrictions and stocking with both pike and pikeperch were found to be appropriate methods for controlling planktivorous fish to moderate densities in reservoir management (see in Benndorf, 1988 *et al.* 1988). Restocking and protection of piscivores by creating a suitable substrate for development of macrophyte cover have also been attempted, in Schmachter See in the former East Germany (Lampe & Schmidt, 1981). In short, the fish-stock management is a more active approach that may lead to relatively stable situations for varying periods of time.

4.3.3.3 Manipulation for improving water quality

The criterion chosen for the improvement is a discernible or a desired increase in Secchi-disc depth. This strategy has received increasing attention from water quality managers, both as a tool in water quality control and management. In the Netherlands in the last six years several lakes of differing trophy and area have been manipulated (see papers in Van Donk & Gulati 1989; Gulati 1990; Gulati *et al.* 1990). The water managers have gone as far as producing a manual for fish-farmers/sport fishers with a questionnaire relating to *Daphnia* numbers, algal densities, algal blooms, Secchi-disc depth (turbidity) and benthic fish, etc. (Hosper & Meijer, 1993). A score list based on the results of the questionnaire gives indications about the feasibility of carrying out fish manipulation and the estimates of costs. This is perhaps a maiden attempt in this direction. The validity of the guidelines given in the manual has to be tested in long-term studies, realizing that trophic cascades can be very enigmatic. The manual certainly has aroused interest among sport-fishers and managers to scrutinize the problems and prospects of their waterbodies, before deciding on the choice of remedial measures. Undoubtedly, such a manual offers certain basic guidelines, a helping hand rather than tailor-made solution to water quality problems in general.

4.3.3.4 Manipulations with multiple objectives

Most examples of fish manipulation belong to this category. The cases where effects were short-lasting are those of selective fishing for cyprinids as in Lake Trummen (Andersson & Diehl 1988). Hrbácek *et al.* (1986) stocked Hubenov reservoir in Czechoslovakia with brown trout, but roach and perch stocks increased. In some cases the effects were somewhat longer-lasting, 1-2 years. Manipulations involved either selective fishing and stocking with perch (Kazprazak *et al.* 1988), or removal of the cyprinids and restocking with O^+ perch as in Bleiswijkse Zoom (Meijer *et al.* 1990) or with pike fingerlings as in Lake Zwemlust and Lake Wolderwijd (Van Donk *et al.* 1989, 1990 a; Meijer *et al.* 1994 a). Leah *et al.* (1980) stocked one compartment of the Broads at Brunall (UK) with pike leaving a second one untreated for comparison. Also poisoning of a whole fish community and stocking with piscivorous fish (Hrbácek *et al.* 1961) did not produce improvement lasting longer than one or two years.

Benndorf (1990) cites at least four cases in which effects of manipulation were noticeable for longer than three years or so, including his own work in Bautzen reservoir in which stocking of piscivores was coupled with catch restrictions for perch, pike and eel. The effects produced lasted more than five years as indicated by the improvement in Secchi-disc transparency (see further under case studies).

4.4 CASE STUDIES

Several lakes in North America and northern Europe were restored in the last decade or are under restoration. In many cases lake manipulation was used either as a complementary or as a sole measure to improve water quality (see in Cooke *et al.* 1986, 1993; and Gulati *et al.* 1990; Benndorf 1988; Mortensen *et al.* 1994). Some representative cases in which biomanipulation was used are briefly described.

4.4.1 North American lakes

Lake Washington. Lake Washington has a long and well-documented case history of nutrient reduction and subsequent improvement in the water quality (Edmondson & Litt 1982: Lehman 1988). The 'return' of *Daphnia* sp. (*D. pulicaria*) and the improved light climate in the lake are associated with the decrease of *Oscillatoria* spp, *O. rubescens* and *O. agardhii.* But preceding the decline in cyanobacterial densities between 1968 and 1976, other interesting events occurred. Between 1962 and 1967 *Neomysis mercedes,* the opossum shrimp, which predates on *Daphnia,* decreased by about 90% in its densities because of increase in abundance of longfin smelt (*Spirinchus thaleichthys*). That the decrease in *Neomysis* contributed to the resurgence of Daphnia was investigated and confirmed by intensive studies (Edmondson 1991: page 42). However, it was only in 1976 that the *Daphnia* numbers really increased. An examination of phytoplankton records showed a progressive decrease in the *Oscillatoria* sp. between 1968 and 1976. Thus, the delayed reappearance of *Daphnia* was caused by food conditions. Edmondson & Abella (1988) attributed the increase in smelt to improved conditions for reproduction due to a revetment construction in the Ceder River, a source of supply to Lake Washington. Therefore, though the nutrient reduction and hydrological factors did play complementary roles, a trophic cascade was most likely involved in reducing the algal biomass and water quality improvements and its sustenance.

Lake Michigan. Cooke *et al.* (1993) cite several studies dealing with the biomanipulation of Lake Michigan. Both intensive commercial fishery earlier in the nineties and the invasion of sea lamprey (*Petromyzon marinus*) into the lake, caused a decrease in the density of the lake's top piscivore, the lake trout (*Salvelinus namaycush*). This led to an increase of planktivorous fish during the mid-fifties, especially the alewife (*Alosa pseudoharengus*). Size-selective feeding by alewife caused the zooplankton to shift to small-sized species. This resulted in reduced grazing intensity and increase in the algal mass, which led to decreased light penetration in the lake. These trophic alterations were accompanied by a steady increase in nutrient inputs to the lake. The fishery management measures included stocking and maintenance of the Pacific salmon populations. In the early 1980s alewife biomass had decreased apparently due to increased piscivory. Reappearance of large-sized zooplankton-especially, *Daphnia pulicaria,* was new to the lake. The dominance of the daphnids in the subsequent few years led to a very significant improvement in water quality. Between 1960 and early 1980s the Secchi-depth has increased more than three-fold, from 5 m to 15 m. Also, an accompanying shift in the phytoplankton species to small flagellates occurred. Though the roles of the nutrient control measures and food web measures are difficult to quantify, most probably the latter mainly caused the observed improvement in underwater light-climate. However, starting in 1985 the *D. pulicaria* declined in numbers under intensive predation pressure of planktivorous fish, especially of bloater chub (*Coregonus hogi*). This nullified some of the observed improvements in the Secchi-depth transparency. The zooplankton grazing apparently was no match to the phytoplankton growth rates. It had only a small influence on the algal mass which was reduced both in 1983 and in 1987, the years with very different densities of *D. pulicaria* (Lehman 1988). Evans (1990) who reanalysed the evidence based on the earlier observations casts doubts on the success of the top-down management measures in large and ecologically complex systems like Lake Michigan and the other Great lakes, and goes on to say that such management strategies may be more appropriate in smaller and moderately eutrophic lakes. Apparently, the noticeable foodweb effects are related to decrease in P loading of the lake since 1972 when the control measures were initiated. But it is not clear from the studies if the lake is still going through a food web change, or if the short-term changes observed are, indeed, in direct response to food web manipulations.

Peter, Paul and Tuesday lakes. Carpenter and co-workers (Carpenter *et al.,* 1985, 1987; Elser & Carpenter, 1988; see also in Cooke *et al.* 1993) carried out intensive experimental work on these three small (<2.5 ha) and deep (5-10 m) lakes in

Michigan. Whereas both Peter and Paul lakes had large populations of piscivore, the largemouth bass, they lacked planktivores. Tuesday lake had a substantial population of planktivorous minnows; all lakes had *Chaoborus*. In 1985, a reciprocal exchange of fish was effected in Peter and Tuesday lakes. The piscivore bass from the Peter Lake were exchanged with minnows in the Tuesday Lake. Paul Lake was used as a reference. Subsequently, the domination of Lake Tuesday by large-sized *Daphnia pulex* and increase in density of *Chaoborus sp* but decrease of phytoplankton were consistent with the predictions. The response to the manipulation was more complex in Peter Lake: though phytoplankton biomass and productivity were likely to increase because of predation by planktivores (minnows) on daphnids, the mechanism differed. The young-of-the-year (YOY) bass that had escaped removal from the Peter Lake preyed on the minnows which were 'driven' to littoral to escape predation. Thus, in Peter Lake the bass that escaped transfer - rather than the minnows - caused the decline of zooplankton, particularly *D. pulex*. Consequently, the primary productivity increased. On the other hand, in the Tuesday Lake *D. pulex* became dominant, *Chaoborus* population increased and small zooplankters (rotifers) were reduced following the removal of minnows. The decrease of planktivory and increase of herbivory led to dramatic decreases of phytoplankton, specially flagellates, and phytoplankton primary production. Despite the failure to completely remove bass from Peter Lake, the study on these lakes demonstrates both the complexity of food webs and the importance of piscivores in food web structure.

Other N. American lakes. In Lake George (Ontario, Canada), a small waterbody (10.6 ha; max. depth 16.2 m) fish/zooplankton experiments were carried out in enclosures by McQueen and co-workers (McQueen & Post 1988: Post & McQueen 1987; McQueen *et al.* 1989). These studies also benefited from observations on the effects of winter kill in 1981-1982 that eliminated *ca* three-quarters of the largemouth bass population. The study extended for six years and included the period in which the piscivores and planktivores re-established. In the enclosure experiments, as expected, a strong top-down effect was detected. However, the effect was strongest near the top. Also when the daphnids were large (>1 mm), all the variability in the total-P/chlorophyll-*a* regression could be explained by zooplankton grazing. Similarly, almost all the variability in the chlorophyll-*a*/zooplankton regressions was explained by the planktivorous biomass and predatory mortality of *Daphnia.*

The winter kill provided an opportunity to compare some of the enclosure work with the lake data (1980-1986). As predicted from the enclosure work, a strong cascade: *piscivores → planktivore → zooplankton* was noted. But the final link in the cascade, *viz* zooplankton → chlorophyll, was found lacking. The chlorophyll-*a* concentration as predicted from the enclosure study was correlated with total-P. McQueen *et al.* (1989) suggested that bottom-up processes (resource availability) are the long-term processes which, in fact, determine the trophic-level biomass and the short-term ones - the cascades - the 'realized biomass'.

4.4.2 European lakes

Danish lakes. Effects of both short-term and long-term manipulation in shallow, eutrophic lakes in Denmark have been evaluated by Jeppesen *et al.* (1990a, b). They used empirical data on total-P, phytoplankton, submerged macrophytes and fish and examined the data sets in the light of the results from whole-lake fish manipulation experiments. After about 80% removal of the planktivorous fish, trophic cascade were studied in three lakes. In Lake Vaeng, which is relatively much less eutrophic than the other biomanipulated lakes in Denmark, a 50% removal of planktivorous fish caused marked improvement in the transparency. Important causal factor for this was a seven-fold increase of zooplankton biomass in the first year, specially of *Daphnia* and *Bosmina sp.*, and a shift in the dominance from rotifers to cladocerans. These changes produced a marked reduction (*ca* 50%) in the mean phytoplankton biomass in the first year as well as a shift in the dominance from cyanobacteria and small diatoms to larger diatoms and green-algae and cryptophycean forms. The improved light climate contributed mainly to an increase in abundance of submerged macrophytes (*Potamogeton crispus* and *Elodea canadensis*). The internal P-loading was reduced markedly and total-P concentration in the lake decreased. In Frederiksborg Castle Lake, the planktivorous fish biomass was reduced by nearly 80% to about 80 kg ha^{-1}. About 15 kg ha^{-1} perch *Perca fluviatilis* was stocked. In contrast to Lake Vaeng, only minor changes were observed in Frederiksborg Castle Lake, which is eutrophic and dominated by cyanobacteria. In hypertrophic Lake Sϕbygärd, dominated by green-algae, a 16% reduction in planktivorous fish led to notable alterations in trophic structure: a 40-60 fold increase in the biomass of filter-feeding cladocerans (*D. longispina* and *B. longirostris*) over a three-year period. Nevertheless, the total-P level in the water column did not decrease. In addition, marked trophy-related differences were observed in these lakes in the ratio of >10 cm planktivorous fish to >10 cm piscivorous fish. In Lake Sϕbygärd no changes occurred in the ratio after the reduction of roach and rudd. In Lake Frederiksborg Castle (Riemann *et al.* 1990) the changes in the proportion of the two fish types were only minor. In the relatively least eutrophic Lake Vaeng the proportion of planktivorous fish >10 cm declined drastically - from 99% before the manipulation to ca 14% three years later. This differences in response were related to the total-P concentrations in the lakes.

Jeppesen *et al.* (1990 b: Fig. 4.4) developed the *threshold hypothesis*, based on the empirical regression relationship between the ratio of the numbers of planktivore >10 cm to the total fish >10 cm (planktivores and piscivores) as the dependent variable and mean total-P (May-Sept.) as the independent variable. This relationship is based on data from 30 lakes, all >10 ha in area. The main generalization from the regression model is that a critical relationship exists around the total-P concentration of 100-200 µg P l^{-1} and the fish ratio of 0.8 or 0.9. A decrease in the P level at this point leads to a precipitous decrease in the fish ratio. An important implication of this is that total-P should be reduced to below the 100 µg l^{-1} level to ensure a reduction in the ratio of planktivorous fish to total fish below 0.8. In other words, the proportion of the piscivores increases. This is interesting in that the top-down approach when complemented with the bottom-up strategy to accelerate the process of recovery. The P reduction can occur in two ways: first, indirectly by the top-down approach - the planktivore reduction as such and second, by direct reduction of the P-load. This latter operates as follows: *P-reduction → decreased algal biomass → improved transparency → more macrophytes → more piscivores.* From this point the top-down effects will effectively 'take over' so that the fish-management measures are likely to produce the desired changes in the water quality.

No response implies that neither the macrophytes will develop in shallow areas nor will the Secchi-disc transparency increase to >0.6 m depth. Apparently, in such cases the removal of planktivorous fish from lakes with high P-levels is not compensated by an increase in proportion of piscivores. Instead, there is seemingly an increased recruitment in such lakes of the planktivores, caused probably by an improved food supply. This short-term successes or failures of the measures applied plead for continuous management (removal) of planktivorous fish or re-stocking of piscivores, or perhaps both. However, a feasibility of such steps is questionable considering the exorbitant costs of fish removal/stocking, more so in large and deep lakes. Lastly, the studies on Danish lakes suggest that long-term success of measures will depend on: 1) the establishment of submerged macrophytes which generally do not develop if P is not reduced to well below

200 µg $^{-1}$; and 2) that ability of lakes to develop "self perpetuating increases in the ratio of piscivorous to planktivorous fish" is related to P level, i.e. only if the P level is reduced to below 100 µg l $^{-1}$ will the ratio switch in favour of piscivorous fish.

Norwegian lakes. In Norway, biomanipulation has been carried out with two main objectives: as a complementary measure to reduce algal biomass (see papers in Lyche *et al.* 1990; and Sanni & Wævågen 1990) and to improve sport fishery (Langeland 1990). Lyche *et al.* (1990) and Sanni & Wævågen (1990) have described three cases (lakes Gjersjoen, Helgetjern & Mosvatnet) of lake biomanipulation. All these are lakes are small (<2.7 km^2) but vary greatly in their maximum depths: from 3.2 m in Mosvatnet to 64 m in Gjersjoen. The magnitude of response was reflected in the intensity of the manipulation measures used. Two of them, Lake Helgetjern (area 0.12 km^2; depth 3.5 m) and Lake Mosvatnet (area 0.46 km^2; depth 3.2 m) were rotenone-treated to remove the planktivores. Both lakes showed dramatic responses to the drastic measure. In Helgetjern the phytoplankton decreased by an order of magnitude in the year following the rotenone treatment. A year later the zooplankton biomass doubled, with *D. pulex* and *D. longispina* forming 90% of the zooplankton biomass. This was probably also partly due to hatching of epihippia added in the preceding autumn to the lake. However, with the increase in the roach density 'the response trajectory of phytoplankton versus zooplankton carbon shows large fluctuations' (Lyche *et al.* 1990). In Lake Mosvatnet, the phytoplankton decrease, based on chlorophyll was more than three-fold. The cyanobacterial densities decreased too. There was both a five-fold increase in the biomass of *D. galeata* and a doubling of the individual weight of this daphnid. Though grazing rates were not measured the studies imply high clearance rates (30-50% d^{-1}) by *Daphnia* population. The Secchi-depth increased to >2.3 m (bottom visibility). Though presumptuous, the observed decrease in total-P concentration may be related to increased sedimentation of detritus originating from *Daphnia* egestion and gelatinous algae which probably sank faster. But it may be remarked that what appears to be a decrease in total-P may be partly due to a trophic shift of total-P to zooplankton which many workers do not include in the total-P determinations. The large, deep and mesotrophic lake Gjersjoen, was stocked with piscivorous fish, the pikeperch, after the density of planktivorous fish (roach) was reduced by about 80-90%. The lake showed a more moderate response, with the daphnids (*D. cristata*) showing an increase only five years after the roach reduction, even though the mean daphnid size had considerably increased shortly after the fish manipulations. Lyche *et al.* (1990) conclude under conditions of P-limitation the increased zooplankton grazing can decrease algal biomass through two separate mechanisms: one, reduction of the P-pool in the phytoplankton and, second, reduction of the internal C: P ratio in the phytoplankton cells.

Langeland, 1990, has summarized several case in which manipulation was used to improve sport fishery rather than water quality. Use of rotenone to eliminate fish in Lake Haugatjern, a eutrophic waterbody (Reinertsen *et al.* 1989) led to dramatic decrease (80%) of algal biomass and cyanobacteria dominance. The changes were attributed to daphnids which increased both in numbers and mean individual size. General conclusion from studies on the lakes of varying trophy was: up to three-fold increase in Secchi-disc transparency accompanying a substantial decrease in phytoplankton biomass and production (Olsen 1989: Olsen & Vadstein 1989: cited in Langeland 1990). The recommended criteria, evolved from the studies are expressed as "water cleansing efficiency" (Langeland 1990: Tab. 2). A high efficiency envisages small and fast-growing algae and gelatinous greens with a P/B ratio of > 0.3 d^{-1} and a C/P ratio of $<70:1$ for the algal biomass produced; algae to zooplankton biomass ratio of <3; large-bodied zooplankters with mean daphnid length of >1.2 mm; and fish with trout, pike, pikeperch as the main fish and biomass of planktivorous fish not exceeding 30 kg ha^{-1}. Nonetheless, these are only suggested criteria determining ecological status for desired water quality. Their validity in lakes of differing trophic status and loading rates has not been tested.

German Lakes. Among the first and most well known study in lake biomanipulation in Germany is the work of Benndorf (1987, 1988a, b, 1990) on Bautzen reservoir (area 553 ha: Z_m 7.4 m). The pike which was abundant in the reservoir after its impoundment in 1974-1975, declined due to intensive angling. Consequently, planktivorous fish, perch, belonging to the year-class 1977 became abundant. Starting in 1977, except in 1978, 1979, and 1983, pikeperch (*Stizostedion lucioperca*) fingerlings were introduced yearly in to the reservoir in autumn. In addition, the maximum number of piscivores caught daily and the minimum catch size (60 cm) were restricted. The predation pressure of piscivores reduced the abundance of zooplanktivorous fish, mainly small perch, but without restricting its larger, piscivore age classes. This was apparently the key factor controlling the young-of-the-year of all fish. Already in 1980 the biomass of the most important filter-feeding cladoceran, *Daphnia galeata,* increased three-fold and the mean individual body-size of the herbivore crustaceans doubled as well. A strong initial increase of invertebrate predators, *Chaoborus flavicans* and *Leptodora kindtii*, was controlled by moderate densities of the remaining planktivorous fish. Larger-bodied daphnids were effective in inflicting high grazing mortality on phytoplankton. Consequently, there was an extended clear-water phase with the annual maximum of Secchi-disc depth ranging between 4 and 9 m during the summer periods of 1981-1988 - an increase of about 40% in the manipulation period excluding the years with low water-level. Significantly, the mean and maximum biomass levels of phytoplankton were, except in 1984, higher during the manipulation period than in the period before. This is probably caused by a major shift in the species composition of algae resulting in the dominance of Microcystis, in response to intensive grazing pressure of zooplankton. Also net retention in the reservoir of the incoming P decreased because the external loading rates increased. According to Benndorf (1990), "some responses of the ecosystem to the biomanipulation revealed remarkable instability which cannot be attributed to year-to-year variations in the fish communities". Benndorf attributes these instabilities to strong fluctuations in the invertebrate predators as well as to summer phytoplankton and further concludes that by a proper management of the piscivore stocks, abundance of zooplanktivores can be kept low, though a fast reduction of O^+ fish when recruitment is strong, because of the improved food conditions, is a key problem which needs more attention in the biomanipulation works.

Dutch lakes. The eutrophication of Dutch lakes, the majority of which are shallow (1-2 m), has resulted in deterioration of the under-water light climate (Secchi-disc depth, 30-50 cm), marked increase in densities of cyanobacteria and a virtual disappearance of submerged macrophytes. The fish species composition shifted from predominantly roach, rudd, tench, perch, and pike to that of bream and pikeperch (Lammens 1989). The fish standing crop in the lakes is generally very high (200-1000 kg ha^{-1}), in which the planktivore and benthivore, especially bream, dominate. The success of bream is attributed to: one, its laterally compressed body-form and protruding back, especially as the fish grows in size; second, to its delayed maturity and larger size at maturity than the other cyprinids. These factors make the fish much less prone to predatory mortality. Thus, large bream (20 cm) coexists with pikeperch and as well partly shares with it the pelagic food. Both cladocerans and copepods form the main prey of the bream until it becomes about 25 cm long. Thereafter, they are primarily benthivorous and the chironomids form 50% or more of its food menu but can switch to column feeding mode, capturing pelagic animal. In contrast, other planktivorous fish (roach and white bream) measuring >15 cm can hardly feed on cladocerans which are too small to be retained on the gill rakers. Since the lakes differ markedly in size-class distribution of bream, predation pressure by bream also differs considerably so that composition and densities of preferred prey, mainly daphnids, can vary considerably from lake to lake. Thus, in many of these eutrophicated lakes, the increase in bream standing crop and disappearance of large-sized zooplankters, *Daphnia* spp, have gone hand in hand. Moreover, bream >25 cm, as mentioned, switches to benthivorous diet. It stirs up bottom material and thus contributes to increase in turbidity of water. These lakes are characterized by the dominance of cyanobacteria, especially *Oscillatoria* spp (50-100*10^3 filaments ml^{-1}) and chlorophyll-*a* levels of up to 300 µg l^{-1} are reached.

Measures involving P-reduction by sediment removal, flushing and by precipitation were invariably unsuccessful (Van Liere & Gulati 1992). Additional measures envisaged a manipulation of planktivorous fish (Gulati 1989, 1990; Gulati *et al.* 1990; Meijer *et al.* 1990; Meijer *et al.* 1994 a, b; Van Donk & Gulati 1989; Van Donk *et al.* 1990 a, b; Hosper & Meijer 1993). Food-web manipulation has since 1987 been attempted in more than a dozen shallow, eutrophic water bodies ranging greatly in size (1-2700 ha). Among these, in three lakes, Lake Zwemlust, Lake Breukeleveen and Lake Wolderwijd, response to food web measures at different trophic levels was simultaneously investigated. The salient features of the studies are described here.

Lake Zwemlust (area, 1.5 ha; Z_m, 1.5 m) had recurrent blooms of *Microcystis* and very high standing stock of fish (ca 1000 kg ha^{-1}), mainly planktivorous fish (bream), up to March 1987 when it was biomanipulated. The fish was completely removed using different capture methods simultaneously with a complete emptying of the lake. The lake got refilled by seepage water in a few days and was stocked with pike and rudd. Together with fish, *Daphnia magna* and *D. galeata* were introduced. Seedlings of *Chara* sp and rhizomes of *Nuphar lutea* were planted along the shoreline and refuges daphnids and spawning area for pike were created by fixing stacks of willow twigs to the lake bottom. Despite high nutrient loadings (2.4 g P m^{-2} y^{-1} and 9.6 g N m^{-2} y^{-1}) *via* underground seepage water from a nearby river and precipitation (Van Donk *et al.* 1993) and development in the early spring period of high algal standing crop, Secchi-disc depth transparency improved considerably, reaching up to lake bottom (± 2.0 m) from late spring through summer, except in 1991. This was caused by high grazing rates of crustaceans on seston (Gulati 1990) as well as by macrophyte abundance (Ozimek *et al.* 1990), which caused severe nitrogen limitation of phytoplankton. Fish standing crop, predominantly rudd, increased from about 50 kg ha^{-1} in 1988 to 300 kg ha^{-1} in 1992. However, besides predating on zooplankton rudd also exploited alternate food resource, the submerged macrophytes (Van Donk *et al.* in press). In 1991, rudd was estimated to have consumed *ca* 40% of maximum macrophyte biomass, implying a reduced predation of planktivorous fish on zooplankton. Thus, rudd is probably both a suitable and desired replacement for bream. Since rudd appears to prefer *Elodea* to *Ceratophyllum,* a change in the dominance to the latter is likely. But longer-term studies should show if some of the positive effects of biomanipulation will be mitigated or maintained.

Lake Breukeleveen (area 180 ha; Z_m, 1.5 m) is one of the Loosdrecht lakes under restoration, since 1984, by reduction of P in the inflows. Nevertheless, up to 1990 seston concentrations, dominated by filamentous cyanobacteria, did not decline, nor did the light climate improve. Zooplankton was dominated by small-sized daphnids (*D. cucullata*) and bosminids (*B. longiristris, B. coregoni*) and rotifers. The lake was biomanipulated in March 1989 by a 60% reduction of the fish standing crop of ca 150 kg ha^{-1} by seining. It was restocked with 400 ind ha^{-1} of pike fry (2-3 cm) as well as 'inoculated' with roughly 12 ind m^{-3} of large-bodied *Daphnia* spp (*pulex, galeata*) (Van Donk *et al.* 1990b). No improvement was observed in the transparency of water during the subsequent summer period. But within six months after the fish reduction the fish standing crop increased to a level as high as before the fish reduction. Surprisingly, this increase was 4-5 times higher than that expected from the growth of the fish alone. This can only be partly ascribed to rapid growth of the bream on its reduction. Moreover, the invertebrate predators (*Leptodora kindtii*) seemingly caused a massive daphnid mortality. In addition, since the lake is open to prevailing winds, continuous sediment resuspension and wave action prevented the light climate to improve and macrophytes to establish. It is obscure if the reduction of fish standing stock in Lake Breukeleveen was ineffective or if the migration of fish via the sluices from the neighbouring lakes contributed to the failure of the measure.

Lake Wolderwijd is the largest (area 2700 ha; depth range 0.5-2.5 m and Z_m 1.5 m) of the lakes biomanipulated in the Netherlands. Between November 1990 and June 1991, the initial fish-stock (mainly bream, and roach) of 200 kg ha^{-1} was reduced to *ca* 45 kg ha^{-1} by seine netting, trawls and fykes (Meijer *et al.* 1994a). In May 1991, 600,000 specimens of pike fry were introduced in the littoral region to control young-of-the-year planktivores. In a few weeks, chlorophyll concentration decreased to extremely low levels (5 µg l^{-1}) and concomitantly the

Secchi-disc depth increased to 1.8 m, and remained high for five weeks. The values observed are the highest in two decades. These changes were triggered by high community grazing of zooplankton (76-100% d^{-1}) of crustaceans, in which *Daphnia galeata* (300 ind l^{-1}) was the most important (Gulati *et al.* 1993). However, the *Daphnia* population collapsed at the end of June and seston mass rose causing a sharp decrease in Secchi-depth transparency. Fecundity data in mid-summer indicate that the decline of *Daphnia* was probably caused by predation rather than food. Interestingly, compared with preceding years, densities of *Neomysis integer*, the mysid shrimp in summer (400 ind m^{-2}) were ten times higher than in preceding summer. Thus, mysids probably also contributed to the heavy daphnid mortality, but also bream and roach contributed to this. In contrast to the smaller lakes, the ratio of area with a macrophytes cover to area of the open water in Lake Wolderwijd was much lower. The pike population did not develop most likely because of inadequate vegetation. In 1992, the "clearwater phase" lasted for only three weeks and Secchi-disc depth did not exceed 1.2 m. In 1993, the lake reverted to the pre-manipulation phase. However, in the areas colonized by *Chara* and other macro-vegetation, transparency has remained higher after the measures than in the more inshore areas. Future monitoring will show if perch will control the mass development of *Neomysis*, and 2) if increase in predation on zooplanktors by O^+ planktivorous fish will be curbed by an 'optimal' development of perch stock. That the pike has failed to establish only confirmed the observation on other lakes.

4.5 CONCLUDING REMARKS

The studies dealing with top-down control in the food web in the last one decade or so have not provided any tailor-made solutions for a reduction of algal biomass and sustainable improvement in light climate. Nevertheless, it has become abundantly clear that, quite analogous to the measures for reducing phosphorus, fish manipulation is an indispensable, complementary technique if the goal is to obtain improved under-water light climate. The fish affect both the nutrient dynamics and food web relationships.

The studies both in Europe (e.g. Benndorf 1990; Meijer *et al.* 1994 a, b) and North America (Edmondson & Abella 1988) show that fish removal may lead to increased densities of invertebrate zooplankton predators (*Chaoborus, Neomysis,* or *Leptodora*). Therefore, a complete removal of the planktivorous fish will not *per se* lead to optimal conditions for daphnids to establish and stabilize. On the other hand, if the biomass of planktivorous fish exceeds a certain critical level the larger crustacean herbivores will not be able to dominate, nor regulate phytoplankton densities and biomass. Standing stock of O^+ fish below which larger-bodied *Daphnia* can develop well apparently varies between 20 and 50 kg ha^{-1} (see references in Benndorf 1990). But there are cases in which *Daphnia galeata* was not decimated at much higher fish biomass levels, e.g. smelt (*Osmerus eperlanus*) in Lake Tjeukemeer (Lammens *et al.* 1985), or rudd in Lake Zwemlust, with a standing stock of 300 kg ha^{-1}. In the latter case there is evidence that predation pressure on daphnids, as mentioned in this paper, was markedly reduced due to the rudd switching to macrophytes (*Elodea* sp.) as an alternate food resource. Besides the alternative food resources, the availability of refuges for zooplankters will increase upper critical level of fish standing stock. Therefore, in addition to size, the species composition and abundance of fish, the existence of refuges will determine the chance of larger-bodied *Daphnia* to withstand the predation pressure of fish. Important here is also the densities of *Daphnia* needed to effectually regulate the phytoplankton densities in these lakes. Based on zooplankton grazing data and Daphnia numbers in the manipulated Dutch lakes, Gulati (1990) computed densities of the larger daphnids to vary between 35 and 60 ind. l^{-1} for a 25% d^{-1} removal of seston mass, roughly the level to sustain the clear-water phase initiated by the grazers in spring.

We know that shallow lakes respond generally more rapidly to biomanipulation, more so when concentration of total-P does not exceed 50 µg l^{-1} (Lammens *et al.* 1990). There are, however, exceptions to this. For instance, in Lake Zwemlust total-P was always >1.0 mg l^{-1} and yet the biomanipulation measure was successful for several years (Van Donk *et al.* 1990a). Benndorf (1990) derived from long-term, whole-lake studies a *biomanipulation efficiency threshold*-of P-loading of *ca* 0.6 g total P m^{-2} y^{-1}, below which the top-down effects are positive. Though this value is not a universal yardstick to guarantee success, it does, however, imply that bottom-up measures aimed at P-reduction will only increase the chances of success, especially if this threshold level is not exceeded. But such threshold concentrations of total-P will become more meaningful in predicting the success of planned measures should they take in to account the sources and sinks of P in the system, viz the dynamics of P reserves in the macrophytes and fish, which most likely serve both as a store but also as a source of supply of P. Surprisingly, what has hitherto not been attempted is the classical *fish-farm approach* of an equitable balance between the nutrients inputs and their harvesting as biota, the fish biomass. This is apparently a very sustainable and economically viable approach for at least the small shallow lakes.

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CHAPTER 5

MANAGEMENT OF EUTROPHICATION OF LAKES TO ENHANCE FISH PRODUCTION[1]

Péter Bíró

5.1 INTRODUCTION

Eutrophic and especially hypertrophic ecosystems are disturbed and unstable. They include lakes, reservoirs and ponds which develop noxious algal and bacterial blooms and which experience extreme fluctuations in water quality and productivity on a diurnal and seasonal scale. This results in production of gases, off-flavours and toxic substances. They undergo periods of oxygen depletion which results in massive fish kills. Hypertrophic lakes are in fact the ultimate state of eutrophication. Whole systems may collapse in an ecological catastrophe (Barica 1980; van Nguyen & Wood 1979).

"Natural" (lakes) and "artificial" (reservoirs, fertilized fish-ponds) eutrophication is in general favourable for enhanced fish production. The most simple and most universal idea concerning counteracting eutrophication assumes intensive fishery management, that is high production and high catches, leading to the removal of nutrients when the fish are removed (Opuszynski 1980). But fishery management practices vary widely according to the structure and functioning of the habitats, and to the fish carrying capacity and exploitation (Bíró 1993 a, b).

5.2 ECOLOGICAL CHARACTERISTICS OF NATURAL AND ARTIFICIAL WATERS

Because of the high diversity of natural lakes and artificial water bodies (reservoirs, man-made lakes or ponds, rice fields, etc.,) it is difficult to give a general characterization of physical, chemical and biological processes.

Taub (1984) has shown that in natural lakes the major chemical and energy trans-

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[1] Substantial sections of this chapter have been taken from another review of management of the pond ecosystems and trophic webs by the same author (Bíro 1993b).

fers have been organized by inputs, internal lake processes, and outputs. The **inputs** include climatic energy transfers of solar energy and wind, and chemical inputs of precipitation and terrestrial contribution. The **internal lake processes** include mass water movements, biological transformation, and chemical precipitation. The **outputs** include river outflow, fish harvests and insect emergence. According to these characteristics, the lakes vary considerably and respond differently in the function of their trophic state (Oláh 1980).

Any ecosystem may be analyzed from the functional point of view in terms of the following (Overbeck 1989), which are of crucial importance in managing the eutrophication for increased fish production: 1) energy circuits; 2) nutrient cycles; 3) distribution pattern and productivity of the organisms in space and time; 4) food chains (grazing food chain and detritus food chain); 5) control (cybernetics, regulation of metabolism).

There are three major categories of eutrophic/hypertrophic ecosystems (Barica 1980):

1) Lakes and reservoirs with high and uncontrolled nutrient input;
2) Fertilized aquaculture systems including fish ponds being used for maximum organic production of fish and shellfish;
3) Sewage purification systems including sewage lagoons and stabilization ponds.

The main characteristics of eutrophic and hypertrophic waters are:

1) Shallowness, limited water circulation, lack of stratification, re-suspension of sediments, minimal water exchange, long retention time;

2) Unbalanced nutrient and oxygen regimes. Periods of oxygen supersaturation ($<300\%$) are often followed by oxygen depletion or total anoxia. External loading of nutrients from diffuse sources is many times higher than that of point sources. Internal loading of nutrients can exceed the external load in relation to redox conditions at the mud-water interface and pH regime. N:P ratios are generally low in eutrophic and hypertrophic waters. In an advanced state, self-accelerated eutrophication through positive feedback mechanisms of anaerobic phosphate release often occurs, considerably reducing the turnover time of dissolved phosphate (for a few minutes) in the P-budget of the lakes (Bíró 1984; Oláh 1975; Oláh 1978). Extremely high, fluctuating productivity when daily rates of primary productivity as high as 5.8 g C m^{-2} day^{-1} followed by respiration only as a result of

algal bloom collapses and decomposition (Barica 1975). Ecological stability is low. Secondary production is usually dominated by benthic macroinvertebrates but zooplankton is less abundant. This short-cut in the food chain is a result of non-grazeable filamentous algae. Fast growth rate and high fish production up to several tons ha^{-1} year^{-1} in fish ponds. Mass mortalities often occur (Barica 1980).

As trophic state advances, the number of species decreases and remarkable shifts in species composition and their ecological niches occur (Colby *et al.* 1972; Leach *et al.* 1977; Hartmann 1977) (Fig. 5.1). Primary productivity maxima of different waters in the northern hemisphere vary from 4,000 to 253,000 kJ m^{-2} yr^{-1} and in the southern hemisphere from 7,600 to 84,000 kJ m^{-2} yr^{-1}. Fish productivity or yield in the northern hemisphere ranges between 5 and 3,000 kJ m^{-2} yr^{-1} (in intensively managed tropical fish-ponds it may be much higher; Sinha & Oláh 1982), and in the southern hemisphere (Antarctic waters) it is <50 kJ m^{-2} yr^{-1} (no other data is available) (Bíró 1993 b).

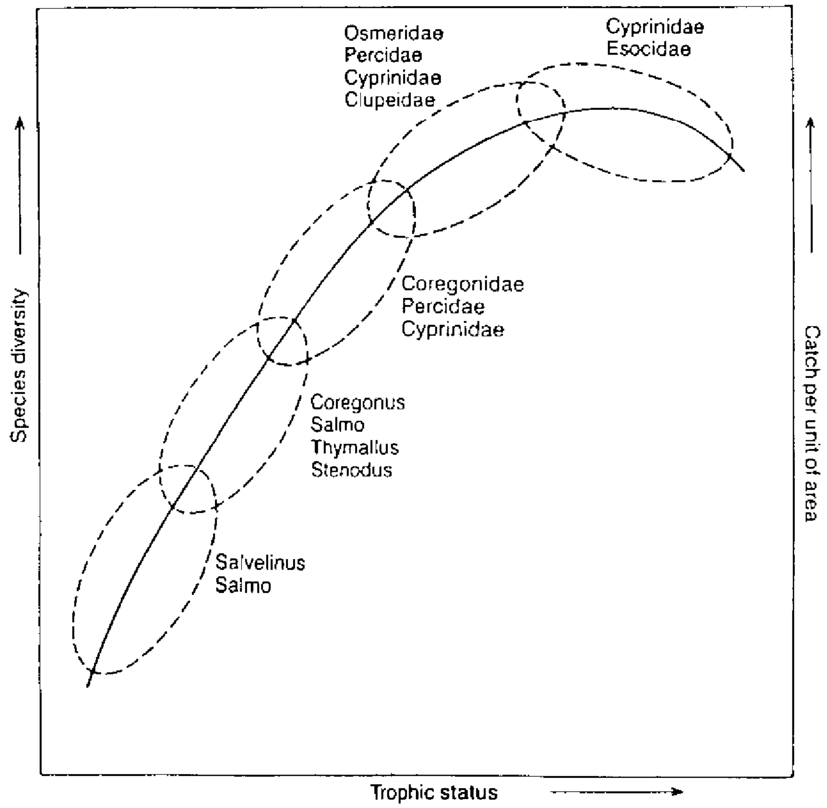

Fig. 5.1 Relationship between the trophic status of a lake and the fish community structure (after Colby *et al.* 1977).

Because lakes in different parts of the globe have been used for different purposes (drinking water supply, recreation, sports, commercial and sport fisheries, etc.), they are "buffer zones" of various interests. In this context, the best fisheries management should take into consideration all of these points (usually not possible) and should be based on the current productive as well as fish carrying capacity of the water. This allows an optimal exploitation strategy of fish resources of natural lakes.

5.3 ECOLOGICAL BACKGROUND OF FISH PRODUCTION

Fish production in lakes depends upon natural productivity that has been influenced by abiotic and biotic factors. Food webs exhibit channels of energy-flow of the lake systems, and the efficiency of energy transfer from primary producers to fish varies widely in the function of the above factors. Exchange of nutrients in the water-sediment interface is the governing factor of fish productivity, because sediments can store, by some 100-1000 times, more nutrients than the water. The exchange rate of nutrients, e.g. phosphorus, basically depends on the pH-regime: higher pH results in more intensive release of P-forms thus allowing an increased primary productivity and an accelerated energy-flux (Bíró 1984; Istvánovics 1988).

There is a concept of "ichthyoeutrophication" which assumes existence of positive feedback between the eutrophication process and changes in the fish species complex. According to this concept, fishery management in counteracting the process of eutrophication should consist of complex measures to maintain the initial ichthyofauna community structure, or at least to retard its changes (Opuszynski 1980).

A great deal of data has been published on the efficiency of energy transfer from primary producers to fish in a wide variety of lakes, reservoirs and fish ponds (Bíró 1993b; ILEC/UNEP 1988-90; Kajak & Hillbricht-Ilkowska 1972; Korinek 1972; Morgan 1980; Taub 1984; Winberg *et al.* 1972) (Tab. 5.1, Fig. 5.2).

It is commonly believed that temperate eutrophic or hypertrophic shallow lakes (e.g. Lake Balaton) may generally produce higher and sustainable fish yields than deep, thermally stratified ones. Increasing lake trophy results in more or less increased overall fish productivity to a certain level, thereafter it tends to decrease or becomes stabilized. Modelling of trophic relationships may help to understand

Tab. 5.1 Gross (g)/net (n) primary (P_p) and fish production (F_n) or yield (Y) in ponds, lakes and reservoirs. Most values are recalculated for kJ m^{-2} y^{-1} (*), or given in kJ m^{-2} d^{-1} (**), or in kJ m^{-2} 100 days (***) (after Bíró, 1993b, modified). B = biomass; P = production; + + + = values referring for *Notothenia neglecta* were recalculated for three months.

Area	Range of P_n	Range of F_n	Trans. efficiency (F_n/P_p – %)	Authors
Carp (1+, 2+) pond	–	–	(1.7-24.4)	Korinek (1972)
Smyloy, Bohemia	2008-10460	75.4-196.8*	1.9-3.75	〃 〃
Fish ponds, Poland	–	–	3.3-6.9^{n}	Wróbel (1962)
	–	–	8.3-16.7^{g}	〃 〃
Carp ponds, Israel	57-175**	–	1.6	Hepher (1962)
Polish lakes	–	41.2^{Y*}	0.2^{g}	Kajak *et al.* (1972)
Fish ponds	–	–	4.0^{g}	Morgan (1980)
Lakes & reservoirs	–		3.3-6.9^{g}	〃 〃
Slapy Res. Cz. Rep.	5359	171.2-185.5^{Y*}	3.2-3.5	Hrbácek (1984)
Klicava Res. Cz. Rep.	7888	41.5-111.8*	1.0-2.7	Hrbácek (1984)
L. Pääjärvi, Finland	1426	15.6	1.09	Sarvala (1978)
L. Naroch, former USSR	6478	18.0	0.28	Winberg *et al.* (1972)
L. Myastro, 〃	7417	26.2	3.65	〃 〃
L. Esrøm, Denmark	10715	88.5	0.86	Jónasson (1972, 1977)
L. Leven, Scotland	15715	123.0	0.78	Morgan & McLuscky (1974)
L. Balaton, Hungary	3880	20.9	0.34	Oláh (1975)
	7615-33890*			Herodek (1977)
	7531-36401*	3.18-19.4^{Y*}	0.04-0.1	Bíró & Vörös (1990)
L. Fertõ, Hungary	3598.2^{g*}	2.1^{Y*}	0.058	ILEC/UNEP I-III (1988-90)
Little Balaton reservoir Hungary	18200t^{g***}	1.21-7.0^{Y*}	0.007-0.038	Bíró (MS)
Zurichsee, Switzerland	7531-16317.6^{g*}	12.2^{Y*}	0.16-0.075	ILEC/UNEP I-III (1988-90)
L. Yunoko, Japan	3723.8*	75.3*	2.0	Mori *et al.* (1984)
L. Suwa, Japan	18116.7*	<171.5*	0.95	〃 〃
L. Kojima, Japan	18242.2	656.9*	3.6	〃 〃
L. Tatsunuma, Japan	318.0	14.6*	4.6	〃 〃
L. Biwa	234.3*	0.42*	0.18	〃 〃
East Lake, Wuhan, China	17850*	16.3-228.6^{Y*}	0.09-1.28	Liu (1984)
L. Kinneret, Israel	37.7-104.6*	41.5*	4.4-12.2	Serruya & Leventer (1984)
L. Nasser, Egypt	1231-1887**	1.42*	–	Latif (1984)

L. Parakrama, Sri Lanka	167360^{g*}	$1883\text{-}2092^{Y*}$	0.13-1.1	Fernando (1984)
L. Lanao, Philippines	25940.8^{n*}	20.1^{Y*}	0.08	Fernando (1984)
Lowland Res., India	$24411\text{-}44560^{*}$	$67.8\text{-}78.3^{Y*}$	0.18-0.3	Fernando (1984) Sreenisavar (1977)
L. Victoria, Africa	25104^{*}	—		cit. Fernando (1984)
L. George, Uganda	83680^{*}	—	—	Ganf (1969)
Pink Lake, Australia	1008^{*}		—	Hammer (1981) cit.Williams (1984)
Lake Phewa, Nepal	40271^{n*}	33.5^{Y*}	0.083	ILEC/UNEP I-III
	253132^{g*}	33.5^{Y*}	0.013	(1988-90)
L. San. Roque, Argentina	20920^{g*}	—	-	Bonetto & Di Persia (1984)
Los Molinos, Argentina	24686^{g*}	—	—	〃 〃
Embalse del Tercero, Argentina	30543^{g*}	—	—	〃 〃
Waldsea Lake, Canada	1590^{*}	—	—	Hammer (1984)
L. Mälaren, Sweden	$4184\text{-}5648.4^{g*}$	1.36^{Y*}	0.024-0.033	〃 〃
L. Hjälmaren, Sweden	7112.8^{g*}	1.59^{Y*}	0.022	〃 〃
L. Wättern, Sweden	1673.6^{g*}	0.57^{Y*}	0.34	〃 〃
L. Vänern, Sweden	836.8^{g*}	0.4^{Y*}	0.048	〃 〃
L. Päijänne, Finland	1368.2^{g*}	4.56^{Y+}	0.33	〃 〃
L. Mjøsa, Norway	$836.8\text{-}4184^{*}$	2.5^{Y*}	0.06-0.3	〃 〃
Southern Indian Lake, Canada	2092^{g*}	$0.23\text{-}0.8^{Y*}$	0.011-0.039	〃 〃
Char Lake, Arctic	297^{*}	1.25^{*}	0.42	
		$43.5\text{-}65.7^{B}$	14.6-22.1	Hobbie (1994)
Antarctic Lakes	53.1-	81.2^{B+++}	1.08.152.9	Laws (1977)
	7531.2^{+++}	27.6^{P+++}	0.37-52.0	〃 〃

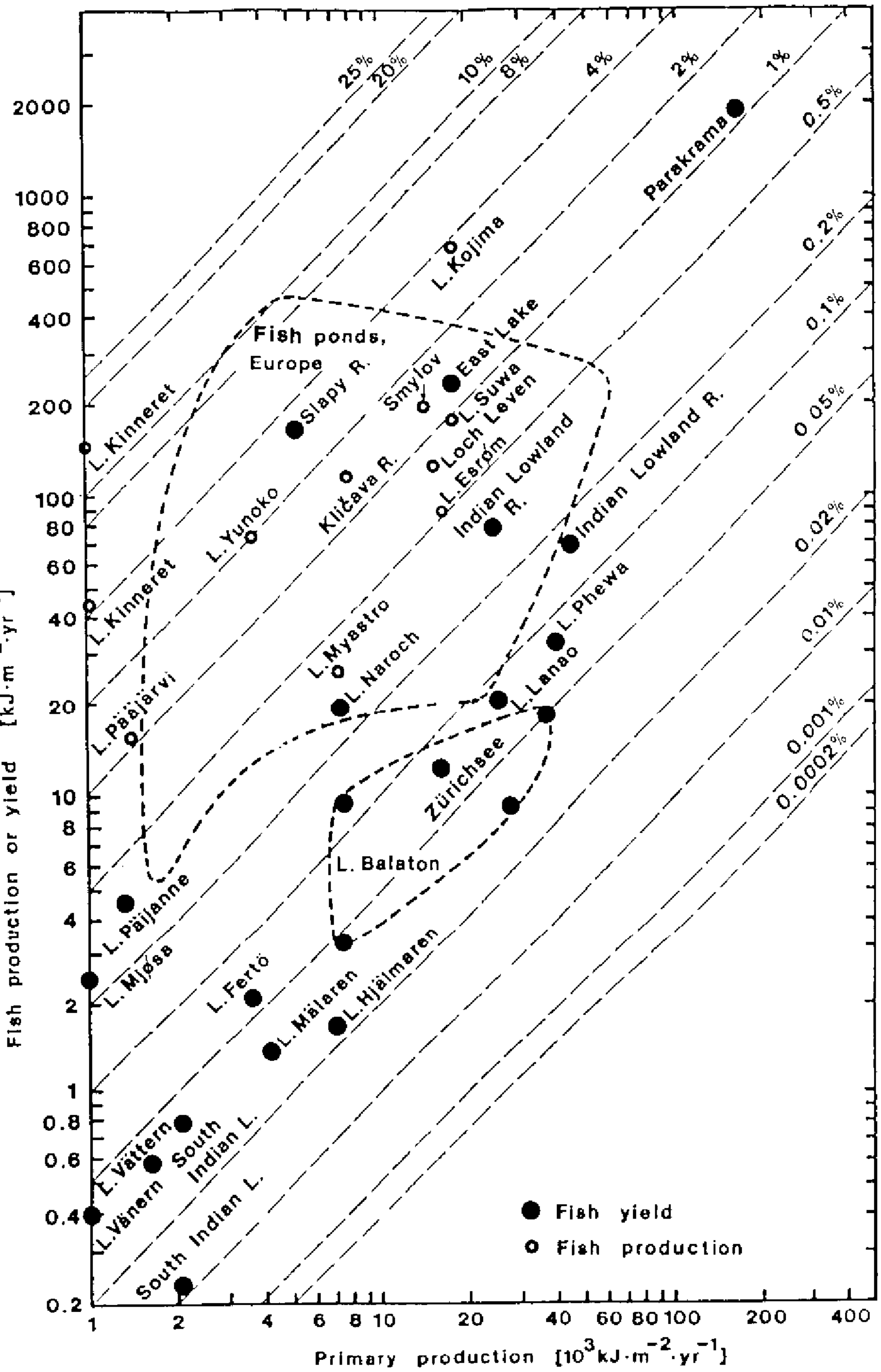

Fig. 5.2 Efficiency of energy transfer from primary producers to fish in a variety of fish-ponds, lakes and reservoirs (kJ m^{-2} year^{-1}) (from Bíró 1993b, modified).

these processes (Jørgensen 1986). In highly productive, well buffered shallow lakes there is usually a surplus primary productivity (e.g. Lake Balaton: 300-800 g C $m^{-2}y^{-1}$) along with intensive bacterial decomposition. Because of faster nutrient circulation through various feedback mechanisms, the energy dissipation within the lake system becomes more significant, and the energy flow or the efficiency of energy transfer to fish is also reduced (Bíró 1984). According to the literature data, the efficiency of energy transfer from primary producers to fish varies between 1 and 2% in natural lakes (or even less) in the function of their trophic state. The higher the primary productivity, the lower the efficiency of energy transfer to fish, and contrary, the shorter the food-chain, the higher the efficiency. A fairly high number of case-studies led to a better understanding of the functioning of eutrophic lakes and resulted in optimal strategies for exploitation of fishery resources (Bíró 1993a) (Tab. 5.2).

Tab. 5.2 Efficiency of energy transfer in Lake Balaton (kJ $m^{-2}d^{-1}$)

Energy level	BASINS		Authors
	NE	SW	
Primary production			
open water (1986)	7531 (100%)	36401 (100%)	Bíró & Vörös 1990
(1990)	6456	30264	Gorzó-G. Toth
Secondary production			
open water (1977)	170 (2.26%)	300-400 (0.99-1.32%)	Ponyi 1985, 1992
littoral (1992)	61.84 (0.82%)	618 (1.7%)	Simonian *et al.* (in press)
Tertiary production (fish yield)			
open water (1971-80)	3.18-4.52 (0.04-0.06%)	16.3-19.4 (0.045-0.053%)	Bíró & Vörös 1990
pikeperch (1987)	(0.002-0.0053%)	(0.0071-0.022%)	Bíró (1991)
littoral (1992)	15.0-26.5 (0.23-0.41%)	15.2-23.6 (0.05-0.078%)	Simonian *et al.* (in press)

5.3.1 Exploitation of food webs by fish

The term "biomanipulation" has been defined as management of aquatic communities by controlling natural populations of organisms aimed at water quality improvement (Shapiro *et al.* 1975). Biomanipulation aims to decrease the trophic stage of natural lakes (oligotrophication), however, the management of eutrophication for enhanced fish productivity of these waters on the contrary focuses on the optimal exploitation of higher primary productivity and accelerated energy-flux to achieve higher fish production (yield) without depleting the natural lake structure and processes.

The term "biomanipulation" is similar to others presently used by several authors: top-down forces, trophic cascade or food web manipulation (Benndorf 1987; Carpenter *et al.* 1985; Gophen 1990). All these terms refer to manipulation of secondary or tertiary producers and its impacts on the community structure of aquatic ecosystems. At present, the complexity of the ecosystem response and the role of bottom-up forces (nutrients) and/or nutrient-mediated effects of planktivorous fish on plankton community structure are considered (Carpenter *et al.* 1985; Gophen 1990; van Donk *et al.* 1990). Gulati *et al.* (1990) present several approaches concerning food web manipulation in different water bodies.

Food web management practices applied for increasing fish production are trying to enrich the "natural productivity" of fish-ponds (or exploit eutrophication of natural lakes), and simulate those circumstances which were characteristic for highly productive flood plains of rivers prior to their regulations. However, in moderately or intensively managed ponds, controlled application of nutrients enhance the biomass and productivity of food-chain components (Bíró 1993b). Control of aquatic vegetation in fish ponds and natural lakes is another problem concerning increasing natural food, because aquatic vegetation can seriously interfere with fish pond operations (Ghittino 1972). The sophisticated management of eutrophication to increase fish production depends on the same process which has been induced by human impacts or resulted in a stepwise, slow, successive geochemical alteration of the lake systems.

5.4 PRODUCTION/DECOMPOSITION INTERACTIONS AND THE ROLE OF NUTRIENTS

Fish pond management techniques depend on the controlled inputs of fertilizers (P, N), manure from animal husbandry, treated/untreated domestic sewage as well as water supply. In intensively managed fish ponds, the addition of fertilizers does not usually result in a significant increase of fish productivity as it is observable in nutrient-poor waters. Excessive application of fertilizers may lead to environmental pollution and sanitary problems. Fairly high fish production can be achieved through the use of organic fertilizers. In the decomposition of organic materials and mediating the energy through superimposed levels, the role of the heterotrophic food web (microbial loop) proved to be very significant. The mineralization in eutrophic lakes with predominant participation of bacteria are considerable: more than 80% of the primary production is decomposed in the upper layers. Only about 20%, in many cases much less, sinks down to the sediment surface (Overbeck 1989). Due to fish-pond circumstances these ratios might be different in relation to their shallowness, sediment disturbances by cyprinids, or metabolic coupling of phytoplankton and bacteria. Primary productivity is correlated with fish productivity because primary producers are used both directly by fish and indirectly as a substrate for heterotrophic bacterial production. Consequently, a 5 g C m^{-2} d^{-1} input highly increases the fish productivity according to temperature regime without concomitant water quality problems. About 40% (or more) of the primary production is channelled immediately through the bacterial metabolism in an annual range. This demonstrates the important role of bacteria in the carbon cycle: extracellular dissolved organic matter, produced by the autotrophic algae, is converted by bacteria into particulate organic matter, which thus again is available for the food chain. On average in eutrophic lakes with a production of 500-1000 mg C m^{-2} day^{-1}, the heterotrophic potential amounts to 1 µg C l^{-1} h^{-1} (Overbeck, 1989). In many fish ponds and eutrophic lakes, blue-green algae (cyanobacteria) constitute the greater part of the summer phytoplankton biomass causing regular water blooms and massive fish mortalities by depletion of oxygen after the bloom collapses. Cyanobacteria which are able to assimilate dissolved atmospheric nitrogen gain a selective advantage over competitors when combined nitrogen fails, and many of them are capable of vertical migration due to buoyancy regulation, this particularly being another competitive advantage in stratified ponds. Blue-green algae are of poor food value to zooplankton, their large size making them inaccessible to the filter-feeding entomostraca. Even the substances produced by many species of cyanobacteria are toxic to aquatic plants and animals (Sevrin-Reyssac & Pletikosic 1990).

Temperature dependent recycling of waste water (sewage effluents) has also been used to enrich ponds and lakes in several countries (tropical, subtropical and temperate habitats, respectively). Toxic compounds in fish farm effluents need further consideration. In natural lakes the treated or untreated communal sewage results in significant eutrophication.

Atmospheric nitrogen fixation in lakes and fish ponds is also a significant nutrient source of algal (mainly blue-green) production. In fertilized, hypertrophic fish ponds the planktonic N-fixing on an average was 0.57 g N m^{-2} y^{-1}, and in sewage-oxidation fish ponds was 0.21 g N m^{-2} y^{-1}, and in Lake Balaton, along its eutrophic-hypertrophic cline, it varied from 0.15 to 12.93 g N m^{-2} y^{-1} (Oláh *et al.* 1981).

Food web components can be varied with introduction of predatory and non-predatory invertebrates (i.e. Mysidaceae etc.). In combined stocking, the fish species partition the planktonic and benthic food resources resulting in higher conversion efficiencies (and also increased interspecific competition). It has been shown that a selective removal of planktivorous fish has a positive influence on the trophic state of a water body. It is plausible that this is caused not only by predation on zooplankton but also by the predation on zoobenthos, that activates the mobilization of phosphorus from the bottom-sediments (Mur 1980). Another possibility for the exploitation of trophic state by fish may have been to apply a combination of cascade reservoirs (Stepanek 1980) stocked by suitable fish assemblages. In these reservoirs the trophic conditions are characterized in Table 5.3.

Tab. 5.3 The approximate relation of the trophic condition of phosphorus and nitrogen content in surface water reservoirs (after Stepanek 1980).

Trophic state	Total P (mg m^{-3})	Inorg. N (mg m^{-3})	Ratio N:P
Strictly oligotrophic	<5	<200	>40:1
oligo-mesotrophic	5-10	200-400	40:1
meso-eutrophic	10-30	300-650	30-22:1
eu-polytrophic	30-100	500-1500	17-15:1
polytrophic	>100	>500	<15:1

5.5 COMBINED STOCKING OF FISH SPECIES

Relationships between the stocking density and the growth rate of common carp have been discussed by Backiel & Le Cren (1967), Walter (1934) and Wolny (1962). Overpopulated stocks show retarded or stunted (density-dependent) growth under natural conditions when the food availability is limited.

Stocking practice (introductory, maintenance, supplementary) can further increase utilization of the aquatic food webs through stocking a proper combination of several fish species (primary, secondary and predatory species) at adequate densities which feed on different natural resources (Ghittino 1972). Several fish species can increase or decrease the productivity of certain food web levels through their interactions (Benndorf, 1990). Dense stocking of fish ponds with carp (*Cyprinus carpio* L.- a benthos and zooplankton consuming species) and the plankton consuming silver carp (*Hypophthalmichthys molitrix* Val.- a phytoplankton and zooplankton consuming species), stimulate an increase in primary production and an increase in the biomass of planktonic algae. Under both temperate and tropic conditions, the effect of fish on these characteristics of the ecosystem is remarkable (Opuszynski 1980). In the tropics other species (e.g. *Tilapia* spp, etc.) can better exploit the food-chains.

Fish population strongly influences the nutrient turnover of the pond; e.g. when herbivorous fish are kept together with common carp, they generally require 20-40% less fertilizers for maintaining planktonic life (recycling of nutrients) than those with common carp in monoculture. In natural eutrophic lakes the bioturbation of sediments by cyprinids increases the internal loading of nutrients and their availability for the planktonic communities (Tátrai *et al.* 1990).

Food-webs can also be influenced directly with stocking of cross-breeds of common carp x phytophagous fish species characterized by mixed-feeding pattern which may occupy vacant niches. However, the introduction of phytophagous fish into natural habitats may result in severe destruction of food webs with the selection of filter-feeder invertebrates (cladocerans, etc.).

Most species show alternating fast and slow growth rates, the possible reasons of which might have been the scarcity of appropriate food stuff and the competition with other species combined with changing environmental conditions, e.g. high water temperature.

In Europe the calculation of stocking density both in monoculture or polyculture depends on the known production and fertility of the pond (Ghittino 1972). Stocking ratios vary widely depending on the area and according to the intensity of techniques used. In natural, eutrophic lakes maintenance stocking is usually used.

The algaecides applied to limit the development of cyanobacteria are effective but are often detrimental to the environment. Another solution would be to increase the N:P ratio to 5 or more, which benefits chlorophyceae and reduces the number of cyanobacteria. The use of aerators to break vertical stratification and avoid low concentration of oxygen also makes water conditions unfavourable to blue-green algae (Sevrin-Reyssac & Pletikosic 1990).

The predation pressure (grazing) of the fish stock on zooplankton plays an important role in lakes. This activity has a direct impact upon the biomass and the species diversity of the phytoplankton.

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CHAPTER 6

MANIPULATION OF AQUATIC PLANTS

Brian Moss

6.1 MACROPHYTES IN THE FOOD CHAIN - DIRECT AND INDIRECT INFLUENCES

The word 'macrophyte' simply means large plant. It has come into use among aquatic scientists to distinguish the thalloid algae, mosses and liverworts, ferns, conifers and flowering plants that grow in fresh and saline waters, from the microscopic algae that are suspended as plankton in the open water or grow, loosely or firmly attached, in association with underwater surfaces such as sediment, rocks or macrophytes. Aquatic macrophytes comprise a varied group (Sculthorpe 1967) that ranges from the tiny floating duckweeds, some of which are only 1mm in length, to large trees such as the cypresses (*Taxodium* spp) of the swamps of the southern United States. Various complex classifications based on life form exist (Hutchinson 1975) but a simple one is most useful for present purposes.

Thus there are first the emergent macrophytes, which are firmly rooted in underwater soils with their bases underwater in the wetter seasons, but rising above the water surface with stem, leaf and flower structures similar to the land plants from which they have relatively recently evolved. Examples include reed (*Phragmites*), *cattail* (*Typha*), bulrush (*Scirpus* and *Schoenoplectus*), papyrus (*Cyperus papyrus*), and a variety of other grasses and sedges, all of which are monocotyledonous flowering plants on the one hand, and a variety of trees and shrubs on the other. Woody emergents include swamp cypress (*Taxodium*), willows and sallows (*Salix*), and alder (*Alnus*). If the floodplain forests of the tropics are examined a much greater variety will be found.

Secondly there are floating-leaved macrophytes, typical of which are the nymphaeids or water lilies. These also are rooted and their inflorescences emerge above the water surface but their leaves typically float at the water surface. They may also have leaves of quite different appearance and anatomy which remain completely submerged. Both emergents and floating leaved plants are generally confined to shallow waters, down to about 2-3 m but the emergents are more tolerant of drought when water tables fall to the soil surface or below. Floating-leaved plants are usually killed by such conditions unless they last for a very short time.

The third functional group is that of the totally submerged macrophytes. These also are usually rooted but may not necessarily be so. If they are rooted, the root systems, although functional in uptake of nutrients from the soil or sediment, are not usually extensive. The anchoring and water uptake functions they have in terrestrial plants and in emergent macrophytes are less crucial or redundant underwater. The leaves of submerged macrophytes are very different from those of emergent or floating-leaved plants for they are usually thin with very thin cuticles on their surfaces, and sometimes highly dissected. These features appear to be helpful in coping with the major problem for plants growing underwater of low diffusion rates of nutrients and carbon dioxide through the medium (Madsen & Sand-Jensen 1991). Thinness of leaf minimises the length of the diffusion pathway. It also helps to maximise the availability of light energy to the leaf, for the underwater environment is a shade environment because of the strongly absorptive properties of water and the substances dissolved and particles suspended in it.

Finally there are macrophytes like the duckweeds (*Lemna, Spirodela,* and *Wolffia*), the water hyacinth (*Eichhornia crassipes*), and the floating ferns, (*Salvinia* spp and *Azolla* spp) which float at the water surface, often forming substantial mats, interconnected by stolons and absorbing all their nutrients from the water rather than from the sediment. Availability of light is no problem for them but they are vulnerable to the destructive effects of wave action and thus are confined to sheltered habitats. They are also disadvantaged by their size in the competition for nutrients with phytoplankton in the water, but have the counteradvantage, once their mats have built up, of overlying the plankton and hampering its growth through shading and stilling of the water column.

The macrophytes contribute in two groups of ways to the food chains of lakes - directly and indirectly (Carpenter & Lodge 1972). Directly they are sources of primary production and are grazed by a variety of animals, from invertebrates to hippopotami. Because of their high water and air content, (many macrophytes have internal air spaces or lacunae, often linked with solutions to the problem of aerating root systems that are surrounded by anaerobic sediments) it was formerly thought that grazing on them was minimal. In fact it may be as extensive as in land plants. Gajevskaya (1969), Fassett (1957) and Lodge (1991) give useful compilations of grazer relationships. Furthermore the macrophytes form platforms on which a community called the periphyton may grow (Sand-Jensen & Borum 1991). This comprises algae, bacteria, protozoa and various associated inorganic and organic detritus. It may be deleterious to the growth of the plants for it may compete with them for light and perhaps carbon dioxide, but it forms a nutritious food source for a variety of invertebrates, like snails, trichopteran and chironomid larvae, which in turn are food sources for invertebrate predators and fish.

Productivity, particularly of emergent macrophytes is often very high (Moss 1988) and a greater abundance of organic matter is produced than is directly consumed by grazers. Aquatic habitats have limited oxygen supplies because of the low solubility of oxygen in water and so organic deposits (peat) may build up underneath emergent plant beds or be exported downstream in riverine habitats to form sediment elsewhere. Peat raises the soil surface and may promote successional processes which result in the progressive filling in of a lake though the process is usually very slow, whilst sediment deposited elsewhere forms the substratum for further growth. The water under dense beds of floating macrophytes, particularly in warm climates, becomes anaerobic through decomposition of sloughed-off material. In emergent and floating swamps the reduced oxygen concentrations have led to evolution of an animal community that is dependent on devices such as atmospheric air breathing for its survival. Nonetheless animal production in such places can be very high. There may also be major seasonal movements of large mammals and of birds into swamps and their surrounding seasonally flooded grasslands to take advantage of the great availability of macrophyte-originated food supplies (Welcomme 1979). A great many indigenous peoples in the tropics are completely dependent on floodplain systems with their aquatic and semi-aquatic plant communities for their traditional subsistence.

Indirect contributions to the foodwebs by macrophytes come through the architectural structure they provide to the lake and through influences on the processes of nutrient cycling (Wetzel 1990). Macrophyte dominated zones in a lake are almost always far more diverse in animal species (Macan & Kitching 1972) than the open water zone dominated by the plankton. The macrophytes provide the physical basis for niches, resting sites, lurking sites for predators, spawning sites and sites for the attachment of fertilised eggs. Through diversity comes the greater ability to exploit the available natural resources provided by light and nutrients, for a diverse community must have specialisation in diets of its members if energy is not to be wasted in interspecific competition.

Because of the generally high productivity of macrophyte-dominated habitats, a high rate of metabolism is maintained within them (Mickle & Wetzel 1978 a, b). This is particularly true of the microorganism communities that colonise the plant surfaces and the organic detritus that falls from them to the underlying sediment. The sediment surfaces are usually microaerophilic or anaerobic and considerable releases of nutrients such as phosphorus can occur. The nutrient cycling within the beds is complex and largely unexplored but it would be very surprising if a whole range of inorganic and organic transfers did not take place between the macrophyte beds and the open water zone, with its important plankton communities and dependent fisheries.

6.2 IN WHAT SORTS OF LAKES ARE MACROPHYTE COMMUNITIES MOST IMPORTANT ?

Macrophytes occur in all lakes, except some extremely saline ones and in those where severe pollution has destroyed their growth. However they are not equally important in all lakes. In large, deep lakes, although they may form a littoral fringe, the geometry of the lake may give much greater overall importance to the open water community. However in terms of areal importance, the littoral zone may be of much greater significance because the deeper waters are frequently very infertile and consequently unproductive. Especially for lakeside dwellers dependent on the fishery, the inshore waters may be much more crucial than those offshore. This may arise because of the export of organic material and nutrients from the macrophyte dominated areas to the inshore waters with a consequent enhancement of their production. The fish communities of the macrophyte zone itself, fished using small-scale artisanal methods, may contribute a substantial catch also (Goulding 1981), though they are not exploitable using large scale mechanical methods which destroy the ecosystem structure.

Large lakes, however, despite their prominence on the map, occupy a much smaller overall area than the millions of small, shallow water bodies that are of greatest importance for human societies. These lakes are the ones in which macrophytes assume a much greater importance in all respects. They include shallow natural basins formed by glacial action, shallow depressions in floodplains, lagoons in swamps, pans and many small man-made dams. They are major components of extensive wetland systems which cover, (or covered, for in some instances they have been severely damaged by drainage or by flooding to form large deep reservoirs), large areas of the land surface. Because of the importance of such habitats and the extensive losses they have suffered, it is especially important that any interference with those that remain should be very carefully considered before any action is taken.

6.3 CHANGES IN AQUATIC PLANT COMMUNITIES

There is usually a pattern of occurrence of aquatic plant communities in lakes, reflecting the depth of the water and the exposure of different shorelines to wind and wave action (Spence 1982). Where the latter do not prevent colonisation the usual pattern is for a zone of emergent plants to straddle the region between dry land and the shallower water with floating-leaved, floating and submerged plants occurring to increasing extents among the emergents as water depth increases. In the deepening water, down to the depth at which insufficient light remains for plant colonisation, submerged plants predominate. Floating plants may occur wherever wind and water movements allow them to persist. There may be cyclic changes in the particular species, particularly of submerged plants, that are dominant in a particular year (McCreary 1991) because of annual variations in weather and other environmental factors and this is quite normal. However there may sometimes be unidirectional changes in which particular species of plant become extremely abundant and others in which plants may disappear altogether. Either of these instances may create problems but it is important that such instances be carefully distinguished from normal cyclic changes before remedial action, which in the wrong circumstances could be damaging, is undertaken.

Aquatic plant crops frequently increase when nutrient inputs (of phosphorus and nitrogen) from the catchment increase (Mitchell 1974). The nutrient inputs come from more intensified agriculture, from the discharge of sewage effluent, and from miscellaneous causes. These might include concentration of wild ungulates into a smaller area than they normally range over, or increases in the flocks of roosting birds resulting from conservation measures or changes in their habits. Increased input of nitrogen may be occuring from atmospheric sources in Africa resulting from the increased incidence of bush fires, and from the burning of gasoline in Europe and North America.

It is generally the floating and submerged plants which respond most to eutrophication for they depend on the water for some or all of their nutrients, particularly nitrogen (Denny 1980; Barko & Carpenter 1991). The emergent and floating-leaved plants are strongly rooted and obtain most of their nutrients from the sediments which are almost always relatively rich in phosphorus. However, in some places, where the sediments are sandy, increase in nutrient load in the water can stimulate growth of emergent and floating-leaved plants or change the species composition of the community. Where submerged and floating plant growth increases on moderate eutrophication, it may cause navigation and fisheries problems through the sheer bulk of plant material produced, though overall the fish production probably increases along with that of the plants. However, nets may become clogged with weed and underneath dense floating mats and at night within submerged beds, there may be severe deoxygenation through decay of sloughed-off plant material. The problem is particularly acute where non-native floating species have been introduced such as the fern *Salvinia molesta*), and the water hyacinth, *Eichhornia crassipes*. Some exotic submerged species have also caused severe problems of clogging small water bodies (Mitchell 1974).

With increasing levels of eutrophication the nature of the submerged plant community changes, with short species (Phase 1, Fig. 6.1) being out-competed by taller ones (Phase 2, Fig. 6.1) which respond to the increasing nutrient supply with greatly increased biomass. It is likely that in many lakes, though the limiting nutrient for the phytoplankton is phosphorus, the nutrient causing increase in aquatic plant growth is nitrogen. This is because the sediments contain large reserves of phosphorus which the plants are able to exploit with their root systems (Barko & Carpenter 1991). Floating plants respond to the same nutrients as the phytoplankton, being dependent entirely on the water column for their supplies. In different places phosphorus or nitrogen may be the key limiting nutrient but for production of nuisance growths it will usually have been necessary for both nutrients to have increased significantly. With high nutrient inputs, there may be a complete loss of submerged and floating plants (Phases 3 & 4, Fig. 6.1). There may also be some loss of emergent and floating leaved plants.

The mechanisms for loss of plants with eutrophication are complex. Formerly it was thought that as the nutrient input increased the phytoplankton increased and eventually simply shaded out the plant community. However, though some experiments seem to show a decline in plant growth with simple addition of large loadings of nutrients, others indicate that in many circumstances other mechanisms are at work (Moss 1990; Scheffer *et al.* 1993). Vigorous plant communities seem to be able to buffer the effects of increased loading for quite some time and experiments have shown no loss of plants with high loadings (Howard-Williams 1981; Balls *et al.* 1989). The buffer mechanisms (Fig. 6.1) include competition between the

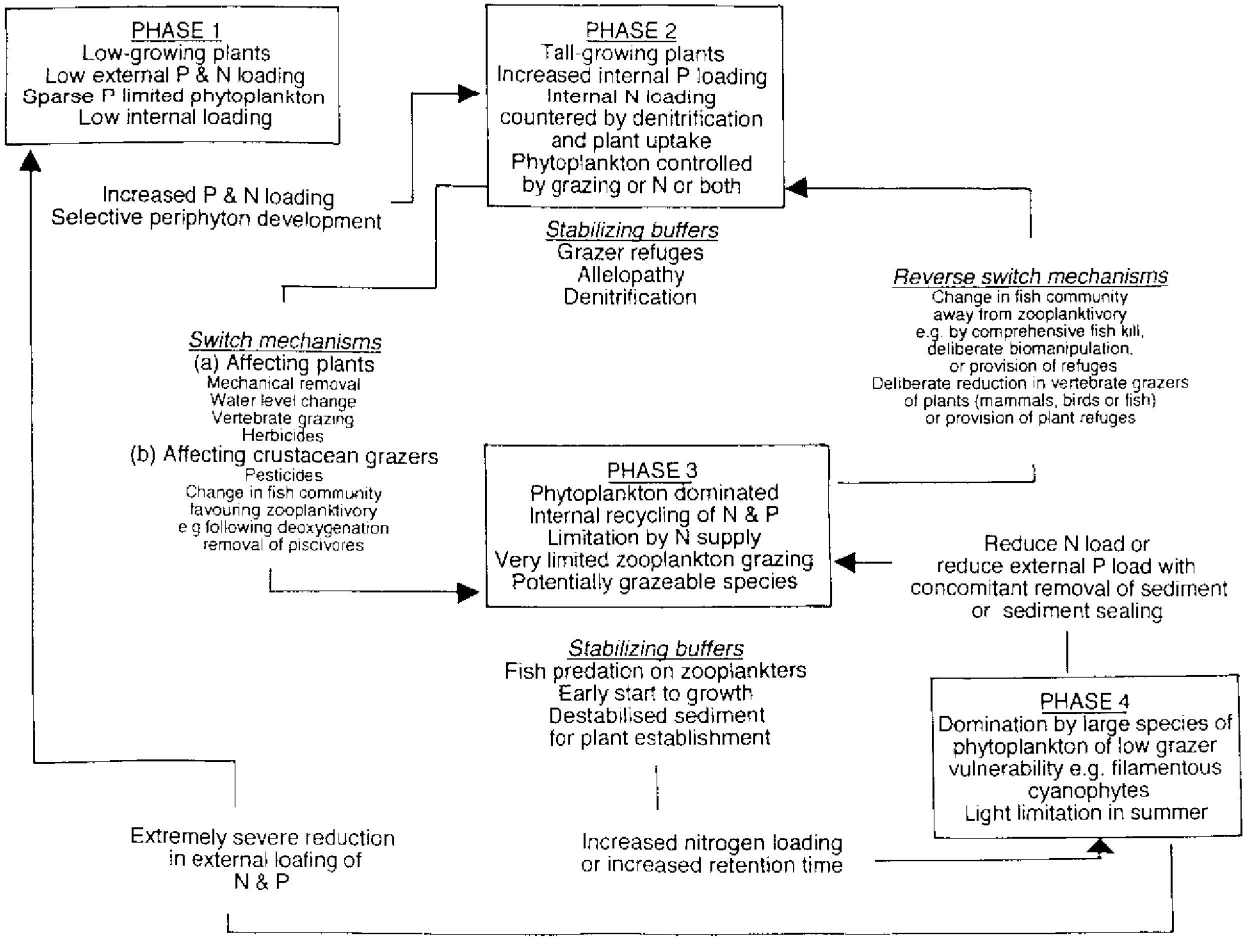

Fig. 6.1 Relationships between macrophyte dominated communities and phytoplankton dominated communities and nutrient loading in very shallow lakes.

plants and the phytoplankton for nitrogen, possibly intensified by the denitrification which takes place as a result of bacterial activity in the microaerophilic or anaerobic regions at the base of dense weedbeds. A second mechanism is allelopathic inhibition of algal growth by the plants (Elankovitch & Wooten 1989; Planas *et al.* 1981) and a third is the harbouring of huge populations of crustacean grazers in physical refuges against predation by fish (Timms & Moss 1984; Irvine *et al.* 1989). The crustaceans are able to move out at night to graze in the open water when fish are unable to see and therefore catch them. The plants also anchor sediment against wind disturbance and deterioration of light climate caused by sediment resuspension (Scheffer *et al.* 1993).

Where loss of plants occurs in the earlier stages of eutrophication, it is necessary, therefore, for these buffer mechanisms to be overcome. This may occur as a result of switch mechanisms (Fig. 6.1) that destroy the plant cover, allowing algae to take advantage of the increasing nutrients and to establish algal dominance as an alternative stable state (Phase 3 versus Phase 2, Fig. 6.1). The same may occur indirectly through food chain effects that reduce the numbers of crustacean grazers and relieve the phytoplankton community of grazing pressure. The former direct mechanisms may include cutting and clearing of the plants, use or accidental run-off of herbicides, damage by boats, or overgrazing, particularly by exotic species of mammals or birds (Moss 1991). Crustacean activity can be destroyed directly by run-off of pesticides (Stansfield *et al.* 1989), increased salinity (Bales *et al.* 1993; Irvine *et al.* 1993) or by alterations in the fish community which favour zooplanktivores (Bronmark & Weisner 1992). Deoxygenation in summer or in winter under prolonged ice cover may do this by selective removal of the more oxygen-demanding piscivores. Once a phytoplankton-dominated community has been established, it too has stabilising buffers which make the re-establishment of macrophytes very difficult (Moss 1991). The buffers include the exposed nature of the open water habitat, which offers little refuge for crustacean grazers against fish predation, the earlier seasonal growth of the algae, the unstable nature of the sediment for establishment of plant propagules, and the vulnerability of inocula of re-establishing plants to bird grazing.

At extremely high nutrient loadings, the nature of the phytoplankton community may change towards production of large species of algae, such as cyanophytes, which may be uningestible by crustacean grazers (Phase 4, Fig. 6.1). In such cases it is possible that a rapid increase in nutrient load may directly lead to production of such algae and this in itself may cause the switch from macrophyte dominance to phytoplankton dominance.

6.4 DECIDING WHETHER A PROBLEM EXISTS OR NOT

Change is inevitable in freshwaters through natural change in the catchment and through natural processes of filling in and shallowing in the lake basin itself. Superimposed on natural changes are anthropogenic ones and it may be difficult to distinguish the natural from the man-made. Even in the latter cases, the degree of change may not cause a particular problem or, in large waterways, it may be a localised one. It is thus wise to be conservative before enacting measures to decrease or increase aquatic plant populations (Nichols 1991). Sometimes the measures undertaken may lead simply to further but different problems or the problem may sort itself out, given time. For example, in the early stages of reservoir construction, the newly forming lake may be highly productive as nutrients are released from flooded soils and decomposing terrestrial vegetation. There may be initial algal blooms or coverage of large areas of water with floating plants, hampering navigation and fisheries. Within a few years however, the lake fertility will decline as incoming river water displaces the nutrient rich water initially present. The floating infestations then decline also and the problems they have caused diminish (McLachlan 1974). On the other hand, if sewage effluent, or water draining intensively farmed areas, is draining into the lake, weed infestations may be permanent and constitute a problem requiring solution.

In general, where aquatic plants have declined there will be a problem, for the loss in habitat structure will lead to loss in the diversity of the fish community and wildlife habitat. There will be declines in water bird populations, increases in sediment resuspension and perhaps in bank erosion. In such cases remedial action will be required although local perceptions may mitigate against this. In the Peoples Republic of China, for example, macrophyte-dominated lakes may be less prized than phytoplankton-dominated ones because large scale and mechanical fishing methods cannot be used where water weed is abundant. 'Restoration' of such lakes may thus involve deliberate destruction of the plant populations with the intention of making the fish more available. Such action will not increase the absolute total fish production in the long term but it may switch it into species that are r selected rather than K selected and from which a greater fishing yield may be safely taken. In the longer term, however, the fish community, being less diverse, may be more susceptible to catastrophes like deoxygenation and in some years the fishery may fail. Extreme caution is thus advised in implementing management measures to lakes except where it is manifestly obvious that a deleterious man-made impact has occurred. Proposals to increase fish production should always be viewed with extreme caution.

6.5 MANIPULATIONS TO REDUCE EXCESSIVE PLANT GROWTHS.

Where aquatic plants are infesting a water body as a result of eutrophication and causing obvious problems, there are a number of possible solutions. The most fundamental is to reduce the nutrient loading. This must first involve establishment of which nutrient it is best to control. Many lakes are limited by phosphorus and it is generally easier to control phosphorus than nitrogen, the other likely limiting nutrient. Some lakes however may be nitrogen limited and phosphorus control will be ineffective unless it is severe enough to create conditions of phosphorus limitation. The first step will thus be to construct phosphorus and nitrogen budgets for the lake to identify the major sources of these elements and to determine the relative availability of N and P in the inflow water. As a rule of thumb, if the N:P ratio by weight is much greater than 10, the lake will be phosphorus limited. If it is less than 10, the lake will be likely to be nitrogen limited.

Sources of phosphorus and nitrogen include those coming from discrete places (point sources) such as sewage or sewage effluent pipes and those coming from diffuse sources such as drainage from the land. Point sources are easier to control by diversion elsewhere or, better, by treatment of the effluent to remove and recover the nutrients. The technology for phosphorus removal is well advanced and involves precipitation by iron or aluminium salts; that for nitrogen is still being developed and is presently expensive.

Diffuse sources present much greater problems. Amounts of phosphorus running off from the land are generally small because soils retain phosphorus efficiently but nitrogen compounds are very soluble and run off in large quantities under some circumstances. Measures to reduce such loads include the establishment or preservation of swamplands or other natural vegetation along inflow streams and the edges of the lake. In such natural vegetation, denitrification and plant uptake can greatly reduce the loads of nitrogen. Agricultural practices which leave soil bare for the minimum time, conserve fertilizer, use slow release fertilizers, and apply them at times when crop uptake is greatest are also to be recommended.

It is possible also to precipitate phosphorus within a lake with calcium or aluminium compounds which also may seal the sediment surfaces and reduce internal loading by release from the sediments. It is also possible to remove some of the nutrient stock by harvesting of aquatic plants, particularly floating ones. Harvesting of rooted plants will generally be ineffective for they draw the bulk of their nutrients from the sediments where supplies are extremely large and only likely to be depleted after many years. Such methods should only be used where no alternatives are possible because they may cause side effects or offer only temporary solutions or both.

Where nutrient reduction is not possible or has been ineffective, various treatments of the symptom of excessive plant growth are possible (Nichols 1991). The first is to remove weed by cutting, followed by disposal away from the lake. This is expensive for the weed is bulky and cutting needs to be continuous to have any major effect. One of the features of the biology of many aquatic plants is their ability to propagate vegetatively very rapidly. Use of herbides is cheaper but much less selective and leaves quantities of dead plant material to decay and cause deoxygenation. Herbicides may destroy the vegeatation entirely if over-used thus creating a new problem; if under-used they may have very little effect. The balance between over- and under-use is a fine one not easily determined before the treatment is carried out. A number of specific biological control agents are available for particular species and these offer the most precise targeting of weed problems. Finally the Chinese grass carp, *Ctenopharyngodon idella,* is a voracious feeder on plants and if used wisely, in areas where it is unable to breed without artificial help, can be used in a fairly precise way. Where conditions are warm enough for it to breed naturally, however, it may be so destructive as to cause similar problems to the over-use of herbicide.

6.6 METHODS FOR STIMULATION OF AQUATIC PLANT GROWTH WHERE COMMUNITIES HAVE BEEN LOST

Aquatic plants will have been lost generally as a result of extreme hypereutrophication alone or following moderate eutrophication, coupled with action of a switch mechanism (Fig. 6.1). Two prerequisites are then needed for reestablishment. First the nutrient loading must be reduced, if it is extreme, to levels where either aquatic plants or grazeable phytoplankton can persist as alternative states. This usually means that total phosphorus concentrations should be not more than about 100-150 µg l^{-1} under phosphorus-limited conditions or total nitrogen 1-1.5 mg l^{-1} under nitrogen-limited conditions. Such levels will allow re-establishment of a relatively species-poor aquatic plant community with water lilies and some of the ranker growing pondweeds. Establishment of diverse plant communities, for example for conservation purposes, will require much more severe nutrient control (<50 µg l^{-1} P or <0.5 mg l^{-1} N).

Nutrient control is only the first step, however, and is unlikely to displace the phytoplankton, which can still form substantial biomass at these nutrient concentrations. The second step is to re-establish the buffer mechanisms (Fig. 6.1) that stabilise the plant-dominated state. This means reducing the water turbidity by husbanding the crustacean grazer communities. In turn this means either provision of artificial refuges against fish predation or removal of fish for a period long enough for the plants to establish sufficiently for them to be able to support their own natural buffer mechanisms.

In practice, provision of artificial structures as refuges (e.g. buoyant rope, netting, bundles of twigs) has proved ineffective or too expensive (Irvine *et al.* 1990) and methods that involve removal of fish have proved to be necessary. Complete removal of all fish works extremely well whilst introduction of piscivores, although theoretically workable, has not been tried in very shallow lakes. Difficulties may involve availability of suitable native piscivores and the maintenance of piscivore to zooplanktivore ratios that are inherently unstable (Moss 1992). A combined approach is to create enclosures at the edges of a lake that are impermeable to fish but allow free movement of water through mesh windows in them (Moss 1990). Fish are removed from within the enclosures in which plant beds are allowed to build up in water kept clear by crustacean grazer activity. It may be necessary to reintroduce suitable plant inocula particularly if the lake has been devoid of plants for some time. Very little is known about the longevity of aquatic plant seed and propagule banks (Madsen 1991). Permeability of the enclosures to flushing is necessary to prevent stagnation which may lead to development of uningestible cyanophyte communities (Shapiro 1990) in the plankton. When significant areas of the lake have been enclosed and allowed to develop plant beds (perhaps 50% of the area of shallow lakes) the enclosure walls can be removed and fish alowed access again. The system should then be able to maintain itself. It has proved necessary in some lakes to protect the initial plant inocula against grazing by birds such as coot and geese, but this is not always needed. A very useful practical guide as to the potential success of these biomanipulative techniques in restoration of aquatic plant communities is Hosper & Meijer (1993).

6.7 CONCLUSION

Aquatic plants are very important components of the ecosystems of shallow lakes. They provide production and habitat and the ecosystem and its uses are likely to suffer if the plant populations either become superabundant or depleted as a result of human activities. Decisions to manage the plant populations should not be taken casually but only after a close inspection of whether a problem really exists, what its ultimate causes have been and what possibly deleterious consequences remedial management may have elsewhere in the ecosystem. It is ultimately better to prevent a problem developing by careful use of the catchment to minimise nutrient run-off, by conservation of natural and semi-natural terrestrial and wetland systems close to the lake and in the valleys of inflow streams and rivers, and by avoidance of the introduction of non-native species. If a problem of excessive growth of weed has developed, the best approach is to remedy the cause and to treat the symptoms only if this is not possible. In doing so it is best to use highly targetted methods rather than coarse general remedies. Where aquatic plants have been lost and require restoration this needs not only removal of the cause of loss but also a further biological engineering of the system to restore biological mechanisms that stabilise the aquatic plant-dominated system. This may not be an easy task.

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CHAPTER 7

MODELLING AND BIOMANIPULATION

S. E. Jørgensen

7.1 INTRODUCTION

The success of biomanipulation varies considerably from case to case, as discussed by Kasprzak in Chapter 2. Modelling seems therefore the obvious tool to use in the selection of biomanipulation, as the primary task of management models always is to predict the results of any alterations in the ecosystem. However, biomanipulation implies, that the structure of the ecosystem (the lake) is changed, which is much more difficult to capture with a model than a simple change in forcing functions, for instance the inputs of nutrients. Structural dynamic models are on the other hand emerging (see for instance Jørgensen 1992a and 1992b), and models are increasingly used as an experimental tool, that sometimes can be used to explain ecosystem behavior (Jørgensen 1990 and 1992b), for instance in association with chaos and catastrophe theories.

As model developments based upon case studies with structural changes are still very scarce, only one case study will be presented (Lake Søbygård; see Chapter 4 by Gulati) later in this chapter. However, as models to a certain extent can explain, when and why top-down control is working, the next section is devoted to a short presentation of the use of catastrophe theory in lake eutrophication models, followed by a section with a model illustration on how and particularly under which circumstances bottom-up and top-down are working. The fourth Section contains the above mentioned structural dynamic case study, followed by a section, where the results of Sections Two to Four are discussed. The Sixth and final Section summarizes the conclusions of using modelling to explain the effects of biomanipulation and as a management tool in selection of biomanipulation strategies.

7.2 USE OF CATASTROPHE THEORY IN LAKE MODELLING

The short term results of biomanipulation are encouraging, but it is unclear whether the manipulated system will inevitably return to the initial eutrophic and turbid conditions. Some observations (see Hosper, 1989 and Van Donk *et al.* 1989), seem to indicate that if low nutrient concentration is combined with a relatively high concentration of predatory fish, a stable steady state will be attained, while high nutrient concentration and high predatory concentration will lead to an unstable clear water state, compare also with Chapter 1 by de Bernardi and Giussani. On the other hand turbid conditions may prevail even at medium nutrient concentrations, provided that the predatory fish concentration is low. By introduction of more predatory fish, the conditions may, however, improve significantly, even at medium nutrient concentrations.

Willemsen (1980) distinguishes two possible conditions:

1. A "bream state" is characterized by turbid water, high eutrophication at least relatively to the nutrient concentration. Submerged vegetation is largely absent from such systems. Large amounts of bream are found, while pike is hardly found at all.
2. A "pike state" is characterized by clear water and low eutrophication relative to the nutrient level. Pike is abundant, while significantly fewer bream are found compared with the "bream state".

Willemsen's work shows that the pike/bream ratio is strongly correlated with water transparency and that the separation between the two states is relatively

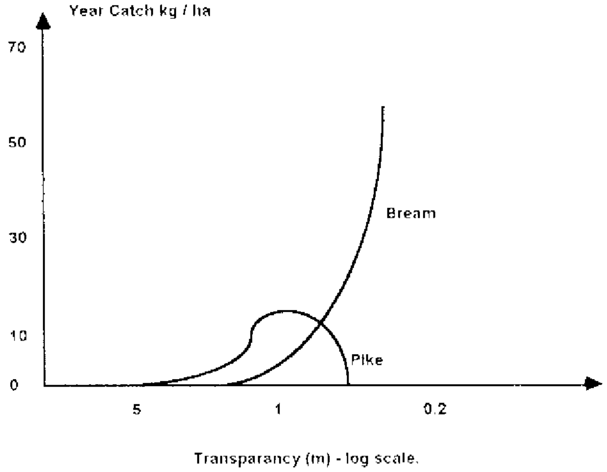


Fig. 7.1 Annual catches of pike and bream (kg/ha^{-1}) plotted versus transparency (m).

distinct; see Fig. 7.1.

Scheffer (1990) has used a mathematical model to describe these shifts in structure, which may be of a catastrophic character. The conceptual diagram of the model is presented in Fig. 7.2. The components of the model are connected by

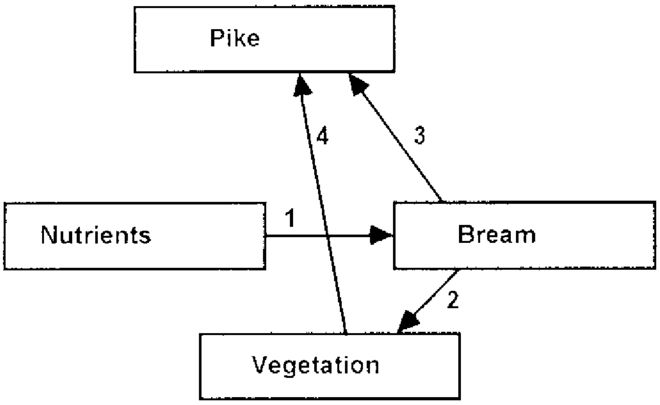


Fig. 7.2 Conceptual model applied to describe shifts from "bream state" to "pike state" and *vice versa.*

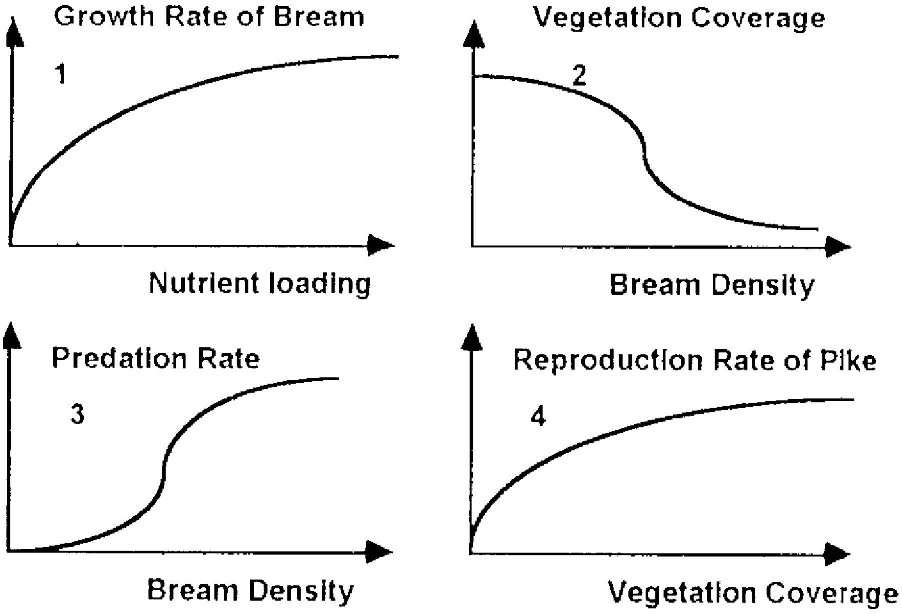


Fig. 7.3 Relations incorporated in the model in Fig. 7.2.

four relations, which are incorporated in the model as a simple Monod and Hill function; see Fig. 7.3.

The general features of the model are reflected by the plot of the isoclines. Figure 7.4 shows the zero isoclines of bream and pike. The low position of the pike isocline at high bream densities is explained by the decrease of vegetation in these situations.

The rise of the bream isocline at low bream density is a result of the functional response used in the model. The isoclines intersect at three points, i. e., the net growth of both pike and bream is equal to zero at these points. The three points therefore represent equilibrium points of the model. While points 1 and 3 are stable equilibria, point 2 represents an unstable equilibrium.

The slightest perturbations will cause the system to shift away from this point. The two stable points appear to correspond to the pike (1) and bream state (3). The effect of eutrophication on the system may be visualized by plotting isoclines for different values of the nutrient level. The pike isocline is not affected by the nutrient concentration, but the bream isocline changes, as shown in Fig. 5, with the nutrient level - the higher the nutrient concentration, the higher the position of the isocline in the diagram; see Fig. 7.5.

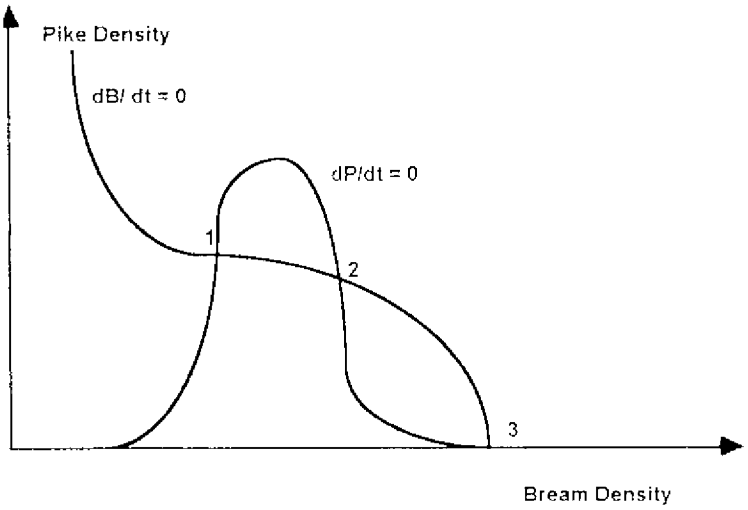


Fig. 7.4 Zero isoclines of the bream ($dB/dt = 0$) and pike ($dP/dt = 0$).

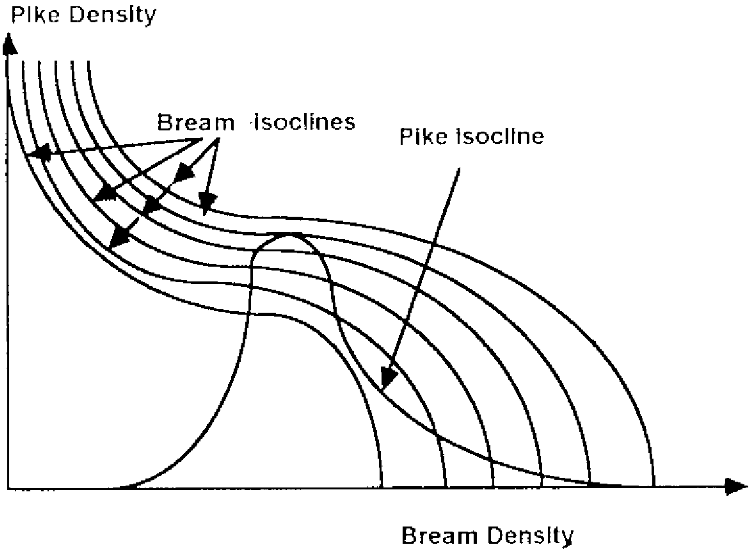


Fig. 7.5 The position of isoclines and stable equilibria at different nutrient levels. The highest position of the bream isocline corresponds to the highest nutrient concentration.

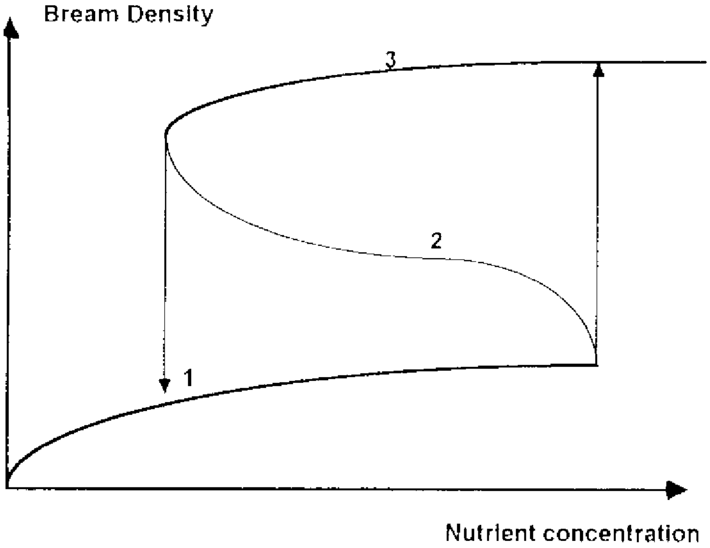


Fig. 7.6. A catastrophe fold is shown by means of projection of the intersection line of isocline planes of bream and pike on the nutrient-bream plane.

The behavior of an oligotrophic situation can easily be derived from Fig. 7.5. The lower bream isocline applies to the oligotrophic state. A low pike equilibrium is the only possible steady state under these conditions.

At increasing nutrient concentration the equilibrium will shift upwards slowly. Pike density will thereby increase, while bream density does not change much. This type of response continues until the bream isocline reaches a position where the intersection point disappears. At this point the pike population will collapse. The turbid bream equilibrium is attained. If we change the nutrient from high to low concentration, however, the picture will be different. By reduction of the nutrient level the system will stay in the bream type of equilibrium to a very low nutrient concentration, although the bream concentration will decrease slightly. Only at very low nutrient concentrations does the intersection point representing the bream equilibrium disappear and the system return to a pike state. Clearly this behavior is analogous to other examples described by catastrophe theory applied to biological systems; see Jørgensen (1992a and 1994).

Figure 7.6 shows the catastrophe fold, where a bream isocline is plotted versus the nutrient concentration, assuming that pike is in steady state. The isocline consists of the stable parts 1 and 3. The unstable part 2 corresponds to the "jump" between the two stable points. The discontinuous response to the increase and decrease of nutrient level implies that decreased nutrient levels will not cause a significant decrease in the eutrophication and a significant increase in water transparency before a rather low level has been attained. However, it may be possible to "push" the equilibrium from point 3 to point 1 by addition of predatory fish, for instance pike.

7.3 THE USE OF MODELS AS AN EXPERIMENTAL TOOL IN BIOMANIPULATION.

The modelling example in Section 2 illustrates that two different concentrations of planktivorous fish can coexist with a certain nutrient concentration, which explains the hysteresis reaction shown in Fig. 7.6. The general modelling experience is, that a given set of forcing functions gives a certain set of the state variables including the concentration of plantivorous fish, but when the set of equations that describes the ecosystem has a formulation causing catastrophical behavior in the mathematical sense, we can observe the reactions described in Section Two. To explain these observations further, models have been used as an experimental tool in the sense that the model description is in accordance with well working

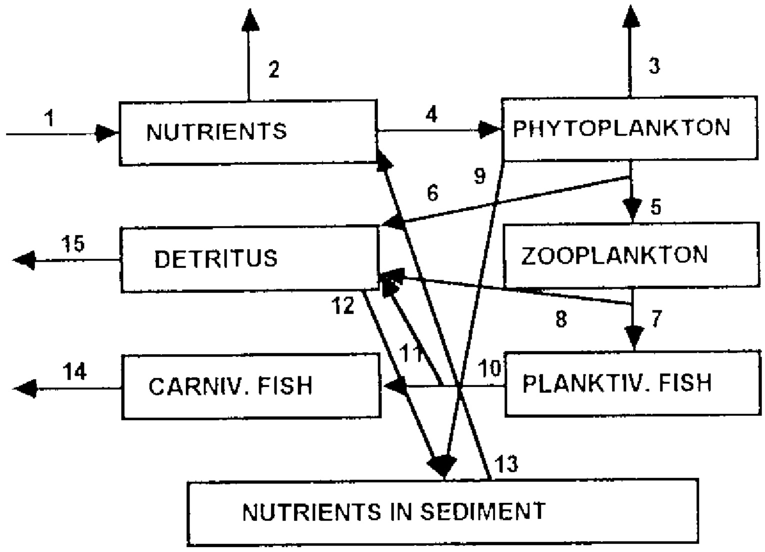


Fig. 7.7 The model used as an experimental tool in this Section is shown. The state variables are nutrients (only phosphorus is considered in this case), phytoplankton, zooplankton, plantivorous fish, carnivorous fish, nutrients in sediment and detritus. The processes are: 1. inflow of nutrients, 2. outflow of nutrients, 3. outflow of phytoplankton, 4. uptake of nutrients by phytoplankton for growth, 5. grazing, 6. loss of detritus by grazing, 7. predation on zooplankton, 8. loss of detritus by this predation, 9. settling of phytoplankton, 10. predation by carnivorous fish, 11. loss of detritus by this predation, 13. release of nutrients from the sediment, 14. catch of fish, 15. outflow of detritus.

lake models, but simulations with forcing functions for which there are no data available to control the model output are carried out.

The model used for these experiments is shown in Fig. 7.7. Only phosphorus is considered as a nutrient in this case, but it is of course feasible to consider both nitrogen and phosphorus. The model encompasses the entire food chain. The problem of modelling in the case of different inputs of nutrients is however, that the phytoplankton, zooplankton, plantivorous fish and carnivorous fish are all able to adjust their growth rate within certain ranges. It is therefore necessary to test a series of simulations with different combinations of growth rates to find which combination can give the highest probability of survival for all four classes of species. The results of these simulations can be summarized in the following points:

1. Between a total phosphorus concentration of 70 µg/l to 180 µg/l two levels of planktivorus fish give a stable situation with high probability of survival for all

four classes of species, but the level with the lowest level of plantivorous fish give the highest concentration of zooplankton and of carnivorous fish, while the phytoplankton concentration is lowest. This interval from 70 µg/l to 180 µg/l is of course dependent on the model-description of the lake and must not be taken as fixed values for all lakes, but indicate only that there is an interval approximately corresponding to mesotrophic conditions with two more or less stable situations.

2. The stable situation with the lowest level of plantivorous fish corresponds to the lowest growth rate of zooplankton and phytoplankton, which normally implies that it is a species that is bigger in size.

3. Above 180 µg total P/l or below 70 µg total P/l only one stable level is achieved. The two levels correspond to a high respectively a low level of plantivorous fish, and a high respectively a low level of phytoplankton. The zooplankton is relative to the level of phytoplankton highest below 70 µg total P/l and relatively low above 180 µg total/l.

4. When the plantivorous fish is at a low concentration either below 70 µg total P/l or between 70 µg and 180 µg total P/l the phytoplankton is clearly controlled by the relatively high zooplankton level, i. e., the grazing pressure, while phytoplankton is at the high planktivorus level above 70 µg total P/l, is controlled by the nutrient concentration.

As already underlined this exercise should only be considered qualitatively, but the results indicate that the use of biomanipulation seems only to be successful by an intermediate nutrient level, which is in accordance with Chapter 1 by de Bernardi and Giussani and Chapter 4 by Gulati. Unfortunately, the studies referred in these two chapters and throughout this volume have not been modelled, which would have given a better basis for quantifications. The range, where biomanipulation can be used successfully, is most probably to a high extent dependent on the specific conditions in the considered lakes, which unfortunately makes it problematic to use the results obtained here more than qualitatively. Furthermore, the role of applying a food web, which is of course more realistic, has not been investigated by application of models and therefore cannot be stated.

7.4 MODELS OF STRUCTURAL DYNAMIC CHANGES

The example in Section Three used a test of many combinations of growth rates to find the best combination of parameters from a survival point of view. This adjustment of the parameters corresponds to adaptation within some ranges and for more radical changes of the parameters to a change in the composition of species in the lake. If models have to be used as management tool in cases where significant changes in the nutrient level will take place or where biomanipulation is considered, it is necessary to develop models that can account for structural dynamic changes. This model development is, however, in its infancy and therefore only limited experience is available.

Our present models have generally rigid structures and a fixed set of parameters, reflecting that no changes or replacements of the components are possible. We need, however, to introduce parameters (properties) that can change according to changing general conditions for the state variables (components). The idea is currently to test if a change of the most crucial parameters produces a higher so-called goal function of the system and, if that is the case, to use that set of parameters. The type of models that can account for the change in species composition as well as for the ability of the species, i. e., the biological components of our models, to change their properties, i. e., to adapt to the prevailing conditions imposed on the species, are sometimes called structural dynamic models, to indicate that they are able to capture structural changes. They may also be called the next or fifth generation of ecological models to underline that they are radically different from previous modelling approaches and can do more, namely describe changes in species composition.

It could be argued that the ability of ecosystems to replace present species with other, better fitted species, can be considered by construction of models that encompass all actual species for the entire period that the model attempts to cover. This approach has, however, two essential disadvantages. The model becomes first of all very complex, as it will contain many state variables for each trophic level. It implies that the model will contain many more parameters that have to be calibrated and validated and, which will introduce a high uncertainty to the model and will render the application of the model very case specific (Nielsen 1992a and 1992b). In addition, the model will still be rigid and not give the model the property of the ecosystems of having continuously changing parameters even without changing the species composition (Fontaine, 1981).

Several goal functions have been proposed, but only very few models, that account for change in species composition or for the ability of the species to change their properties within some limits, have been developed. Straskraba (1979) uses a maximization of biomass as the governing principle (the above mentioned goal function). The model computes the biomass and adjusts one or more selected parameters to achieve the maximum biomass at every instance. The model has a routine which computes the biomass for all possible combinations of parameters within a given realistic range. The combination that gives the maximum biomass is selected for the next time step and so on.

The thermodynamic variable, exergy, has been used most widely as a goal function in ecological models, and one of the available lake case studies will be presented and discussed below in this section. Exergy has two pronounced advantages as goal function compared with entropy and maximum power (proposed by H. T. Odum, 1983): It is defined far from thermodynamic equilibrium and it is related to the state variables, which are easily determined or measured. As exergy is not a generally used thermodynamic function, we need, however, first to present this concept.

Exergy expresses energy with a built-in measure of quality. Exergy accounts for natural resources (Eriksson *et al.*, 1976) and can be considered as fuel for any system that converts energy and matter in a metabolic process (Schrödinger 1944). Ecosystems consume exergy, and an exergy flow through the system is necessary to keep the system functioning. Exergy measures the distance from the "inorganic soup" in energy terms, as will be further explained below.

Exergy, Ex, is defined by the following equation:

$$Ex = T_o{}^*NE = T_o{}^*\, I = T_o{}^*\,(S_{eq} - S) \qquad (1)$$

where To is the temperature of the environment, I is the thermodynamic information, defined as NE, NE is the negentropy of system, i. e., $= (S_{eq} - S) =$ the difference between the entropy for the system at thermodynamic equilibrium and the entropy at the present state. It can be shown (Evans, 1969) that exergy differences can be reduced to differences of other, better known, thermodynamic potentials, which may facilitate the computations of exergy in some relevant cases.

As can be seen the exergy of the system measures the contrast - it is the difference in free energy if there is no difference in pressure, as may be assumed for an ecosystem - against the surrounding environment. If the system is in equilibrium with the surrounding environment the exergy is zero.

Since the only way to move systems away from equilibrium is to perform work on them, and since the available work in a system is a measure of the ability, we have to distinguish between the system and its environment or thermodynamic equilibrium alias the inorganic soup. Therefore it is reasonable to use the available work, i. e., the exergy, as a measure of the distance from thermodynamic equilibrium. Survival implies maintenance of the biomass, and growth means increase of biomass. It costs exergy to construct biomass and biomass therefore possesses exergy, which is transferable to support other exergy (energy) processes. Survival and growth can therefore be measured by use of the thermodynamic concept exergy, which may be understood as *the free energy relative to the environment*; see equation 1.

Darwin's theory may therefore be reformulated in thermodynamic terms and expanded to the system level, as follows: The prevailing conditions of an ecosystem steadily change and the system will continuously select the species that can contribute most to the maintenance or even growth of the exergy of the system.

Notice that the thermodynamic translation of Darwin's theory requires that populations have the properties of reproduction, inheritance and variation. The selection of the species that contribute most to the exergy of the system under the prevailing conditions requires that there are enough individuals with different properties so that a selection can take place - it means that the reproduction and the variation must be high and that once a change has taken place due to better fitness it can be conveyed to the next generation.

Notice also that the change in exergy is not necessarily $\geqq 0$, it depends on the changes of the resources of the ecosystem. The proposition claims, however, that the ecosystem attempts to reach the highest possible exergy level under the given circumstances and with the available genetic pool ready for this attempt (Jϕrgensen and Mejer, 1977 and 1979).

It is not possible to measure exergy directly-but it is possible to compute it, if the composition of the ecosystem is known. Mejer and Jϕrgensen (1979) have shown by the use of thermodynamics that the following equation is valid for the components of an ecosystem:

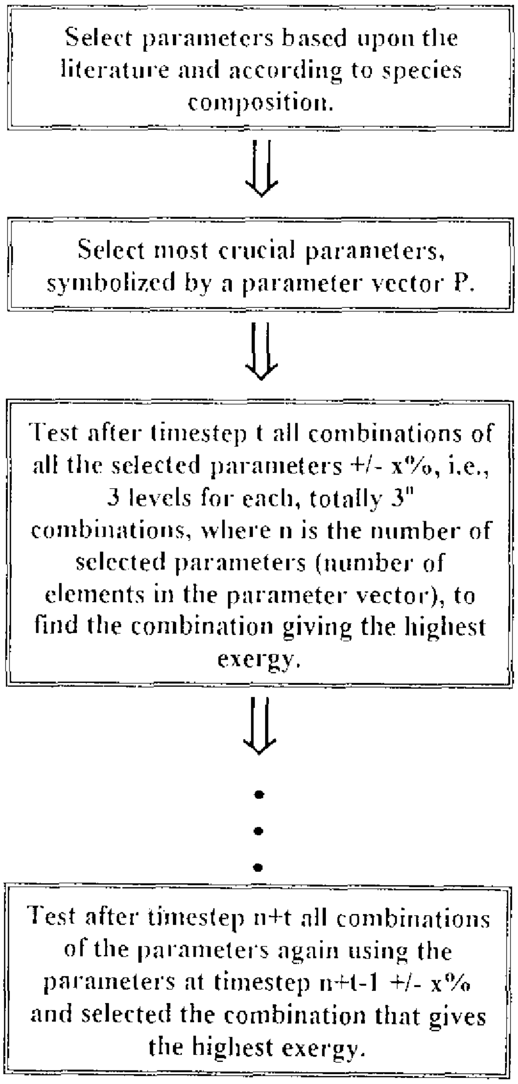
$$Ex = RT \sum_{i=n}^{i=n} (C_o{}^{*} \ln (C_i / C_{eq,i}) - (C_i - C_{eq,i})), \qquad (2)$$

where R is the gas constant, T the temperature of the environment (Kelvin), while C_i represents the i^{th} component expressed in a suitable unit, e. g., for phytoplankton in a lake C_i could be milligrams of a focal nutrient in the phytoplankton per liter of lake water, $C_{eq,i}$ is the concentration of the i^{th} component at thermodynamic equilibrium, which can be found in Morowitz (1968) and n is the number of components. $C_{eq,i}$ is, of course, a very small concentration of organic components, corresponding to the probability of forming a complex organic compound in an inorganic soup (at thermodynamic equilibrium). Morowitz (1968) has calculated this probability and found that for proteins, carbohydrates and fats the concentration is about 10^{86} $\mu g/l^{-1}$, which may be used as the concentration at thermodynamic equilibrium.

For more complex compounds such as unicellular organism, it will be even smaller and these compounds would therefore, even if they are present in a very small concentration, also contribute significantly to the exergy. The probability of forming one coli bacterium or a simple phytoplankton cell can be estimated from the number of genes. It has been found by this method that $C_{eq,i}$ for phytoplankton or coli bacterium is around 10^{1100} $\mu g/l^{-1}$ see Jφrgensen *et al.,* (1994).

The probability of forming multi-cell organisms at thermodynamic equilibrium is even lower, because additional exergy is required to make up the more complex structure and cover the information embedded in this structure. $C_{eq,i}$ for zooplankton has therefore provisionally been estimated to be around $10^{65,000}$ $\mu g/l^{1}$ and $C_{eq,i}$ for fish to $10^{130,000}$ $\mu g/l^{-1}$ for a total concentration, ci, of 1 mg/l^{-1}. The exergy contributions of higher organisms are, however, still under discussion, although some theoretically based rules have been developed; see Jφrgensen *et al.,* (1994). These proposals for the concentrations of various biological components at thermodynamic equilibrium do not, of course, lead to any exact value of exergy or even of the relative change of exergy. It will, however, account for relative changes due to changes in the properties (parameters) of the organisms. The inorganic constituents of an ecosystem do not create similar computational difficulties, but the thermodynamic equilibrium concentrations will here be the total concentrations of the various elements, corresponding to the fact that all chemical compounds were in inorganic form in the primeval soup, which we often use as reference state for our exergy calculations.

The idea of the new generation of models presented here is to find continuously a new set of parameters (limited for practical reasons to the most crucial, i. e., the most sensitive parameters) that is better fitted for the prevailing conditions of the ecosystem. "Fitted" is defined in the Darwinian sense by the ability of the species to survive and grow, which may as indicated above be measured by the use of exergy (see Jϕrgensen, 1982, 1986, 1994 and 1990, Jϕrgensen and Mejer, 1977 and 1979 and Mejer and Jϕrgensen, 1979). Figure 7.8 shows the proposed modeling



Select parameters based upon the literature and according to species composition.

Select most crucial parameters, symbolized by a parameter vector P.

Test after timestep t all combinations of all the selected parameters +/- x%, i.e., 3 levels for each, totally 3^n combinations, where n is the number of selected parameters (number of elements in the parameter vector), to find the combination giving the highest exergy.

Test after timestep n+t all combinations of the parameters again using the parameters at timestep n+t-1 +/- x% and selected the combination that gives the highest exergy.

Fig. 7.8. The procedure used for the development of structural dynamic models.

procedure, which has been applied in the cases presented below.

The use of exergy calculations to vary continuously the parameters has only been used in four cases of biogeochemical modeling. One of the case studies (Søbygård Lake) will be shown here as an illustration of what can be achieved by this modeling approach. The results from Søbygård Lake (Jeppesen *et al.*, 1989) are particularly suitable to test the applicability of the described approach to structural dynamic models.

Søbygård Lake is a shallow lake (depth 1 m) with a short retention time (15-20

Tab. 7.1 Equations of the model for Søbygård Lake.

```
fish = fish + dt* (-mort - predation )
INIT (fish) = 6
na = na + dt* (uptake-graz-outa-mortfa-settl-setnon )
INIT (na) = 2
nd = nd + dt* (-decom-outd + zoomo + mortfa )
INIT (nd) = 0. 30
ns = ns + dt* (inflow-uptake + decom-outs + diff )
INIT (ns) = 2
nsed = nsed + dt* (settl-diff )
INIT (nsed) = 55
nz = nz + dt* (graz-zoomo-predation )
INIT (nz) = 0. 07
decom = nd* (0. 3)
diff = (0. 015)* nsed
exergy = total__n* (Structura-exergy)
graz = (0. 55)*na* nz/(0. 4+na)
inflow = 6. 8* qv
mort = IF fish > 6 THEN 0. 08*fish ELSE 0. 0001* fish
mortfa =(0. 625)*na* nz/(0. 4+na)
outa = na*qv
outd = qv*nd
outs = qv*ns
pmax = uptake*7/9
predation = nz*fish*0. 08/(1-nz)
qv = 0. 05
setnon = na*0. 15*(0. 12)
settl = (0. 15 )*0. 88*na
Structural-exergy =(nd+nsed/total__n)*(LOGN (nd+nsed/total _n) + 59) +
(ns/total__n)* (LOGN (ns/total__n) - LOGN(total__n))+(na/total__n)*
(LOGN(na/total _n) + 60) + (nz/total _n)*(LOGN(nz/total__n) + 62)+
(fish/total__n)*(LOGN (fish/total__n) + 64)
total _n = nd+ns+na+nz+fish+nsed
uptake = (2. 0-2. 0*(na/9))*ns*na/(0. 4+ns)
zoomo= 0. 1*nz
```

days). The nutrient loading was significantly reduced after 1982, namely for phosphorus from 30 g $P/m^{-2}y^{-1}$ to 5 g $P/m^{-2}y^{-1}$. The reduced load did not, however, cause reduced nutrients and chlorophyll concentrations in the period 1982-1985 due to an internal loading caused by the storage of nutrients in the sediment (Søndergård, 1989 and Jeppesen *et al.*, 1989).

Yet, radical changes were observed in the period 1985-1988. The recruitment of plantivorous fish was significantly reduced in the period 1984-1988 due to a very high pH caused by eutrophication. Because zooplankton increased and phytoplankton decreased in concentration (the summer average of chlorophyll A was reduced from 700 $\mu g/l^{-1}$ in 1985 to 150 $\mu g/l^{-1}$ in 1988). The phytoplankton population even collapsed in shorter periods due to extremely high zooplankton concentrations. Simultaneously the phytoplankton species increased in size. The growth rate decreased and a higher settling rate was observed (Kristensen and Jensen, 1987). The case study shows, in other words, pronounced structural changes, caused by biomanipulation-like changes. The primary production was, however, not higher in 1985 than in 1988 due to a pronounced self-shading by the smaller algae in 1985. It was therefore very important to include the self-shading

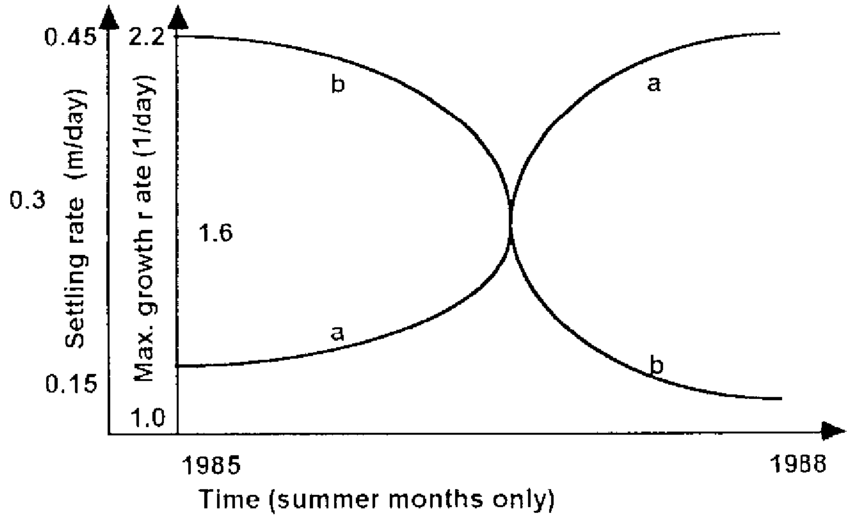


Fig. 7.9 The continuously changed parameters obtained from the application of a structural dynamic modeling approach to Søbygård Lake are shown. a covers the settling rate of phytoplankton and b the maximum growth rate of phytoplankton.

Tab. 7.2 Parameter Combinations giving the highest Exergy.

	Maximum Growth Rate (day^{-1})	Settling Rate (m*day^{-1})
1985	2. 0	0. 15
1988	1. 2	0. 45

effect in the model. Simultaneously a more sloppy feeding of the zooplankton was observed, as zooplankton was shifted from *Bosmina to Daphnia.*

The model applied has 6 state variables: N in fish, N in zooplankton, N in phytoplankton, N in detritus, N as soluble nitrogen and N in sediment. The equations are given in Tab. 7.1. As can be seen, only the nitrogen cycle is included in the model, but as nitrogen is the nutrient controlling the eutrophication in this particular case, it may be sufficient to include only this nutrient.

The aim of the study is to describe by use of a structural dynamic model, the continuous changes in the most essential parameters using the procedure shown in Fig. 7.8. The data from 1984-1985 were used to calibrate the model and the two parameters that it is intended to change from 1985 to 1988 received the following values by this calibration:

Maximum growth rate of phytoplankton:	2. 2 day^{-1}
Settling rate of phytoplankton:	0. 15 day^{-1}

The state variable fish-N was kept constant = 6. 0 during the calibration period, but an increased fish mortality was introduced during the period 1985-88 to reflect the increased pH. The fish stock was thereby reduced to 0. 6 mg N/l - notice the equation "mort = 0. 08 if fish >6 (may be changed to 0. 6) else almost 0".
A time step of t = 5 days and × % = 10% was applied; see Fig. 7.8. This means that 9 runs were needed for each time step to select the parameter combination that gives the highest exergy.

The results are shown in Fig. 7.9 and the changes in parameters from 1985 to 1988 (summer situation) are summarized in Tab. 7.2. The proposed procedure (Fig. 7.8) can simulate approximately the observed change in structure.

The maximum growth rate of phytoplankton is reduced by 50% from 2. 2 day^{-1} to 1. 1 day^{-1}, which is approximately according to the increase in size. It was observed that the average size was increased from a few 100 μm^3 to 500-1000 μm^3, which is a factor of 2-3 (Jeppesen *et al.* 1989). It would correspond to a specific growth

Tab. 7.3 Exergy and Stability by different Combinations of Parameters and Conditions

Parameter	Conditions	
	1985	1988
1985	75. 0 Stable	39. 8 (average) Violent fluctuations. Chaos.
1988	38. 7 Stable	61. 4 (average) Only minor fluctuations.

reduction by a factor $f = 2^{2/3}\text{-}3^{2/3}$ (see Jϕrgensen, 1994)

It means that:

$$\text{growth rate in 1988} = \text{growth rate in 1985}/f, \qquad (3)$$

where f is between 1. 58 and 2. 08, while in the above Tab. 7.2 is found by use of the structural dynamic modeling approach.

Kristensen and Jensen (1987) observed that the settling was 0. 2 m day^{-1} (range 0. 02-0. 4) in 1985, while it was 0. 6 m day^{-1} (range 0. 1-1. 0) in 1988. By the structural dynamic modeling approach an increase was found from 0. 15 day^{-1} to 0. 45 day^{-1}, the factor being the same - three - but with slightly lower values. The phytoplankton concentration as chlorophyll-A was simultaneously reduced from 600 µg/l to 200 µg/l, which is approximately according to the observed reduction. All in all it may be concluded that the structural dynamic modelling approach gave an acceptable result and that the validation of the model and the procedure in relation to structural changes was positive. It is, however, necessary to expand the model to account for *all* the observed structural changes, including zooplankton, to demonstrate an even more convincing case study. This will therefore be done at a later stage, when all the data from the case study are available. The structural dynamic modelling approach is of course never better than the model applied, and the presented model may be criticized for being too simple and not accounting for the structural dynamic changes of zooplankton. For further elucidation of the importance of introducing a parameter shift, it has been tried running the 1985 situation with the parameter combination found to fit the 1988 situation and vice versa. These results are shown in Tab. 7.3; they show that it is of great importance to apply the right parameter set to given conditions. If the parameters from 1985 are used for the 1988 conditions a lower exergy is obtained and the model to a certain extent behaves chaotically while the 1988 parameters used on the 1985 conditions give a significantly lower exergy.

7.5 DISCUSSION: TO WHAT EXTENT IS IT POSSIBLE TO USE MODELS IN SELECTION OF BIOMANIPULATION ?

Three modelling experiences have been presented in the three previous sections. They show that models can be applied to explain why biomanipulation works under some circumstances and why it does not work under other circumstances. The use of catastrophe theory is able to explain the appearance of hysteresis in the relation between nutrient level and eutrophication, as shown Fig. 7.10. Qualitatively, the results in Section Three can be used to explain that this hysteresis relationship exists in an intermediate nutrient level, which explains why biomanipulation in this range of nutrient concentrations has worked properly (it means with long term effects), but not above or below this intermediate range.

Models have, in other words, been an applicable tool in our effort to understand the obtained biomanipulation results, but a more quantitative use of models in the selection of biomanipulation will most probably require application of structural dynamic models. These types of models have been developed, but the experience is

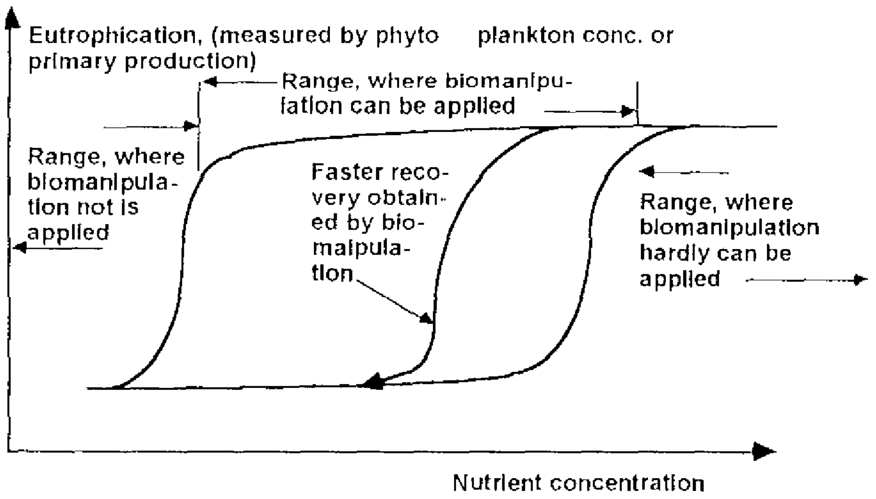


Fig. 7.10 The hysteresis relation between nutrient level and eutrophication measured by the phytoplankton concentration or the primary production is shown. The possible effect of biomanipulation is shown. As seen it will be able to short cut between the high eutrophication structure and the low eutrophication structure. An effect of biomanipulation can hardly be expected above a certain concentration of nutrients, as indicated on the diagram. Below a certain nutrient concentration biomanipulation will not be applied, as the eutrophication is too low to expect any effect.

still quite limited and the required data set is still not completely defined.

These results may be summarized in the following recommendations of the use of models for management of biomanipulation:

1. Attempt either to use a structural dynamic model such as the one presented in Section Four or use a more general model as the one shown in Fig. 7.7 to examine the possibilities of using biomanipulation. In the case that the general model Fig. 7.7 is used, it is necessary to test various parameter combinations at every nutrient level. The computation of exergy may help to select the best parameter combination for each nutrient level.
2. Consider the results only as approximations unless very good data for the application of structural dynamic models are available.
3. Consider intermediate nutrient levels, somewhere between 50 μg total P/l^{-1} and 200 μg total P/l^{-1} or 7 times higher concentrations for nitrogen, if it is the limiting nutrient, as the range, where biomanipulation most probably will work.

The results obtained by modelling and in situ biomanipulation experiments may be explained by the presence of ecological buffer capacities and time lag in structural changes. When the nutrient level is increased, see Fig. 7.10, the eutrophication, will in the beginning, not increase much. The lake ecosystem has an ecological buffer capacity, which can be explained by increased grazing and settling of the phytoplankton formed by increased nutrient level. However, at a certain nutrient level, the zooplankton can not any longer control the phytoplankton concentration, which becomes limited only by the nutrient level. The result is that the eutrophication level increases considerably by increased nutrient level. The entire structure of the ecosystem is changed, because the phytoplankton is now limited by nutrient, zooplankton by the predation from plantivorous fish and not any longer by the available food source, the phytoplankton, and the plantivorous fish is now limited by food source, the zooplankton, and not any longer by the carnivorous fish. It implies that other properties are selected, for instance other growth rates. Furthermore, the carnivorous fish will be scarce, as they are mostly hunting by sight and the increased eutrophication makes, therefore, hunting more difficult.

If we now decrease the nutrient level, for instance by discharge of waste water with significant lower nutrient concentration, this "high eutrophication structure" with low concentration of carnivorous fish, high of plantivorous fish, low of zooplankton and high of phytoplankton will not change immediately.

The low transparency will therefore still make an increase in the carnivorous fish difficult, and the grazing is still not able to control the phytoplankton concentration, because they are relatively low in concentration, as they still have a considerable predation pressure by the plantivorous fish. In this situation biomanipulation will either by removal of plantivorous fish and/or introduction of more carnivorous fish, give a clear effect, as shown in Fig. 7.10. The biomanipulation provides a simple, faster recovery to the "low eutrophication structure", where the grazing controls the phytoplankton concentration. Outside the intermediate nutrient level the forcing functions, i. e., the input of nutrients, determine the eutrophication which is also indicated on Fig. 7.10.

7.6 CONCLUSIONS

Models seem a useful tool to understand the function of biomanipulation, taking into account that they sometimes give positive results, and sometimes negative results. Models in general should be used as a tool to try to understand qualitatively the behavior of complex systems as for instance lake ecosystems. Sometimes, when a good data base is available models can be used quantitatively in environmental management, for instance for the control of eutrophication by waste water management, see Jørgensen and Vollenweider, 1988 and Jørgensen (1986 and 1994). The use of models quantitatively for selection of biomanipulation is possible by the application of structural dynamic models, but as the experience with this type of models is very limited, it can not be recommended to rely completely on the modelling results in this case, although they may be used qualitatively. There is, however, a clear need for the use of models in management and selection of biomanipulation to answer such questions as: Can biomanipulation give the desired results ? How many plantivorous fish must be removed and/or how many carnivorous fish must be added ? How many times and with which frequency should the biomanipulation be used to ensure the anticipated results ? Such questions can only in rare cases (the data requirement would be too high in most real case studies) be answered today by the use of models. It should therefore be strongly recommended to provide more and better case studies and use models on such case studies, well supported by good data. Only through increased experience on the use of models for selection of biomanipulation can we provide the management tool, that we need so urgently.

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CHAPTER 8

Case study: LAKE CANDIA (Northern Italy)

G. Giussani and G. Galanti

8.1 INTRODUCTION AND PRE-TREATMENT CHARACTERISTICS

Lake Candia is a small eutrophic lake located near the city of Torino (Northern Italy), and represents an important natural resource in that area (Fig. 8.1 and Tab. 8.1).

The most important water supplies, apart from precipitation and run-off, are internal springs, and the theoretical renewal time has been evaluated to be 6. 7 years. Despite its shallowness this lake presents a permanent stratification from April to October; usually is ice covered in January and February, and oxygen depletion is present in hypolimnetic water from July to complete overturn (October).

Tab. 8.1 Morphometric characteristics of Lake Candia.

Surface	1. 5 km^2
Shoreline length	5. 7 km
Maximum depth	7. 7 m
Mean depth	3. 8 m
Lake volume	7. 1 10^6 m^3
Drainage area	9. 9 km^2 (between 226 and 354 m a.s.l.)

Chemical water analyses carried out in July 1979 on the occasion of a fish mortality (Giussani *et al.* 1980) and one year later in March and September give us a picture of the pre-treatment situation of the lake for what concern total phosphorus, nitrate and ammonia nitrogen, Secchi disc transparency and total chlorophyll concentration (Tab. 8.2).

The pelagic phytoplanktonic population was rich both in number of species (107 different species have been identified) and in number of individuals (higher than 100 10^6 l^{-1} during summer, in integrated samples 0-5 m). Blue green algae, mainly ***Microcystis aeruginosa***, together with Chrysophyceae were the dominant groups. Total chlorophyll concentration was higher than 30 μg l^{-1} and occasionally

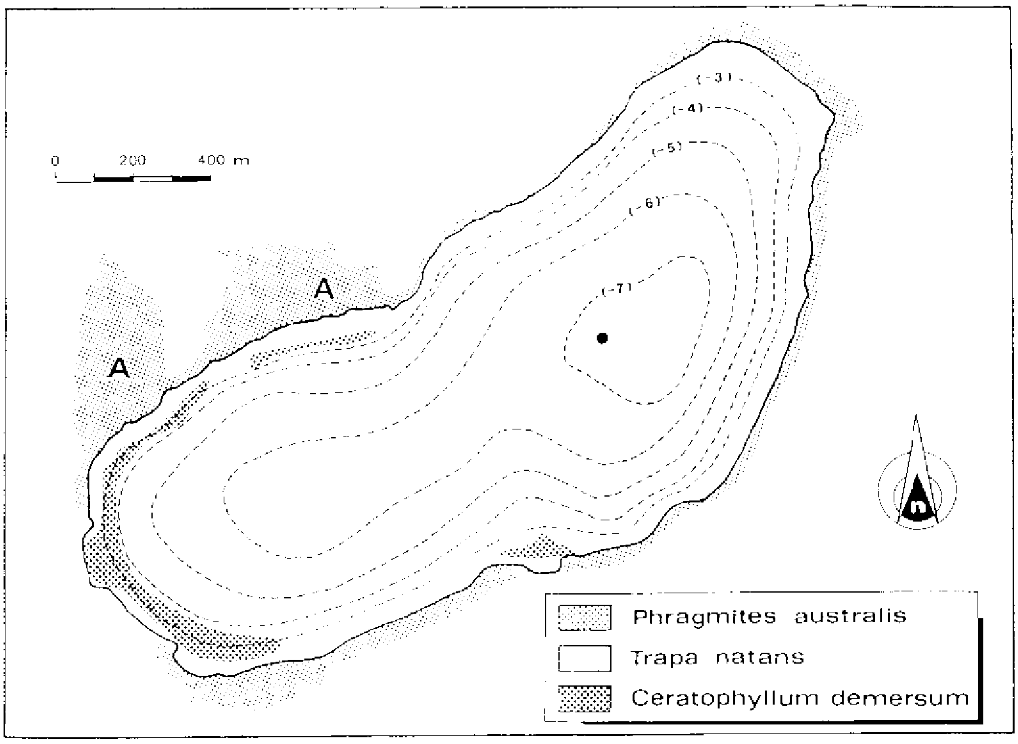

Fig. 8.1 Lake Candia: bathymetric map. The most important aquatic macrophyte populations are shaded (see legend); ● sampling station; A: marsh area recovered as spawning site.

Tab. 8.2 Values of the most important parameters that identify the pre-treatment situation in Lake Candia.

	P_{tot} ($\mu g\ l^{-1}$)	N-NO_3 ($\mu g\ l^{-1}$)	N-NH_4 ($\mu g\ l^{-1}$)	S. disc (m)	Tot.Chl. ($\mu g\ l^{-1}$)
VII-1979	86	36	314	1.2	48
III -1980	60	107	213	1.8	40
IX-1980	58	36	416	2.3	129

exceeded 100 $\mu g\ l^{-1}$.

The pelagic zooplankton population was dominated by small cladocerans: *Ceriodaphnia quadrangula* and *Eubosmina coregoni longirostris*. *Daphnia hyalina* was also present with a spring peak. Copepods were present with *Mesocyclops leuckarti* and *Thermocyclops crassus* and to a lesser extent of importance *Cyclops vicinus* and *Eudiaptomus padanus*.

The fish population of the lake, after the disappearance of the bleak (*Alburnus alburnus alborella*) caused by the fish-kill occurred in 1979, was dominated by the invasive presence of the rudd (*Scardinius erythrophthalmus*). The most efficient fish predators, pike (*Esox lucius*) and black bass (*Micropterus salmoides*), did not succeed in controlling the rudd population most probably for the following reasons: 1) pike and black bass are the preferred catch of anglers, while rudd is neglected; 2) three year old rudd are out of the predability size; 3) young rudd can easily find hiding-places in the dense stem tangles of *Trapa natans*; 4) the spawning areas of pike are accessible only with difficulty by mature individuals.

Also present was catfish (*Ictalurus melas*) with a fairly important population which, apparently, did not interfere with the food chain object of biomanipulation, perch (*Perca fluviatilis*) and tench (*Tinca tinca*), the latter actively caught with nets by a few authorized fishermen.

Total fish-stock in the lake has been estimated higher than 300 kg ha^{-1}, broken down as follows: 55% rudd, 25% catfish, 11% tench, 5% pike, black bass, perch and 4% other species.

Total macrophyte cover was 52.9 ha, representing 35% of the lake surface (Fig. 8.1) (Galanti *et al.* 1990). The helophyte community, dominated by *Phragmites australis*, covers 28 ha, whereas the floating-leaved *Trapa natans* (water chestnut) colonizes 19.7 ha, all the lake around, yielding annually 1420 t wet wt (120 t organic matter). Other floating-leaved species like *Nymphaea alba, Nuphar luteum, Nymphoides peltata* and *Hydrocharis morsus-ranae* cover 0.1 ha. The submersed community is dominated by *Ceratophyllum demersum* and *Myriophyllum spicatum* (6.4 ha in total, 1.4 ha of which mixed with *Trapa natans*).

The presence of a blooming aquatic macrophyte community gave us the opportunity to enlarge the spectrum of the biomanipulation strategies usually devoted to recovery of the aquatic ecosystems from eutrophication.

In fact, besides having the capacity to control the biomass of planktonic algae toward a bottom-up direction, submersed macrophytes may also influence the interactions at the top of the food web, acting directly on the predation equilibria that regulate the population of piscivorous fish, zooplanktophagous fish and zooplankton (Breck & Kitchell 1979; Carpenter *et al.* 1985; Loucks 1985; Carpenter & Lodge 1986). Creating the conditions for a shift of these equilibria in favour of an increase of zooplankton density and biomass has been the main task of the aquatic plant management in Lake Candia. The mere presence of macrophytes cannot be relied upon for the achievement of this goal. In fact, a very dense stand would retain the intensity of predation by piscivorous fish.

Thus, a reduction of plant density is often necessary to increase piscivorous fish activity, to reduce predation on zooplankton and to enhance grazing on phytoplankton according to the 'cascade effect'. At the same time, the reduced predation on zooplankton is expected to create a shift to larger individuals with lower remineralization rate of phosphorus (Breck & Kitchell 1979; Loucks 1985). Therefore, plant management for biomanipulation purposes may concern the increase or the decrease of the macrophyte biomass, as well as the preservation and the exploitation of an intermediate optimal structure. Increasing or creating macrophyte stands is the most difficult venture because it requires the modification of basic environmental features (i.e., type of substratum, slope of the shoreline and water level) or a preliminary partial reduction of the phytoplankton and suspended organic matter which attenuate light penetration for submersed plants. Decreasing or maintaining a given macrophyte density is certainly a simpler goal, even though the costs may be high. Physical removal by dredging or harvesting is a more suitable method than herbicide application which is more disruptive and poorly selective.

8.2 THE TREATMENTS

During late 1986 and early 1987, more than 12 t of rudd (1^+ and 2^+ years old) were removed from the lake, using seine nets, in addition to the amount (2 t) usually caught by local fishermen. So, total fish biomass has been lowered to about 200 kg ha $^{-1}$.

The accessibility to the marsh area, located along the northern shore of the lake (Fig. 8.1), has been opened, by digging a series of channels, to allow an increase of spawning areas for pike and black bass. The lack, in the past, of an appropriate management has led this area to be lost from its pristine function of nurturing of ichthyophagic fish species.

The hydrophyte harvesting operations started in 1986. From mid-August to early-October, about 50% of the total cover of the water chestnut was harvested yearly, by means of a Rolba Aquamarine 400 harvester, on about 130 sites (each about

50 m wide), regularly distributed along the lake perimeter. Except for a few experimental plots, 50% of the sites were treated in 1986, 1988 and 1990, whereas the remaining 50% was treated in 1987, 1989 and 1991. This harvesting scheme was chosen to ensure a satisfactory annual regrowth of *T. natans* and to keep enough residual plant mass as shelter for fish, waterfowl and inhibiting agents for phytoplankton.

The annual average of harvested water chestnuts for the six year period amounts to 370 t wet wt, corresponding to 32 t of organic matter, 899 kg of nitrogen and 74 kg of phosphorus. This latter quantity exceeds the external run-off loading, of 69 kg P y^{-1}, (Durio *et al.* 1983), representing most of the total external loading of the lake.

8.3 RESULTS AND DISCUSSION

The general increase of total zooplankton biovolume during the six years of the survey appears to be relevant. Total biovolume, expressed as annual average, increased from 7.9 cm^3 m^{-3} in 1986 (the control year) to 9.5-10.5 cm^3 m^{-3} in the following years, with a maximum of 11.3 cm^3 m^{-3} in 1991. Fig. 8.2A shows the

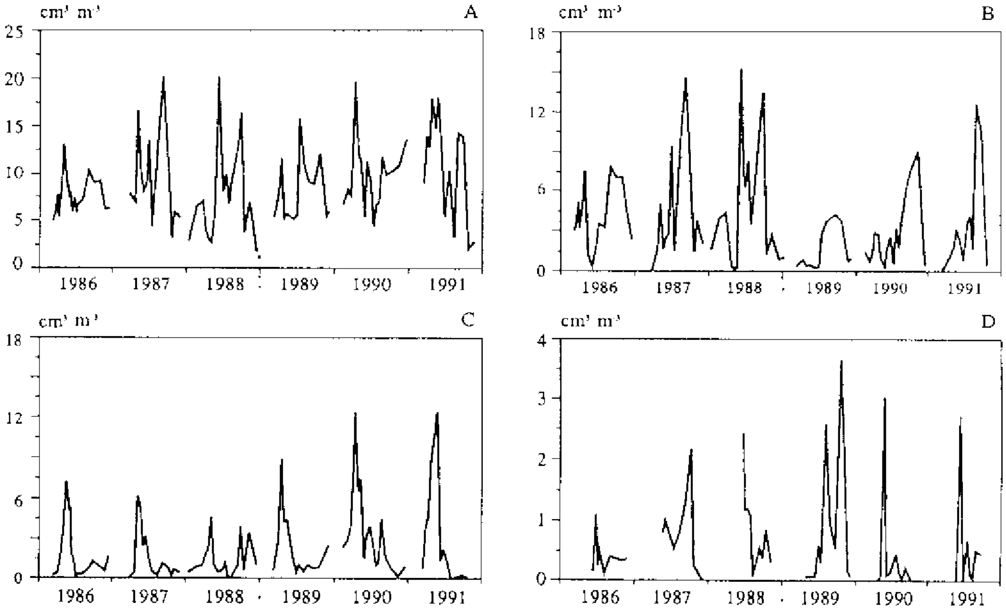

Fig. 8.2 Evolution of the biovolume of zooplankton population in Lake Candia: A: total zooplankton population; B: micro-filter-feeder cladocerans; C: *Daphnia hyalina*; D: *Leptodora kindtii*

seasonal trend of this pluri-annual evolution in which it is possible to distinguish two different peaks, in spring and in autumn.

The analysis of cladoceran populations shows that the spring-peak is attributable to *Daphnia hyalina* (Fig. 8.2C), the most important macro-filter-feeder present in the lake, whereas in autumn it is the sum of several species of small cladocerans (*Eubosmina coregoni, Bosmina longirostris,* and *Ceriodaphnia quadrangula*) that show a peak (Fig. 8.2B). These micro-filter-feeders have mainly increased soon after the lowering of the fish stock (1987-1988).

Daphnia hyalina biovolume remained at about the same value during the first two years after the reduction of the fish stock. This observation confirms similar results obtained in previous studies in semi-natural experiments (de Bernardi *et al.* 1986). Those experiments documented an increase in micro-filter-feeders after the removal of planktivorous fish, but not an appearance of large bodied crustaceans. One reason that can explain this delay in the success of the *Daphnia* population after fish reduction can be found in the fact that food selection by the planktivorous fish in Lake Candia is not strongly size selective, but appears as opportunistic, preying food items more abundant at a given time independently from their size (Giussani, unpublished data). Since 1989 the spring-peak of *D. hyalina* has grown-up over 12 $cm^3 m^{-3}$ in 1990 and 1991, doubling the values surveyed in 1986, 1987 and 1988).

The progressive increase of the predator *Leptodora kindtii,* reaching its maximum in autumn 1989 (Fig. 8.2D), can probably explain the decrease of importance of micro-filter-feeders, that in 1989 revealed a real collapse (Fig. 8.2B).

The increase of the importance of the large invertebrate predators, due itself to lower fish predation pressure, has somewhat affected smaller zooplanktonic populations. Further analyses of the data, now in progress, will deepen this important aspect of the population dynamics of small zooplanktonic preyed species.

For what concerns species composition of zooplankton populations, no dramatic changes occurred during and after the application of the treatments. We should note only the disappearance of *D. cucullata,* coexisting with *D. hyalina* with a low number of individuals during 1986, in the following years.

To a lesser extent, also the copepods *Eudiaptomus padanus* and *Mesocyclops*

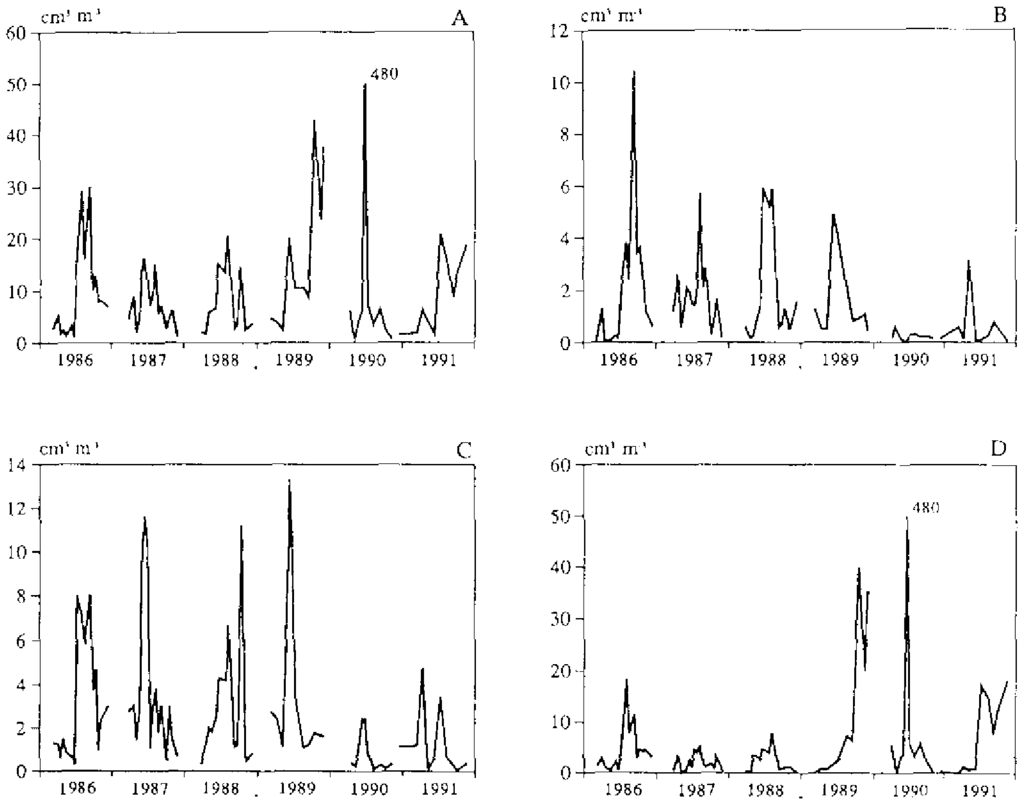

Fig. 8.3 Evolution of total phytoplankton biovolume (A) and of different individual or colony size classes (B: < 15 µm; C: 16-50 µm; D: >50 µm).

leuckarti and *Thermocyclops crassus* showed an increase. The total phytoplankton biovolume decreased from 1986 (the pre-treatment year) until the end of summer 1989 when a bloom of *Anabaena spiroides* took place; in 1990 the phytoplankton biovolume was, on the whole, lower than the previous years with the exception of an isolated peak due to the dinoflagellate *Ceratium hirundinella.* The annual trend of the algal size fractions <15µm and between 16 and 50 µm showed a marked decrease in 1990 and 1991 when *Daphnia hyalina* attained its highest biomass (Fig. 8.3), while the size fraction >50 µm decreased from 1986 to 1988 and then increased from 1989 to 1991.

The most representative phytoplankton taxa were the Cyanophyta (in summer and autumn) and the Cryptophyceae (throughout the year). As it concerns the biovolume, Chlorophyceae and Cryptophyceae decreased from 1986, while the Cyanophyta, after a decrease in the year 1986-1988, increased in the last few years;

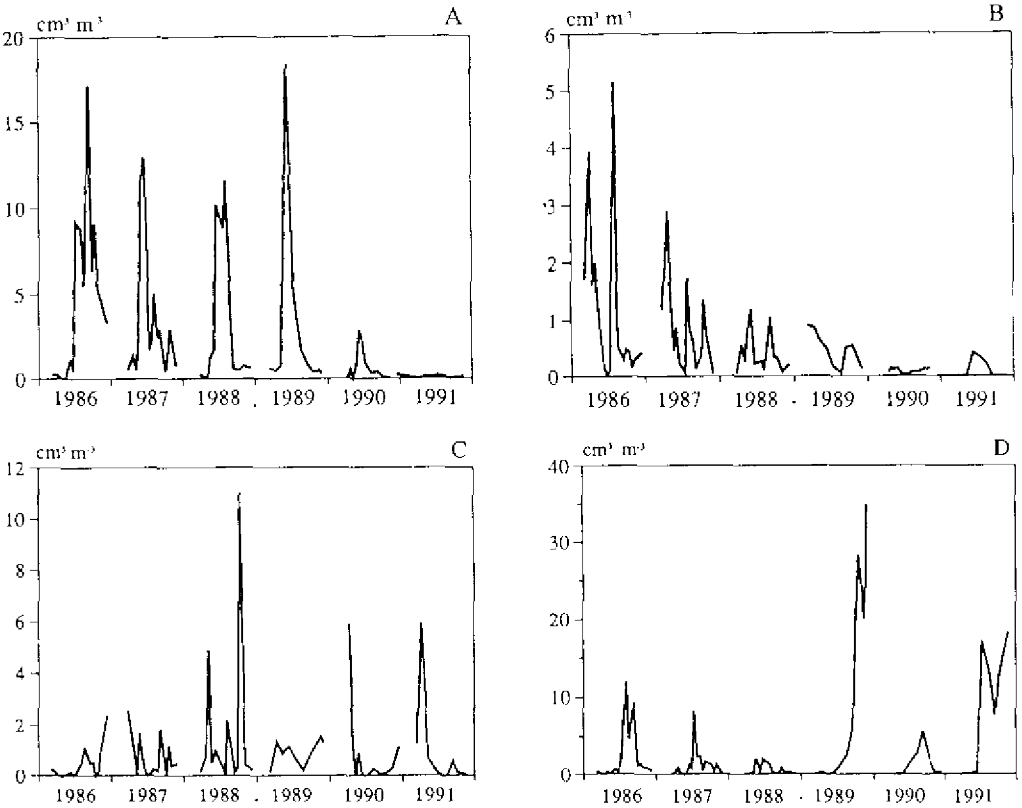

Fig. 8.4 Evolution of the biovolume of the most important algal groups: Chlorophyceae (A), Cryptophyceae (B), Chrysophyceae (C), Cyanophyta (D).

the Chrysophyceae did not show any particular annual trend (Fig. 8.4).

Changes in the relative abundance of some species occurred: until 1988 *Microcystis aeruginosa* was the prominent blue-green while *Anabaena spiroides* and *Gomphosphaeria naegeliana* became dominant respectively in 1989 and in 1990-1991; *Sphaerocystis schroeterii* characterized the green algae but, in the years before 1990, it was alternatively associated with other species that attained high biomass (*Staurastrum* spp, *Coelastrum* spp, *Cosmarium* spp, *Closterium* spp). Among the Chrysophyceae, *Mallomonas caudata, M. akrokomos* and *Chrysococcus* sp. were commonly present in the study period; the biomass peak observed in 1987 was due to *M. caudata,* while the spring relative maxima in 1990 and 1991 were determined by *Synura petersenii* and *Uroglena* sp. that were not observed in the previous years. Different species of *Cryptomonas* and *Rhodomonas* characterized the Cryptophyceae community.

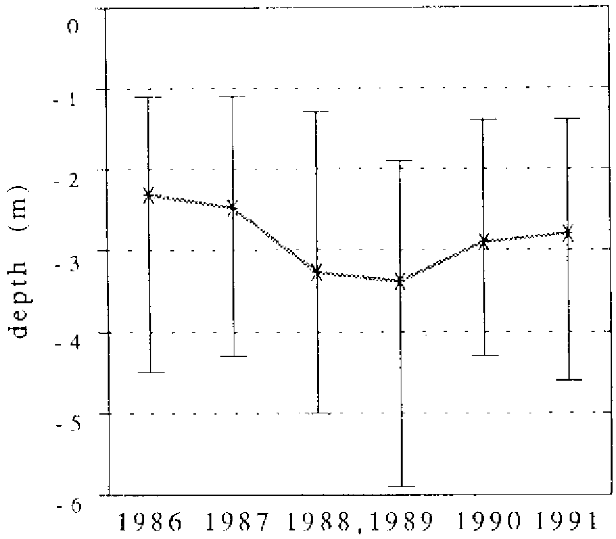

Fig. 8.5 Trend of the annual average of Secchi disc transparency and maximum and minimum values.

The variations of the annual average, maxima and minima of Secchi disc depth are given in Fig. 8.5: transparency increased from 1986 to 1989 (from 2.3 to 3.3 m) and then decreased in 1990 (2.9 m) and in 1991 (2.8 m). The expected inverse relationship between transparency and phytoplankton biomass was found just for the first three years of the research. Although a number of trophic state indexes (Carlson 1977, 1980) assume that the Secchi disc depth is primarily determined by algal biomass, it is well known (Canfield & Hodgson 1983; Lind 1986) that other variables also (in particular, light scattering by non-algal particles and non-particle light adsorption) control the transparency and may interfere with this classic inverse relationship.

In Lake Candia the light attenuation coefficient, calculated according to Kirk (1983), indicated that the non-phytoplankton component is quite important: in these conditions, when even moderate non-algal turbidity is present, the transparency variations are only in part explained by the phytoplankton biomass changes, and can be affected in an unpredictable way by turbidity variations. The survey of the main chemical parameters in the water showed that despite the reduction of organic nutrient loading by the macrophyte harvesting, the hypolimnetic oxygen concentration did not improve and the total phosphorus remained constant around the annual mean of 30 μg P l^{-1}.

The application of biomanipulation techniques on a real scale to natural environments has focused on several problems to which the attention of the scientists must be concentrated on in the future.

One of the most puzzling problems in controlling fish population is the high variability in the natural recruitment of the fish stock, mainly due to the annual variation of the spawning time, larval mortality, onset of spring production, rather than to the magnitude of parent stock (Ivlev 1961; Cushing 1982; Giussani & Ruffoni 1985). In small lakes, to which biomanipulation is addressed, fisheries overexploit top predator fish and neglect zooplanktophagous, altering the abundance and the structure of the fish community. The management of naturally occurring hydrophytes or their introduction may be a further variable influencing fish community ecology. At last, the availability and the accessibility of spawning areas, appropriate for the different species habits, have great importance in determining fish population structure in many small lakes.

Several problems, more directly pertaining to the field of limnology, are still open. If the effects of selective predation by zooplanktophagous fish are relatively well known in the short term, the knowledge in the medium and long term is scanty. In fact, as a secondary effect, it is possible to observe an increasing predation trend by invertebrate such as *Chaoborus* and *Leptodora* (de Bernardi *et al.* 1987). Later on, selective grazing on dimensional basis can produce a reduction of a few algal species and the fertilizing effect due to *in situ* nutrient release (Goldman *et al.* 1979) can be of particular relevance during summer epilimnetic depletion. As phytoplanktonic species are not liable to the same grazing pressure and an increase of nutrient concentrations is, competitively, more favourable to larger algal individuals (Berquist & Carpenter 1986; McQueen 1990), feeding activity by herbivorous zooplankton may change species composition, transferring nutrients from smaller edible to larger non-edible species (Lehman & Sandgreen 1985; Bush & Brooks 1988).

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CHAPTER 9

FOOD-CHAIN MANIPULATION AS A TOOL IN MANAGEMENT OF SMALL LAKES IN THE NETHERLANDS: THE LAKE ZWEMLUST EXAMPLE

R. D. Gulati

9.1 INTRODUCTION

In the Netherlands the control of eutrophication of inland waters is among the major issues in environmental policy (Hosper & Jagtman 1990). The Netherlands being a delta country, the problem is rather acute because of a virtually complete dependence of surface water supplies on transboundary rivers (Rhine, Meuse and Scheldt). These rivers, as they enter across the national boundaries, are already highly polluted and their nutrient loads are very high. The River Rhine alone contributes >80% to the total loads of P and N from across the national boundaries. In addition, intensive agricultural practices and animal husbandry are the cause of an excessive use of fertilizers. For example, in 1990 the nitrogen application to agricultural soil in the Netherlands, including both manure and fertilizers, was about 450 kg N ha^{-1} y^{-1} (GLOBE-Europe 1992). This is about six times as high as the average for Europe and perhaps the highest average rate of use for any country. Nutrient control policy and international programmes (Rhine Action Programme, North Sea Action Programme) have led to detectable reductions in levels of total-P in the inflow waters. However, the loading with P of the inland waters is still high. The national Environmental Policy Plan, operative since 1989, envisages an even more comprehensive reduction of eutrophication of surface waters. To prevent algal blooms, reductions of total-P to <0.15 mg l^{-1} and N to 2.2 mg l^{-1} are considered as acceptable levels. Surface pollution laws have also been enforced and regional water authorities are now very active in taking steps to improve water quality in the lakes by both reductions of the external P loadings and active management measures.

In the Netherlands, eutrophication of the shallow lakes, which outnumber the deep-water bodies, started in the early 1950s. The allochthonous inputs to these lakes cause high loadings of P and N *via* water, mainly, from the rivers Rhine and Meuse. These lakes are now characterized by very high concentrations of cyanobacteria (blue-green algae) in the phytoplankton and poor underwater light climate.

The in-lake restoration measures to reduce P, involving sediment dredging and removal (Van der Does *et al.* 1992) and chemical inactivation of P by treating lake water with ferric chloride (Van der Vlugt & Aldenberg 1982) produced only short-term ameliorations. Ineffectiveness of such measures is attributable generally to the continuing high release from the sediments as well as inability of the measures to reduce external P loading rates to <0.3-0.4 g C m^{-2} y^{-1}. Also, P reduction by flushing with water poor in P (Hosper & Meijer 1986; Jagtman *et al.* 1992) met with temporary successes. In a long-term extensive study of Loosdrecht lakes the reduction in external P loading produced only minor changes in the biotic factors (see paper in Van Liere & Gulati 1992). Both, chlorophyll and seston levels remained virtually unchanged, especially the former. Also, underwater light climate did not improve, nor did the phytoplankton and zooplankton exhibit changes in the species composition or biomass (Gulati *et al.* 1992). The failure of the measures in the Dutch lakes, as in the Loosdrecht lakes (Van Liere & Janse 1992), is probably because of high P-loading rates even after the rehabilitation measures, besides the unabated sediment release of P. Besides, P release via the in-lake P sources, both by mineralization of organic matter in the water column and metabolic excretion of zooplankton and fish, apparently retarded the P reduction rates (Gulati *et al.* 1991; Van Liere & Janse 1992). Thus, the measures involving external P reductions and hydrological management have proved insufficient. This has necessitated the use of complementary restoration techniques, viz ecological management of aquatic ecosystems (Van Donk & Gulati 1991), the so-called foodweb manipulation.

In this paper I describe a case study of the Lake Zwemlust, which was restored by foodweb manipulation alone, since nutrient loadings, being primarily via underground seepage, could not be reduced. In the six-year follow-up investigations, the effects of planktivorous fish removal/reduction were examined without changing the external nutrient loading so that recovery was attributable to biomanipulation measures alone.

9.2 PREVAILING BIOLOGICAL CONDITIONS: A RESUME

Most freshwater lakes in the Netherlands are shallow (1-2 m) and vary greatly in area (<1 ha to > 1, 000 ha). In most cases they owe their origin to peat dredging and are, therefore, humus-rich, but alkaline and highly productive. They are invariably interconnected waterways with significant influence of underground seepage, including loss of water in many cases. The nutrient enrichments in these lakes via the surface inflows is generally quite high, such that total-P and total-N levels exceed 1 mg P l^{-1} and 5 mg N l^{-1}. Consequently, the primary productivity is high (300-600 g C m^{-2} y^{-1}) so that seston mass is high too (5-20 g C m^{-3}) and mostly dominated by filamentous cyanobacteria (*Oscillatoria* spp or *Microcystis* sp.) which reach bloom conditions (200 10^{6} fil. l^{-1}) in summer. This leads to poor underwater light conditions and very low Secchi-disc depth (SD) values (0. 20-0. 50 cm) in summer, resulting in virtual disappearance of macrophytic vegetation. Consequently, the pike (*Esox lucius*), a piscivorous fish that uses littoral vegetation as a substrate for spawning and a refuge against predation, has disappeared, making place for pikeperch (*Stizostedion lucioperca*). The pikeperch, contrary to the pike, cannot predate effectively on the relatively large fish (>15 cm) as bream (*Abramis brama*), with laterally compressed body. In short, the habitat deterioration and poor condition of the pike have generally caused the pikeperch and cyprinids to increase, especially the bream. The planktivorous bream (<15 cm) predates more selectively on microcrustaceans (small daphnids, *Bosmina* spp and *Chydorus* sp.) and when somewhat older it switches to a predominantly benthivorous diet (benthic crustaceans, chironomids and oligochaetes). The pikeperch, on the other hand, predates more efficiently on the larger-bodied cladocerans, the *Daphnia* spp. Thus, in most of these shallow, eutrophic lakes the larger *Daphnia* generally have become rare, or disappeared altogether. This has resulted in the zooplankton grazing pressure to decrease markedly. Thus, the phytoplankton increase that ensued these changes in the food-chain led to increased limitation of nutrients or light so that the filamentous cyanobacteria became predominant. Large-bodied grazers (*Daphnia*) cannot effectively feed on these filamentous blue-greens. In short, both high predation by fish and poor food condition caused the larger grazers to vanish, to be replaced by the relatively smaller-sized cladocerans, (*Daphnia cucullata* and *Bosmina* spp). Fish standing crop in the lakes, dominated by cyprinids, particularly by bream, is quite high (200-1, 000 kg ha^{-1}). The browsing activity in the lake bottom for food of the adult bream, which is predominantly benthivorous, contributes to resuspension of sedimented material (Meijer *et al.* 1990). The wind-induced mixing is, however, the main cause of stirring up of the bottom sediment in shallow lakes (Gons *et al.* 1986) leading to poor light climate and enhanced nutrient availability.

The prevailing limnological characteristics and failure or non-feasibility of the other restoration measures, generally form the basis of biomanipulation strategy. The Lake Zwemlust, which is the most extensively and long-term studied biomanipulated lake in the Netherlands, is used here as a case study.

9.3 LAKE ZWEMLUST: A CASE STUDY

Lake Zwemlust is one of more than a dozen lakes that were biomanipulated recently in the Netherlands. These lakes are shallow (Zm, 1-2. 5 m) but differ greatly in area (1 to 2700 ha). Lake Zwemlust is a shallow (Zm, 1. 5 m: Zmax, 2. 5 m) water body, located in the village of Nieuwersluis (Province of Utrecht), and serves as an outdoor swimming pool for the local community. The input of water to the lake, rich in both P and N, is mainly *via* seepage from the polluted River Vecht running nearby. The nutrient loadings of the lake *via* the seepage water are *ca* $\geq$2g P m ^{2} y ^{1} and >9 g N m^{-2} y^{-1}, including also the atmospheric deposition in case of N (Van Donk *et al.* 1993).

Thus, the lake developed recurrent blooms of *Microcystis aeruginosa* in summers, with high chlorophyll (*ca* 250 mg l^{-1}) and turbidity (SD *ca*, 0. 30 m). Consequently, macro-vegetation disappeared almost completely, and the structure of the fish community was altered: the pike vanished and bream became dominant. In 1968, an unsuccessful attempt was made to control cyanobacterial blooms, by dredging and sediment removal, and by applying Karmex AA (80%), a herbicide (Van Donk *et al.* 1989).

9.3.1 Lake and biomanipulation measures

The present biomanipulation measures were taken in March 1987 (Van Donk *et al.* 1989; Gulati 1989, 1990). The study involved cooperation among the lake managers, limnologist, fishery biologists and engineering bureaus and a six-year long (1987-1992) data collection of various parameters.

Three main steps were taken to manipulate the lake. First, in the second half of March 1987 the lake was emptied by pumping out the water to a nearby ditch and the fish (mainly bream) were removed by seine netting and electro-fishing. Second, before the lake got refilled with seepage water from the River Vecht, taking about three days, stacks of willow twigs were affixed to the lake bottom in the northern part, to serve as shelter and spawning ground for the pike as well as a refuge for zooplankton. Third, 1,600 pike fingerlings (4 cm) and 140 specimen of adult rudd (*Scardinius erythrophthalmus*) were introduced to serve as a food for the pike. Together with this, about 1 kg (wet weight) of daphnids (*D. magna, D. galeata*), which served as food for the fish in the containers during transport, was also introduced. Lastly, seedlings of *Chara globularis* were introduced and some 200 roots of *Nuphar lutea* were planted in the shore line area. The pike introduction was repeated in April 1988.

9.3.2 Main events following biomanipulation

Within a few weeks of biomanipulation, *Pteromonas*, a chlorophyte, exhibited an explosive increase despite the low water temperature (10 ℃). Together with some diatoms and flagellates this nanoplankter caused chlorophyll *a* to increase to 50 mg l^{-1}. The Secchi-disc transparency decreased to *ca* 0. 50 m. Later in April, rotifers, especially *Brachionus calyciflorus, Polyarthra* sp. and *Filinia* sp., reached densities of >4000 ind l^{-1} but declined sharply by early May. The crustacean maximum following the rotifer, decrease consisted chiefly of copepods and nauplii. Thereafter, *Bosmina* sp. increased and three *Daphnia* spp (*D. galeata* , *D. cucullata* and *D. magna*) followed one another in quick succession, culminating in *D. pulex*. In July the zooplankton concentration decreased drastically (Fig. 9.1). In late

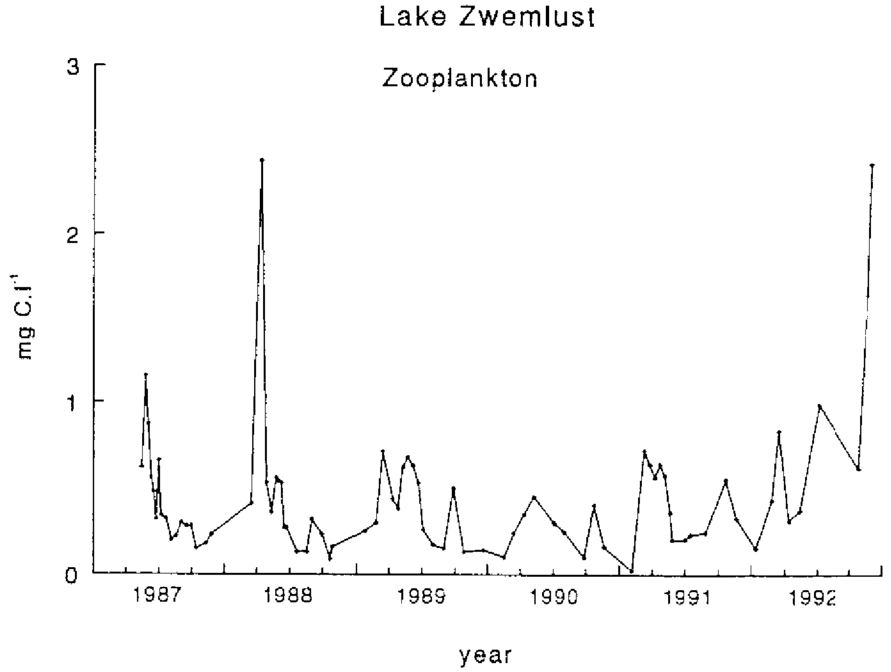

Fig. 9.1 Zooplankton (< 150 µm) biomass in Lake Zwemlust from the time of its biomanipulation in March 1987.

summer, ***Eudiaptomus gracilis***, a calanoid copepod, and the large-bodied daphnids (***D. pulex*** and ***D. magna***), though low in numbers, caused the phytoplankton to decline through their high grazing impact (Gulati 1989). The grazing pressure

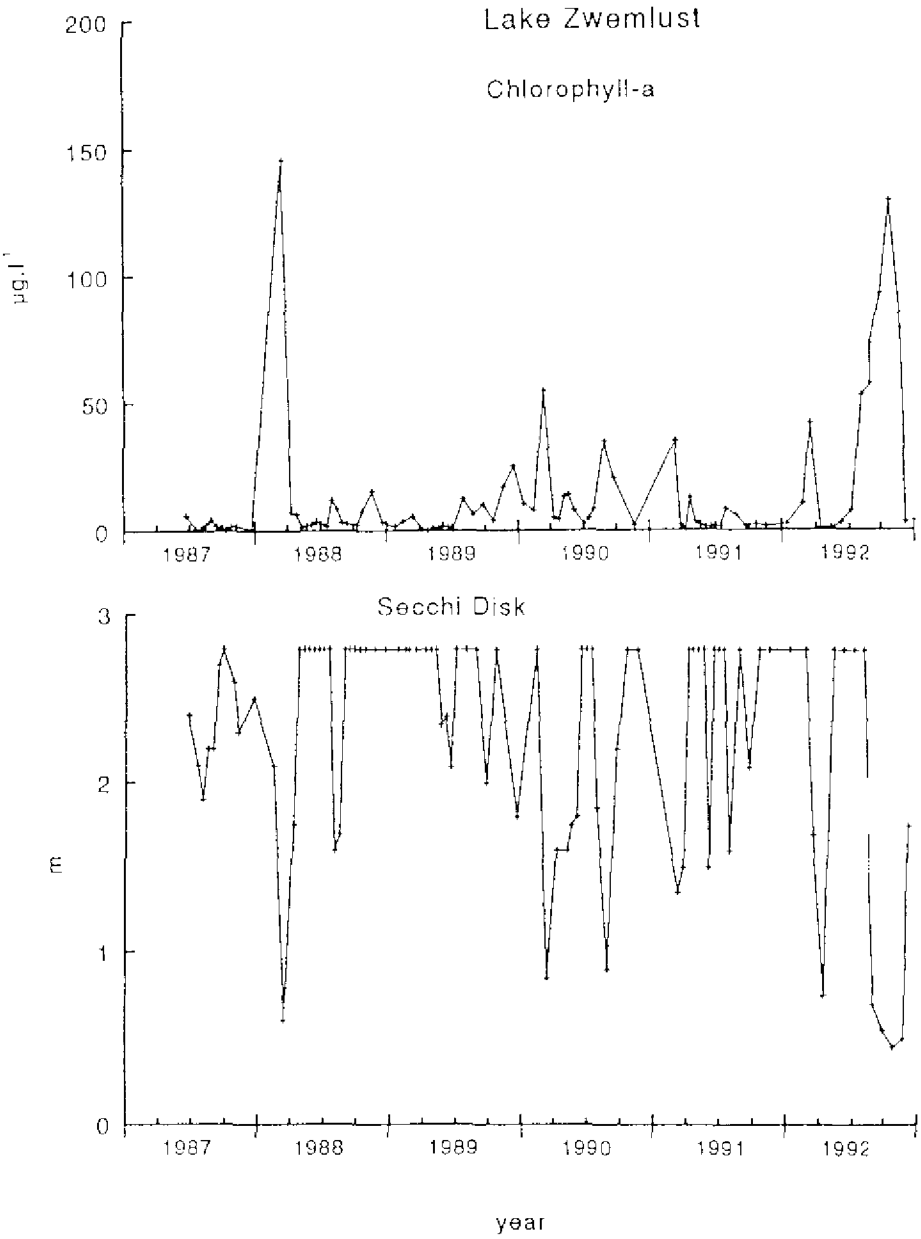

Fig. 9.2 Chlorophyll-a and Secchi-disc depth (metres) in Lake Zwemlust. The horizontal areas of the measurements indicate visibility up to the lake bottom.

remained high, resulting in a decrease in the chlorophyll level to <5 mg l^{-1} and Secchi-depth to increase to >1. 5 m (Fig. 9.2). The planted rudd did not spawn until July 1987, and only 20% of the pike that was introduced survived. The fish standing stock in the lake was about 30 kg wet weight. Chironomids, mainly, *C. plumosus*, attained a maximum of 8, 000 ind m^{-2}.

In 1988, *Ankyra*, a green alga peaked in mid-March, causing the annual chlorophyll maximum (140 mg l^{-1}). *Daphnia pulex* (130 ind l^{-1}) was the main grazer in spring 1988. Its fecundity was very low, generally with 1 egg ind^{-1}, with somewhat bigger clutch sizes (3 eggs ind^{-1}) for larger animals (2. 50 mm). The macrovegetation was well developed by mid-summer, with *Elodea nuttallii* and *Chara globularis* as dominant forms. High densities of ostracods (1, 000 ind l^{-1}) and microcrustaceans, *Simocephalus vetulus* and to some extent *Chydorus sphaericus*, were encountered in open water. Zoobenthos developed a rich diversity (Kornijow & Gulati, 1992a, b): in the 63 species recorded, *Lymnaea corvus* and *Planorbis planorbis* were abundant. The snail *Valvata piscinalis* was very common. Also *Gammarus pulex* and *Stictochironomus*, typical inhabitants of clear-water, were encountered. The high water transparency was caused mainly by N-limitation of phytoplankton (Van Donk *et al.* 1990) apparently due to competition with macrophytes which acted as N sink.

In 1989, contrary to 1987 and 1988, there was no spring bloom (chlorophyll, <5 mg l^{-1}) (Fig. 9.2). Subsequently, however, *Volvox aureus* became common and chlorophyll increased to 14 mg l^{-1}. Among the rotifers *Keratella cochlearis* (3, 000 ind l^{-1}) was the principal species. Annual primary productivity in 1989 of 70 g C m^{-2} was only 50% of that in 1988. There was a shift in *Daphnia* species with the appearance of *D. galeata* (140 ind l^{-2}). Macrophytes standing crop was estimated at 2, 093 kg ha^{-1}; they covered about 80% of the lake's surface area. Again, *Elodea nuttallii* was very important (Ozimek *et al.* 1990). This vegetation contained about 75% total-N and total-P in the lake (Tab. 9.3 in Van Donk *et al.* 1990). The diversity of macrofauna was quite high (Kornijow *et al.* 1990; Kornijow & Gulati 1992 a, b). The snail *Lymnaea peregra* which used *Elodea* as a substrate, reached densities of up to 102 ind m^{-2}. The snail acts as an intermediate host of a trematode, *Trichobilharzia ocellata*, which parasitizes birds. The cercariae of this trematode caused complaints of swimmers' itch. The zooplankton grazing rates ranged between 125 and 340% d^{-1} from spring through summer. Water transparency improved markedly (SD >2 m) so that the lake bottom was visible (Fig. 9.2): The rudd spawned thrice in 1989 forming a standing crop of

106 kg ha^{-1} (Van Donk *et al.* 1990). The 1^+ and 2^+ year classes of the pike were in poor condition.

During 1990 and 1991 diatoms (*Stephanodiscus*) and green algae peaked in spring. Chlorophycean maximum was dominated by *Oocystis* in 1990 and *Eutetramorus* in 1991. In 1990, a major reversal of the improvements, observed in water quality during 1987-1989, occurred. For the first time since 1987 *Bosmina longirostris* dominated the cladocerans. Also copepod numbers increased and the crustacean density exceeded 1,000 ind. l^{-1} (Fig. 9.3). The rotifer numbers (mainly *K. cochlearis* and *Kellikottia longispina*) were up to four times higher than during 1987-1989. Besides, the zooplankton community grazing rates remained below 50% d^{-1} and the light climate deteriorated (SD <1 m) already in early spring. This was observed also for primary productivity in 1990, which was 3.5 times that in 1989. Lastly, these major shifts starting in 1990 caused the macrophyte standing crop to decrease distinctly. *Elodea nuttallii* was replaced by *Ceratophyllum demersum* (Van Donk *et al.*, in press). As regards fish, the standing crop of rudd in 1990, ca 395 kg ha^{-1}, was constituted about 50% of the 0^+ and 1^+ fish; the 0^+ pike (5.4 kg ha^{-1}) and the $>1^+$ pike formed about 45 kg ha^{-1}. The condition of rudd deteriorated in 1991 and its standing-crop dropped to 110 kg ha^{-1}.

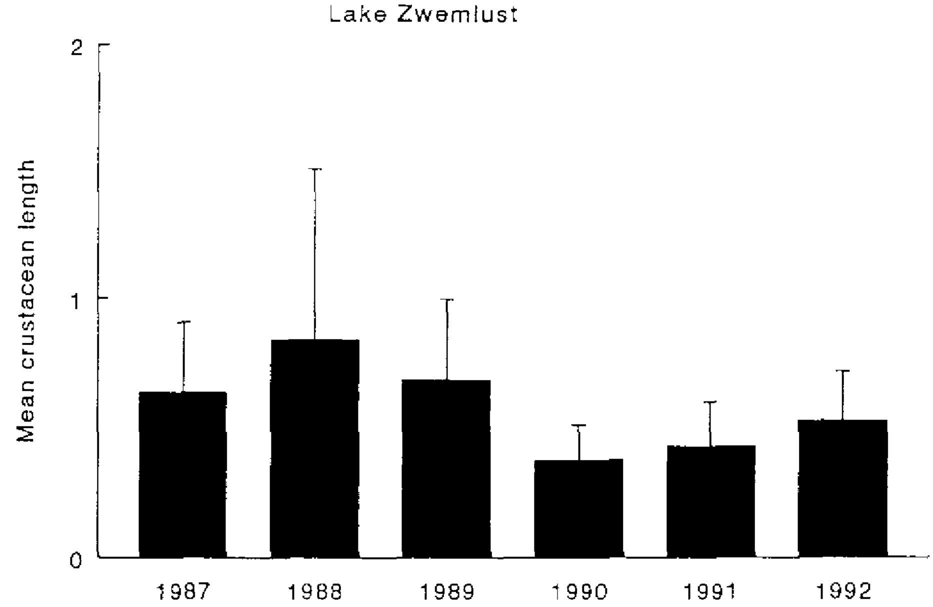

Fig. 9.3 Changes in the mean length (mm) of the crustacean community in lake Zwemlust.

In 1992 phytoplankton production rates were markedly higher than in 1991, caused mainly by *Microcystis*. The annual production maximum (>3 g C m^{-2} d^{-1}) was observed in early August. Also the chlorophyll a level was high and exceeded 50 mg l^{-1} in summer, was the second highest in the six years (Fig. 9.2). But the production per unit chlorophyll (<50 mg C mg^{-1} chlorophyll *a* d^{-1}) was the lowest in the six years. The average seston concentrations more than doubled since 1987. This explained the concomitant, sharp decreases in Secchi-depth. The spring peak of the zooplankton was absent; and the annual maximum occurred in early September. *Bosmina longirostris* exhibited an unprecedented increase (950 ind. l^{-1}: Fig. 9.1). *D. cucullata, the smallest among the Daphnia* spp encountered in the lake, became the dominant daphnid, with their numbers always exceeding 80 ind. l^{-1} during April-October. The annual maximum was observed in early winter of 1992/1993 rather than in the spring especially because *D. cucullata* persisted in high numbers. The grazing rates exceeded 100% d^{-1} during early summer, caused mainly by the *Daphnia* population. A six-fold increase in the seston mass in the mid-summer followed the sharp decrease in the zooplankton grazing rates. The bosminids were important grazers in 1991, whereas in 1992 it was the daphnids.

The average length computed from the changes in the average weight, decreased during the six years (Fig. 9.3). In 1988 when *D. pulex* was dominant the average weight per individual zooplankters in the community (except nauplii) was 5. 40 mg C ind^{-1} but in 1990 it decreased to 1. 70 mg C ind^{-1} with a slight increase thereafter.

9.4 DISCUSSION

9.4.1 Role of zooplankton and appearance of macrophytes

The biomanipulation of Lake Zwemlust was a pioneering study to restore a lake in the Netherlands by food-web manipulation alone: neither inlake nutrient reduction nor external nutrient reduction was employed. The purpose of the experiment was to improve the underwater light climate, i. e., to increase the depth of Secchi-disc visibility from ca 0. 30 m before the measures to 1. 0 m thereafter - the basic water quality norms for outdoor swimming waters in the country. The experiment was fairly successful, in that a prolonged clear-water phase was achieved and generally persisted for long spells during the six-year follow-up study. This is in contrast to the other manipulated lakes in the country, both big and small, in which the improvements were only transient. The success of the measures in Lake Zwemlust can be attributed chiefly to its small size and shallowness of the lake. Because of the small size, the wind fetch is much lower in Lake Zwemlust than in large lakes. This, together with the high water clarity and the high nutrient concentrations promoted a luxuriant development of macrophytic vegetation which caused nutrient limitation and thus contributed to the decrease of the phytoplankton. The lake, therefore, did not have the drawbacks associated with size scales (DeMelo *et al.* 1992) which make the management measures much less effective. In addition, the isolation of Lake Zwemlust from other surface waters facilitated a complete emptying to ensure a 100% fish removal, besides preventing the problem of entry of fish from adjacent waterbodies. This latter was a major obstacle and a factor in the failure of the biomanipulation measures in one of the Loosdrecht lakes, the Lake Breukeleveen (Van Donk *et al.* 1990).

An interesting feature of the experiment in Lake Zwemlust was the high and uninterrupted nutrient (N & P) loadings *via* the seepage inflows, even after its manipulation. In other Dutch lakes food-web manipulation measures were invariably preceded by some nutrient reduction measures, despite poor success (Gulati *et al.* 1990; Gulati 1990; Meijer *et al.* 1990; Van Donk *et al.* 1990). Moreover, in these lakes the nutrient inputs were relatively much lower when foodweb manipulations were initiated. Some examples are: 1) Lake Breukeleveen (Van Donk *et al.* 1990), as already mentioned, in which nutrient loading was reduced beforehand; 2) Lake Klein Vogelzang, in which nutrient-rich sediment was dredged and removed, besides P-stripping in the water column (Van der Vlugt *et al.* 1992); and 3) Lake Wolderwijd, which was flushed intermittently with P-poor and algae-poor water before and during its biomanipulation (Meijer *et al.* in press). Compared with these and other lakes, in Lake Zwemlust the increase in Secchi-disc transparency was greater, reaching the lake bottom (2 m depth). It was persistent virtually throughout the summer periods except in 1990. Moreover, vis-a-vis other studies in the Netherlands (Gulati 1990; Meijer *et al.* 1990), and elsewhere (Carpenter & Kitchell 1993), there was no reference waterbody for Lake Zwemlust. However, even though the information on the lake before its manipulation period is anecdotal (Van Donk *et al.* 1989, 1990), the improvement in water quality following the manipulation was unequivocal.

The lake's emptying and quick refilling with nutrient-rich river water *via* seepage created a situation analogous to putting up a batch culture. The lake's sediment served as an inoculum for algae and as a nutrient source. At the start, top-down biotic factors were virtually non-existent and the nutrients were continuously in excess supply. Therefore, temperature and light were influential in controlling the phytoplankton growth and development. Thus, in this "simplified" lake ecosystem phytoplankters (*Pteromonas*) were the first to develop, followed by rotifers (*Brachionus* spp), which were most likely inoculated *via* their eggs from the lake sediment. The rotifers benefitted from the absence of predators, and competition for food and increased rapidly. They were the first consumers in the lake ecosystem, with nutrient → algae → rotifers forming the simplified food chain governed by bottom-up control. Among the cladocerans, the smaller-bodied forms, *Bosmina longirostris* and *Daphnia cucullata*, the 'native' species (Van Donk *et al.* 1990), developed first to be quickly superseded by the larger daphnids. The succession of larger *Daphnia* spp (*D. magna, D. galeata, D. pulex*) in the spring and summer was quick, but restricted to 1987. Their pronounced decreases indicated food limitation, which is confirmed by dips in chlorophyll and seston concentrations, besides the increase in Secchi-disc depth. Also, high clearance rates of the zooplankton (Gulati 1990) indicate low food concentrations. Thus, the top-down factors steadily became more important than bottom-up factors.

Because of very weak zooplanktivory, the large-bodied daphnids developed and exerted strong influence on seston. But the food shortage caused the large grazers to diminish rapidly so that the bottom-up effects became dominant again. In short, in this simplified ecosystem, the zooplankton served as a nexus through which the cascading effects were very effective in decreasing primary production rates and increasing water clarity (see, e.g., in Carpenter & Kitchell 1992). Based on analysis of extensive data sets they found the top-down response to weaken at the zooplankton-phytoplankton level in most cases. Virtual absence of predatory fish was a crucial factor in the success of our experiment in 1987 when grazing rates of large *Daphnia* population (Gulati 1989, 1990) caused phytoplankton to keep low. Although the Secchi-disc depth norm was achieved, the system lacked stability.

In 1988 despite the initial similarities to 1987 with respect to high zooplankton grazing activity and the light climate, the lake exhibited some stability due the development of macrophytes, a new element to the system's edifice. Macrophytes also contributed to N-limitation of phytoplankton growth in the summer (Van Donk *et al.* 1990). This was more important in restricting phytoplankton development than mortality caused by zooplankton grazing (Gulati 1989, 1990). However, in spring 1988, the grazing rate of *Daphnia pulex*, released of predation pressure, reached an extremely high level (430% d^{-1}) and was undoubtedly the cause of exceptionally high algal mortality. Consequently, macrophytic vegetation and macro-algae developed luxuriantly in 1988 (Ozimek *et al.* 1990) and in the first-half of 1989. Phosphorus supply *via* seepage water being unlimited, nitrogen decreased to below detection levels, mainly due to its withdrawal by *Elodea nuttallii* (Van Donk *et al.*, in press). Thus, the macrophytes acted as N sink thereby limiting the phytoplankton growth during most of the vegetation period.

9.4.2 Shifts in macrophytes and increase in fish-stock

The year 1990 was marked by an array of changes resulting in a shift in the lake's trophic status. First, fish standing stock increased to 440 kg ha^{-1}, comprising mainly rudd (398 kg h^{-1}), about half of which was 0^+ and 1^+ fish. Both rudd and pike predated on the zooplankton (unpublished data), including *D. pulex* which thus disappeared. Second, a simultaneous increase in densities of rotifers and small-bodied cladocerans is most likely due to released pressure of competition for food from the larger grazers. These changes in zooplankton structure were sustained in 1991, despite some fall in the standing stock of rudd and pike. Even though the zooplankton tended to revert to the pre-biomanipulation state, the grazing was still relatively high, mainly attributable to *Bosmina* populations. But the primary production rates and chlorophyll concentrations increased. Besides, a shift in dominance from *Elodea* to *Ceratophyllum demersum* pointed to trophic changes and deterioration in water quality. There is evidence that rudd selectively consumed *Elodea,* rather than *Ceratophyllum* (Van Donk *et al.,* in press). This will help explain the shift from *Elodea* to *Ceratophyllum.* This switch in feeding behaviour of rudd, from zooplanktivory to herbivory, is certainly a crucial factor in relieving predation on zooplankton. Apparently, only the smaller-sized zooplankton (bosminids) benefitted relatively the most from it. Should the *Ceratophyllum* continue to dominate in the coming years, the standing crop of *Elodea* will be kept low due to grazing on it by the rudd. Floating forms such as *Ceratophyllum* are known to draw their nutrients from the water column (Best, 1977) rather than from the interstitial water in the lake bottom. Therefore, it remains to be seen if its dominance will lead to a decrease of internal P-loading *via* the sediment.

Contrary to some other Dutch lakes, planktivore reductions did not lead *Neomysis integer,* an invertebrate predator, to manifest itself in the lake (Meijer *et al.,* in press). This and other invertebrate predators (*Chaoborus* spp) (Elser *et al.* 1987) can effectively predate on small-sized and juvenile cladocerans. But this does not help explain the well-known mid-summer declines of the zooplankton which often occur even when the invertebrate predation is low. In such cases food limitation may play a more crucial role. In Lake Zwemlust, the situation is, however, alarming with regard to the standing crop of fish, especially the rudd which has reached 400 kg ha^{-1}, a level very similar to that reached by cyprinids in most eutrophic lakes. In spring/early summer the fish strongly influence the zooplankton structure and densities.

Lastly, even though the food-web manipulation of Lake Zwemlust is often considered as a complementary restoration technique, rather than an alternative to measures involving nutrient reduction. The situation in case of Lake Zwemlust is unique in that food-web manipulation was the only workable restoration option. The nutrient reduction measure is not a feasible control measure since the seepage water is the sole source of N and P. Thus, the 'positive' results obtained in the lake can be considered as an exception rather than a rule. Because of the multidisciplinary and the long-term nature of the study after the lake's biomanipulation, the study was both informative and instructive. More recently, the delayed and secondary effects have, nevertheless, cast some doubts on the long-term stability of the clear-water 'phase' in which macrophyte will continue to play a crucial role. The zooplankton plays a more direct role in reducing phytoplankton and triggering improved light climate. Nonetheless, the macrophytes and planktivorous fish may be the crucial aspects in management and control of water quality in the small lakes like Zwemlust.

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CHAPTER 10

Case studies: LAKE BALATON (Hungary)

Í. Tátrai

10.1 INTRODUCTION

As a result of intense eutrophication in Lake Balaton, especially in the last decades of this century, the fish fauna has changed greatly. Undesirable changes include a decline in fish stocks of the most commercially valuable species such as pike-perch (*Stizostedion lucioperca* L.), pike (*Esox lucius* L.) and catfish (*Silurus glanis* L.) and an increase in a low-value cyprinid species principially bream (*Abramis brama* L.) and roach (*Rutilus rutilus* L.). The proportion of the most valuable fish species in catches was an order of magnitude higher (while the proportion of bream has increased by some 30-40%) at the beginning of this century compared to catches made in the last 10-15 years.

In water quality research increased attention is being paid to the effect of fish on phytoplankton biomass. A large number of studies shows that reduction of the fish stock (a form of biomanipulation) can cause a significant decrease of chlorophyll-a content and turbidity of the water (Hanson & Buttler 1990; Sondergaard *et al.* 1990). This is especially of interest for the restoration of turbid shallow lakes where biomanipulation can cause the system to switch to an alternative stable clear water equilibrium (Moss 1990). A simple causal link between fish stock and phytoplankton productivity is the increased nutrient release from the sediment that can result from benthivorous behaviour of fish (Tátrai *et al.* 1990). To aid the arrest of 'degradation' of the fishery by decelerating the rate of eutrophication, an extensive research programme was implemented aimed at studying the eutrophication processes by benthivorous fish in 'lake in lake' systems in Lake Balaton.

10.2 MATERIALS AND METHODS

Lake Balaton has a large surface area (596 km^2) but its average depth is only 3.2 m (length 77 km; maximum width: 16 km). A rapid eutrophication of the lake started at the end of the 1960s. The SW area of this elongated water body, with some 35 inflows and one outflow, is nowadays hypertrophic while its eastern part is still mesotrophic.

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. One enclosure served as a control (CE) while the other was stocked with varying biomass of bream (*Abramis brama* L.) (FE) corresponding to biomasses in the different basins of Lake Balaton (Tab. 10.1).

Water samples for physical, chemical and biological analyses were taken every 2-5 days from the two enclosures and Lake Balaton (LB) nearby the enclosures with a surface-mud tube sampler 12 cm in diameter.

Tab. 10.1 The number and size of bream (*Abramia brama* L.) used for the experiments.

Date of the experiments	Average water temp. °C	No & Biomass of fish (g m^{-2})	Average weight (g) of fish (range)	Total increment in weight (%)
01-06-11.09 1984	18.7	9 60.7	47.9 (10.0-106.5)	82.8
21.06-18.07 1985	19.0	6 79.7	94.3 (8.0-158.0)	49.6
04.07-11.09 1986	21.9	4 46.4	82.4 (69.0-107.0)	21.4

10.3 RESULTS

10.3.1 Bacteria

In 1985 and 1986 the production of the bacterioplankton was highest in the presence of fish (Fig. 10.1). But in 1985 the bacterial production in FE was very close to that measured in the eutrophic basin of the lake.

10.3.2 Phytoplankton

A total of 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. In FE, however, the diatoms were replaced by filamentous blue-greens (*Aphanizomenon flos-aquae* and *A. issachenkoi*). The number of filaments doubled within 4-5 days and accounted

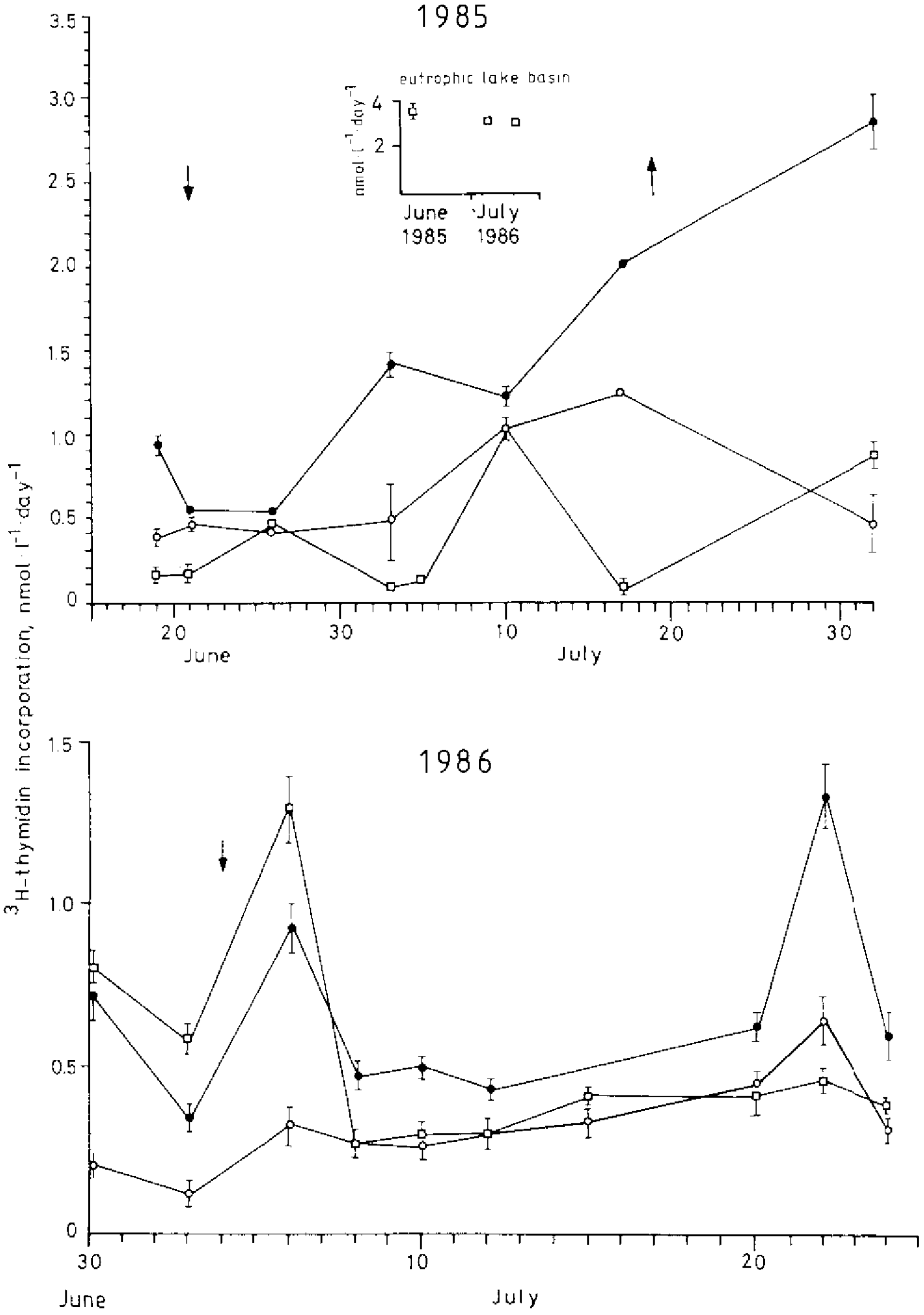

Fig. 10.1 The activities of bacterioplankton in the fish (●) fish and fish free (o) enclosures and in Lake Balaton ( ).

for more than 90% of the total biomass at the end of the experiments. Blue-greens appeared in CE and LB as well, but their biomass was only 20% of that found in FE. In CE the biomass of phytoplankton, apart from the small fluctuations, decreased throughout the study. Primary production was lower at higher fish biomass in 1984, always coinciding with the peaks in algal biomass. However, the trend in primary production was very similar in both years (Fig. 10.2).

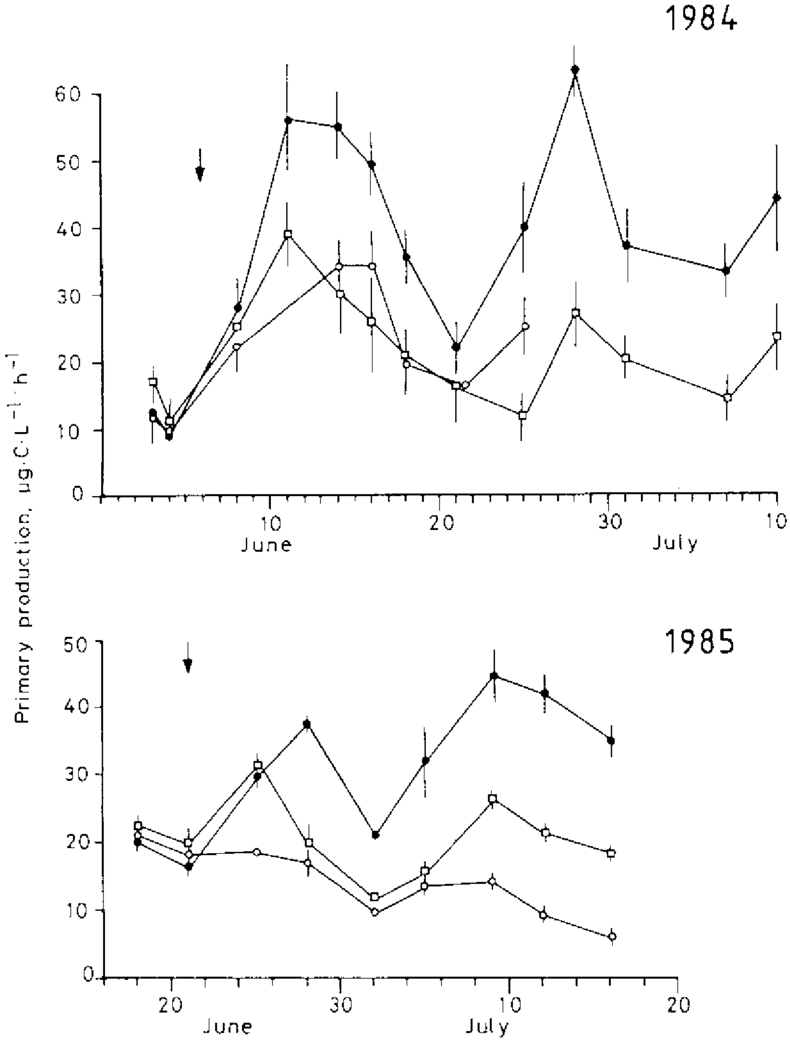

Fig. 10.2 The rates of primary production in the enclosures and in the lake (symbols as in Fig. 10.1).

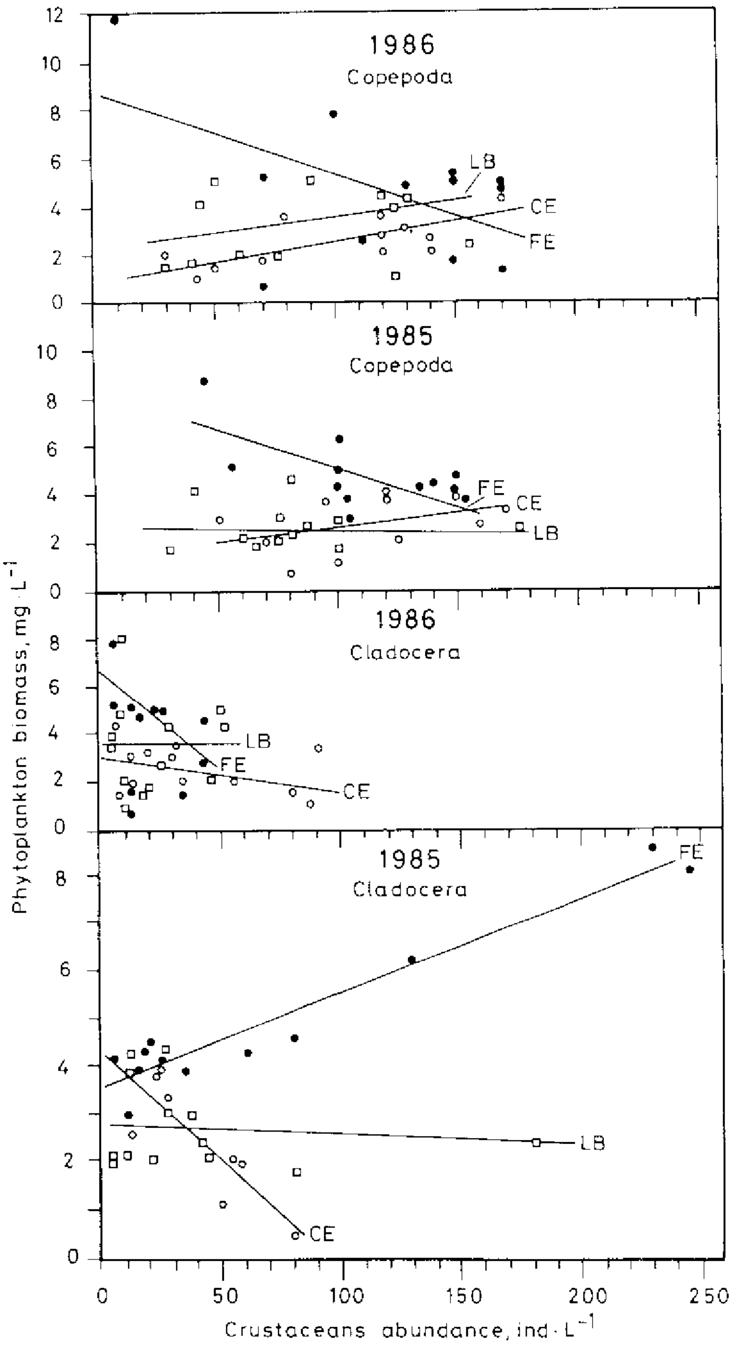

Fig. 10.3 The relationship between crustaceans abundance and phytoplankton biomass for the enclosures and the lake (FE = Fish Enclosure, CE = Control Enclosure, LB = Lake Balaton) (symbols as in Fig. 10.1).

10.3.3 Zooplankton

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 (Fig. 10.4). 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.

Regressions of crustaceans abundance against the phytoplankton biomass in FE show significantly positive relationships for cladocerans in 1985 and negative ones for copepods only in 1985 (Fig. 10.3). Positive correlation in FE suggests that large sized (mainly females more than 0.8 mm in size) *D. brachyurum* might also contribute to changes in algal biomass.

10.3.4 Benthos

Changes in abundance of the benthic macroinvertebrates, mainly chironomids in the enclosure with fish suggest (Tab. 10.2) that bream feeding chiefly on animals burrowing to the deeper sediment layers, might have released a sufficient amount of nutrients by resuspension of sediment particles.

Tab. 10.2 Abundance of macroinvertebrates (ind m^{-2}) 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).

Groups	Control enclosure		Fish enclosure		Lake Balaton	
	04.07.85	16.07.85	04.07.85	16.07.85	04.07.85	16.07.85
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	9,456	7,992	12,432	9,003
Others (Eph. Coleop.)	0	0	44	0	89	44
Total	13,894	12,610	14,541	11,678	15,628	11,693

10.4 DISCUSSION

Our results from enclosure experiments contradict, in some points, the data in the literature. The top-down effects, due to the low stockings of the planktivorous fish populations, are less important in Lake Balaton than in other lakes. McQueen *et al.* (1986) showed that top-down effects are only obvious in less eutrophic lakes and these effects are very limited in hypertrophic lakes. 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 Lammens's (1988) conclusion we, however, believe that bream removal will probably decrease the nutrient effects (Tátrai & Istvánovics 1986) and thus change the phytoplankton dynamics in Lake Balaton. 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 foodweb manipulation.

To aid the nutrient reduction programme as well as improving the stock of commercially valuable species Lake Balaton's foodweb should be manipulated in the topmost trophic level by stocking piscivorous fish. This should be done in conjunction with the lowering of standing stocks of benthivorous species, principially bream.

The removal of benthivorous fish will reduce the resuspension of the sediments disturbed by these fish's foraging action and the potential nutrient release into the water column from the sediments which fuels algal growth. Increasing the stock of commercially valuable species (pike-perch, pike and catfish) will hopefully reduce the population of breams.

10.5 CONCLUSIONS AND MANAGEMENT STRATEGY

The stocking of piscivorous fish and the reduction of benthivores should be conducted at the following levels.

1) The critical biomass of the cyprinids should be lowered from 500-600 kg ha^{-1} to 100-150 kg ha^{-1} in the eutrophic basins and from 200-300 kg ha^{-1} to 50-100 kg ha^{-1} in the mesotrophic basins. The removal should concentrate on the population older than $2^+ - 3^+$.
2) The biomass and the diversity of piscivorous fish stock should be increased by

introduction of young specimens. The proportion of piscivores to prey species should be a minimum of 35% that is between 20-40 kg ha^{-1}. The biomass of the pike-perch stock should be increased to 14-28 kg ha^{-1} from 1. 6-4. 8 kg ha^{-1} by stocking juveniles over 10 cm. The size limit of individual pike-perch in commercial catches should also be increased from 35-40 cm to 60 cm in order to maximise the sustainable yield of the population.

3) The depressed communities of pike and catfish which tend to inhabit the well developed area of macrovegetation should be increased ten-fold from 0.2% to 2% of the community in order to limit planktivorous fry populations.

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CHAPTER 11

LONG TERM (1970-1990) WHOLE LAKE BIOMANIPULATION EXPERIENCE
Case Study: LAKE KINNERET (Israel)

M. Gophen

11. 1 INTRODUCTION

The subtropical, warm monomictic (15-28 ℃, ranges of monthly average epilimnic temperatures) Lake Kinneret is the only natural freshwater lake in Israel. The lake is in the north east of the country (Fig. 11.1) (between 32° 42' and 32° 53'N) in the "Jordan" part of the Syrian-African rift valley. The lake is below mean sea level (bmsl) with water surface maximum fluctuating amplitude between 208.90 m and 213.00 m bmsl. The maximum and mean depths of the lake are 44 and 26 m respectively, and surface area is approximately 168 km^2 (at 209 m bmsl). The lake supplies 25% of Israel's total water demands (450 10^6 m^{-3} y^{-1}) and 50% of the drinking water requirements. Lake Kinneret is mesotrophic with a meso-oligotrophic summer (7-8 months) epilimnion (Wetzel 1983). Lake features, water balance, fish stock and harvest, plankton biomass, chlorophyll and nutrient concentrations, pH and conductivity values are given in Tabs. 11.1 and 11.2 (Gophen and Nishri 1993). The purpose of this paper is to evaluate long-term changes in limnology and fishery of Lake Kinneret related to the introduction of new fish species.

11.2 LAKE UTILIZATION

Until 1964, the lake was utilized for tourism, minor water supply for drinking and agricultural irrigation for the population living close to the lake, and top priority was given to fishery. During 1932-1947, lake water overflows were used for electric production in the hydroelectric station at Naharaim, located downstream 5 km south from the lake.

On 10 June 1964, the largest water system ever constructed in Israel, the National Water Carrier (NWC) was put into operation. From 1964 to1968 the NWC was not operated at full capacity. Since 1969 this system has been in full operation: in

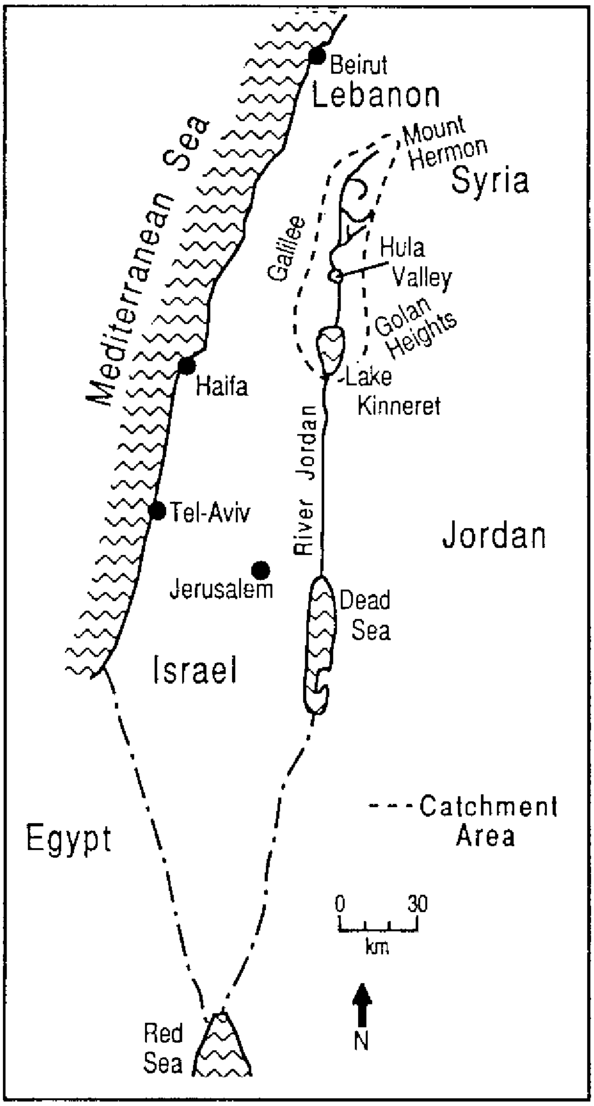

Fig. 11.1 Map of Israel. Lake Kinneret and its watercatchment area are indicated.

winter water is pumped to recharge underground aquifers and for drinking and in the summer, for irrigation and drinking. After 1964 water supply became the top priority of lake utilization and water quality has been the major concern of lake managers.

Tab. 11.1 Limnological features of Lake Kinneret.

Catchment area	2730 km^2
Surface Area	168 km^2 (at 209 m below MSL)
Maximum annual amplitude of water level altitudes	209-213 m below MSL
Shoreline	55 km
Length	21 km
Maximum width	12 km
Total volume	$4\ 10^9 m^3$
Total Inflows	$0.9\ 10^9 m^3 y^{-1}$
Evaporation	$0.3\ 10^9 m^3 y^{-1}$
Total pumping	$0.5\ 10^9 m^3 y^{-1}$
Overflow	$0.1\ 10^9 m^3 y^{-1}$
mean phytoplankton biomass*	69 g (ww)/ m^2(+ 16)(Max. 250/gm^{-2})
Mean chlorophyll	6.0 µ (± 0.8)
Mean zooplankton biomass	21 gww m^{-2}
Fish stock assesment*	4000-6000 t
Fishery*	100 kg $ha^{-2} y^{-1}$

Sources: Berman et al 1992; Gophen 1992; Walline et al. 1992.
Sarid and Golani 1958-1991.

Tab. 11.2 Chemical features (ranges: max-min) of Lake Kinneret winter. Concentrations are given in mg l^{-1} (ppm) in the homothermic water column in winter and in the anoxic hypolimnion in summer. (LKDB-Lake Kinneret Data Base) (Gophen and Nishri 1993).

Parameter	Value, Concentration (mg l^{-1})	Period
pH (pH units)	7.4-8.9	Annual
Conductivity	1167-1501 µmho/cm^{-1}	Annual
DO	5.3-20.0	Epilimnion
Cl^-	200-252	Winter homothermy
$S^=$	2.6-9.2	Hypolimnion
Total-N	0.646-1.124	Winter homothermy
Total-N	0.689-1.827	Hypolimnion
N-NH_3	0.021-0.222	Winter homothermy
N-NH_3	0.098-1.802	Hypolimnion
N-NO_3	0.067-0.500	Winter homothermy
N-NO_2	0.013-0.034	Winter homothermy
Total-P	0.016-0.035	Winter homothermy
Organic - P	0.007-0.027	Winter homothermy
Total Dissolved - P	0.006-0.150	Winter homothermy
Total Dissolved - P	0.022-0.084	Hypolimnion
Ortho - P	0.002-0.012	Winter homothermy
Ortho - P	0.015-0.070	Hypolimnion
Organic - C	2.8-6.0	Winter homothermy
SiO_2	6.0-10.0	Winter homothermy
$SO_4^=$	54-56	Winter homothermy
Ca^{++}	37-55	Winter homothermy
Na^+	100.0-130.0	Winter homothermy
Mg^{++}	27.0-33.0	Winter homothermy
K^+	5.0-6.0	Winter homothermy
Alkalinity(mg l^{-1} $CaCO_3$)	100-150	Winter homothermy
CO_2	1.6-8.3	Winter homothermy
CO_2	9.3-14.5	Hypolimnion
Suspended Matter	2-7	Winter homothermy

11.3 THE HISTORY OF FISHERY MANAGEMENT

Consideration of fishery management (biomanipulation) has to be divided into two periods with different challenges: 1) before 1964, when fishery was top priority and 2) after 1964 when water supply and quality were given highest priority. Fishery management through stocking was initiated in 1920, but intensively done only from the 1950s. Three species of fish were introduced to Lake Kinneret before 1950: *Gambusia affinis* (mosquito fish) (1920), aimed at prevention of malaria. This fish established stable populations in the lake competing with the native *Aphanius mento* in the littoral. *Cyprinus carpio* (common carp) was introduced in 1931 and several times later but its present population is very small. *Tinca tinca* (tench) was introduced once in 1948, but subsequently completely disappeared (Gophen *et al.* 1983a).

Intensive activity of fish stocking began early in the 1950s and continued onward (Gophen *et al.* 1983 b). The introduced species were: a) *Anquilla anquilla, Ictiobus cyprinella, Aristichthys nobilis,* and *Dicentrarchus labrax* are exotics which were planted once or twice and then no further: b) *Hypopthalmichtys molitrix* and 3 mugilids are exotics which have been stocked annually since 1958 (mugilids) and 1970 (*H. molitrix*) until present. *Oreochromis aureus* (= *Tilapia aurea*; blue tilapia) was very rare in the lake prior to its introduction (started in 1958) and became more abundant later and known to compete with the native *Sarotherodon galilaeus* for territorial and food resources (Gophen *et al.* 1983a,b; Vinyard *et al.* 1987; Sarid and Golani 1958-1991). The Galilee Saint Peter's fish (*S. galilaeus*) is native in Lake Kinneret and also has been heavily stocked annually since 1952 (Gophen *et al.* 1983a). I eliminate the sporadic introductions of fish before 1952 for the consideration of biomanipulation in Lake Kinneret as a long-term whole (1952-present) "experiment".

The limnology of the lake was intensively studied only from the late 1960s, therefore lake dynamics (foodweb and chemical processes) are analysed for a shorter period of 25 years.

11.4 LAKE KINNERET FISH AND FISHERIES (1958-1991)

There are 24 fish species in the lake, of which 15 are commercial, yielding annually approximately 100 kg/ha (Sardid and Golani 1958-1991). Among the commercial species, four (2 bleaks and 2 tristramellids) are endemic to Lake Kinneret, four (3 mugilids and *H. molitrix,* silver carp) are exotics, and *O. aureus* was very rare prior to its introduction and became abundant during 1975-1991. The most abundant genera are the zooplanktivorous bleaks (*Mirogrex* sp. and *Acanthobrama* sp.). Most Lake Kinneret fishes are planktivorous, several are benthivorous and piscivory level is low (Gophen *et al.* 1990). In spite of high food source diversity, most of the Kinneret fish species consume zooplankton, several of them throughout all seasons, and some mostly during summer-fall. Predation pressure of fish on zooplankton in Lake Kinneret by both particulate (fingerlings of most species and adult bleaks) and filter (adult cichlids and silver carp) feeders is heavier in summer-fall than in winter. The high pressure in summer-fall is caused by food deficiency and the high metabolic costs affected by the temperatures (25° -30° C in upper 10 m) prevailing in this season (the "Kinneret Summer-Paradox"; Serruya *et al.* 1980). Winter zooplanktivory of bleaks and their stock biomass increase during the 1960s and 1970s was documented by Landau *et al.* (1988), Azoulay and Gophen (1992) and Zohary *et al.* (1993). Zooplanktivory by *H. molitrix* (silver carp) was documented by Spataru and Gophen (1985). Changes of fish community structure with increasing broodstocks of Silver carp, *O. aureus* and bleaks and planted fingerlings were accompanied by intensification of zooplanktivory (Gophen 1992).

The native species, *S. galilaeus* (Galilee Saint Peter's fish) is known as a filter feeder at adulthood which selectively feed on the witner-spring bloom-forming dinoflagellate *Peridinium gatunense.* The conversion of *Peridinium* biomass to body tissues by *S. galilaeus* was better than that of blue tilapia (Gophen 1983a; Vinyard *et al.* 1987).

Data presented in Tabs. 11.3-5 indicates the following: stocking of *S. galilaeus* was enhanced from an average of 1.1 10^6 fingerlings per annum during 1958-77 to 2.8 10^6 year during 1978-84 and 4.0 10^6 year in 1985-91. Stocking of blue tilapia declined, averaging 1.5 10^6 year, 0.6 10^6 year and 0.03 10^6 year, in 1958-77, 1978-84 and 1985-91 respectively. Introductions of mugilids during 1958-91 were stable (0.9-1.1 10^6 year on average) while stocking of silver carp averaged for 1969-77, 1978-84 and 1985-91 was 0.6, 1.1 and 0.1 10^6 fingerlings y^{-1} respectively (Sarid and Golani 1958-91). The stocked tilapia catches when averaged for all three periods indicated a greater than two-fold increase for *S. galilaeus* and 40% for blue tilapia, while stocking for *O. aureus* almost stopped during the late 1980s and introduction of *S. galilaeus* was enhanced. The annual catches of silver carp during 1985-91 were two-fold lower than in 1978-84, but the stocking in this later period

Tab. 11.3 Fish stocking (total introduced fingerlings) in Lake Kinneret during 1958-1991, in millions (10^6) (Sarid and Golani 1958-1991).

Species	1958-77	1978-84	1985-91	Total (%)
S. galilaeus	21.7	16.6	23.7	62.0 (44)
O. aureus	29.0	3.3	0.2	32.5 (23)
Mugilids	22.2	5.5	5.1	32.8 (23)
*H. molitrix**	5.5	6.7	0.8	13.0 (10)
Total	78.4	32.1	29.8	140.3 (100)

*started in 1969

Tab. 11.4 Landings of stocked species (tons/period) during planting period and catch success: kg harvest standerdized per 10^3 introduced fingerlings (Sarid and Golani 1958-91).

	Landings		(tons)	Catch success (kg/10^3 fingerlings)		
Species	until 1977*	1978-1984	1985-1991	until 1977	1978-1984	1985 1991
S. galilaeus	3466	1611	2695	158	96	112
O. aureus	1382	571	840	54	159	4667
Mugilids	2519	1448	834	153	268	154
H. molitrix	98	920	506	55	139	843

**S. galilaeus*: from 1958 *O. aureus*: from 1960
Mugilids: from 1962 *H.molitrix*: from 1974

was only one tenth that previously. This suggests that the standing stock of this fish is presently high, and dominated by old and large specimens whilst younger specimen are less vulnerable to common fishing gears.

It has been suggested that stocked *O. aureus* established stable populations that compete with *S. galilaeus.* The competition for food sources between between these two cichlid species was demonstrated by Drenner *et al.* (1982), Gophen *et al.* (1983 a), and Vinyard *et al.* (1987). Observations in spawning grounds also indicated territorial competition (Gophen unpublished data) with the more aggressive *O. aureus* being favoured. Consequently, *S. galilaeus.* catch success declined (30% and 40% during 1978-84 and 1985-91 respectively) (Tab. 10.4). The outcome was intensified pressure on zooplankton by *O. aureus* and silver carp and reduced pressure on ***Peridinium*** (Serruya *et al.* 1980; Gophen *et al.* 1990; Gophen 1992).

11.5 THE PLANKTON OF LAKE KINNERET: STRUCTURE AND TEMPORAL CHANGES

11.5.1 Phytoplankton

The Lake Kinneret phytoplankton is characterised by an annual late winter to early spring bloom of the thecate dinoflagellate *Peridinium gatunense*, while in summer and fall algal assemblages consists mainly of nanoplanktonic green and blue-green species and diatoms (Serruya *et al.* 1980). Picocyanobacteria were present in low numbers during winter-spring season with maximum abundance of 10^5 cells/ml (Malinsky-Roushansky 1991). During 1975-1989 there was a more than two-fold increase of annual means of phytoplankton biomass, with significant rise of summer-fall levels of nanoplankton (mostly by Chlorophytes which are favoured by zooplankton as food (Fig. 11.2) (Gophen *et al.* 1990; Gophen 1992).

11.5.2 Zooplankton

The zooplankton of Lake Kinneret are primarily (>93% biomass) consisting of ***Mesocyclops, Thermocylops, Eudiaptomus, Diaphanosoma, Bosmina, Ceriodaphnia, Keratella, Asplanchna, Sychaeta,*** and ***Polyarthra.*** Cladocerans, young (nauplius and I-IV copepodite stages) cyclopoids, calanoids and rotifers (except *Asplanchna*) prefer to graze on small algal cells and other supplemental food sources like detritus (external import, internal resuspension, fish and zooplankton feces, degraded *Peridinium* cells, bacteria and protozoans). Fifth stage copepodite and adult cyclopoids are raptorial feeders which prey on other zooplankters (mostly *Ceriodaphnia*) and detrital particles (ca. 30-40% of their diet). I also found (Gophen, unpubl.) that a minor part of supplemental food resources of raptorial copepods consists of microbial loopers.

It is clear (Gophen *et al.* 1990; Gophen 1992) that during the last two decades, the biomass of Copepoda, Cladocera and Rotifera declined gradually but significantly (Fig. 11.3). The overall decrease of zooplankton biomass resulted in increased densities of smaller-bodied cyclopoids and cladocerans, which is an indication of intensification of fish predation pressure on particulate feeders. Moreover, densities of several common small-bodied zooplankters (*Keratella*, nauplii) also declined, presumably due to increased pressure from filter feeder fish.

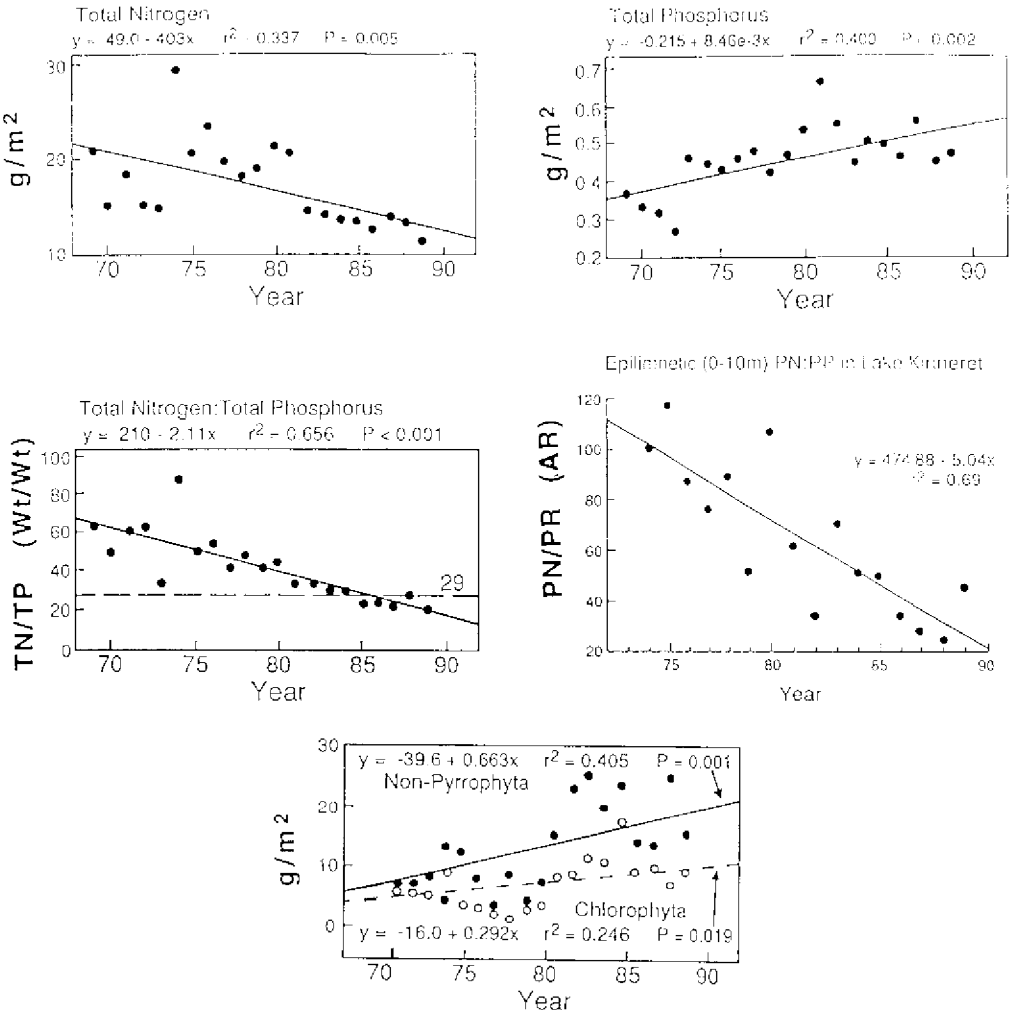

Fig. 11.2 Annual (1969-89) averages (g m^{-2}) of total nitrogen (TN) and total phosphorus (TP) in whole water column (top) and TN/TP (W_t/W_t) ratios (middle-left) in Lake Kinneret; Annual (1974-89) averages of the ratios between particulate nitrogen (PN) and particulate phosphorus (PP) in the upper 10 m (top, right): Annual (1970-89) averages of nonpyrrhophytes (●) and chlorophytes (o) biomass ($g_{(ww)}$ m^{-2}) in the trophogenic zone of Lake Kinneret (bottom). Regressions between parameters and time are given. Redrawn data from: Berman *et al.* 1992 for phytoplankton: Gophen 1992 and Gophen & Paz 1992-for nutrients.

11.6 NUTRIENT: TEMPORAL CHANGES

Nitrogen concentrations in Lake Kinneret were low during 1969-73 when they rose abruptly in 1974 to their highest recorded level (Gophen *et al.* 1990). Since 1974, nitrogen concentrations have decreased steadily (Fig. 11.2). Total and particulate phosphorous increased steadily from 1969 to their highest level in 1981 (i. e. increasing available phosphorous; Berman *et al.* 1992) and declined slightly afterward (Fig. 11.2). During 1974-1985, total particulate nitrogen significantly declined (Fig. 11.2). As a result of these changes the TN/TP(W_t/W_t) declined from above 40 throughout the 1970s (with the exception of 1973 when the TN/TP was 31) to less than 30 for the late 1980s (Fig. 11.2) The atomic ratio between particulate N (PN) and particulate P (PP) significantly declined during 1974-1989 (Gophen 1992). These changes in nutrient concentration may cause modifications and instabilities of phytoplankton community structure. Considerable changes in nutrient limitation in algae under different N/P supply ratios, and have dissolved P and N remain low, were documented by several authors (Rhee 1978; Tilman *et al.* 1986). The significant changes of TN/TP (and/or PN/PP) in Lake Kinneret and their effects on phytoplankton were considered by Berman *et al.*

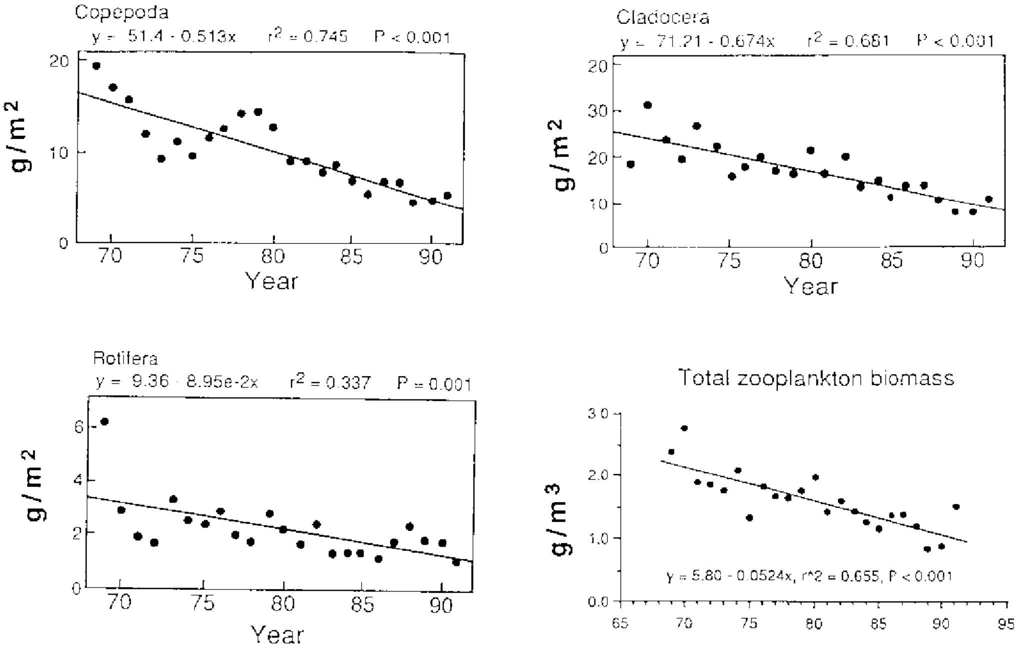

Fig. 11.3 Annual (1969-91) averages of Copepoda. Cladocera and Rotifera biomass ($g_{(ww)}$ m^{-2}) and total zoomass ($g_{(ww)}$ m^{-3}). Regressions between parameters and time are given.

(1992). However, the way their analysis was done is confusing. Jordan River (63% of lake discharge) loadings represented multi-annual (1969-1988) stable ratios between SRP and $NH_4+NO_3+NO_2$ (NO_2 is negligible in Jordan waters) (Berman *et al.* 1992) but these are not all sources of available N and P. Total dissolved P, organic P and N availabilities to the Kinneret biota were not considered by Berman *et al.* (1992). Moreover, internal P-fluxes from the sediments and N-removals (Smith *et al.* 1990) must be considered as well. Nitrate influxes through winter discharges (major external sources) are subject to competition between denitrifiers and algae (Cavari 1979). If N-removal through denitrification was enhanced during the 1980s, a consequent potential N-limitation to algae is suggested and PN reduction is anticipated (Smith *et al.* 1990; Gophen and Paz, 1992).

The decline of organic nitrogen in the Jordan River loading was documented by Gophen *et al.* (1990). Enhancement of P-supply from the sediments and N-removal (sedimentation and denitrification) from the water and decline of organic nitrogen in the lake were documented (Fig. 11.2) (Berman *et al.* 1992; Smith *et al.* 1990). Therefore, for efficient lake management (biomanipulation, and/or external loads operations) it is a misconception to not consider changes or sources other than SRP and $NH_4+NO_3+NO_2$ in Jordan River loadings (Berman *et al.* 1992). Dissolved N and P are not well correlated with algal community structure. Total N and P are however. This is because the algae respond to the supply ratio of N and P but the dissolved pools are often very low and somewhat variable. The N and P content in the Lake Kinneret biota was undoubtedly changed, reasonably reflecting changes in N/P supply. For an efficient design of biomanipulation management, comprehensive consideration is required. In the case of Lake Kinneret, a wider spectrum of N/P change studies and consequent algal community structure response is ultimately needed. Rhee (1978) showed physiological differences in a single algal species under different N/P loadings but with no detectable difference in dissolved NO_3. The Kinneret phytoplankton community changes probably reflected the overall N/P supply more than the dissolved N/P. If the phytoplankton of Lake Kinneret during the 1980s represented different N/P ratios from that measured during the 1970s it is probably because of a change in the overall supplied N/P.

11.7 FOOD WEB STRUCTURE AND MANIPULATION

There are three major food-consumer linkages in the Kinneret ecosystem: 1) the nanoplanktonic algae-zooplanktonic grazers and zooplanktivorous fish (bleaks, fingerlings of most species, and adult cichlids, silver carp and mugilids); 2) *Peridinium* and several fish species but most efficiently *S. galilaeus*, and to a lesser extent other species. *Peridinium* is not grazed by zooplankton except *Asplanchna*; and 3) Microbial loopers which are mostly active during the abrupt degradation of the *Peridinium* bloom (May-early June) and a minor part of their biomass is channeled to higher trophic levels including filter feeding zooplankton. This structure of the Kinneret foodweb was outlined as based on microscopical studies of food compositions and on experimental studies of feeding habits of zooplankton and fish (Serruya *et al.* 1980). Recently, these linkages were substantiated by long-term analysis of stable isotopes of carbon ($^{13}C/^{12}C$ ratios) (Zohary *et al.* 1993).

11.8 LAKE MANAGEMENT OPTIONS

A comprehensive analysis of background information on food-consumer interrelationships in the Kinneret ecosystem (Serruya *et al.* 1980; Zohary *et al.* 1993), considerations of temporal trends (Figs. 11.2 and 11.3) and water managers' required constraints is based on the following conceptual principles: 1) Lake water quality as set by formal standards must be such that it can be supplied with minor treatment (chlorination), i.e., no increase of nanoplankton in summer-fall and controlled biomass of *Peridinium* in winter; 2) Reasonable annual income for commercial fishery; 3) The lake is open for unlimited tourism and recreation activities. To achieve these goals we incorporated limnological information collected during 1970-1989 and fisheries statistics (1958-91), to establish a master plan design. Inverse relations between zooplankton grazers and nanoplankton, but also positive relations between increased available P and chlorophytes during the 1980s were indicated. Because of food limitation for fish during at least 7-8 summer-fall months (Serruya *et al.* 1980), the absence of free trophic niche for exotic fish is suggested. It is impossible to conclude what had the most substantial link to increase of chlorophytes: zooplankton decline or available P increase. Nevertheless, I think that grazing zooplankter biomass in Lake Kinneret should be higher that at present (closer to early 1970s values) to increase consumption capacity of nanoplankton. To achieve this goal, it is recommended that exotic fishes not be stocked and enhancement of the native, high market value (Tab. 11.5) cichlid *S. galilaeus* is desired by improving its spawning conditions of fishing restrictions in its reproductive area during spawning season and enhanced fingerling introduction. Elimination of silver carp stocking will have only minor impact on fishermen's income (Tab. 11.5) and enhancment of *S. galilaeus* population is a fair compensation (Tab. 11.5). Reduction of the standing stock biomass of the

Table 11.5 Financial value (US $ 10^3) of annual fish harvests (tons) in Lake Kinneret for the period 1990-91 (Sarid and Golani 1958-1991).

Species	Catch		Price	
	tons	%	US $ 10^3	%
S. galilaeus	542	25	2547	50
O. aureus	181	8	652	13
Mugilids	222	10	1154	23
H. molitrix	73	3	73	1
Others	1167	54	630	13
Total	2185	100	5056	100

zooplanktivorous bleaks is also recommended. The potential effectiveness of this program requires a thorough additional study of the reasons for the decline of N/P in the lake and its implications on phytoplankton composition with consequent decisions on nutrients management.

CONCLUSIONS

In a case like Lake Kinneret in which water quality is a national concern and lake utilization includes commercial fishing, it is recommended: 1) to carry out a comprehensive, thorough study of the ecosystem long-term changes in nutrient dynamics and 2) immediately eliminate exotic fishes. If nutrients supply (external and internal loadings) are under fair control, biomanipulation by native fish might have a positive effect on water quality. Target species for biomanipulation in Lake Kinneret should be selected on the basis of four major factors: 1) to be natural (native) components of the system; 2) effective and non-expensive stocking; 3) fair market value and vulnerability to fishing gear and 4) potential positive impact on water quality.

EPILOGUE

Ironically, during the summer of 1994, a heavy bloom of *Aphanizomenon ovalisporum* (Pollinger, unpublished data) developed in Lake Kinneret. The concept presented by Berman *et al.* (1992) of long-term phytoplankton stability, no eutrophication and no blue-green blooms was shattered. The paper I have presented in this book about Lake Kinneret explains why the Berman *et al.* (1992) concept is irrelevant and backgrounds for predicted eutrophication and blooms of Cyanobacteria are given. The very dense population of *A. ovalisporum*, observed in

Lake Kinneret in summer-fall 1994 (started in August) clearly indicate the corroboration of the predictions I made: the lake is eutrophied and blue-green is heavily bloomed.

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CHAPTER 12

MANAGEMENT BY FOOD CHAIN MANIPULATION OF LAKE BIWA (Japan)

Akira Kurata

12.1 INTRODUCTION

Lake Biwa is the biggest water source in Japan with a surface area of 674 ㎢, a maximum depth of 104 m and a mean depth of 41 m that supplies drinking and industrial water for some 14 million residents in the Kyoto, Osaka and Kobe megalopolis. The quality of lake water was profoundly influenced by economic development since the 1960s through rapid eutrophication. In order to reduce problems caused by eutrophication, various ordinances have been enacted and many improvements have been made by responsible authorities. However, eutrophication still progresses slowly but steadily by the increase of nutrient loading from a number of sources, especially non-point sources such as domestic wastewater and cultivated field run-off. Nowadays, therefore, removal of nutrients from the water inflowing to the lake is one of the most important approaches to solving the environmental problems of the lake.

In this chapter, an unintentional but typical skillful biomanipulation utilizing natural lagoon ecosystems adjacent to the lake is made to clarify quantitatively from the function of nutrient removal point of view.

12.2 SITE DESCRIPTION

There are many large and small natural lagoons around the lake. Most of them are connected to the lake through narrow channels and have the same water level as the lake, as reported in an earlier paper (Kurata & Kira 1986). The main biomanipulation dealt area is in Nishinoko Lagoon, which is one of the largest lagoons, though shallow (maximum 2.0 m depth). Surrounded by paddy fields, the surface area is 2.9 ㎢ and the shoreline reaches 18.5 ㎞. In this lagoon, *Phragmites australis* grows well with very high densities, covering about 167 ha. The reed zone of the lagoon is shown in Fig. 12.1. The total catchment area of the lagoon is 83.9 ㎢, and 77.3% of it is flatland. Although about a dozen rivers flow

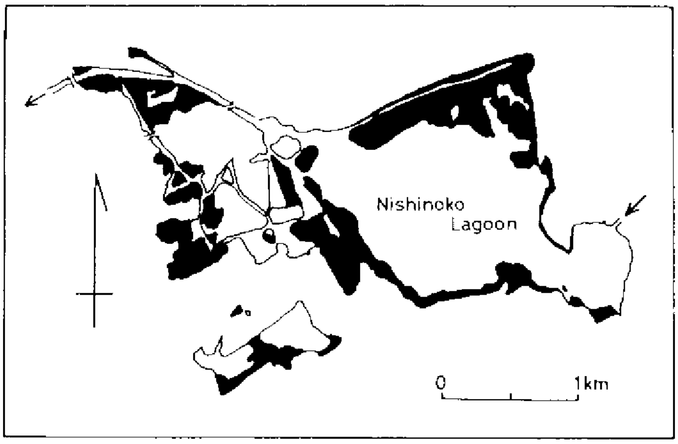

Fig. 12.1 Profile of Nishinoko Lagoon which is the exiting largest lagoon around Lake Biwa. Solid parts represent reed zone. Arrows indicate the inlet and the outlet.

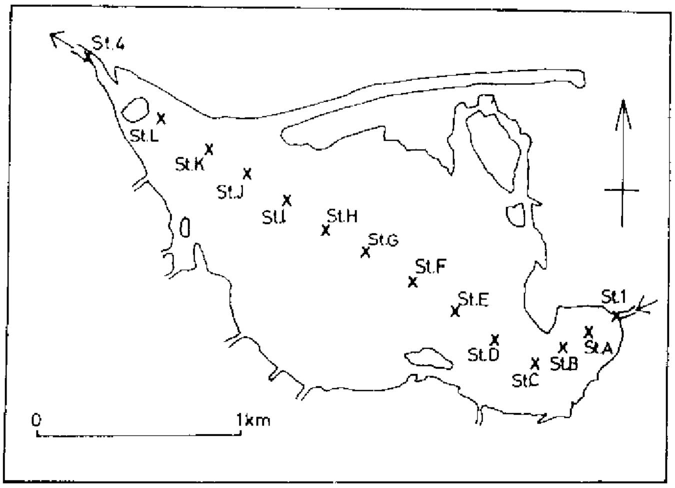

Fig. 12.2 Routine sampling stations were set up linearly from the inlet (St. 1) to the outlet (St. 4) in the lagoon.

into this lagoon, the catchment area of Hebisuna River, which is the main inflowing river, occupies 72.8% of the total catchment area. Chomeiji River is the main, almost the only, outflowing river from the lagoon. Fourteen water sampling stations were set up linearly from the main inlet to the outlet as shown in Fig. 12.2. The other stations were set up as a rule at the mouths of 15 inflowing rivers or channels to the lagoon.

A great amount of inorganic and organic particulate matter contained in the inflowing water was sedimented rapidly in the lagoon within several hundred meters from the inlet. The results are shown in Figs. 12.3 and 12.4. Comparison of size-fractionated particulate matter at Station 1 and 4 is shown in Fig. 12.4. The greater part of particulate matter in the inflowing water was large size particulate matter, such as larger than 14 µm and smaller than 35 µm in diameter. The fact coincides with rapid sedimentation of particulate matter in the lagoon. A little increase in small size fraction must be attributed to active multiplication of small size microorganisms including phytoplankton in the lagoon. After flowing into the lagoon, the temperature of influent was raised several centigrades in the lagoon and it must accelerate the activity of mineralization by very high population density of heterotrophic microorganisms compared with that in the lake water. As shown in Fig. 12.5, the COD value was also raised several mg l^{-1} in the lagoon and it must be attributed to active multiplication of small size microorganisms and phytoplankton in the lagoon. Concentration of nutrients in inflowing water was higher generally than that of outflowing water throughout the year in all lagoons investigated. A comparison of seasonal changes of PO_4-P concentration in inflowing and outflowing waters in three lagoons is shown in Fig. 12.6. Phytoplankton population density was very high in lagoons and outflowing water

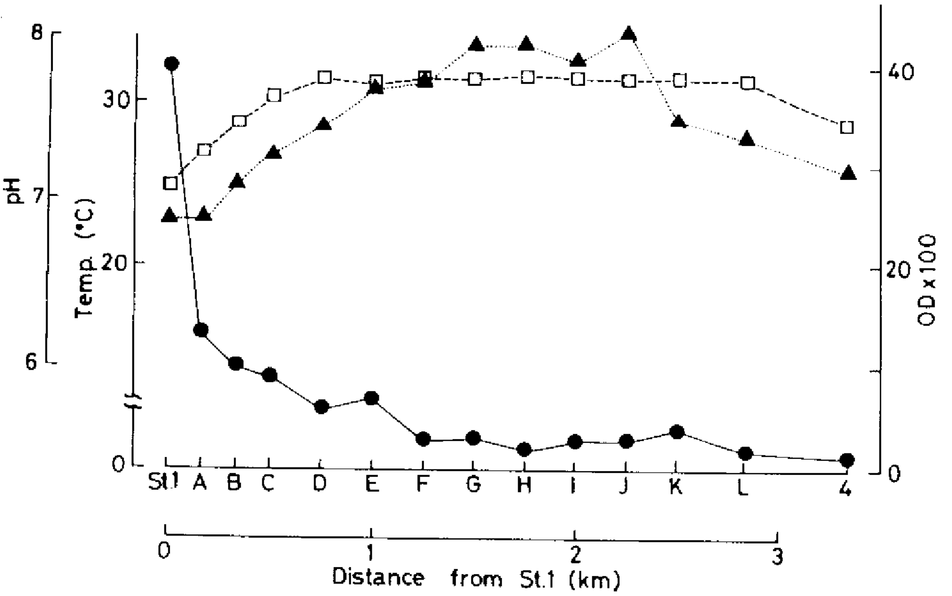

Fig. 12.3 Horizontal change of water temperature (white square), pH (black triangle) and SS (black circle) at each station.

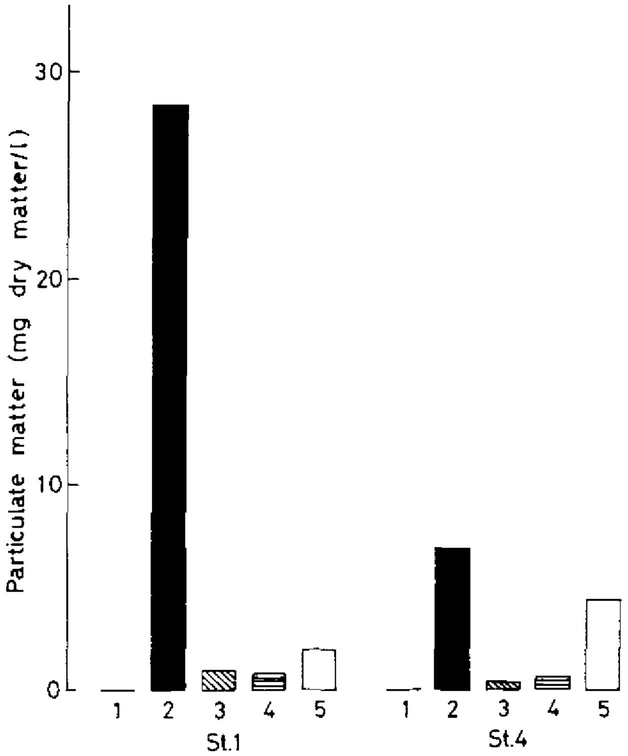

Fig. 12.4 Comparison of the size-fractionated particulate matter at St. 1 (inlet) and St. 4 (outlet). 1:>35μm; 2: <35μm, >14μm; 3: <14μm, >7μm; 4; <7μm, >1.2μm; 5:<1.2μm, >0.5μm.

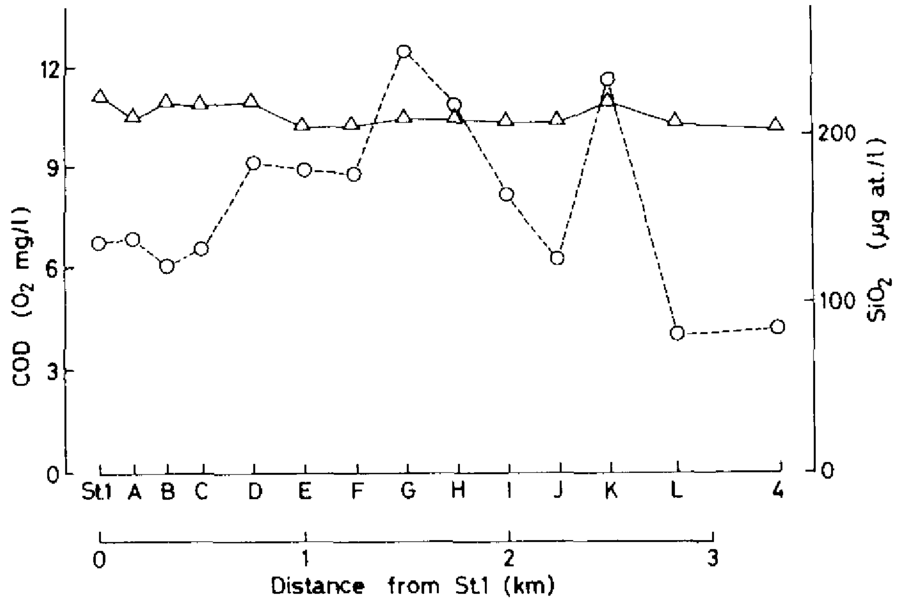

Fig. 12.5 Horizontal change of the COD value (white circle) and the concentration of SiO_2 (white triangle) at each station.

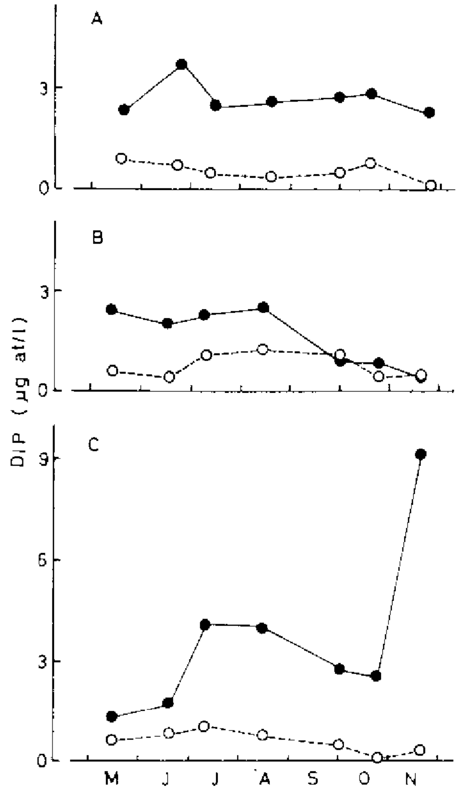

Fig. 12.6 Comparison of the seasonal change of PO_4-P concentration in inflowing water (black circle) and outflowing water (white circle) in three lagoons (A: Nishinoko Lagoon; B: Komatsunuma Lagoon; C: Katata Lagoon).

although phytoplankton were hardly recognized in inflowing water throughout the year in each lagoon. One of the results in the lagoons investigated is shown in Fig. 12.7. Very high population density of phytoplankton must actively utilize nutrients in water of the lagoon. Therefore, phosphorus content converted from dissolved-form reactive phosphate to particulate-form organic phosphate by phytoplankton was calculated and its inter-relationship with the population density of phytoplankton in water of the lagoon is shown in Fig. 12.8. As shown in this Figure, it is suggested that population density of phytoplankton in water of the lagoon depends considerably on the concentration of reactive form phosphorus supplied by inflowing water to the lagoon.

Surrounded by paddy fields, the lagoons receive a very high nutrient load. However, it is thought the activity of mineralization by heterotrophic microorganisms is very high both in water and on the surface of bottom sediments in the

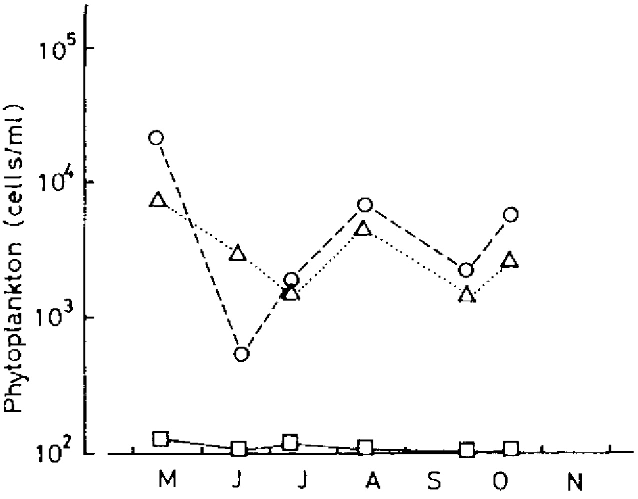

Fig. 12.7 Comparison of the seasonal change of phytoplankton population density in water of the lagoon (white triangle), inflowing water (white square) and outflowing water (white circle) in Katata Lagoon.

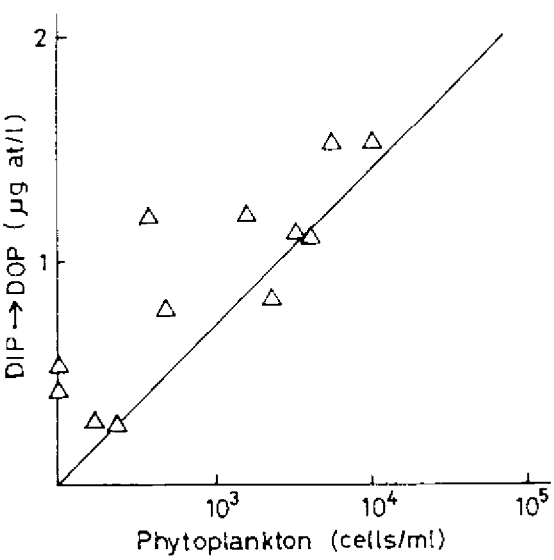

Fig. 12.8 Relationship between phosphorus content converted from dissolved form reactive phosphorus to particulate form phosphorus by phytoplankton and population density of phytoplankton in water of the lagoon.

lagoon. The activity sustains the very high population density of phytoplankton, 100 times or more, compared with that in the lake. The total cell number of phytoplankton ranged usually from several thousand to ten thousand *per* ml seasonally (maximum 17,000 cells ml $^{-1}$). The algal community was dominated by flagellates, such as *Cryptomonas*, *Chlamydomonas*, together with a smaller quantity of the diatom *Cyclotella* and the green algae *Scenedesmus*, *Crucigenia* and some smaller monads belonging to the group of *Euglena*. These phytoplankton species are very profitable for the growth of plankton feeder shellfishes from a nutritional point of view (Kurata *et al.* 1976). It is supposed that the dissolved-form nitrogen compounds must be reduced through denitrification in the reed zone by nitrate and nitrite reducers as shown in Fig. 12.9.

The shellfish *Hyriopsis schlegeli*, one of the indigenous species of shellfish in the lake, is cultivated to produce freshwater pearls in Nishinoko Lagoon as shown in Fig. 12.10. The larvae of the shellfish are also collected in the central part of this lagoon. A high biomass of phytoplankton is consumed for the growth of *H. schlegeli*, namely, for the production of freshwater pearls. In this lagoon, no fertilizer is used for acceleration of the growth of phytoplankton and no bait is given to the shellfish. Accordingly, it is concluded that loaded nutrients from the surrounding cultivated fields and from upstream villages and towns are converted to freshwater pearls by a number of *H. schlegeli*, although requiring skillful technique, troublesome work and delicate management of environmental conditions of

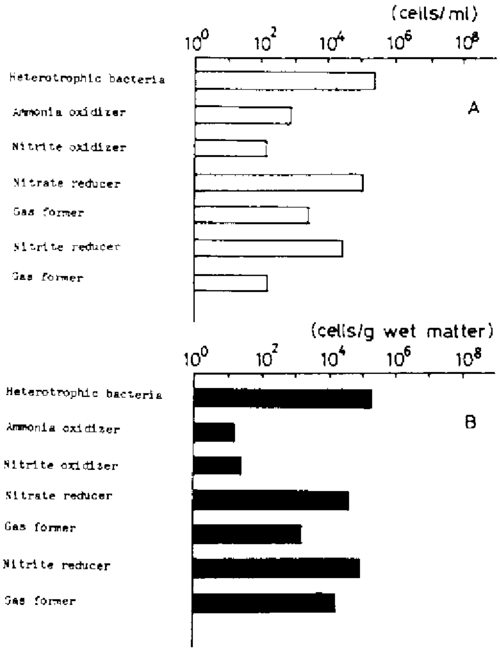

Fig. 12.9 Bacterial population density having various functions in water (A) and in the bottom sediments (B) in Nishinoko Lagoon.

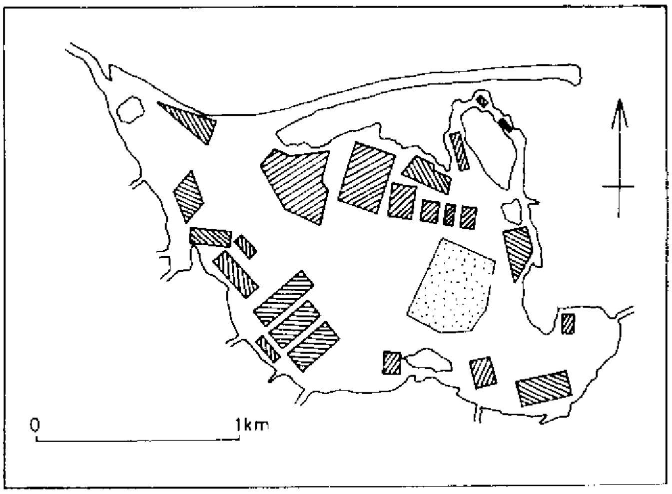

Fig. 12.10 Freshwater pearl cultivation farms (parts of oblique lines) in the lagoon. A dotted part represents the area in which is collected the larvae of *Hypriopsis schlegeli*.

cultivation farms. Generally, a rather eutrophic nutritional level of water with high population density of nannoplankton is profitable for the prosperous growth of the shellfish. It is estimated that approximately 700,000 *H. schlegeli* are harvested annually from the lagoon. After carefully removing the pearls from 20 cm large shellfishes that have been cultivated for about five years, these are usually fit for edible consumption. These unintentional biomanipulation processes are effective in removal of nutrients from the lagoon. One of the results is shown in Tab. 12.1. However, its production is decreasing year by year because of the deterioration of the water quality of cultivation farms.

Phragmites australis grows well in Nishinoko Lagoon as shown in Fig. 12.1. During the winter, *P. australis* is harvested annually and it is used for different kinds of daily life products, for example, sunshade screens, domestic screens and souvneirs etc. Approximately 910 t (dry wt) of *P. australis* is harvested annually from this lagoon. Accordingly, the same amount of organic matter is removed

Tab. 12.1 Removal of shellfish biomass from the lagoon by the cultivation of freshwater pearl.

Number of the freshwater pearl cultivation factory	10
Total number of shellfish (*Hyriopsis schlegeli*)	7, 000, 000 ca.
Total weight of shellfish (wet base)	680 t
Total weight of shellfish (dry base)	94 t
Total nitrogen removal	16 t

annually from this ecosystem. Nitrogen and phosphorus contents contained in *P. australis* were assayed and the total amount of nitrogen and phosphorus removed from the lagoon was calculated. The results are shown in Tab. 12.2.

The submerged macrophytes grow well in the open area of this shallow and nutrient-rich lagoon. During the summer, therefore, macrophytes have been harvested by many fishermen to improve environmental conditions for navigation and cultivation of freshwater pearls in the lagoon. Approximately 3, 000 t (wet wt) of *Elodea canadensis* has been harvested annually and used as a manure in orchards. Since 1984, an automatic macrophyte harvesting vessel was introduced into the lagoon. In addition to this process, sport-fishing equivalent to 8 million yen is carried out throughout the year. These kinds of effective processes for the removal of nutrients from this ecosystem are summarized in Tab. 12.3. In all, 31.2 metric tons of nitrogen and 4.09 metric tons of phosphorus are removed throughout the year from the lagoon by unintentional biomanipulation through different kinds of human activities, such as harvesting of reeds and macrophytes, freshwater pearl cultivation and fish catch, although 81.1 metric tons of nitrogen and 4.4 metric tons of phosphorus from the loaded nutrients remain in the lagoon. Thus harvesting of nitrogen and phosphorus by the above methods contributed 38.5% and 93.0%, respectively, to the entire nutrient retention of the lagoon.

Tab. 12.2 Annual removal of nitrogen and phosphorus from the lagoon by the harvest of *Phragmites australis*.

Total area of *P. australis*	60 ha
Average number of *P. australis* m^{-2}	52
Nitrogen content in *P. australis* m^{-2}	36. 6 g
Phosphorus content in *P. australis* m^{-2}	4. 3 g
Total harvest of *P. australis* (dry wt)	910 t
Total nitrogen removal	16. 4 t
Total phosphorus removal	2. 3 t

Tab. 12.3 Removal of nitrogen and phosphorus from the lagoon by various human activities.

	Total N (t)	Total P (t)	Annual harvest (10^6 yen)
Harvest of *P. australis*	16. 4	2. 3	180
Harvest of *H. schlegeli*	4. 0	0. 27	1,500
Harvest of *E. canadensis*	10. 5	1. 5	
Fish catch	0. 3	0. 02	8
Total	31. 2	4. 09	1, 688

Nitrogen, however, is undoubtedly reduced actively through denitrification in the reed zone by epiphytic microorganisms, as reported in an earlier paper (Kurata 1983).

Nishinoko Lagoon plays an important role as a whole ecosystem in removing nutrients from the inflowing wastewater into Lake Biwa, as if it were a natural ecological wastewater treatment system through unintentional but skillful biomanipulation techniques. A simplified model of the system is shown schematically in Fig. 12.11. This is a first estimate of an ecological engineering model applied to the environs of Lake Biwa from the point of view of biomanipulation techniques by utilizing natural ecosystems. This biomanipulation model must be studied further in other types of lagoons and applied to more lake environments suffering from eutrophication.

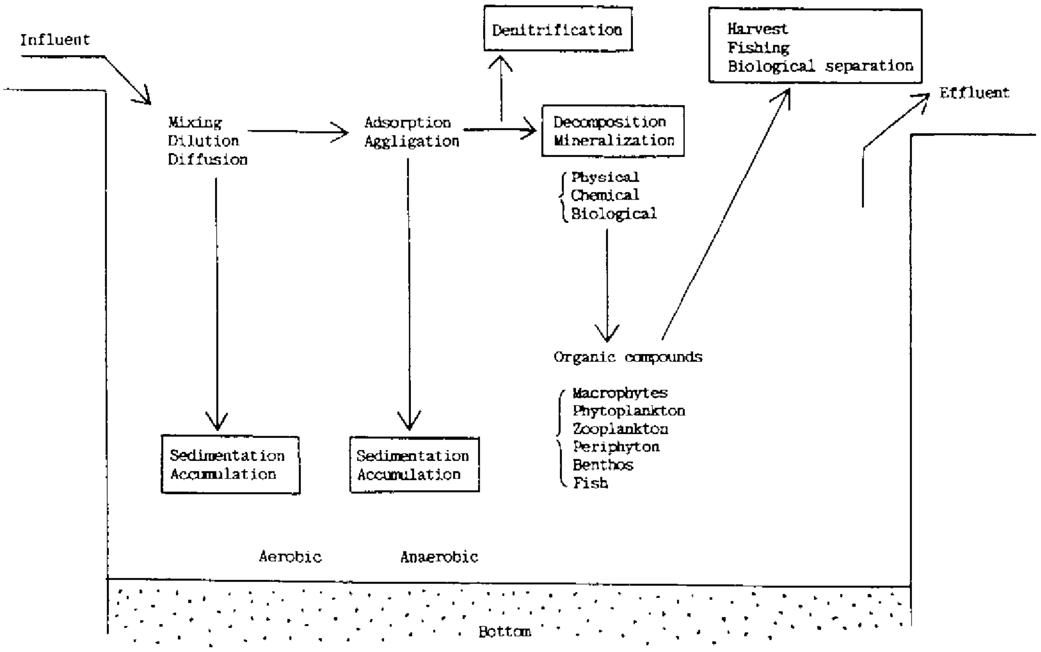

Fig. 12.11 Schematic diagram of the self-purification activity in lagoons including different kinds of biomanipulation techniques.

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CHAPTER 13

RESERVOIR MANAGEMENT USING FOOD CHAIN MANIPULATION

C. H. D. Magadza

13.1 INTRODUCTION

The establishment of reservoirs is immediately accompanied with successional processes that lead to the formation of aquatic communities where once terrestrial ones existed. The rapidity of the succession process to a dynamic climax and complexity of the ensuing ecosystems depends on a number of factors. The morphometric features of the impoundment, the pre-impoundment lotic community structure, the hydrology and operation of the new impoundment all determine the successional process that follows the impoundment and the complexity and completeness of the new ecosystem.

Within the tropics, seasonality of the hydrological events determine both the pre- and post-impoundment communities. Furthermore the operation of the reservoir, particularly the period of draw down, also affects the nature of the post impoundment communities, which in extreme cases can remain in an early successional stage due to repeated resetting of the ecological conditions.

Furthermore post impoundment conditions of high nutrient availability, lack of ecological competitors, and, in tropical situations, high growth rates often create ideal conditions for their proliferation of alien species, which can greatly influence the course of post impoundment succession. Where the end results of such post impoundment succession leads to unsatisfactory management situations, human intervention by food chain manipulation has been able to modify the outcome.

This paper will briefly examine some African tropical cases in which biomanipulation has been exercised, and also contrast such efforts of human interference with a natural aquatic ecosystem.

13.2 LAKE KARIBA.

13.2.1 The pelagic fishery

A pre-impoundment survey of the middle valley by Jackson revealed that the middle Zambezi Valley had a poor species diversity, with a total fish species list of only 14. The paucity of fish biodiversity was attributed to a lack of habitat diversity, particularly during the low water flow period when the river was reduced to sand banks with little vegetation cover. This lack of cover resulted in heavy predation by *Hydrocynus vittatus* during the low water season (Jackson 1961).

The construction of Lake Kariba created a large inland sea, with a vast pelagic zone. In the initial stages of the filling *Alestes imberi,* which was originally confined to the upper Zambezi flood plains, appeared to displace *Alestes lateralis,* in the Middle Zambezi (Balon 1971). However even the *A. imberi* did not become truly pelagic. Some early reports of the limnology of the pelagium indicated large populations of zooplankton, made up of the copepoda *Tropodiaptomus kraepelini, Diaptomus syngenens, T. simplex* and *Thermocyclops sp*; the cladoceran *Daphnia lumholtzi, Ceriodaphnia cornuta* and *Bosmina longirostris.* It soon became clear that unless a pelagic fishery was introduced a large part of the lake would remain unutilized for fisheries. Balon (1974) had estimated that the riverine fish species could only utilize the inshore habitats which comprised 38% of the lake surface. In view of the failure of the indigenous fishes of the Zambezi River to effectively colonise the pelagium food chain in this sector of the lakes, habitat would have consisted of a short pathway between phytoplankton and zooplankton and thence to the decomposer system.

Thus in 1969 and 1970, under the auspices of the FAO, *Limnothrissa miodon* Bulenger, a pelagic clupeid from Lake Tanganyika, was introduced into Lake Kariba to utilize the planktivore niche. The introduction was at Sinazongwe, about midway along the lake axis, on the Zambian shore, (Bell-Cross & Bell-Cross 1971).

At the same time *Limnocaridina tanganicae,* a freshwater shrimp also common in Lake Tanganyika, was introduced as a food source for *Limnothrissa.*

Large populations of *Limnothrissa* developed in Lake Kariba (Balon 1971). Experimental fishing for the clupeid in Lake Kariba soon revealed sizeable catches of *Hydrocynus vittatus* juveniles in the pelagium. The availability of abundant supply of prey in the pelagium had induced the juveniles stages of this riverine carnivore to become pelagic in pursuit of the new prey. Previously *H. vittatus*, like the other riverine species previously present in the pre-impoundment Middle Zambezi, had been restricted to the littoral zone of the lake. The establishment of pelagic fish population also attracted fish eating birds such as the Grey Headed gull, *Lards cirrocephalus* and the white winged tern, *Chlidonias leucopterus*. Thus the introduction of *Limnothrissa* resulted in an increase in bodiversity of the pelagium and consequently a more elaborate food web.

Figure 13.1 shows the development of the fishery after its point introduction of *Limnothrissa* at Sinazongwe. Although the management of this fishery has been by trial and error due to the lack of basic data on its biology in Lake Kariba in contrast to its biology in Lake Tanganyika, the data above shows that the introduction of *Limnothrissa* has been a great success.

After the establishment of the *Limnothrissa* population there were further changes in the pelagic populations (Fig. 13.2). The large zooplankters (Calanoids and Daphnids) became very rare. Cyclopoids replaced calanoids in dominance, while *Bosmina longirostris* replaced the Daphnids (Magadza 1980, Masundire 1989). However the earlier components of the zooplankton community occasionally develop in river mouths during the rainy season. Although *Limnocaridina* has

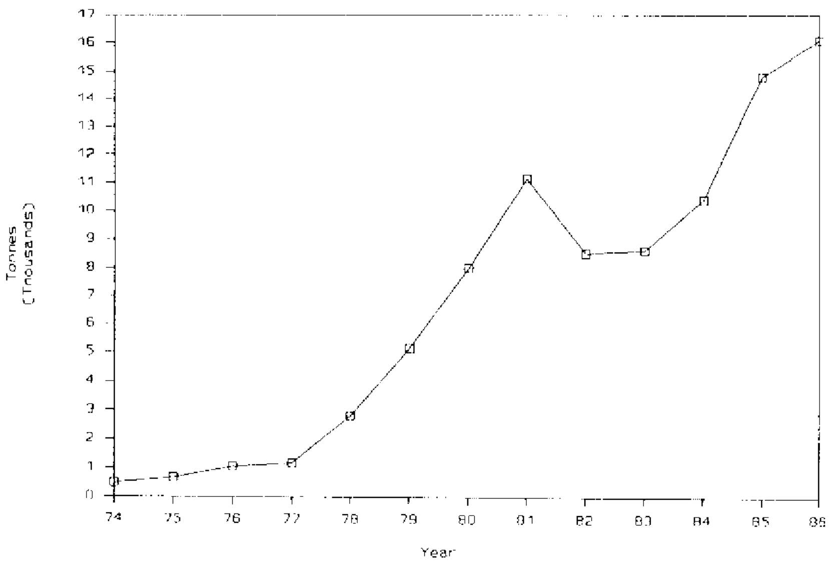

Fig. 13.1 Growth of *Limnothrissa miodon* fishery in Lake Kariba (after Magadza, 1993).

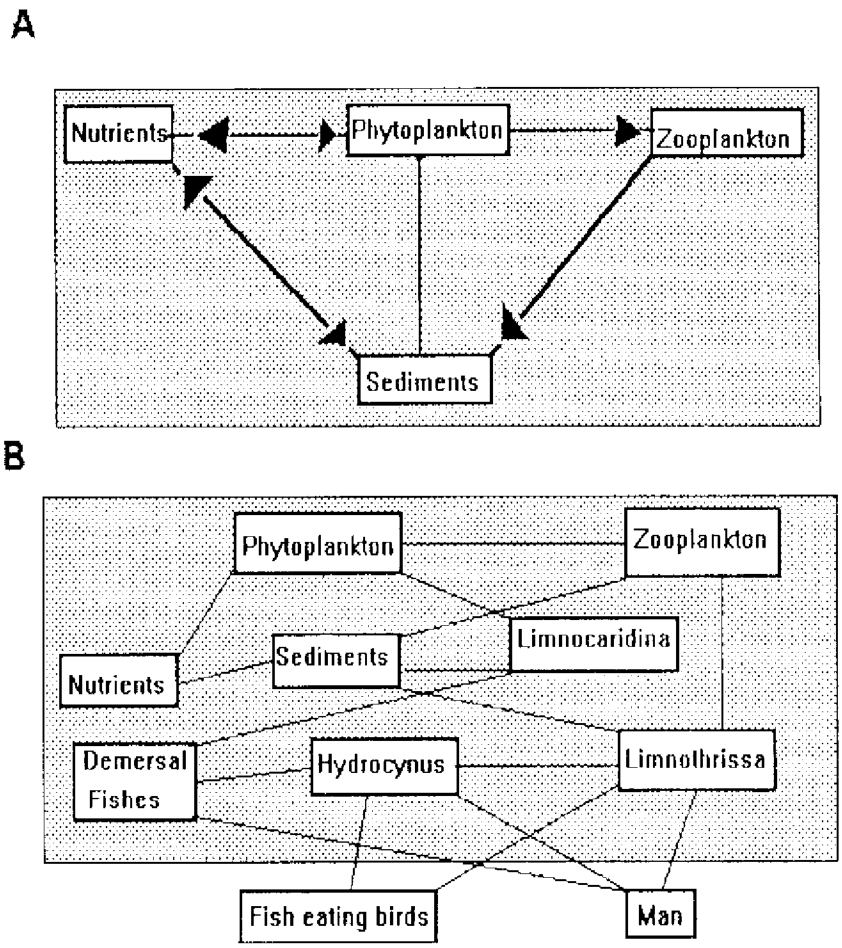

Fig. 13.2 Food chain in the L. Kariba pelagium before (A), and after (B), introduction of *L. miodon* and *L. tanganicae*. Note that before the introduction there were no opportunities for human exploitation of the pelagial production.

survived the introduction it never was dominant in the pelagium, remaining confined to the littoral area where its population dynamics is determined, *inter alia*, by the draw down regime.

The economic significance of the introduction of *Limnothrissa miodon* into Lake Kariba is that it transformed a country that had no significant traditional fishery into one of the major fisheries of southern Africa with an economic value of several million dollars. The fish landings of Lake Kariba now exceed those of Lake Malawi, the third largest inland lake in Africa.

13.2.2 The inshore species

Tropical savana rivers, on account of their hydrological seasonality, often have very few fish species. Jackson (1960) noted that the middle Zambezi River had only 14 species, a condition he ascribed to the blandness of the river channel, which reduces to monotonous sand banks in the dry season. Similarly in Namibia he showed that in contrast to wetlands and marshes, rivers had had very limited fish species. Thus when reservoirs are constructed on such rivers the initial lake will have very limited fish species and a simplified food chain. The management of such reservoirs for fish production then involves the introduction of alien fish species to create a more complex food chain.

Thus in Lake Kariba, in addition to the introduction of pelagic organisms *Tilapia machrochir* was introduced to supplement the inshore fishery species complex. The inshore fishery from Lake Kariba produce about 9,000 tonnes of fish, mostly consisting of *T. machrochirs.* and *T. rendalli,* an immigrant from the Kafue River system. Similarly the introduction of these ciclids in Lake Chivero (formerly L. McIlwaine) enabled the establishment of a profitable fishery in this water body (Fig. 13.3).

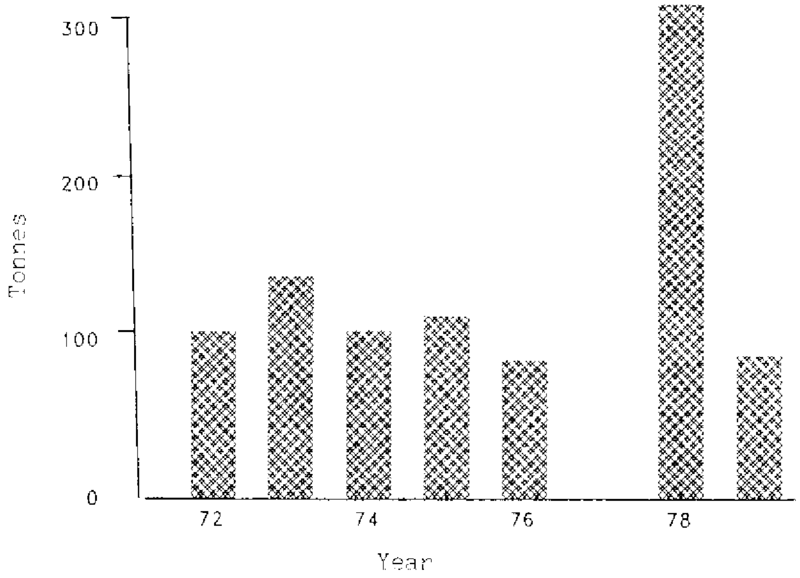

Fig. 13.3 Fish catches in L. Chivero based on introduced *T. machrocir.* (after FAO (1990)).

13.3 CONTROL OF AQUATIC WEEDS

The obstruction of dams usually creates trophic conditions that favour the explosive growth of alien opportunistic aquatic plants, notably *Eichhornia, Salvinia, Pistia, Azolla, Lagarosiphon, Ceratophyllum* and *Eigeria.* These weeds invariably interfere with the normal uses of the reservoir by blocking intakes, excessive growth and decay, giving the water an unpleasant taste and smell, and also by interfering with the biology of other aquatic organisms due to alteration of water quality. Extensive growth of floating weeds often leads to fish kills due to restriction of oxygen. Such changes in water quality also lead to changes in species composition of fish communities. The restriction of light penetration curtails planktonic communities, in turn leading to a collapse of planktonic food chain systems.

There are basically two options for the control of aquatic weeds: chemical control and biological control. In the former there are often undesirable side effects, such as the sudden depletion of oxygen following herbicide application and direct toxic effects of the chemical compounds both to humans and other aquatic organisms. Biological control agents utilize natural food chain systems without the adverse effects of chemical agents.

The case of Lake Kariba is illustrative of this principle. When the lake was created the decay of forests released large amounts of nutrients into the forming lake. *Salvinia molesta,* a South American native, had been introduced into the Zambezi River system. As an ecological alien it lacked local herbivores that would normally graze on it. Thus the absence of predators and the abundant supply of nutrients were ideal conditions for unchecked explosive growth of this weed in the lake. Furthermore the extensive areas of partially submerged dead trees, still present now, provided shelter for the expanding weed mats.

There were some attempts at chemical control, but the extent of the weed was such that it soon became clear that such a strategy was economically unsustainable.

Three biological control agents; *Paulinia acuminata, Cyrtobagus singularis,* and *Samea singularis,* were introduced into Lake Kariba to provide herbivores for the weed. Only *Paulinia* seemed to have survived (Mitchell & Rose 1979).

Figure 13.4 shows the growth and decline of *Salvinia* before and after the

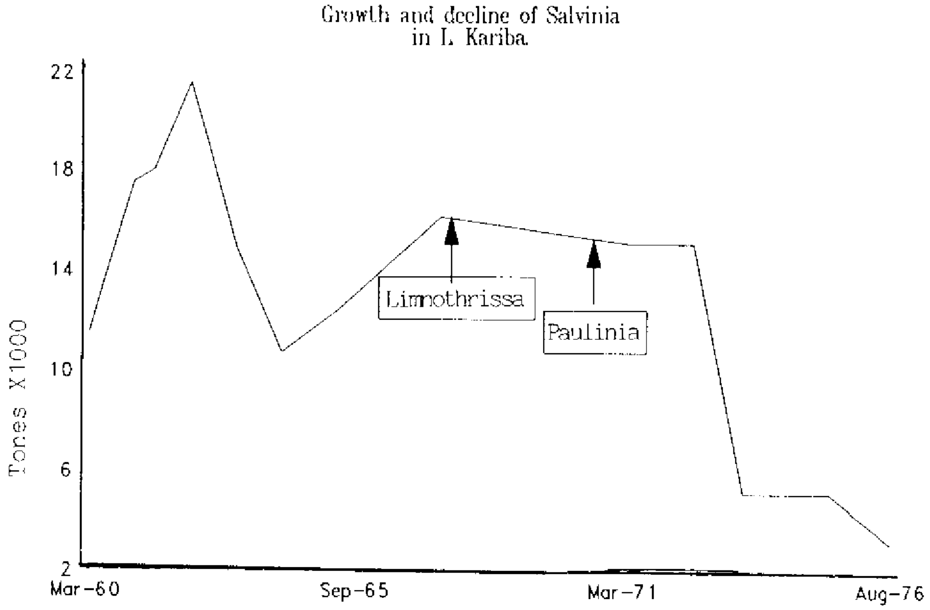

Fig. 13.4 The growth and decline of Salvinia molesta in Lake Kariba, before and after the introduction of *Limnothrissa miodon* and *Paulinia acuminata.* Note that the decline of Salvinia was pronounced after the introduction of the grasshopper.

introduction of the grasshopper. The figure also indicates the time of the introduction of the clupeid *Limnothrissa miodon.*

The figure shows a marked decrease in the area covered by *Salvinia* following the introduction of *Paulinia acuminata. Cyrtobagus singularis,* which was introduced on the Zambian side of the lake, did not establish itself.

The relative role of the introduced biological control agents remains controversial. Mitchell and Rose (1979) reported that *Paulinia* nymphs were in great abundance few months after the introduction, and were seen to feed on the young growing leaves of *Salvinia,* and thus ascribe the rapid decline in the area of lake covered by *Salvinia* to the grazing pressure exerted by *Paulinia.* They further reported that *Paulinia* was instrumental in checking the spread of *Salvinia* in Kabora Bassa reservoir.

The period between 1980 and 1993 may shed additional light on the causes of the decline of *Salvinia* in L. Kariba. In the early part of the decade the weed was frequently seen floating on the lake in small colonies. Growth forms of the plants suggested nutrient deficiency as observed by Mitchell (1975). In contrast weed mats in estuarine areas were well formed into compacted mats. *Paulinia* was still present in the lake. Towards the end of the decade the grasshopper was less evident. There were no signs of *Paulinia* herbivory in the young leaves of *Salvinia*, a situation that would have encouraged the resurgence of the weed. However the weed continued to decline until in 1993 the weed was not evident in the Sanyati Basin of the lake, being replaced in the river mouths by *Pistia stratoides*.

Mitchell and Tur (1975) noted that *Salvinia molesta* on the open lake had a lower growth rate than that in the river mouths and isolated bays. He noted that open lake phosphorus level ranged between 0 and 0.05 mg l^{-1} in open waters in comparison to a range of 0 to 0.21 mg l^{-1} in sheltered waters. Magadza et al (1987) give mean phosphorus levels of less than 0.01 mg l^{-1}. At the time of their study Mitchell and Tur did not cite phosphorus as limiting growth. They also indicate that the fishing of *Limnothrissa miodon* now constitutes a major nutrient sink, particularly phosphorus. These data suggest that *Limnothrissa miodon*, by its grazing on the plankton, sequesters significant amounts of phosphorus which are exported as fish products, thus maintaining a level of phosphorus too low for the growth of *Salvinia*. Kautsky has also suggested that the filtration of pelagial water by mussels also constitutes a significant nutrient drain.

13.4 CONTROL OF DISEASE VECTORS IN RESERVOIRS

The establishment of reservoirs and the subsequent increase in human water contact promotes a variety of water borne diseases, particularly schistosomiasis. These endoparasites are transmitted by pulmonate snails, particularly of the general *Bulinus* and *Limnaea*. The abundance of these moluscs is encouraged by the presence of aquatic vegetation, such as *Potamogeton spp*, *Nympheia* and *Vaelisneria*. A combination of herbivorous fish, such as *Tilapia andersoni* as well as various carp species and moluscivores such as *Sargochromis chodringtonii* can help suppress the populations of the schistosome transmitting snails, and hence control the prevalence of the disease in small water bodies and irrigation canals. In the control of the malaria vector mosquitoes the gambusid fish species have been used to predate on the mosquito larvae.

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