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THE FEASIBILITY OF BIOMANIPULATION IN RESERVOIRS AND DEEPER LAKES

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Statement of Use

This document records the results of a feasibility study of the possibilities for biomanipulation of reservoirs and recommends the management steps necessary for effective action by the NRA.

Research Contractor

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CONTENTS

EXECUTIVE SUMMARY

Biomanipulation is a technique for the ecological re-structuring of the pelagic food web which can be used in eutrophic lakes to achieve lower algal biomass and improved transparency. The effectiveness of the technique has been conclusively demonstrated in shallow lakes.

It is targeted upon zooplankton populations of the open water, with the objective of maintaining large-bodied species that effectively suppress phytoplankton through their grazing, reducing algal and cyanobacterial biomass and thus improving lake transparency.

Biomanipulation is primarily achieved through alterations to the fish community, such that the enhancement of piscivorous predators maintains a lower population of planktivorous fish (usually cyprinid) whose predatory impact upon zooplankton is thus minimised, allowing large-bodied zooplankton to thrive.

Reservoirs and deep lakes differ from shallow lakes primarily in that they stratify for longer periods. This stratification is usually more stable (over weeks-months) in summer unless artificially prevented. Reservoirs and deep lakes also have longer retention times. As a result of these two features, their biology usually responds to reductions in external nutrient loading more strongly than do shallow lakes where internal (sediment) loading has seriously delayed recovery in some case studies.

The increased size of reservoirs poses potential problems for biomanipulation, through greater practical and political difficulties in managing fish communities. Nevertheless, several case studies have demonstrated that successful biomanipulation can be achieved in reservoirs, although none have remained stable for long periods. Moreover the annual variability in external environmental effects on fish recruitment success (such as temperature, water levels, food availability to 0+ fry) has a strong and unpredictable influence upon success.

The ideal prerequisites for successful biomanipulation are:

a) a reduction of phosphorus inputs to below a threshold level, currently believed to be about 20 g TP /l/day

b) efficient artificial circulation which reduces phytoplankton production and also reduces the risk of cyanobacterial population development breaking away from grazing control

c) maximum possible control of fish species composition, which enables a portfolio of methods to be used for piscivore enhancement and planktivore suppression.

d) efficient monitoring of key food web variables – particularly zooplankton size structure and fish recruitment success each spring.

Those reservoirs in the literature which demonstrate biomanipulation most consistently are wholly artificial concrete-sided, rather than valley-dammed reservoirs, because they meet pre-requisites b) and c) at least.

In the Northern Area of the Anglian Region of the NRA, only Covenham Reservoir and Rutland Water contained data extensive enough for the evaluation of their potential for biomanipulation. Limited data from Pitsford Reservoir suggested that its zooplankton were more heavily suppressed than the other two by planktivorous fish.

Rutland Water has a zooplankton community moderately stable from year to year, dominated by one species of Daphnia, *D. galeata*. This indicates that fish predation is moderate. There is limited evidence that this exerts control of late spring-early summer algal populations, and is itself controlled by moderate-strong planktivory in summer. The reservoir is not mixed effectively enough to prevent late-summer cyanobacterial dominance.

Covenham Reservoir has a zooplankton community whose structure fluctuated widely in the three years for which data exist. In two out of the three years large-bodied cladocerans predominated. These indicate that predation pressure by planktivorous fish is low. Evidence suggests that these zooplankton suppressed phytoplankton in years when large-bodied species dominated, which coincided with low spring temperatures which (we infer) led to reduced cyprinid spawning success.

It is recommended that Covenham Reservoir be considered for a full-scale experiment in biomanipulation because:

a) its zooplankton size structure indicates the biological feasibility of such a course of action

b) its lack of angling indicates that biomanipulation could be politically feasible.

It is further recommended that a large-scale experiment at Rutland, enclosing one of the bays in the northern arm (Barnsdale is suggested) be undertaken to establish whether biomanipulation is consistent with a trout fishery. It is envisaged that the coarse fish populations in the enclosed bay will be reduced by repeated fishing effort but that the trout density and angler effort should remain the same as the main reservoir.

The framework for such experiments is discussed.

This feasibility study should be built upon by a detailed analysis of the full limnological data for the reservoirs. Current research and monitoring at the reservoirs should immediately be extended to include Pitsford, and at all three reservoirs should take into account the extent of piscivory and planktivory, the quantification of cyprinid spawning and recruitment, and the role of the littoral zone.

The feasibility (biological, technical and political) of a reduction of cyprinids and enhancement of piscivores (pike, eel, large perch) in experiments at Covenham and Rutland should be further evaluated by discussions with Anglian Water. The timescale considered should be six years at each reservoir; three years of coarse fish removal, carefully monitored, followed by three years of re-structuring of the coarse fish populations to provide a favourable piscivore balance, also carefully monitored.

The general conclusion is that biomanipulation is a realistic technique for eutrophication management in reservoirs which should be seriously pursued in conjunction with the other techniques known to be synergistic with it, but that it is a technique which will require continual monitoring and adjustment once established.

1 THE DEVELOPMENT OF BIOMANIPULATION IN LAKES

1.1 Introduction

Over the past fifty years there has been a progressive decay in aquatic habitats as a consequence of human disturbance. Investigations since the 1940s, in Europe and the US, have identified nutrient (particularly phosphorus) enrichment, primarily from sewage effluent and secondarily from agriculture, as the cause. This was well understood by the late 1970s. Since that time the scientific community has progressively become more active in seeking management solutions as well as mere explanations for change. A series of management-oriented publications (Sas 1989, Harper 1992, Harper and Pacini 1995) have reflected that stage of knowledge and the background is not considered further here.

In the last 5-10 years it has become clear that, despite long-term research efforts, the reduction of phosphorus alone has not achieved the desired restoration of aquatic ecosystems. The Norfolk Broads are a good example of this problem (Phillips and Moss 1994, Phillips and Pitt 1994). This stems from the realisation that the OECD models (Vollenweider and Kerekes 1982) for eutrophication assessment, which assume strong and direct dependence from a single identifiable element, i.e. phosphorus, and which were powerful tools for the initial classification of waterbodies, have failed as predictive tools for explaining changes in single ecosystems. An international investigation project devoted to the assessment of eutrophication management by nutrient reduction (Sas, 1989) conclusively disproved the expectations built upon single nutrient loading relationships. The development of "ecotechnological" management; a pragmatic, biologically-based approach to the integration of physical, chemical and biological changes in the structure of an ecosystem, is now leading to water quality improvement using internal mechanisms (Benndorf, 1995) which support the external mechanisms (reduction of nutrient loading).

1.2 Biomanipulation

Biomanipulation, in the sense of its early definition given by Shapiro, Lamarra and Lynch (1975) as the use of biotic processes to manipulate lakes, is the primary example of this 'ecotechnical' approach in lake management (but is part of a portfolio of ecotechnical approaches in the catchment-scale management of eutrophication, Straskraba (1994)). It originated with work on Czech fishponds in the 1960s and is based upon ecological theory later elaborated in North America as the 'trophic cascade' or 'top-down *versus* bottom-up' theory of ecosystem regulation (McQueen, Post and Mills 1986; Harper, 1992).

A variety of examples from the field and laboratory have now demonstrated the importance of grazing by larger bodied species of water fleas (Cladocera) in determining algal crop sizes in freshwaters (Pace, 1984) and thus supported the concept of biomanipulation (Shapiro *et al.*, 1975; Shapiro, 1990; Gophen, 1990; Moss, 1992).

Successful biomanipulation (Shapiro and Wright, 1984) is based on the prediction that increased piscivore abundance will result in decreased planktivore abundance and hence increased zooplankton abundance. Increased zooplankton grazing pressure then leads to reductions in phytoplankton abundance and improved water clarity. Successful biomanipulation is thus measured in terms of the reduction of phytoplankton biomass and the parallel increase in water transparency.

Biomanipulation has a successful history in shallow lakes, and has been well reviewed in such water bodies (Gulati *et al.*, 1990; Reynolds, 1994; Phillips and Moss, 1994) such that little further comment is necessary here.

1.3 Shallow and deep lakes

There is frequently a difference in the behaviour of shallow and deep lakes, which stems from the basic difference in response to nutrient loading observed in these two types of waterbodies. Shallow lakes only intermittently stratify, and are often strongly influenced by nutrient release from sediments. Deeper lakes and reservoirs on the other hand are more strongly influenced by external loading, and are likely to stratify more consistently during the summer (unless artificial measures are applied to prevent this). An approximate mean depth of 3 m was identified as a boundary between shallow and deep lakes in a recent review (Phillips and Moss, 1994).

There are several implications of this distinction into shallow and deep lakes for the application of biomanipulation:

- The trophic structure of communities in stratified waterbodies is more complex so that cascade effects have less impact at lower trophic levels (Carpenter *et al.*, 1985).
- Cyanobacteria are relatively more favoured by higher water column stability (deep lakes).
- Deep lakes are characterised by longer retention times which also tend to favour slow-growing, larger, inedible phytoplankters such as *Aphanizomenon* and *Planktothrix* (Reynolds, 1994).
- In deep lakes there is a high ratio between the pelagic and the littoral zone which reduces the influence of macrophyte beds and the possibility of control of zooplanktivorous fish by pike.
- Responses to biomanipulation are obtained more readily in systems characterised by strong resource limitation (Phillips and Moss, 1994). Light and nutrient limitation are

often observed in reservoirs and deep lakes during part of the year unless they are naturally or artificially mixed.

- Fish contribute little to the nutrient pool of deep lakes while they may have significant effects in shallow bodies of water where standing stocks are high and water volumes low (Nakashima and Leggett, 1980). This effect may be important in enhancing phytoplankton growth (bottom-up). However it is difficult to separate it from the impact of fish on phytoplankton through predation on zooplankton (top-down) (Lammens, 1988).
- In deep lakes biomanipulation cannot rely upon "secondary" bottom-up effects that may play an important role in shallow lakes (Benndorf 1990).
- Stratified systems offer chemical refuge to zooplankton from predation. Nyctemeral vertical migrations are commonly observed as a result of this.

All of the published reports available for review (Benndorf *et al.*, 1984; Carpenter *et al.*, 1987; McQueen *et al.*, 1989; McQueen, 1990; Scavia *et al.*, 1986; Lehman, 1988; Shapiro and Wright, 1984; Phillips and Moss, 1994) suggest that for deep lakes there will be significant top-down correlations at the top of the food-web (piscivore-planktivore-zooplankton), but with weak and unpredictable long-term impacts on phytoplankton.

The crucial question to be addressed by this reveiew is whether that statement can be supported by a critical review of case studies on the one hand, and the raw data from the reservoirs of the Northern Area of the Anglian Region on the other.

The evaluation of biomanipulation is considered under five main themes in the following chapters:

- 1. What evidence from the literature is there that biomanipulation might be succesful in reservoirs?
- 2. What evidence from the literature is there about the problems of biomanipulating reservoirs?
- 3. How do the specific characteristics of the Anglian Region reservoirs relate to the requirements of effective biomanipulation and what evidence do we need to review and evaluate ?
- 4. What immediate investigations should be carried out to assess whether biomanipulation could work in these reservoirs ?
- 5. What kind of additional management and supporting research data are needed if it is decided to implement biomanipulation ?

2 THE POSSIBILITIES FOR BIOMANIPULATION IN RESERVOIRS

2.1 Successful biomanipulation in lakes

Successful biomanipulation has been reported now in a large number of publications and is summarised effectively in two recent NRA-sponsored ones; Reynolds (1994) and Phillips and Moss (1994). The top-down food web processes have been demonstrated more strongly in shallow lakes (e.g less than 3m average) than deeper ones (Moss *et al.* 1994) and the oldest experimental lake restoration projects now have over a decade of data (e.g. Moss *et al.* 1995) demonstrating the importance of both the maintenance of piscivorous fish stocks on the one hand and the refuge function of macrophyte zones on the other.

2.2 Indirect effects of biomanipulation

Most research on biomanipulation has focused on the direct effects of predation, while it is also important to take into consideration the resulting feedback effects. These are direct and indirect bottom-up effects caused by changes in ecological equilibria induced by top-down control. Their importance is at least equal to, if not greater than the direct impact of fish predation and zooplankton grazing. The difficulty of separating these complex concurrent interactions in order to evaluate them is presently the main problem limiting the reliability of biomanipulation as a water management tool.

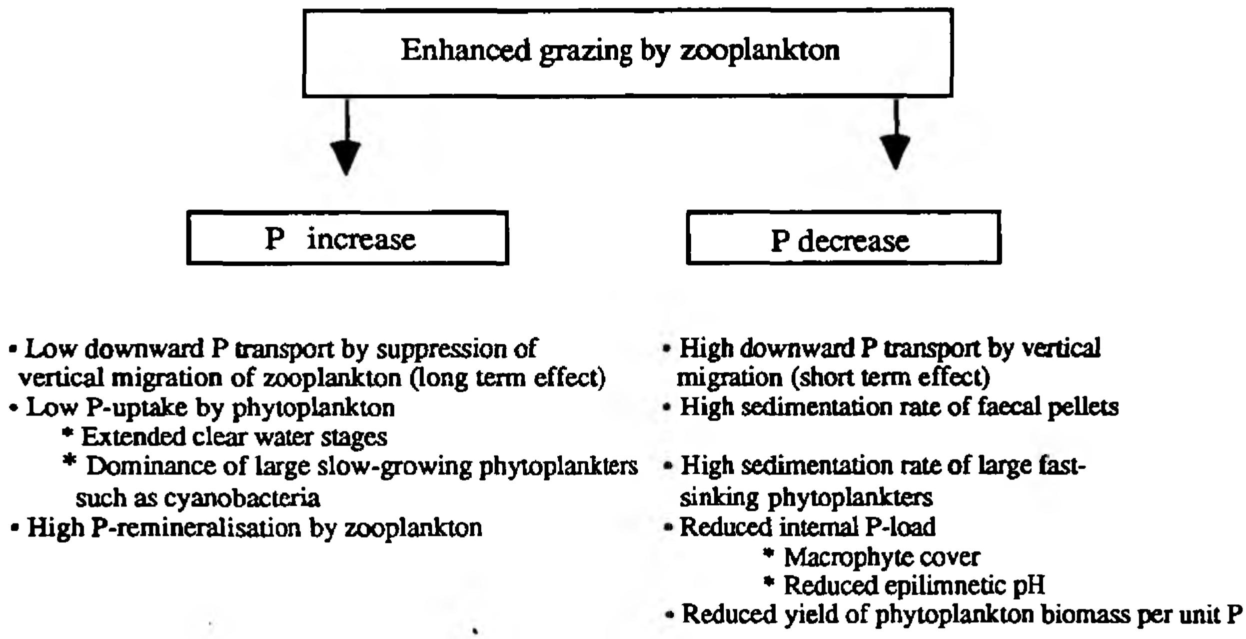
Benndorf (1992) distinguished three types of indirect effects:

- Trophic linkage: a change in quantity or quality of the resource base,
- Behavioural: a behavioural change of the prey,
- Morphological: the development of anti-predator traits.

Trophic linkage effects are the most important. An example is the complex of indirect effects of enhanced grazing by large herbivores on phosphorus dynamics. It has been shown that an increase in zooplankton size increases the phosphorus sedimentation rate as zooplankters produce larger faecal pellets that sink faster (Benndorf, 1992). At the same time large pellets increase water transparency as suspended faecal matter is less dispersed (Benndorf, pers. comm.). Processes and relationships that were relatively unexpected or formerly considered to be of marginal importance are also significant. For example, the level of nutrient enrichment influences zooplankton by changing the nutritional properties of phytoplankton and this alters the reproductive biology of zooplankters (Sommer, 1992; Sterner *et al.*, 1993).

The indirect consequences of inter- and intra-specific competition among zooplankters caused by resource limitation have also been little studied (Sommer, 1992). In particular the relative importance of these mechanisms in relation to other behavioural controls such as chemical communication among planktonic organisms is not understood. It has been shown that chemical substances released by *Daphnia* are able to regulate colony formation in *Scenedesmus acutus* (Lampert *et al.*, 1994) while substances released by some cyanobacteria appear to be toxic to zooplankton (Lampert, 1981; Lampert, 1987; Kirk and Gilbert, 1992; Gilbert, 1994).The baseline phosphorus concentrations needed for successful biomanipulation are thought to be less than 150 µg/l TP (Jeppesen *et al.* 1990). Benndorf suggested that at higher ambient phosphorus concentrations it is still possible to achieve enhanced zooplankton grazing (which he demonstrated in Bautzen reservoir, see 6.5.4). This however may not be translated through into a reduction of algal biomass, as shown in the left-hand pathway in Figure 2.1. The optimal outcome, shown as the right-hand pathway, can only be achieved through additional, concurrent management such as reduction in ambient phosphorus concentration or by artificial mixing or a combination of the two.

Figure 2.1 The indirect effects of biomanipulation (enhanced grazing) on the phosphorus concentration in a water-body (Benndorf, 1992)



2.3 Top-down *vs.* bottom-up control in eutrophic lakes

De Melo *et al.* (1992), Moss (1992) and Reynolds (1994) considered biomanipulation as an effective restoration tool in the absence of any nutrient control, in contrast with observations made by other authors (Lyche, 1989; Elser *et al.*, 1990; Benndorf, 1987; 1990; 1995; Hrbácek, 1994; Koschel, pers. comm.) who considered that it can only work after effective nutrient control has been applied. The increase in nutrient loading which drives the eutrophication processes is typically accompanied by profound changes in physico-chemical equilibria and food web structure. Biomass, productivity and nutrient turn-over (in particular phosphorus) increase in parallel to adjustments in the species composition at all levels of the food-web (Harper, 1992). Positive feedback mechanisms such as the build-up of anoxia in the hypolimnion and the depletion of CO_2 in the epilimnion push the system towards a progressively more hypertrophic state despite attempts at restoration.

These physico-chemical changes are also related to shifts within the phytoplankton which eventually lead to the appearance of large, self-regulating, colonial cyanobacteria populations (Shapiro, 1990; Pick and Lean, 1987). Inefficient phytoplankton grazing is related to an increase of zooplankton predation by fish due to the impairment of piscivores by large changes in oxygen concentrations (depletion to supersaturation within 12 hours) and reduced water transparency.

2.4 Thresholds for the success of biomanipulation

The apparent contradiction between the results cited by different authors led to the formulation of the hypothesis of a *biomanipulation efficiency threshold of phosphorus loading* (Benndorf, 1987). A reduction of mean phytoplankton biomass as consequence of a strong top-down effect can be expected only below a threshold of phosphorus loading which has been set by Benndorf as a surface loading of 0.5-2 g TP m^{-2} $year^{-1}$. Observations in the United States similarly suggested a loading threshold above which grazer control is progressively lost (Cottingham *et al.*, 1994), although their threshold was much lower (a volumetric loading of 1 µg P $l^{-1}d^{-1}$). For Rutland Water, where in the early part of 1994 actual loading into the reservoir was around 30 kg P/day compared to a maximum of 400 kg P/day in 1991 (Krokówski, pers. comm.), Benndorf's figures convert to below 17 kg P/day, Cottingham *et al.*'s two orders of magnitude lower.

The debate between bottom-up/top-down controls on phytoplankton biomass (McQueen *et al.*, 1986) does not resolve the fundamental question which remains: whether biomanipulation is useful in the absence of nutrient control? Moss (1992) and Phillips and Moss (1994) maintained the view that the real trigger for stable phytoplankton dominance is the development of cyanobacteria and argued that under conditions which help to prevent the establishment of cyanobacteria (such as a high flushing rate which gives diatoms a competitive advantage over other groups or a high N:P ratio), biomanipulation is effective in improving water quality.

This opinion supports the possibility that biomanipulation can be used for restoring reservoirs. These water bodies are in general characterised by larger catchments than natural lakes and consequently receive higher loads. Several reservoirs have been designed in such a way to maximise management options by changing their hydraulic parameters. Specifically designed models can be employed to provide high quality water supply by various technical methods. Several theoretical options were reviewed by Straskraba (1994). Moss proposed the careful control of the fish population as a tool for the management of drinking-water reservoirs in Britain coupled with hydraulic conditions aiming at the reduction of cyanobacteria (Moss, 1992). A drastic reduction of the coarse fish stock might be more acceptable in highly managed water bodies such as reservoirs than in natural lakes (Phillips and Moss, 1994), although reservoirs such as Rutland Water, Grafham Water and Pitsford Reservoir have high-profile trout fisheries that both impose restrictions on management possibilities as well as creating a possible additional impact of planktivory.

If the control of water levels is possible (as in valley reservoirs with a natural catchment) then an added advantage that can be used to influence the specific composition of zooplankton (Naselli-Flores and Barone, 1994) and fish (Zalewski *et al.*, 1990a, Tarczynska *et al.*, 1994) is available, through deliberate drawdown to manage fish spawning success.

2.5 Case studies of reservoir and deeper lake biomanipulation

Examples in the literature of top-down control effects in reservoirs (largely in continental Europe) are increasing at the same time as management interest in the control of deleterious effects of eutrophication grows. However, there are still relatively few documented cases of biomanipulation in reservoirs and deeper lakes, as opposed to the many case studies of shallow lakes in the literature. The case studies reviewed here highlight the particular characteristics of reservoirs in relation to food-web control.

2.5.1 Lake Washington, USA

Lake Washington (Edmondson, 1991), often cited as an example of successful lake restoration by nutrient reduction, is a typical case of strong top-down control mechanisms working under conditions of low nutrient loading. This lake recovered after nutrient reduction by the diversion of a wastewater tributary in 1963-1967 following precisely the predictive model of Vollenweider as chlorophyll *a* decreased in a direct proportion to total phosphorus. Phosphorus loading and in-lake concentration decreased and the water transparency increased to levels similar to those characteristic of the years preceding sewage diversion. However an unexpected increase in the population of several *Daphnia* species occurred pushing the lake further towards oligotrophy. A tentative explanation for this effect would be that *Daphnia* increased due to the simultaneous decline of the zooplanktivorous shrimp, *Neomysis mercedes*, linked to the increase in its predator fish, the long-fin smelt *(Spirinchus thaleichtys)*. Another possible cause could have been the decline of *Oscillatoria* due to the nutrient diversion, as the abundance of *Daphnia* is dependent on the rate of its predation by fish but also on suitable food supply: *Oscillatoria* is known to mechanically inhibit filter-feeding (Infante and Abella, 1985). McQueen (1990) found that shifts in phytoplankton composition at high levels of nutrient enrichment favour the establishment of ungrazable phytoplankters and in Lake Washington that situatiomay have been reversed (Fig 2.2). Either explanation is possible, since McQueen *et al.* (1986), Vanni *et al.* (1990) and Lafontaine and McQueen (1991) have also suggested that top-down control is stronger in oligotrophic systems.

The positive result obtained with the restoration of lake Washington seems to be due to its depth (64 m max.), short retention time (0.4 years^{-1}), oxic hypolimnion, and its relatively short period of nutrient enrichment. This case also demonstrates the importance of the past history of a lake for its response to eutrophication management.

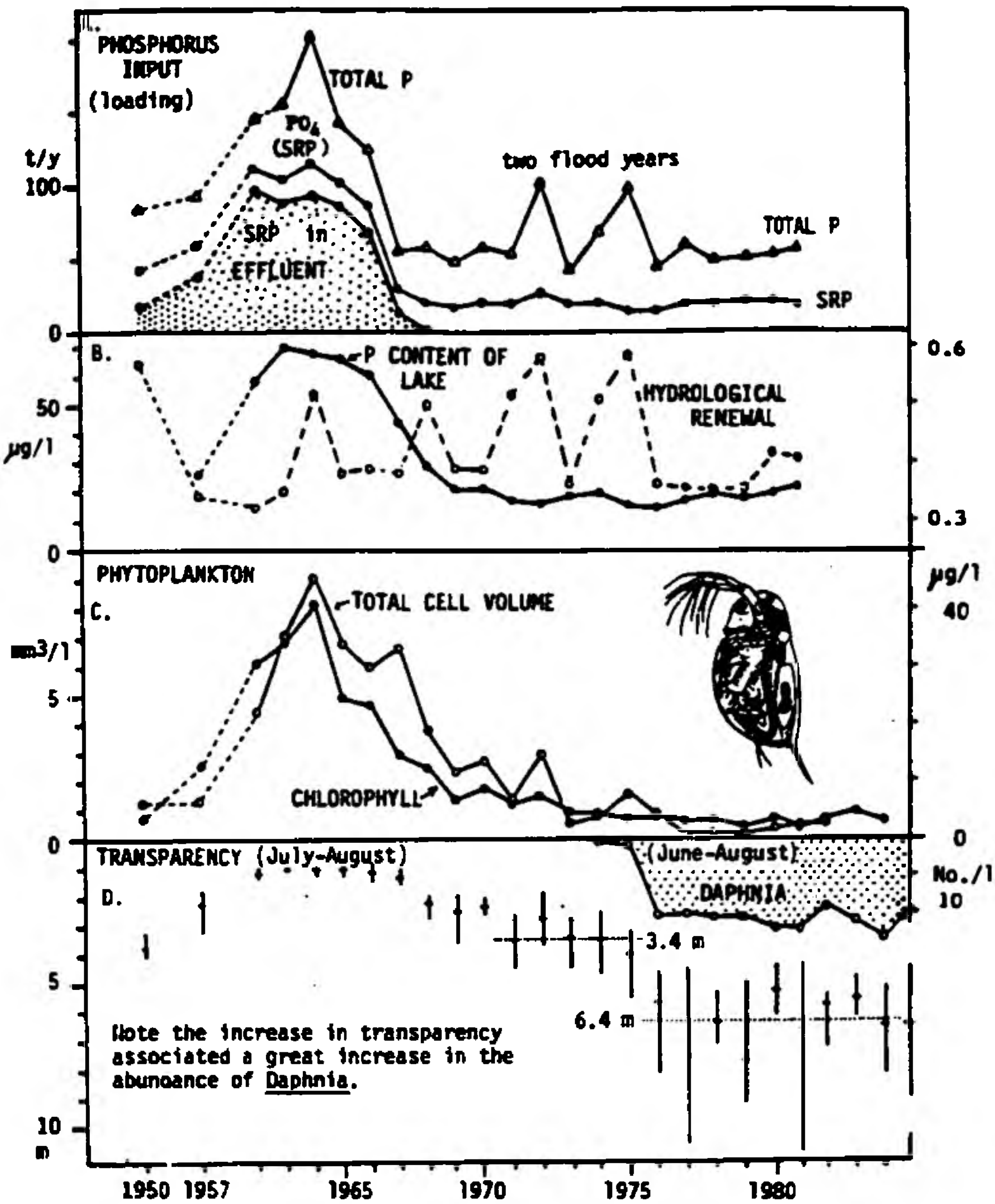


Figure 2.2 Lake Washington, showing changes in phosphorus loading with eutrophication followed by diversion, consequent decline in phytoplankton and transparency increase, and finally the additional increase in trasnsparency and decline in phytoplankton biomass associated with enhanced grazing by *Daphnia*. From Edmonson, W.T. (1985) Recovery of Lake Washington from pollution, *Proc. Int. Congr. Lakes Pollut. Recovery*, Rome.

2.5.2 The Thames Valley reservoirs, London

The combined effect of light limitation and high zooplankton grazing successfully controls phytoplankton development in a series of artificial water supply reservoirs near Heathrow Airport, West London, receiving large amounts of dissolved nutrients from the river Thames. Efficient mixing is achieved by the inlet jets, positioned at the centre of the basin above the reservoir bottom and angled upwards. Steep-sided concrete banks, devoid of vegetation, ensure high impact of wind mixing and limit the development of large fish biomass due to the lack of suitable sites for spawning and of protection for the fry from displacement by wave action and currents. In 1992 fish biomass in Wraysbury reservoir was as low as 6.8 kg ha^{-1} and in some other reservoirs lower than 50 kg ha^{-1}. In Wraysbury reservoir, concrete side walls prevent spawning by fish other than ruffe and perch (Kubecka and Duncan, 1994). This explains the high proportion of perch in a reservoir that would have otherwise been dominated by cyprinids according to Kubecka's classification of reservoir fish composition in relation to nutrient loading (Kubecka, 1993b).

The reservoir phytoplankton, as a result of mixing combined with the high turbidity of input water from the river Thames, experiences a strong light limitation and a short photoperiod coupled with lower temperature which tend to retard spring development. This optimises the impact of grazing by zooplankton which develops later in the spring (Steel, 1972). Zooplankton populations are not entrained by mixing and are less affected by the reduced temperature.

The effects of a constant supply of high quality food resource from river phytoplankton may be as important as the lack of predation for sustaining large-bodied *Daphnia* populations. Studies elsewhere on the physiology of *Daphnia* feeding have shown the importance of the biochemical composition of the food resource on organism and population responses such as growth rate, fertility, clutch size, age at reproduction and mortality (Sterner *et al.*, 1993). Efficient grazing in the London reservoirs is dependent on the continuous input of river water because high throughput makes these systems well flushed (retention time 50-100 days) and river water carries substantial amounts of organic seston. Peaks of algal development in the river Thames are of a much higher biomass than those in Queen Elizabeth II reservoir (Steel, 1972). Vertical circulation within the reservoir retards sedimentation of this allochthonous material and ensures resource availability for zooplankton. This sustains *Daphnia* during crucial periods of low autochthonous phytoplankton development preventing the slumping of the population (Phillips and Moss, 1994). Observations of occasional low fecundity in daphnids and biomass of small edible phytoplankton (Seda and Duncan, 1994) confirm that in these reservoirs zooplankton are potentially resource-limited. This does not translate into a significant relationship between cladoceran biomass and chlorophyll *a*. (Seda and Duncan, 1994) because the food supply depends largely on the irregular river inputs rather than on autochthonous growth.

It is difficult to place within this context the influence of fish diseases that severely reduced the fish populations in the 1960s (Duncan, 1990) and the impact of an invertebrate predator

Leptodora kindtii (Phillips and Moss 1994). The role of invertebrate predation on grazers is controversial. Its impact has been studied in several lakes (Lehman, 1988; Rognerud and Kjellberg, 1990; Lehman and Cáceres, 1993; Meijer *et al.*, 1994b; Phillips and Moss, 1994). In natural unmanaged lakes invertebrate predators are not usually able to control zooplankton biomass. Accidental and experimental biomanipulation has shown that invertebrate predation is triggered by vertebrate predation (Hrbácek *et al.*, 1986) as the number of fish that feed on invertebrate predators is drastically reduced.

These reservoirs seem to disprove Benndorf's postulate that biomanipulation will be inefficient under high phosphorus loading. They confirm the importance of forms of management which complement the direct restriction of zooplanktivorous fish, which on their own may not be successful in obtaining the desired trophic cascade effects. In the London reservoirs the complementary management is destratification by mixing in a concrete bowl-shaped environment.

Eutrophication appears to be increasing in Queen Mary reservoir, which is characterised by a shallower depth, a high chlorophyll *a* and the absence of vertical mixing devices (Seda and Duncan, 1994). In contrast to the other reservoirs of the series, Queen Mary has a relatively high shoreline index, a littoral zone with developed marginal terrestrial vegetation suitable for the spawning of roach and bream, large cyprinids (Kubecka and Duncan, 1994), increasing fish biomass and the presence of small-bodied zooplankton dominated by copepods (Renton *et al.*, 1994; Kubecka and Duncan, 1994). This reservoir lacks both "anti-fish" features (Seda and Duncan, 1994) and the artificial circulation which are the precursors for efficient management in the other reservoirs and tends to strengthen the conclusions drawn from the other reservoirs that biomanipulation is possible if supported by at least one other strong management method.

2.5.3 Sulej6w reservoir, Poland

This shallow (average depth 3.3 m, area 2383 ha), elongated waterbody, filled in 1973, is situated in the lowlands of central Poland. It collects the drainage of an agricultural catchment of which 60% is occupied by intensively fertilised fields. Due to nutrient loading from agricultural areas and pollution by untreated sewage, nutrient concentrations in the major tributary, the Pilica river, are as high as 7 mg P l^{-1} and 11 mg N l^{-1}. Mean in-lake concentrations are 0.3 mg P l^{-1} and 2.5 mg N l^{-1} with occasional peaks of ammonia reaching 1.3 mg N l^{-1} (Galicka, 1992). The relatively short and variable retention time (15–48 days), the frequent mixing and the important seasonal and inter-annual changes in water level render this drinking water storage reservoir a highly unstable ecosystem. Due to the uniformly shallow bottom, changes in water level cause a large variation in reservoir surface area; between 1981 and 1988 the reservoir surface decreased of as much as one third. Chlorophyll levels are moderately high with mean summer values around 30 μg chl *a* l^{-1} and peaks of 45 $\mu g\ l^{-1}$. The phytoplankton biomass is composed mainly of pennate diatoms in spring and in autumn, cyanobacteria in late winter and in summer with the occasional occurrence of high peaks of phytoflagellates at the beginning of autumn (Galicka *et al.*, 1993). Recent investigations revealed the presence of toxic cyanobacterial blooms *(Microcystis aeruginosa)* which coincided with years of high spring water levels (Tarczynska *et al.*, 1994). Zooplankton are composed mainly of *Bosmina coregoni* and *Daphnia cucullata* and tend to peak in late spring–early summer. These periods are accompanied by a change in phytoplankton species composition with a decrease in small, flagellate, edible phytoplankters (Galicka *et al.*, 1992). However, a direct relationship between phytoplankton and zooplankton biomass has not been yet demonstrated.

Percids and cyprinids make up together between 60 and 70% of the fish biomass. There is little substrate suitable for egg deposition and shelter for the fry, due to the frequent changes in water level which leave sandy beaches devoid of vegetation as the main littoral habitat. Perch dominate the fish biomass in the reservoir as they are able to spawn on structurally poor substrates while bream are present and thought to contribute to sediment resuspension (Zalewski *et al.*, 1990b).

Studies on the behavioural ecology of different fish species revealed overlapping food preferences and niche shifts due to competition for large cladocerans. Observation of 24-hour feeding patterns revealed that perch fed predominantly on large zooplankters. Other food items, including their own conspecifics and benthic invertebrates, were consumed only at sites where large zooplankters were unavailable. In years of high perch recruitment, phytoplankton biomass increased as a consequence of the high impact of perch on the zooplankton community. Perch growth rates decreased in years of high recruitment as a consequence of a reduction in the numbers of cladocerans. A correlation between fry density and growth rate confirmed a density-dependent effect (Zalewski *et al.*, 1990 b). At high perch densities, roach were out competed and fed on periphyton and detritus; this is surprising for a species highly adapted for filter–feeding, a technique which is generally considered as highly suited for planktivorous feeding.

Zander (pikeperch) are the main predators in Sulejów but do not seem to exercise significant control on the biomass of the other fish as their numbers do not exceed 3% of the total fish. In 1984 (high water year) hatching of perch and pikeperch were closely coupled. The coincidental occurrence of a strong year class of perch and pikeperch does not favour the pikeperch. Young pikeperch were unable to feed on the abundant perch fry of the same age class because the fish were too large for them to swallow and they developed poor condition as they were also out-competed by the higher ability of perch in feeding on zooplankton (Zalewski et al., 1990b). Large perch do feature in pikeperch diet; under conditions of unlimited prey choice, adult pikeperch tend to prefer soft-rayed cyprinids to the spiny-rayed perch. In Sulejów the impact of predation on perch was unimportant. Because of the low availability of cyprinids in the Sulejów reservoir pikeperch tend to predate on their own conspecifics when there is a lack of alternative food. Recent observations confirmed the occurrence of a bimodal size distribution of pikeperch derived from this mode of feeding proving that cannibalism was the dominant factor regulating the survival of pikeperch juveniles (Frankiewicz et al., 1995). In Sulejów resource–stressed pikeperch has a potential control over cyprinid recruitment but no effect on perch numbers. In general predation does not have a high impact on the determination of fish biomass in Sulejów reservoir, this seems to be more directly related to physical factors.

Temperature is often considered as the most important factor determining fish reproductive success in temperate freshwaters (Koonce *et al.*, 1977). In Sulejów, however, yearly recruitment showed no dependence on spring temperatures but correlated with changes in water levels. Years characterised by high water levels in spring had higher availability of suitable spawning grounds offered by submerged littoral vegetation. In those years in which high water levels persisted up to the spawning time, percids and cyprinids invaded the flooded terrestrial vegetation and achieved high reproductive rates. This observation lead Zalewski and coworkers to estimate the impact of the water level change by an 'area stability index' As (Fig 2.3):

$$As = M + \sqrt{\frac{M}{Var}}$$

where:

M is the mean area of the reservoir during the spawning to post–spawning period (May, June, July in the Sulejów),
Var is the variance of the above mean, expressing the variability of the area due to water–level fluctuations.

The index is intended as an expression of water level variability between the pre- and the post-spawning period (Zalewski *et al.*, 1990a). A positive relationship was drawn between the area stability index and perch and cyprinid fry densities in littoral areas caught by a 1.0 cm mesh, 15 m long seine net (Zalewski *et al.*, 1990b; 1995) over a period of seven years. The year 1982 was characterised by particularly high instability due to engineering works being carried out at the dam. Water levels decreased sharply during the spawning period leaving littoral areas to dry out. Low recruitment of perch was accompanied by low perch densities and larger sizes. Compared to other years in 1982 perch had a higher proportion of *Daphnia* in their stomachs in relation to other food items. Lower predation pressure correlated with the presence of larger *Daphnia* than in other years. In 1984 stability was high and so was coarse fish recruitment. The monthly figures of zooplankton biomass showed a slump corresponding with the feeding of the young-of-the-year coarse fish. General fish condition was poorer than in other years due to density dependent effects. The sharp decrease in zooplankton biomass was not observed in 1983, a year of low area stability.

In recent years *Dreissena polymorpha* has appeared in the reservoir. It is likely that a rapid population growth could have implications for nutrient cycling, phytoplankton grazing and availability of fish spawning substrate.

These observations and parallel studies on nutrient cycles confirmed that the water level and the retention time have a direct impact on the phytoplankton community. The combined effects depend upon a series of factors relating to the release of nutrients by newly inundated areas during high water levels and the occurrence of high coarse fish recruitment. Conversely drawdown periods are characterised by high temperatures and high internal loading (Tarczynska *et al.*, 1994). The extent of the impact of top-down control on the phytoplankton biomass cannot be easily established as both fry recruitment and the release of nutrients from littoral areas are triggered by an increase in water levels and these potential causes cannot be easily separated.

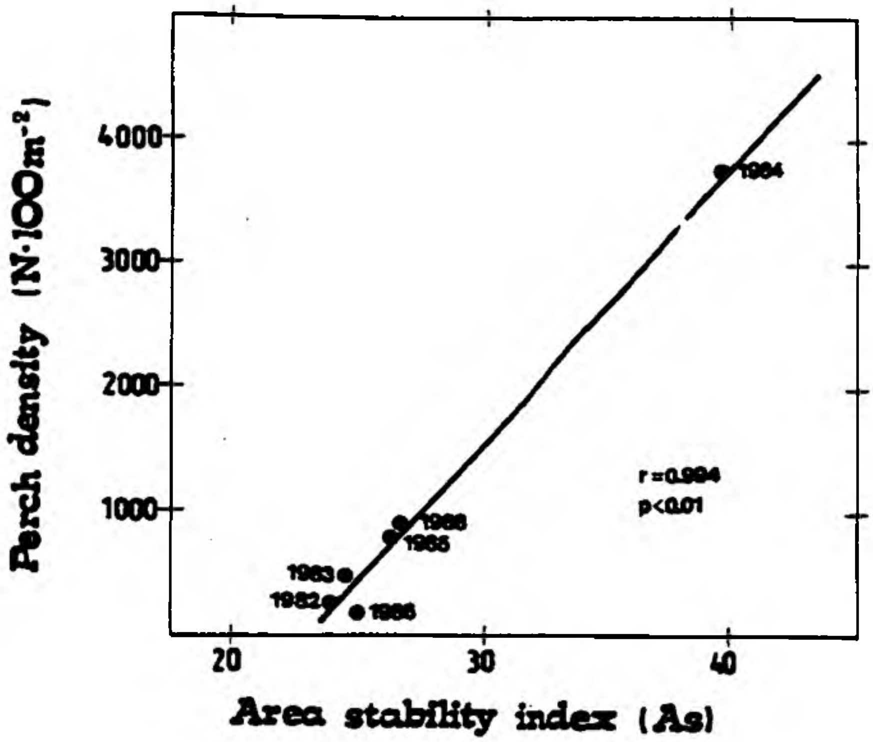


Figure 2.3 The area-stability index of Zalewski

Current research is looking at the possibilities of managing the abundance of fry to boost zooplankton biomass. Strategic changes in water levels were successful in reducing cyprinid and partly percid fish recruitment. An additional means of reducing perch recruitment is provided by removable artificial substrates, designed to attract egg deposition under the inhospitable conditions offered by the sandy bottom. Artificial substrates consist of bundles of brunches of local riparian tree species (spruce, juniper, birch and pine) arranged into pyramids about 50 cm high (Wojciech Rucinski, pers. comm.). Observations of egg deposition on these substrates revealed that perch lay their eggs almost exclusively on birch while roach prefer the structurally more complex spruce (Frankiewicz *et al.*, 1995). It is hoped that future studies on the reproductive behaviour of fish may help in the design of an ideal artificial substrate by progressive refinement. The use of a successful artificial substrate combined with a better knowledge of the timing of the yearly spawn would offer the possibility to manage the fish biomass on a species-by-species basis. Artificial substrates can be removed from the water after spawn and the eggs destroyed to reduce yearly recruitment. Alternatively they can be used to sustain the recruitment of a given species by providing additional eggs.

This form of management conflicts, however, with the general purpose of drinking water reservoirs. Artificial changes in water levels are often not practicable because of the need for a high water level in the reservoir in the spring to counterbalance the strong water deficit that occurs during the Polish summer. The use of artificial substrates in conditions of high water levels at spawning time is controversial. It is not known whether they can be effective in the reduction of fish biomass in the presence of suitable natural substrates such as flooded terrestrial vegetation which are likely to be preferred to the artificial ones.

2.5.4 The Biesbosch reservoirs, The Netherlands

A chain of three reservoirs in the southern part of the Netherlands, built following the design developed for the Thames Valley Utilities reservoirs in London (Steel, 1975), covering 615 ha of surface for a volume of 86 10^6 m^3, provides drinking water to the cities of Rotterdam, Dordrecht and their surroundings. The Biesbosch reservoir complex is supplied by water pumped from the eutrophic river Meuse (0.3 g $TP \cdot l^{-1}$, 5 g $TN \cdot l^{-1}$; Oskam, 1995). Strategic abstraction at times of higher water quality protects the reservoirs from peak loads of river bourne pollutants. Natural self-purification by physico-chemical and biological processes (sedimentation, particle adsorption, mineralisation, biological uptake) further increase the water quality before it reaches the water treatment works after 5 to 6 months' residence within the chain of reservoirs.

Artificial destratification by air-injection is employed to induce light limitation of algal growth and is successful in keeping average yearly chlorophyll levels between 5-20 $\mu g\ l^{-1}$. The application of OECD models shows that this is 5 to 10 times lower than the chlorophyll *a* concentration estimated on the basis of nutrient loading. The highest chlorophyll levels are found in De Gijster reservoir (the first of the chain receiving water directly from the Meuse). In addition a shallow littoral area 3-7 m deep, covering some 25% of the total surface, decreases the efficiency of circulation here.

In De Gijster reservoir spring diatom blooms with peak chlorophyll *a* of 30 to 60 $\mu g \cdot l^{-1}$ were common between 1973 and 1988 interfering with the water treatment (Oskam, 1995). In these years water temperature remained below 10°C during most of the spring preventing the development of effective zooplankton grazing. The spring diatom peak was limited by light and progressively by decreasing silica levels.

Warmer springs from 1988 onwards enabled large cladocerans (*Daphnia magna, D. pulex* and *D. longispina*) to develop which reduced the diatom peak to 10-20 μg Chl *a* l^{-1}. The provision of a zooplankton refuge at greater depths by artificial destratification may provide an additional explanation for higher zooplankton numbers as zooplankters in deeper (dark) waters may be sheltered from fish predation (Pastorak *et al.*, 1980; Klapper, 1991).

Cyanobacteria are present in the reservoir at a relatively low biomass; in summer 1994 for example they constituted less than 20% of the total phytoplankton assemblage (Henk

Ketelaars, pers. comm.). Taste and odour problems since 1984 have been caused however by geosmin produced by benthic *Oscillatoria* (Oskam and van Bremen, 1992).

The high efficiency of zooplankton grazing is caused by the dominance of eel, perch and pikeperch in the fish population. These predators are able to reduce the yearly recruitment of other cyprinid fry which would otherwise have the greatest impact on zooplankton populations (Oskam and van Breemen, 1992; Oskam, 1995). Investigations of the fish population revealed that perch, ruffe and to a certain extent pikeperch can successfully spawn within the reservoirs. Observations carried out by SCUBA divers confirmed that cyprinids also lay their eggs but these do not achieve successful development and are heavily preyed upon by bream (Visser, 1993). Cyprinids are represented mainly by roach, bream and silver bream *(Blicca bjoerkna)*. Their overall numbers are lower than those of percids but the condition factor of those remaining is high. A progressive increase in bream has occurred in recent years; in some cases bream represents up to 75% of the catch of cyprinids (Visser, 1993). The proportion of cyprinids to other fish is higher in the De Gijster than in the Honderd en Dertig and in Petrusplaat as the three reservoirs follow in a chain of progressively less eutrophic conditions. Petrusplaat is characterised by high piscivorous/planktivorous ratio due to the presence of large eels and the availability of spawning grounds for perch but not for cyprinids.

Invertebrate predators are often indicated as potential threat to the success of biomanipulation in lakes and reservoirs. Typical invertebrate predators of the pelagic habitat are the cladocerans *Leptodora* and *Bythotrephes* whose forelimbs are flattened and enlarged, by closing them together they tend to form a basket–like structure in which they trap the prey, constituted mainly by small cladocerans (Lampert and Sommer 1993). The effect of invertebrate predators causes sometimes a left–skewed distribution of the zooplankton biomass as they select preferentially smaller organisms (Henk Ketelaars, pers. comm). The overall impact of invertebrate predators on the trophic chain and on the success of biomanipulation is controversial. In De Gijster reservoir the appearance of *Bythotrephes longimanus* in some warmer years coincided with a shift of the structure of the zooplankton assemblage, with a slight decrease in the proportion of copepods to cladocerans. There was no indication of a significant increase of the algal biomass that may be linked to this invasion probably due to the low numbers of these invertebrate predators. The appearance of *B. longimanus* had no effect on the abundance of the other invertebrate predator *Leptodora kindtii* which is also present in the reservoir (Ketelaars and van Breemen, 1993).

The relatively low algal biomass found in the Biesbosch reservoirs is likely to be related to their particular fish community composition, which in turn is interpreted as a response to the morphology and operation of the reservoirs. In the Biesbosch, reservoir edges consist of steep-sloping concrete banks covered by filamentous algae such as *Cladophora, Ulothrix* and *Spirogyra*, highly unsuitable for egg deposition. The high piscivore/planktivore ratio in the reservoirs is sustained by a continuous invasion by (small) coarse fish from the river Meuse through the inlet and these provide food for a higher piscivore population than could otherwise be sustained by the reservoir alone. This external supply of food is particularly crucial during winter when food resources are scarce and predatory fish population generally suffer poor

Figure 2.4 Artificial spawning substrates used at Sulejow reservoir

condition. Cannibalism was noted in perch and pikeperch but did not seem to significantly affect their numbers. The Biesbosch reservoir perch were found to achieve the highest growth rates in some years of any known perch population in the Netherlands. Food items included invertebrates, fish and zooplankton and varied among individual fish and different periods of the year according to the stage of development and availability. Their growth rate indicated that perch were in a state of virtually unlimited food supply. Pikeperch had a lower condition factor than perch as they seemed unable to adapt to different food items during temporary scarcity of young fish (their preferred prey was ruffe). Eel introduced *via* the water inlet also contributed significantly to the high predation pressure while pike only seemed to have a marginal influence. Pike catches were limited to a few large specimens (80-100 cm) indicating that the species achieves poor recruitment.

These reservoirs also demonstrate that successful biomanipulation coupled with strong mixing can, even under high levels of nutrient loading, be maintained to produce zooplankton grazing leading to lower than predicted algal crops and clear water conditions.

2.5.5 Bautzen reservoir, Germany

This relatively shallow reservoir (mean depth 7.4 m, area 533 ha) was filled for the first time in 1974 to provide cooling water for a large industry. Complete exposure to strong winds ensures frequent mixing of the water column with the exception of a few weeks during summer anticyclones (Benndorf *et al.*, 1988). A very high phosphorus loading (4.1-15.5 g $P{\cdot}m^{-2}$) resulted in cyanobacterial blooms as soon as the reservoir filled, reducing visibility in summer and causing great nuisance to recreation (swimming, sailing, sport fishing and wind-surfing). A biomanipulation experiment was started in 1977 after an agreement between the state water authority and the angling association. The strategy chosen was an introduction of piscivores after intensive fishing of planktivorous fish. Angling was subsequently regulated to reduce catches of piscivorous fish.

Between 1977 and 1993 the introduction of 20,000 pike, 80,000 pikeperch and a lesser number of eels and catfish *(Silurus glanis)* was successful in decreasing the zooplanktivorous fish populations and initially resulted in enhanced grazing pressure on phytoplankton (Benndorf, 1990). The numbers of pike steadily decreased thereafter, but pikeperch were able to reproduce in the reservoir and increased in biomass from 6 to 36 kg ha^{-1} between 1983 to 1991; the overall percentage of piscivorous fish rose from 12 to 35-40% during this period (Mehner *et al.*, 1994). The main contributor to biomass over this period was perch however, which were considered as the main agent in suppression of efficient zooplankton grazing. In the late 80s perch started to decline with replacement by ruffe, carp and bream. At the same time large piscivorous perch began to have an impact on 0+ planktivores, reinforcing the initial effects of food web management. Changes in the zooplankton population structure occurred, primarily the appearance of *Daphnia galeata* replacing smaller crustacean species early in the spring, and causing a clear water phase after the spring diatom bloom. Notwithstanding these changes in zooplankton, the overall summer phytoplankton biomass persisted at high levels. In warm years there is strong cyanobacterial dominance, during cooler years large green algae prevail. Water transparency has improved overall however with Secchi depth peaks of 7 m during the spring clear water phase.

The success of the biomanipulation was achieved by the efficient organisation and support provided by the local angling association which participated in the experiment. The effect of angling had had a highly significant impact on the suppression of predatory fish. As many as 2000 to 3000 large pike had been caught in the reservoir each year between 1974 and 1976 before the biomanipulation experiment commenced (Benndorf *et al.*, 1988). The scheme failed to reduce total phytoplankton biomass, as cyanobacteria have flourished as a consequence of grazing selectivity despite the increase in *Daphnia* population. *Microcystis* toxicity also increased since the more toxic strains were not consumed. A direct effect of cyanobacteria on the consumption rate of perch seems to have assisted the establishment of a large roach population, loosening the established top-down control over the predation of zooplankton (Penig, 1983 cited by Benndorf *et al.*, 1988). Several other interdependent factors seemed to influence the perch-roach relationship.

Thus manipulation of fish species composition and biomass to reduce predation pressure on zooplankton was only partially successful. The role of perch appeared to be crucial as these can be either planktivorous or piscivorous depending on their age and the environmental conditions. The onset of clear water conditions was brought about by the release of *Daphnia* from predation by the switch of perch to piscivorous habits. This was apparent as a change in the length/age relationship of the perch population (Mehner *et al.*, 1994).

The resulting situation is unstable due to the presence of large numbers of predatory fish (perch, pikeperch, pike) with characteristic cannibalistic behaviour which tends to limit their own recruitment. This has caused large variations in the numbers of *Daphnia* between different years which through the trophic cascade has had an impact on the numbers of planktonic flagellates (Köthe and Benndorf, 1994). In general Bautzen Reservoir appears similar to other eutrophic temperate lakes in that it is effectively biomanipulated during the spring period and the first part of summer. In mid summer however, with the appearance of cyanobacteria, the top-down control is lost. A reduction of in-lake phosphorus concentrations might to be able to relieve the reservoir from the heavy cyanobacteria blooms and extend the effects of biomanipulation to the whole summer (Mehner *et al.*, 1994). These are likely to occur in the near future both due to changes in the economic situation of the region (eastern Germany) and due to removal of phosphorus in detergents (Benndorf, pers. comm.).

2.5.6 Rímov reservoir, Czech Republic

A long-term study of the effects of human intervention upon fish composition and biomass was carried out in the dendritic, canyon-shaped Rímov reservoir of Southern Bohemia (Czech Republic). After filling in 1978, this deep (45 m max. depth) reservoir experienced an explosion of fish biomass which stabilised after the first five years. Biomanipulation, and experimental study of possible techniques, commenced in 1982. The main chemical and biological parameters have been measured at three-weekly intervals since then. A two-year mark-recapture experiment was conducted between 1985 and 1987 which included more than 65,000 fish.

Three techniques were used to manage the fish stock:

1) the control of cyprinid spawning success by water level management,

2) the capture and removal of planktivorous fish,

3) enhancement of predatory fish populations.

During years of favourable hydrological conditions (between 1983-89) water levels were kept high in the spawning period to induce coarse fish to deposit eggs among the terrestrial vegetation. Water levels were than rapidly decreased by 40-60 cm stranding the eggs, effectively reducing coarse fish recruitment (Seda and Kubecka, 1995). This technique worked less well with perch which were adapted to spawn on unfavourable substrates and at depths greater than 10 m (Kubecka, 1992). Fishing methods for the reduction of coarse fish included fyke nets, beach seines and electrofishing. Intensive fishing was carried out in littoral areas during spawning periods. Sport fishing was restrained and predatory fish were added to the reservoir. High water levels were kept during pike spawning to increase recruitment of predatory fish; it is possible to carry this out in combination with strategic water level reduction to decrease coarse fish recruitment as pike spawn earlier in the year than other species. These combined efforts achieved a reduction of total fish biomass to from 650 kg ha^{-1} in 1982 to 100-150 in the early 1990s, but despite the specific efforts to increase predatory fish, their biomass was never sufficient to control the abundance of perch, roach and bream.

The zooplankton was dominated by the cladocerans *Daphnia galeata, Diaphanosoma brachyurum* and copepods. *Daphnia cucullata* was also common while large daphnids such as *D. pulicaria, D. magna* and *D. pulex* were sporadic. The analysis of 'large' cladoceran biomass (sieved through a 0.71 mm mesh and comprising exclusively *D. galeata*) showed a clear relationship to fish abundance; the large forms made up as much as 10% of the total zooplankton biomass during periods of fish reduction. Similarly the composition of the cladoceran population during the spring clear water period was directly related to fish abundance as larger species were selected by the fish fry; *Bosmina* became more abundant in such years. Such a relationship was lost during the summer stagnation period (Seda and Kubecka, 1995). Phytoplankton biomass was between 10 and 24 $\mu g\ l^{-1}$ and was not related to fish abundance for any of the seasons and years analysed. Maxima were observed in the spring (diatoms) and in some years in summer (cyanobacteria).

In conclusion, attempts to control zooplankton biomass were partially successful. Strategic lowering of water levels was the most effective. Predatory fish introduction was not very effective probably due to high mortality. The trophic chain of effects did not really cascade to the phytoplankton level, and was only apparent at zooplankton level during Spring. It is probable that a reduction of fish biomass to less than 100-150 kg ha^{-1} is necessary before effective biomanipulation could be achieved (Seda and Kubecka, 1995).

2.5.7 Lake Finjasjön, Sweden

This relatively large (11 km^2), shallow (3 m) lake in the densely populated Scania region of southern Sweden has been suffering conditions of acute eutrophication with dense summer cyanobacterial blooms for the past 70 years. Its close proximity to the city of Hässleholm makes of Lake Finjasjön a very important potential resource in terms of water supply and recreation. The first direct human impacts had been water-level lowering operations carried out on Lake Finjasjön at the beginning of last century. Piped sewage was introduced to the lake in the 1920s. This caused rapid eutrophication with blooms of *Gloeotrichia* and appearance of dense mats of *Potamogeton*. Traditional bathing activities had to be forbidden from 1947 onwards due to skin rashes and fevers reported by swimmers who frequented the lake. Sewage treatment started in 1949 and went through a progressive refinement of techniques but without any major impact on the lake that continued to exhibit heavy cyanobacterial blooms *(Microcystis)*. Such blooms were held responsible for repeated fish kills that occurred towards the end of the 1960s and also decrease in numbers of waterfowl. In 1987 the first sediment removal operations started by mechanical dredging. These covered 25% of the area but were stopped in 1992 when it became clear that they would have been ineffective and prohibitively expensive. The removal of 50 cm of black, reduced sediment had left behind 3 m of eutrophic sediments with relatively high phosphorus contents and limited phosphorus retention capacity. The municipality then opted for a new policy: control of cyprinid biomass combined with a decrease in external loading.

Summer average chlorophyll *a* concentrations reached 130 $\mu g\ l^{-1}$ in 1988–90 with peaks of 200 $\mu g \cdot l^{-1}$ but have declined since, indicating a progressive amelioration of the water quality. Main responsibility for the algal blooms is attributed to the internal load which contributes 10 times more phosphorus to the lake than the external load, the latter now limited to 0.4 $g\ P \cdot m^{-2} \cdot ann^{-1}$. Preliminary investigation in 1992 revealed that microbial activity triggered by high temperatures was a determining factor in the release of sediment phosphorus. In the face of this scenario the municipality of Hässleholm took the advice of an international group of researchers (the 'expert panel' of the Lake Finjasjön project) and embarked on an intensive biomanipulation programme. This included heavy coarse fish reduction and reintroduction of predatory fish. The scale of success that followed went beyond the hopes of scientists and managers.

Fish reduction operations started towards the end of 1992. Most of it was carried out by professional fishermen using marine vessels equipped with powerful engines and large trawls. These cleared fish from most of the regions of the lake deeper than 2 m. Smaller outboard-driven boats were then used in shallower areas; the first trawl in shallow areas totalled catches of as much as 600 kg fish per day. Immediate sorting on the ship allowed piscivore species such as pike and pikeperch to be put back to the lake. A test trawl carried out ten months later showed a significant decrease in the proportion of roach in the total catch and a parallel increase in perch. The year following the first reduction was characterised by a highly successful perch recruitment that is believed to have contributed further in suppressing cyprinid numbers. The average weight of bream and pikeperch increased significantly. The proportion of piscivorous (including perch of all ages) to planktivorous fish became close to 1:1 in 1993, which is considered from experiences in Danish lakes, as a proportion favourable to top–down control (Eric Jeppesen, pers. comm.).

Cumulative catch per unit effort revealed that fish reduction had caused a decrease of the cyprinid population by slightly more than 50% of the original biomass in 1993. By the end of that year estimates indicated that the catch effort was getting closer to its original target: a reduction of 80% of the cyprinid biomass. Large reductions of biomass were achieved during winter and spring, but in summer catch per unit effort did not decrease significantly indicating that fish reduction was counterbalanced by high fish reproduction rates. The team felt that fishing during spawning times was crucial as some fish such as bream congregate, come closer to the shore and become easier to catch. The impact on the reduction of recruitment by catching spawning adults is much greater than trying to reduce the numbers of fry after hatching. Spawning areas were located on the lake and local fishermen gave advice on methods to catch different species. Spawning bream were best caught with seines while roach were trapped in fyke nets. The advisory panel made also provisional plans for the control of fish migrations from tributaries during early spring.

The consequences of the fish reduction exercise on the biology of Lake Finjasjön were profound; they reached virtually all the compartments of the lake ecosystem indicating a general shift towards oligotrophy. In 1993 summer average chlorophyll values decreased to 60 $\mu g \cdot l^{-1}$; diatoms became dominant in the phytoplankton and the spring bloom reduced phosphorus levels in the lake water effectively delaying the summer cyanobacterial bloom. Large diatoms such as *Asterionella* became dominant replacing small centric forms such as *Stephanodiscus* which are characteristic of hypertrophic environments. *Microcystis* was still present in the lake but the blooms were less intense. Between 1992 and 1993 the zooplankton biomass increased by 50%. *Daphnia galeata* had previously virtually disappeared from the lake but was present in samples collected in October and November 1993. The overall zooplankton biomass increased in parallel to an increase of the proportion of cladocerans to copepods, (this is highly encouraging as cladocerans are more efficient grazers). Among copepods, calanoids increased by 2.5 times and became predominant. Macrophyte re–establishment was noticed as *Myriophyllum spicatum* colonised new sites on the western shore. The increase in macrophytes was considered highly positive as it created better conditions for perch and pike. Under conditions of good macrophyte cover perch is favoured in its competition over roach. The significant reduction of toxic cyanobacterial blooms generated considerable public interest. Less than two years after the start of the new management policy, the lake was re-opened to recreation including swimming.

The causes of the rapid recovery of Lake Finjasjön are far from being totally elucidated. It is felt that the lake may have reached a highly unstable transient state such that it is premature to make judgements at this early stage. Several investigators feel that the sediment removal operations might have had an important role in the recovery by reducing the total phosphorus load bringing the whole system closer to Benndorf's phosphorus loading threshold for biomanipulation (see next section). While work was carried out on the lake, in the catchment several areas had been selected for the introduction of buffer strips. Land had been set aside by farmers after compensation by the municipality. The operations were run in association with farmers' knowledge of the terrain and their willing participation. A successful public information campaign resulted in the involvement of farmers' organisations and angling clubs. This participation became crucial (Helène Annedotter, pers. comm.). Farmers organisations provided experienced staff for work in the field and angling clubs designed a policy for the prevention of overfishing of piscivores in the lake. Somebody even managed to find a buyer for the large amounts of fish taken out of the lake: a French zoo bought most of the roach for their pelicans, volunteers helped sorting out the fish!

Although this is a shallow lake and its relevance is therefore, more limited, its importance lies in the fact that it is large, and considerable effort has been expended in its biomanipulation: it therefore gives example of the nature of the fish-removal exercise necessary for successful biomanipulation.

2.5.8 Feldberger Hausee, northern Germany

This is a small (1.3 km^2) moderately shallow (mean depth 6.3 m) lake in the Baltic lake district, which was the subject of classical limnological study in the early years of this century but which became seriously eutrophic in the 1950s, dominated by cyanobacteria. This situation continued until the start of restoration in the 1980s. The restoration strategy was to divert sewage from the catchment at the same time as biomanipulation was applied in-lake, and the results have indicated progressive changes in the state of the ecosystem over the 15 year period of restoration (Krienitz, Kasparzak and Koschel 1996).

The first step in restoration was sewage diversion, in 1980. No beneficial effect on the lake was apparent because of the large sediment phosphorus pool, which sustained algal biomass and species dominance similar to the highly eutrophic state of the 1970s (dense green-algal dominance). In 1985 therefore, selective removal of zooplanktivorous fish was initiated, by beach seine netting 14-20 times per year, covering 50-75% of the lake area each year, alongside stocking with large pikeperch.

Effects did not become apparent until 1989-90, when reduction of fish biomass to around 40 kg ha^{-1} was achieved. Initially this also caused an increase in *Daphnia* proportions in the zooplankton together with a decline in nutrient concentrations believed to be a combination of response to external load decrease together with preciptiation of calcite-bound phosphorus. At the same time phytoplankton diversity increased. In the early 1990s the phytoplankton community passed back from a hypertrophic green-algal dominated state through a eutrophic cyanobacterial dominated state which temporarily suppressed the *Daphnia* increase, into a final low biomass and biodiverse phytoplankton community dominated by picoplanktonic green algae. This 'final' state, achieved in 1994, coincided with increased transparency as a result of low biomass (Secchi depth 2m, the highest since the 1960s) and recolonisation of the littoral zone by submerged macrophytes. Phosphate concentration had fallen below a mean of 100 μg l^{-1} for the previous four years.

This case study, albeit of a natural lake, illustrates the longer timescale necessary for effects to become apparent, as well as the benefits of combined measures which render biomanipulation more efficient and more predictably successful.

2.6 The relevance of these case-studies to Northern Area's reservoirs

The direct imposition of changes to the structure of food webs clearly requires considerable effort. Often what has been seen as indications of a successful biomanipulation are in fact only temporary symptoms of the instability of the affected ecosystem. The use of additional techniques can be essential to the chances of ultimate success Nutrient reduction is ideally the prerequisite for management. A significant decrease of nutrient inflow may impact on the phytoplankton species composition and on the interspecific competition between phytoplankton and macrophytes. This may eventually increase transparency and favour the survival of visually-hunting predatory fish.

It is often impracticable however to reduce nutrients to limiting levels as this would require the reduction of summer orthophosphate concentrations to >5 μg PO_4-P l^{-1}. There are other means of increasing transparency by decreasing phytoplankton biomass, the most promising of which is artificial mixing which, if thorough, increases the time spent by phytoplankton in the deeper dark water column limiting its photosynthesis and growth. This technique also seems to favour zooplankton, which are sufficiently independent from water movements to maintain predation-avoidance vertical migrations in artificially mixed systems. Zooplankton migration is made easier by the uniform temperature and oxygenation of the water column which decrease the physiological costs of such behaviour. It is unfortunate that there are very few studies addressing this issue. In general the large scale impact of artificial mixing is under-investigated in relation to biomanipulation.

In the London reservoirs the presence of low fish biomass correlates with a definite zooplankton population structure. However it has not been established up to now, despite the multitude of models explaining the shading effect experienced by phytoplankton during mixing, what is the extent of this impact on the phytoplankton biomass. Undoubtedly *grazing* and *shading* effects work in combination, but their relative importance is not known. Furthermore it is not clear to what extent grazing is favoured by the mixed conditions.

In both Rímov reservoir (Seda and Kubecka, 1995) as well as the nearby Hubenov reservoir (Hrbácek *et al.*, 1986) and the London reservoirs (Seda and Duncan, 1994) the presence of large *Daphnia* is critical for the achievement of phytoplankton control. The zooplankton species composition is directly related to fish biomass as fish tend to select larger zooplankters favouring the development of smaller organisms such as copepods. A model proposed by Seda (1989) relating species composition to the proportion of large cladocerans in zooplankton indicates that when *D. galeata* was the only species present, cladocerans achieved 22-25% of the total zooplankton biomass. As fish predation is reduced the proportion of large daphnids in zooplankton can increase. In the London reservoirs, as large daphnids in zooplankton reach 50% of biomass and *D. magna* and *D. pulicaria* predominate; control of phytoplankton is achieved. Based on these data a possible threshold for control of phytoplankton was indicated as 30% large daphnids in the total zooplankton biomass (Seda and Kubecka, 1995). In Rímov reservoir there has not been sufficient reduction in zooplankton predation to allow for the development of other large zooplankters next to *D. galeata*. This 30% however, serves as a guide and a target in the examination of potential candidates for biomanipulation.

Reservoirs in the Anglian Region fall into two groups. One group are highly artificial, bowl reservoirs, typified by Covenham Reservoir (Fig 2.5).

The other group consists of valley reservoirs, typified by Rutland Water and Pitsford Reservoir, mostly with extensive littoral zones (Figure 2.6). There is thus the probability that the experiences of the London reservoirs and the Biesboch reservoirs can be directly applied to Covenham Reservoir, whilst some of the principles of shallow water lake biomanipulation, such as the management of the littoral zone, (Reynolds 1994, Phillips and Moss 1994) as well as the experiences of the reservoir case studies, might be applicable to valley reservoirs.

2.7 Conclusion: might biomanipulation work in reservoirs?

Biomanipulation is clearly a tool which becomes more effective as human control over ecological processes in any lake becomes more certain and complete. Small, shallow lakes offer this degree of control and provide relatively small 'upsets' such as growth of benthic algae instead of rooted plants as restoration progresses. Reservoirs in theory should offer the possibilities for even greater human control of the ecosystem because they were designed to give human control of the hydrology. Those with greatest control over the hydrology clearly are the most successful in biomanipulation.

The case studies and the supporting theory show that two aspects of control are essential for effective biomanipulation. The first is suppression of coarse fish reproduction; the second hydrological management with or without nutrient reduction. Restriction of cyprinid recruitment can be achieved most successfully by the provision of an unsuitable littoral zone (as in the London, Biesbosch and also Covenham reservoirs). In valley reservoirs, the littoral zone may be poorly developed because of drawdown (or extensive despite drawdown, as in Pitsford Reservoir and Rutland Water) but nevertheless almost always offers adequate spawning opportunities which have thus to be restricted by other means. If deliberate water level change is not available, then active management of the littoral zone by physical destruction of spawning sites offers the only alternative method. Extensive control of the fish stock by a variety of means, both reduction of undesirable planktivores and enhancement of desirable piscivores, has to accompany spawning prevention. Perch appear to play a key role in the balance between a low and high cyprinid biomass. The sustainability of a stable perch population with more or less evenly distributed size classes minimises cannibalism and increases piscivory, leading to a self-stabilising feedback upon perch population structure. This contributes significantly to the overall proportion of piscivory to planktivory in the fish community.

Figure 2.5. The artificial concrete bowl-type reservoir, exemplified by Covenham Reservoir, Lincolnshire

The successful forms of hydrological management have been either the ability to deliberately draw down in Spring as a means of controlling fish recruitment, or an ability to completely mix as a means of controlling phytoplankton growth and succesion. Bowl reservoirs with the latter capability may also have short retention times, which is an additional advantage as flushing out in itself tends to reduce algal biomass.

Clearly in all cases a strong knowledge of the fish community, population structure,feeding strategy and behaviour and the ability to manipulate these to maintain the stability of the fish community structure are essential for biomanipulation success.

Figure 2.6. The valley-type, shallow littoral reservoir, exemplified by Rutland Water, Leicestershire

3 PROBLEMS FOR IMPLEMENTATION OF BIOMANIPULATION IN RESERVOIRS

3.1 Control of fish biomass

Biomanipulation can only work effectively if fish populations are controlled. The evidence from both shallow and deep lake studies offer a number of techniques which could be evaluated for the Anglian reservoirs.

The most drastic but effective technique for control of fish biomass is complete removal; achieved either by drawdown of the waterbody (Lake Zwemlust, The Netherlands); or rotenone poisoning (as was carried out in the embryonic Rutland Water). In practice these techniques have been employed only in extremely rare cases. Even successful removal of the entire fish community does not guarantee the immediate conversion of the system into the clear water state.

Intensive fishing has been necessary in virtually all case-studies. The best results are achieved when fishing is carried out in winter, for several reasons. In winter fish tend to spend more time near the shore or bottom, aggregate in schools, are less active due to the lower temperature and are of reasonable size and therefore easier to capture using nets. Several techniques have been employed such as trawling, long line fishing, trapping for large benthic bream, fyke nets, long seine nets, fine mesh size gill nets, and bongo nets (hoop nets). Nets should have a minimal mesh size of 8-10 mm (Hosper *et al.*, 1992). Electrofishing is possible for littoral margins overgrown by vegetation while the beach seine is most efficient on free sandy beaches. Using these techniques a water surface of 5 ha could be fished out within 3 days, while 6 weeks would be necessary to complete the operation in a 180 ha lake (Hosper *et al.*, 1992).

During the restoration of Lake Finjasjön (Sweden) particular attention was devoted to the capture of spawning fish (Anon., 1993). Fyke nets were used for catching spawning roach while bream were caught by seine nets as they aggregated to spawn. Similarly in Rímov reservoir, fyke nets were employed for catching spawning perch (Kubecka, 1992). This technique is promising but complicated by the need to locate spawning areas.

Coarse fish, in particular cyprinids, are characterised by such a high recruitment potential that most of the fish taken out of the waterbody can be replaced almost immediately in the next generation. Hosper *et al.* (1992) indicate that the management should aim at removing at least 75% of the total number of bream, roach and carp from a given waterbody to achieve long term effects. They advise the return of large perch, eel and young pike (<40 cm) to the water. In Rímov and Bautzen reservoirs direct capture of fish did not succeed in causing a stable decrease in the fish biomass. Difficulty in capturing the fish increased markedly as the number of fish in the reservoir decreased (Seda and Kubecka, 1995).

The control of fish recruitment by strategic water level change was more successful. In all the case-studies analysed it ensured a considerable decrease of fish in the next generation. The combination of strategic water level change with fishing during spawning periods achieved 95% reduction of cyprinids in Rímov reservoir (Seda and Kubecka, 1995).

Due to different spawning times between pike and coarse fish, strategic change of water levels can limit coarse fish recruitment without damaging the pike population; thus preserving a high piscivore/planktivore ratio. Perch numbers decrease but are less affected than roach and bream. Perch eggs are wrapped in long ribbons of slime and can be laid on a sandy bottom in a reservoir without the risk that single eggs might come into contact with anaerobic zones in the sediment. A moderate decrease of perch might be beneficial. The maintenance of a small perch population in good condition is the prerequisite for development of predatory perch which appears to be an important requirement in biomanipulation as it could be a key factor in controlling the young of the year of all fish including its own species (Benndorf *et al.*, 1988). The necessary changes of water level to optimise the effect of this technique will depend on the morphology of the reservoir littoral zone. In Rímov a drop of 40-60 cm was sufficient.

A technique which is complementary to drawdown is the use of artificial substrates, which has been practiced in Sulejów reservoir. The technique has been only recently developed and its potential benefits are still controversial. The substrates are most effective during low water levels when there are no other 'natural' substrates available. Artificial substrates also provide a method for investigation of coarse fish spawning habit .

The manipulation of fish stocks by the introduction of predators requires a massive stocking of adult fish. The cost-effectiveness of this operation is still doubtful especially since results are not assured. Introduced piscivorous populations are fragile and may not be adapted to the new environment which often has unfavourable conditions, such as low transparency which is crucial for sight-hunting predators. Introduced fish often suffer high mortality (Rímov reservoir). The stability of the new population is often questionable as high stocking tends to produce strong year classes which feed on their own recruits and do not allow the development of a healthy, moderate, predatory population. Nonetheless the achievement of an adequate predatory pressure can yield positive results. From observations conducted in Bautzen reservoir it was estimated that some 85-95% of the cyprinid fry was reduced as a consequence of the efficient predation of perch and pikeperch (Schultz *et al.*, 1992). Hosper *et al.* (1992) recommend that lakes that are suitable for the introduction of pike should be stocked with small pike (<40 cm) while larger pike should be removed. After the completion o coarse fish removal a few large pike (>60 cm) should be introduced to ensure a suitable egg deposition for the next year's recruitment. Pike larvae can be introduced after the spawning period in lakes where at least 5% of the water surface of a depth of 30-70 cm is overgrown by reeds or other emergent aquatic plants. Ideally this littoral strip should be some 2 m wide. Pike fry (4-5 cm length) can be put in the water at a density of 1 per metre of overgrown lake edge, smaller ones (3-4 cm) can be at a higher density. The long term management of the pike population requires the continuous reduction of large cannibalistic specimens and the controlled development of a suitable littoral habitat by actively planting reeds and rushes. The introduction of large perch (>15 cm) is also desirable as it proves to be particularly important in the control of invertebrate predators (such as *Neomysis integer)*; for this reason in the course of intensive fishing for the reduction of planktivores, perch larger than 7 cm should be returned to the lake (Hosper *et al.*, 1992).

The desired piscivore/planktivore ratio is approximately 1:1 when perch is included among the planktivores (Eric Jeppesen, pers. comm.). In Bautzen reservoir predators reached 35-40% of the fish biomass and this was judged sufficient to provoke significant changes in the structure of the trophic chain (Mehner *et al.*, 1994). These latter authors stressed that for the success of the operation it is crucial to keep an even distribution of predatory fish of different species and different size classes so that predatory pressure would be distributed among different size classes of prey. This structure would also break the cyclical appearance of strong year classes followed by several weak ones which tends to result in high cannibalism. In Rímov reservoir at one stage perch were dominant with 4,630 individuals ha^{-1}. The presence of 2,000 individuals ha^{-1} of other species (roach, bream) was still not able to dampen the strong self-regulatory effect by cannibalism in the perch population (Kubecka, 1991). The cyclical appearance (about every 8 years) of strong year classes is typical of perch-dominated fish stocks (Kubecka, 1993b). In Bautzen reservoir however, the occurrence of cannibalism in perch varied in relation to the abundance of alternative prey. In years of high pikeperch recruitment on average 75% of the stomach content of perch was occupied by young pikeperch. This allowed a medium-term stabilisation of the perch population and of the whole predatory fish biomass, as perch were able to control the excessive development of pikeperch along with the regulation of their own recruits (Schultz *et al.*, 1992).

There are severe practical difficulties in controlling planktivorous fish populations in large deep reservoirs which cannot be overemphasised (Phillips and Moss, 1994). This point is crucial as it has been shown in several studies that partial fish removal cannot reduce predation on zooplankton enough due to the successful recruitment of young-of-the-year fish. The use of rotenone or pesticides would be strongly objected to by the National Rivers Authority, Conservation Groups and Angling Clubs. Netting of fish cannot remove the total population if only superficially applied (Parr, 1992) but practical experience in Sweden and Germany (see case studies) shows that intensive fishing does provide the desired end result. The most efficient method that could theoretically be used but might pose practical difficulties of water supply would consist in draining the whole waterbody, as is done during the periodical harvest of fish ponds in Eastern Europe.

The only lentic piscivore considered native to Britain is pike, whose persistence is tied to the presence of macrophytes which do not always occur in reservoirs. Many reservoirs often contain trout, large individuals of which may be piscivorous and some contain established perch populations. Other piscivorous fish species tend to prefer colder waters of rivers. Little information in this country is available on the possibility of employing perch, older individuals of which do show piscivorous habits. Stocking with pike or perch alone will not prevent phytoplankton blooms in reservoirs (Parr, 1992) because this neglects the additional suite of measures necessary to ensure success. The introduction of pikeperch would be not allowed at present as the fish has colonised several lentic and enclosed lotic aquatic habitats in the south of the country causing changes that have been considered deleterious by some. The possibility of an introduction of single-sexed or genetically modified pikeperch remains untested but should be given serious consideration, as pikeperch provide open-water predation which no other piscivores effectively can do.

A knowledge of fish biomass is essential for monitoring the progress of biomanipulation. Rough estimates may be obtained approximately by comparing the proportion of large cladocera in zooplankton according to Seda and Kubecka (1995); or can be obtained using the relationship between zooplankton biomass as Total Nitrogen and fish biomass suggested by Kubecka and Duncan (1994). In the field more accurate estimates can be obtained from direct measurements; field sampling using night shore seining according to (Kubecka, 1993a) or more accurately by dual beam echo-sounding (Kubecka and Duncan 1994).

3.2 Control of cyanobacteria

Several case studies of biomanipulation in shallow lakes show failure despite effective enhancement of zooplankton grazing because cyanobacteria populations 'broke away' from grazer control and reached bloom proportions. It is generally believed that zooplankton can control cyanobacteria when they are in the early stages of population growth, and colonies are small and not clumped together. It is necessary to consider however, that parallel control of cyanobacteria during biomanipulation might be necessary for ensuring its success.

Cyanobacteria interfere with grazing by clogging filtering mechanisms (references cited by Phillips and Moss 1994) and in so doing impair the applicability of top-down control. They contribute to the creation of physico-chemical conditions in lakes (such as high pH, shading, hypolimnetic anoxia) that enhance progressive eutrophication and are known to release toxins whose natural role is to discourage grazers. As a consequence of their presence several lake restoration projects incorporating biomanipulation have failed. For these reasons understanding the primary characteristics that give cyanobacteria their competitive advantage over other phytoplankters and analysis of specific methods for their control is important to biomanipulation as a management tool.

The control of cyanobacteria may be interpreted as a biomanipulation in its own right as it has been shown that these organisms tend to create self-regulating populations (Robarts and Zohary, 1984) that prevent ecosystem recovery to lower biomass levels. Reductions in nutrient loading tend to decrease cyanobacterial dominance. Responses are unpredictable however, they are likely to proceed in a step wise pattern and will be delayed in stratified lakes where cyanobacteria tend to accumulate at the clear, nutrient-rich metalimnion. In these lakes eutrophication recovery would require a greater reduction in phosphorus loading (Sas, 1989). Extreme phosphorus loading in shallow lakes leads to dominance by fast-growing, single-celled chlorophytes (Harper, 1992; Moss *et al.*, 1994, Jensen *et al.*, 1994).

3.2.1 General characteristics explaining the competitive advantage of cyanobacteria

The cyanobacterial species which cause ungrazable, sometimes toxic blooms, are slow-growing, large sized 'K'-strategists that owe their competitive advantage over other species primarily to their ability of adapting to low light environments (Walsby 1992).

In stratified lakes cyanobacteria can slowly build up high populations after more 'r'-selected species have waxed and waned. They do so through growth at lower phosphorus levels (including the ability to store phosphorus in excess of immediate needs) and lower N:P ratios (through the nitrogen-fixing ability of some species). They are more competitive for low nutrients at elevated temperatures (as summer progresses) and more efficient at lower light levels (shading by other phytoplankton). They preferentially utilise CO_2 as a carbon source and are more efficient than other phytoplankton taxa at obtaining this from low concentrations (which prevail at the elevated pH often reached in lakes in summer as a result of intense photosynthesis by other phytoplankton). They may also obtain it directly from the atmospheric pool by bouyancy regulation allowing them to float at the water surface. Protection from light damage at the water surface is provided by reverse migration (over a diurnal cycle) and by the development of carotenoid pigments which protect them from UV damage and enhance photsynthetic efficiency. Once their populations have reached high biomass, they effectively shade and may have allelopathic effects upon other competitors, have low loss rates through sedimentation, and are difficult for zooplankton to graze extensively.

In the more turbulent environment of shallow lakes, the suite of cyanobacterial adaptations is less effective. If Z_m is less than Z_{eu}, buoyancy and low-light adaptations may still be effective in maintaining growth, with some cyanobacterial species such as *Oscillatoria* spp. better adapted to turbulence than others even if Z_m exceeds Z_{eu}. If Z_m consistently exceeds Z_{eu}, then these conditions will tend to enhance nutrient levels by circulation and reduce pH by lowering overall photosynthesis, leading to competitive dominance by other slow-growing turbulent-adapted species such as large diatoms. If the pattern of turbulence is irregular then all the slower growing 'K' strategists may be unable to adapt their light and nutrient gathering physiologies rapidly enough, leading to dominance by 'r' strategists. In fully mixed environments, such as turbulent shallow lakes, 'r' strategists dominate. Cyanobacteria may still persistently occur because the renewal of nutrients and carbon at the cell-water interface favours synthesis of carbohydrates which enhance buoyancy and increases their ability to resist mixing (Visser 1995).

3.2.2 Strategies for the control of cyanobacteria

Mixing

Vertical mixing has been employed to reduce phytoplankton abundance by increasing the time spent by photosynthesising cells below the compensation depth (Reynolds 1984, Brierley, 1985). Water bodies characterised by a total depth greater than double the photic depth are well suited to mixing (NRA, 1990).

Cyanobacteria, due their ability to adapt to low irradiance, may not always be effectively reduced by continuous mixing. Such measures will however reduce their production and hence growth. Intermittent mixing with one to two-week cycles was found effective as cyanobacteria were slow in adapting to the changing conditions (Steinberg and Gruhl, 1992). At the onset of stable conditions cyanobacteria moved rapidly to the surface because of their vacuoles whose buoyancy had increased as an adaptation to mixing. Here the filaments lyse as a consequence of abruptly entering a high-irradiance environment.

Some authors have found that constantly changing conditions of stability eventually favoured colonial *Microcystis* which can adapt to this form of light regime and float to the surface at the onset of calm conditions (Walsby and McAllister, 1987). In particular *Microcystis, Anabaena* and *Aphanizomenon* are able to adapt to short term diel light fluctuations (Robarts and Zohary, 1984; Reynolds *et al.*, 1987). Recent observations suggest however that adaptation is more effective in green algae than in *Microcystis* and the competitive advantage of the latter is due to their unpalatability for grazers and their low sedimentation rate (Ibelings *et al.*, 1994). Species of *Oscillatoriales (Planktothrix agardhii, P. redekei)* are slow to adapt to changing light environments (Berger, 1984) and possibly could be effectively eliminated by mixing.

A mesocosm study in the 'Lund tubes' in Blelham Tarn gave encouraging results under 3-4 week periods of mixing/stratification although the authors questioned the applicability of the technique to large reservoirs (Reynolds *et al.*, 1984). They concluded that low levels of mixing may be more cost efficient as they result in similar conditions by just preventing stratification but with stability fluctuations imposed by weather changes. In the 1980s insufficient mixing in Rutland Water occurred during summer anticyclones and caused variable conditions which prevented dominance by bloom-forming taxa and kept chlorophyll levels below potential capacity as calculated from nutrient loads (Ferguson and Harper, 1982). In the summer of 1989 however, the occurrence of a series of hot calm spells led to a very stable water column in Rutland Water with consequent blooms of cyanobacteria (NRA, 1990). One consequence of this was an upgrading in mixing equipment so that intermittent stratification and mixing rarely now occurs (Krokówski unpublished data).

A general problem with mixing techniques occurs due to the difficulty of mixing the entire cyanobacterial population of a water body during bloom conditions. In the Biesbosch reservoirs, a layer of colonies of *Microcystis* was observed to remain in the upper layers of the water surface undisturbed by water column mixing because of their high buoyancy (Visser *et al.*, 1994). It is thus clear that successful mixing of cyanobacteria requires the application of very thorough destratification, or creation of some other conditions preventing their development. A recent detailed study on the physiological responses of *Microcystis* to turbulence and stratification, (Visser 1995) suggests that continuous, powerful mixing can overcome their dominant bloom-forming populations.

Flushing

Short retention times (<10-30 days; Reynolds, 1992) appear to prevent dominance by slow-growing larger, inedible algae such as *Aphanizomenon* and *Oscillatoria*. At still shorter retention time biomanipulation is unable to control phytoplankton due to wash-out (Reynolds, 1994). Optimum retention times for algal control are therefore about 1 month (compare with Covenham Reservoir 8 months, Rutland Water 24 months).

Collapsing gas vesicles

Gas vesicle collapse constitutes a more specific approach. Ultrasonic radiation has been shown to be successful in bursting gas vesicles in the laboratory and could be implemented on a large scale (Walsby, 1992). A method designed by Clarke and Walsby (1988) to be operated at sewage works, demonstrated the crushing of gas vesicles by circulating water through a pipe sunk deep into the ground. An analogous principle could be applied to a small lake where water would circulate through a pipe at one end and would be put back into the lake at the other end (Walsby, 1992). Explosives provide a fast but drastic method for inducing cyanobacteria to sink out but are unlikely to find much acceptance due to their side effects upon fish and recreational users!

Bacteria and viruses

Microbiological control methods are often cited in reviews on cyanobacterial control (Parr and Clarke, 1992; Cooke *et al.*, 1993) but have not been tried on a large scale. The major advantages of this technique is mainly the specificity of treatment since no other organisms are affected. Preliminary investigations support the idea that inoculation with cyanophages or bacteria will reduce the development of extant blooms but cannot be used to prevent the appearance of new blooms since they need to develop under conditions of high densities of cyanobacterial cells. A similar conclusion was reached about the possible use of bacterial inoculi (Fraleigh and Burnham, 1988). At high pH inoculation may fail as cyanobacteria seem able to avoid contamination (Lindmark and Shapiro, 1982). Further potential problems associated with the technique are the rapid development of resistance and the consequences of massive die-off in the case of successful inoculation.

Mechanical removal

Under conditions of massive cyanobacteria scums it may be desirable to use booms of the type employed to collect oil spills. The units can be dragged by boat and the surface pumped off (NRA, 1990). This temporary remedy however does not prevent further formation of the scum.

CO_2 injection

Although not legal in the UK, it has been considered as a possible control mechanism in the US and Germany for several decades. Field-scale experiments are under way at the University of Dresden to test the possibility of decreasing cyanobacteria which are dominant under conditions of high pH and CO_2 depletion, by pumping CO_2-rich water from the hypolimnion to the epilimnion within the same lake (Benndorf, pers. comm.). The design of these experiments is based on the observation of natural collapses of *Microcystis* during storms causing sudden vertical mixing bringing CO_2 to the surface (Shapiro, 1990).

Copper sulphate

Although not legal in the UK, trace additions of copper are used in some cases for the reduction of planktonic cyanobacteria that are more sensitive to this chemical than are diatoms or green algae (Gohlke, 1972). The aim of the application is not to kill the cyanobacteria as it seems to control them through interference with their growth and the fixation of N_2 (Horne, 1979). However, due to acclimation and the secretion of organic substances able to complex copper salts, actual doses of copper sulphate have often to be higher than predicted by laboratory tests (Parr and Clarke, 1992). In the Biesbosch reservoir additions of copper sulphate were not effective up to a dosage that eliminated the entire benthic population (Oskam and van Breemen, 1992).

Benthic algae and cyanobacteria

Benthic cyanobacteria have caused problems in some reservoirs, and filamentous algae have appeared in biomanipulation restoration experiments in the Norfolk Broads. Special techniques had to be designed to eradicate benthic cyanobacteria at the Biesbosch reservoirs in the Netherlands because high levels of geosmin, a substance produced by benthic Oscillatoriales were giving rise to strong taste and odour problems. SCUBA investigations revealed the benthic cyanobacteria as a narrow band (Oskam and van Breemen, 1992). A harrow attached to heavy chains was designed to disturb the sediment and prevent growth. The device was nearly as effective as copper sulphate addition but in contrast to this latter it was not lethal for other benthic organisms.

3.3 Zooplankton refuges

It is believed that a littoral refuge for zooplankton is necessary to allow them to evade fish predation. Moss (1990) and Irvine *et al.* (1990) demonstrated the complex role played by macrophyte beds in shallow lakes acting as refuges for zooplankton. The observations are in agreement with those of other authors (Timms and Moss, 1984; Meijer *et al.*, 1990; 1994a, Scheffer, 1990; Harper, 1992) The persistence of macrophytes also ensures a higher diversity of herbivores and supplies them with alternative food resources in periods of low phytoplankton standing crop. Without this alternative food supply *Daphnia* populations would collapse (Phillips and Moss, 1994).

Artificial zooplankton refuges including polypropylene ropes, suspended fruit-cage netting or bundles of alder twigs did not successfully re-create shelters for zooplankton in eutrophic lakes lacking macrophytes (Irvine *et al.*, 1990; Moss, 1992). In the Norfolk Broads larger scale experiments now involve isolation of a section of the water body from which fish are removed and recolonisation by macrophytes has followed, albeit in a less than straightforward manner due to difficulties caused by benthic algae and bird grazing. The division is then removed hoping that the newly stabilised system will be able to influence the remaining part. Nutrient precipitation and high flushing rates need to be maintained to reduce the competitive advantage of cyanobacteria (Moss, 1992).

Many reservoirs exist in dammed valleys with a substantial littoral zone (e.g. Rutland, Water and Pitsford Reservoir). The littoral vegetation of these is reduced to a species-poor band occasionally with high summer biomass by a combination of light limitation and drawdown, but high nutrient concentrations in water and sediment. The possibilities for littoral macrophyte recovery through isolation, following the Norfolk Broads experiments, can only be speculated on because of the importance of a relatively stable water level to certain submerged plant species. Other reservoirs, such as Covenham Reservoir are characterised by very reduced, often concrete littoral zones . Modification of the reservoir edge to accommodate the development of rooted macrophytes would be unsuccessful.

There is theory, originally developed by Shapiro but poorly tested empirically, that zooplankton can find refuge in the darker vertical layers of the lake. This possibility is enhanced by artificial mixing, since zooplankton may be entrained in vertical circulatory currents. There is no information which compares the relative importance of the different refuges to zooplankton population development.

3.4 Why reservoirs might not respond to biomanipulation

The twin problems for biomanipulation are lack of human control of the fish community, leading to a dominance of planktivory, and lack of zooplankton grazing control of the phytoplankton, leading to dominance by cyanobacteria. These two may occur together or they may not, depending upon circumstance.

All the case studies discussed above showed partial success in biomanipulation, rather than complete success, with perhaps the most stable success demonstrated by the bowl reservoirs (even though deliberate control of fish population was not always practised). Comparison with Rímov reservoir suggests that it is almost impossible to achieve a tight control of fish in valley reservoirs, and that the best that can be expected is control during the spring period by strong influence upon spawning, leading to an extended early summer clear water phase. Control during the later summer is more problematical, with difficulty in preventing cyanobacterial appearance leading the need for additional measures.

The Bautzen reservoir case-study provides an example of successful control of the fish population structure with the appearance of large daphnids. The experiment failed to produce a significant decrease of the algal biomass due to cyanobacteria development. The lake Finjasjön provides an example of a multi-facted approach to lake restoration which targets the whole catchment (inflow wetlands and catchment buffer strips accompany phosphorus removal from point sources) as well as the lake (sediment removal and intensive fishing). It is cklear that biomanipulation of large lakes is technically feasible.

3.5 Conclusion

The knowledge which is accumulating about biomanipulation shows the directions of successes and failures. One clear indication is that it is unlikely to work in isolation from other eutrophication control techniques in waterbodies other than shallow lakes. The concept of a phosphorus loading threshold, below which it will not work, is an indication of this, although there is not agreement on the exact threshold, and there are suggestions that the threshold can be higher if additional mechanisms, such as in-lake mixing, are also implemented.

The opportunities for biomanipulation should therefore be most promising in reservoirs for which there is already some form of phosphorus reduction technology, and which are capable of being fully mixed. The degree of success in the case studies reviewed suggests that under such conditions, which of course include Rutland Water and Covenham Reservoir, biomanipulation should be seriously but carefully considered. An essential prerequisite however, is the ability to control the fish community structure.

4 WHAT IS THE EVIDENCE THAT NORTHERN AREA'S RESERVOIRS MIGHT RESPOND TO BIOMANIPULATION?

4.1 The reservoirs of the Northern Area

The reservoirs under consideration in their report are Pitsford Reservoir in Northamptonshire, Rutland Water, in Leicestershire and Covenham Reservoir in Lincolnshire. The former two are valley reservoirs and the latter an artificial concrete embankment reservoir, similar to the London reservoirs and the Biesbosch reservoirs. All are pumped storage, with minor or no inputs from their own catchments.

Pitsford reservoir has very little data available and so this review will focus upon the contrast between the valley reservoir type, typified by Rutland, and the artificial embanked type, typified by Covenham. A comparison of the two is provided in Figure 4.1 and 4.2 and Table 4.1,

Figure 4.1 Location of Covenham, Rutland and Pitsford reservoirs.

Rutland Water (Year of filling1975)

Character	Dimension	Quantity
Source		Welland, Nene
Volume	10^6 m^3	124
Surface	km^2	12.6
Littoral surface	km^2	8.0 (= 60%)
Max. depth	m	34
Mean Depth	m	10.7
Circumference	km	35
Shoreline Dev.		2.8
Retention time	weeks	90
Drawdown	m	3
TP (source)	mg/l	0.3
TN (source)	mg/l	5
in-lake SRP	mg/l	0.00-0.20
in-lake NO_3	mg/l	2.8-4.6
in-lake SiO_4	mg/l	0.0-4.0
Secchi Depth	m	2-6
Chl *a*	µg/l	5-15
Phytoplankton	Cyanobacteria Cryptophytes	
Zooplankton	Copepods, Daphnia	

Table 4.1a Physical-chemical summary of Rutland Water

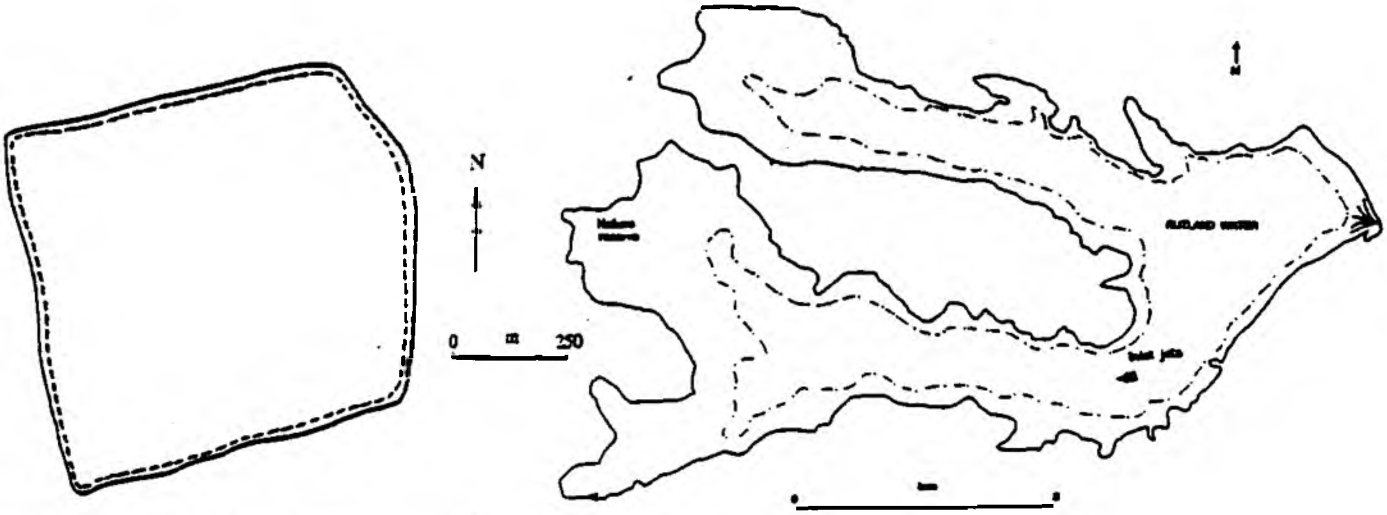
Covenham (Year of filling 1970)

Character	Dimension	Quantity
Source		Louth Canal
Volume	10^6 m^3	10.9
Surface	km^2	0.8
Littoral surface	km^2	0.08 (=10%)
Max. depth	m	16
Mean Depth	m	14
Circumference	km	3.6
Shoreline Dev.		1.1
Retention time	weeks	32
Drawdown	m	1
TP (source)	mg/l	0.2-0.8
TN (source)	mg/l	5-10
in-lake SRP	mg/l	0.00-0.09
in-lake NO_3	mg/l	5.8-8.2
in-lake SiO_4	mg/l	0.2-5.1
Secchi Depth	m	1.5-5.2
Chl *a*	µg/l	3-35
Phytoplankton	Cyanobacteria, Diatoms, Cryptophytes	
Zooplankton	Daphnia spp.	

Table 4.1b Physical-chemical summary of Covenham Reservoir

Figure 4.2 Shape and size of Covenham and Rutland reservoirs

Covenham Reservoir



Littoral zone (- - -) : surface area within depth of 2.5 x Secchi depth

4.2 Design and management features of importance to biomanipulation

Biomanipulation centres on the maintenance of a dense crustacean zooplankton population dominated by large-bodied forms, which reduces standing crop biomass of phytoplankton. This has been achieved in other studies either by close manipulation of fish stock or by manipulation (deliberate or a consequence of reservoir design) of the littoral zone. The littoral zone however, occupies a paradoxical position in biomanipulation because it is on the one hand necessary for zooplankton refuge and on the other for planktivore spawning. Table 4.2 compares the reservoirs in this context.

4.3 Physical management of the reservoirs

Current management of the Anglian Region's reservoirs involves aeration by helixor air guns and bubble curtains in virtually all the water bodies. These are not wholly effective in Rutland but are in Covenham (Fig 4.3): Covenham reservoir also has a jetted input analogous to the type used in the London reservoirs which contributes to its fully mixed state. Ferric sulphate additions have been performed in all the Anglian Region reservoirs since 1990 to reduce in-reservoir dissolved phosphate. As a consequence of these measures the eutrophic state of some of the reservoirs is believed to be slowly decreasing (P. Daldorph, pers. comm.).

Feature	Reservoir	Consequence
1.*Morphology*:		
	Covenham	Uniform littoral habitat, low shoreline index
	Rutland	Irregular littoral habitat, high shoreline index
2.*Bank slope:*		
	Covenham	No littoral area, concrete banks with steep slopes
	Rutland	Moderate littoral area and volume, few steep banks,
3.*Littoral substrate:*		
	Covenham	Concrete; filamentous algae only; poor spawning substratum for cyprinids
	Rutland	Sand/clay with rock reinforcement at edges; tree roots and submerged vegetation; suitable spawning substrata for cyprinids
4.*Management:*		
	Rutland	Water jetted into south arm but imperfectr vertical mixing by helixors
	Covenham	Inlet jetting and air mixing causes full circulation
5.*Fish colonisation:*		
	Rutland	Trout stocked. Cyprinids from feeders streams, screen on river intakes
	Covenham	Screen on river intakes, no feeder streams
6. *Retention time:*		
	Rutland	Long - about 2 years
	Covenham	Moderate - about 8 months

Table 4.2 Comparative management characteristics of Rutland and Covenham of significance to biomanipulation planning

Retention times are relatively long in these latter reservoirs. This characteristic tends to favour slow-growing, buoyant, cyanobacteria instead of diatoms which can sediment readily to the bottom. On the other hand response to biomanipulation can be more efficient as the water bodies might suffer less from the influence of continuous phosphorus inputs and recolonisation by cyprinid fish as occurs in short-retention time pumped-storage systems.

At Foxcote reservoir, a smaller off-river storage reservoir in Buckinghamshire, macrophytes have replaced phytoplankton following ferric dosing for phosphorus control which started in 1983 (Young *et al.*, 1988, Hewston, 1991). In most other reservoirs however cyanobacterial bloom problems have not been eliminated after several years of intensive ferric dosing: of two reservoirs in the south-eastern part of the region, Ardleigh has shown slight declines in chlorophyll but marked reduction in nuisance cyanobacteria, whilst Alton has not (Daldorph and Price 1994). These three reservoirs have been treated with ferric sulphate since 1990, although Pitsford has had far more limited treatment than the other two.

Figure 4.3a Isotherms (upper) and isopleths (lower) in Covenham during 1992. This contrasts with the figures for Rutland and illustrates the more complete mixing of this reservoir.

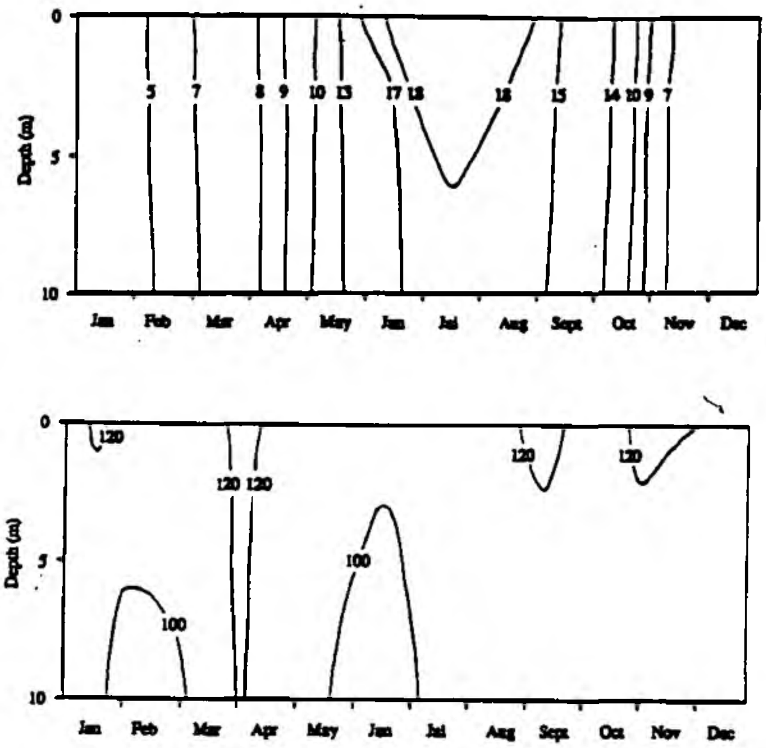
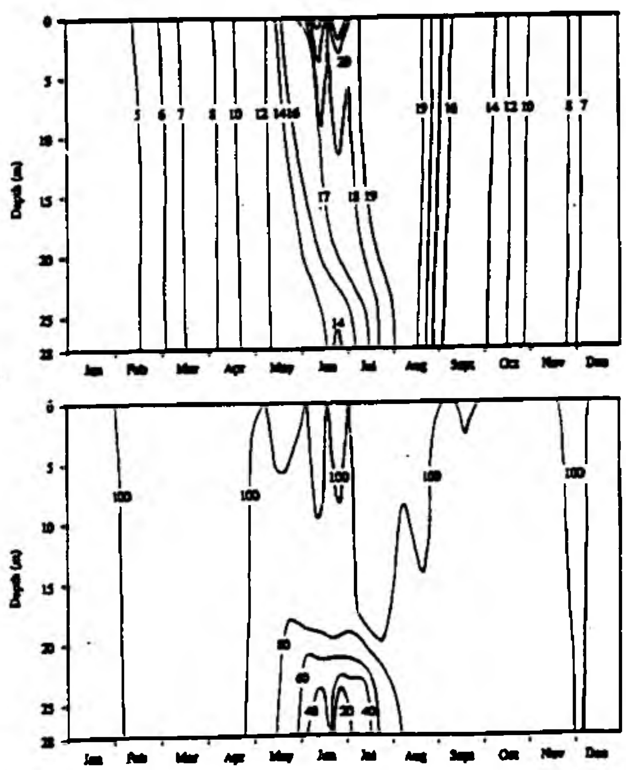


Figure 4.3b Isotherms (upper) and isopleths (lower) in Rutland Water during 1992. This illustrates the slight thermal stratification which occurs and the more substantial oxygen stratification which quite quickly sets in.



4.4 Data available

Reasonable runs of data on physical and chemical parameters exist for Rutland and Covenham, together with measurements of chlorophyll *a* and algal taxonomic composition, from the early 1980s. Zooplankton data exist, generally over the past four years with sporadic data for Rutland for two periods prior to that when specific research projects were carried out, but no formal fish data exist for either reservoir other than those published for the filling phase (Harper & Bullock 1982) and from catch records of the trout fishery. Both reservoirs have fish screens on their river intakes, but multi-species populations have developed through intake of eggs or small fry coupled in Rutland (and also Pitsford) with immigration from feeder streams.

4.5 Fish communities and fishery management

Covenham

In this reservoir there is effectively no littoral zone (Figure 4.2) . The prominent fish species is perch, pike appear to be absent and large bream occur which used to be removed by trapping. Angling is not allowed, because of the steep banks that constitute a hazard. Coarse fish are removed by Anglian Water irregularly and are required for stocking elsewhere.

Rutland Water

The littoral zone is well-developed and weedbeds *(Elodea nutallii and P. pectinatus).* occur to variable extent. The fish community is dominated by stocked brown and rainbow trout, the dominant coarse fish is roach. Perch are relatively common and large brown trout present. Coarse fish occur in the open water in winter, showing shoaling patterns at 20m depth. They spend more time in the littoral zone in summer. Roach shoals are inshore for spawning around April-May-(June). Every year the outbreak of a disease (bacterial furunculosis) precedes spawning. Pike are present in the reservoir and spawn in March-April at the western end of the arms in shallow water devoid of weeds, branches or obstructions. Trout spawning is probably not significant as this species can only spawn in the feeder streams, not in the reservoir.

The reservoir itself is run as a 'put and take' trout fishery and stocking with 80,000 trout (mostly rainbow trout) occurs between March until May. Depending on angler success, additional stocking may take place during the summer. Escape of fish to feeder streams is prevented by electrodes which repel trout.

The management of coarse fish is leased to Framlingham Fisheries, a private company and licensed fish farm. Seine nets of 1000m in length are used for harvesting coarse fish for stocking elsewhere. Pike fishing is allowed during 2-3 weeks in late autumn to reduce predation on trout. According to anglers, pike yields slumped compared to net catches of 10 years ago. No fishing is allowed in the nature reserve and it is thought that this area could serve as refuge for pike due to shallow waters sometimes colonised with rooted macrophytes. It was observed that growth rates of pike were high in the 1970s after flooding and decreased latterly, as commonly happens with reservoir fisheries (Hrbácek, 1994).

Pitsford reservoir is similarly managed as a trout fishery.

4.6 Zooplankton

Zooplankton play a central role in biomanipulation, because the target of management is the maintenance of stocks of large-bodied zooplankton. The objective of biomanipulation is that these zooplankton exert a significant grazing pressure on phytoplankton, thus preventing conditions which favour cyanobacteria, reducing overall algal biomass and increasing lake transparency

Covenham reservoir supports three coexisting species of *Daphnia*, of which *D. galeata* is the smallest. *D. magna* is the largest species while *D. pulex* is of intermediate size, with average adult lengths of 2.9 mm and 1.9 mm respectively. The rotifer community of Covenham is dominated by *Polyarthra* spp. although the other species typical of Rutland also occur at a lower density. Rotifer biomass is usually lower than in Rutland Water, and daphnid biomass higher (Fig 4.4)

Rutland Water has a cladoceran zooplankton community dominated by *D. galeata*. This species typically attains an average adult length of 1.4 mm. Larger species of *Daphnia* are only rarely recorded from the reservoir, and never in great numbers. Rotifer biomass is about an order of magnitude lower than daphnid, and peaks are temporally separate with rotifers typically appearing first (Figure 4.5). Dominant rotifers are *Keratella cochlearis* and *K. quadrata*, with *Polyarthra* and *Synchaeta* spp.

Figure 4.4 Comparison of rotifer and Daphnia biomasses in Covenham reservoir

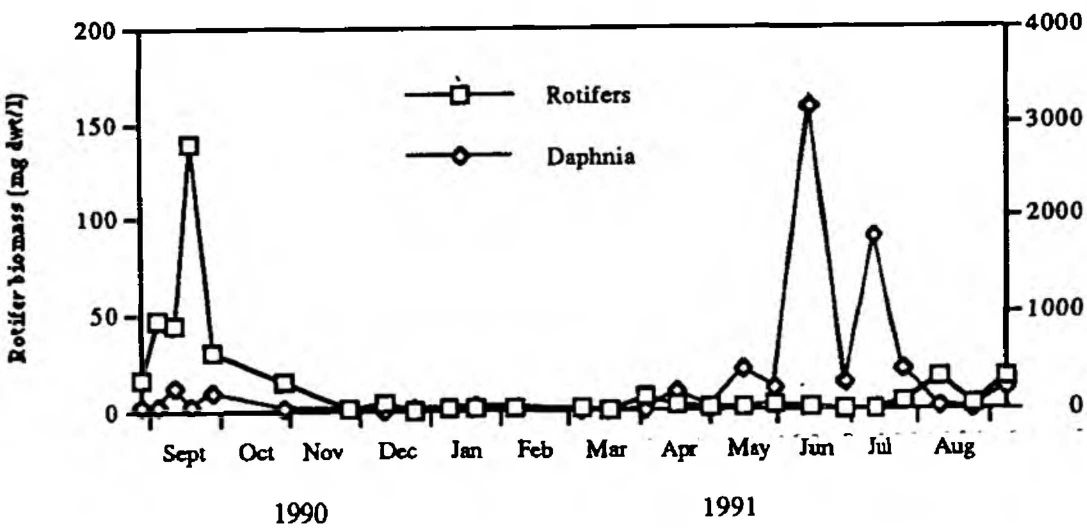
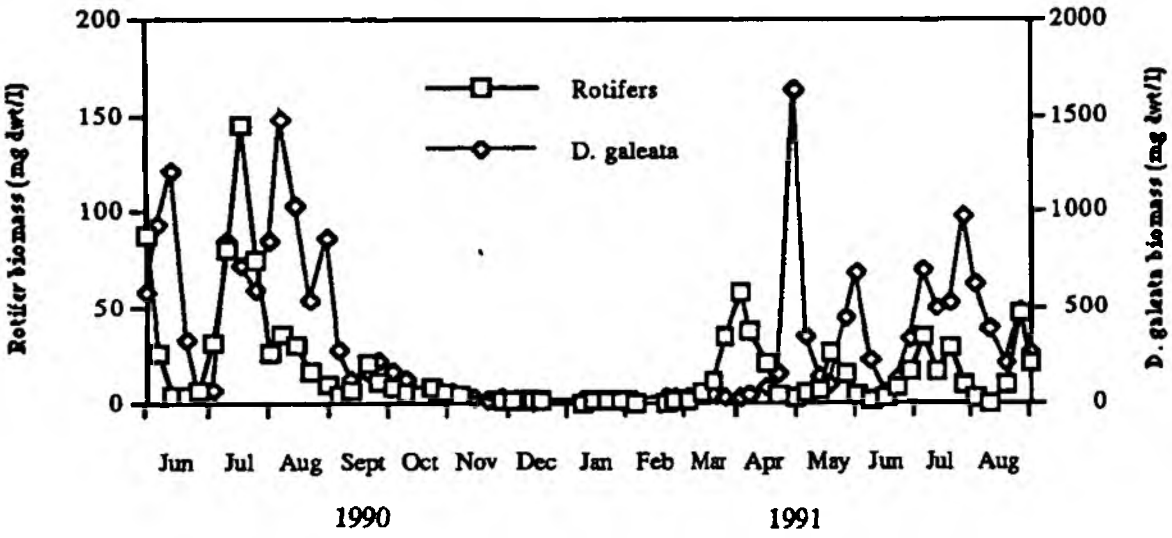


Figure 4.5 Comparison of rotifer and Daphnia biomasses in Rutland Water



4.6.1 Typical species composition 1990-94

Rutland was characterised throughout by dominance of *D. galeata* and very rare occurrence of any smaller species in each year. Typical seasonal patterns have not changed since the reservoir first filled (Harper and Ferguson, 1982) although recent studies by Randall (Randall, 1995) have shown that the average size of mature females at egg production has declined since 1985. The only explanation so far proposed for this change is a slight increase in intensity of fish predation which is not strong enough to cause species shifts. Covenham has experienced greater fluctuations in its zooplankton complement in the three years for which data are available, with dominance by *D. magna* in two years out of three and by *D. galeata* in one.

The zooplankton community in any lake will tend to be dominated by large-bodied grazers in the absence of predation upon them, because these species are competitively superior (grazing efficiency increases exponentially with size as it is based upon volume of water filtered). The presence of efficient larger grazers thus usually causes reduction in populations of smaller-bodied grazers (small cladocera and rotifers): conversely the latter increase in importance if large-bodied *Daphnia* species are suppressed by fish predation. In both Covenham and Rutland small crustacea are effectively absent, but both contain rotifers, the smallest filter-feeding component of the community. It has been hypothesised by Jeppesen *et al.* (1992) that, if fish predation is high and large-bodied grazers suppressed, rotifer biomass will increase; this is one facet of the concept of 'top-down' control of food webs.

Pitsford reservoir rotifers were only sampled over the period August 1990 to August 1991 roughly every fortnight. A similar data set from Rutland Water and Covenham Reservoir over the same time period can be used to compare the biomass of the groups to allow some tentative comparisons about the state of fish predation to be made between the reservoirs (Table 4.3).

Table 4.3 Comparisons of mean zooplankton biomass in the three reservoirs 1990-91

Reservoir	Rotifer biomass (μg/l)	Daphnia biomass (μg/l)
Pitsford	681	*
Rutland Water	425	6560
Covenham	354	7440

* no data available on Pitsford crustacean zooplankton

The biomass of rotifers was larger in Pitsford than in the other two (species composition was similar to Rutland Water). Rotifers exploit a similarly sized food fraction as *Daphnia* but are usually out-competed due to their small size. The increased rotifer biomass in Pitsford Reservoir may thus be the result of increased planktivore activity reducing the biomass of cladocerans to a mean level lower than that of Rutland Water. Pitsford Reservoir is managed as a trout fishery in similar fashion to Rutland Water. It is likely that the reservoir has an established cyprinid community as there is a littoral spawning zone proportionally larger than Rutland Water's. Covenham Reservoir, by contrast, has the lowest mean rotifer biomass and this is consistent with the highest *Daphnia* biomass of the three, itself consistent with the dominance by large-bodied species. We tentatively conclude therefore, in this the only comparison we can make of all three reservoirs, that predatory pressure upon grazing zooplankton is greatest in Pitsford and least in Covenham.

4.7 Phytoplankton community of Covenham Reservoir and Rutland Water

In general terms the trophic state of the two reservoirs is similar. Covenham has annual phosphorus concentrations which are now below 100 μg/l (Fig 4.6) as a consequence of phosphorus sedimentation (and also P-removal in Louth sewage effluent, the major catchment phosphorus source) but in previous years means were around five times this figure and maxima ten times.

Rutland had lower levels than Covenham even before P-control (means around 100, maxima around 200 μg/l) which have been reduced to half the figures or less as a consequence of ferric-dosing in-lake combined with P-removal from the major conurbations of the Nene source (Fig 4.7).

Phytoplankton generally reflect these differences (Figures 4.8 and 4.9). At Covenham, maximum concentrations usually exceeded 75 µg/l chlorophyll *a* before phosphorus removal and are now around 40 (Fig 4.8); annual means have declined from around 25 to 10 µg/l. At Rutland maxima previously exceeded 30, means 10 µg/l. Mean values appear to have decreased, to below 10, more obviously than have maxima (Fig 4.9).

Figure 4.6 Nutrient levels in Covenham Reservoir in a typical post-ferric dosing year (1994)

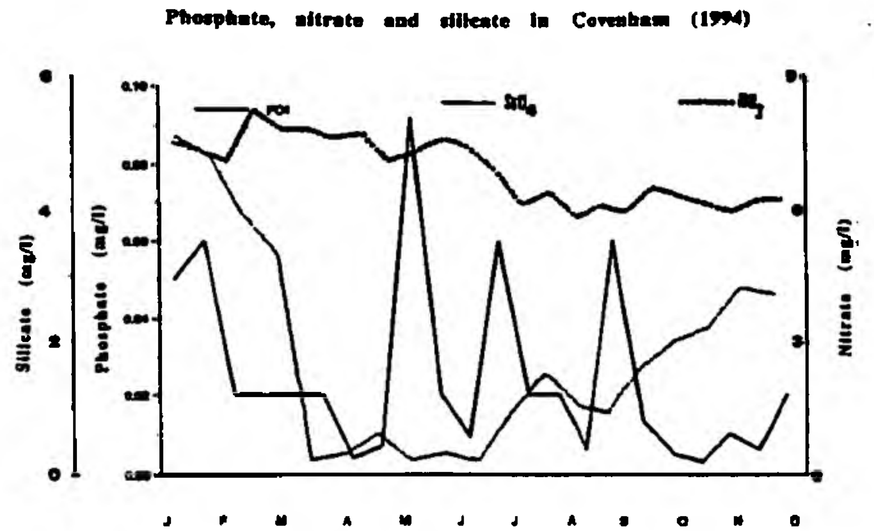


Figure 4.7. Nutrient levels in Rutland Water in a typical post-ferric dosing year (1994)

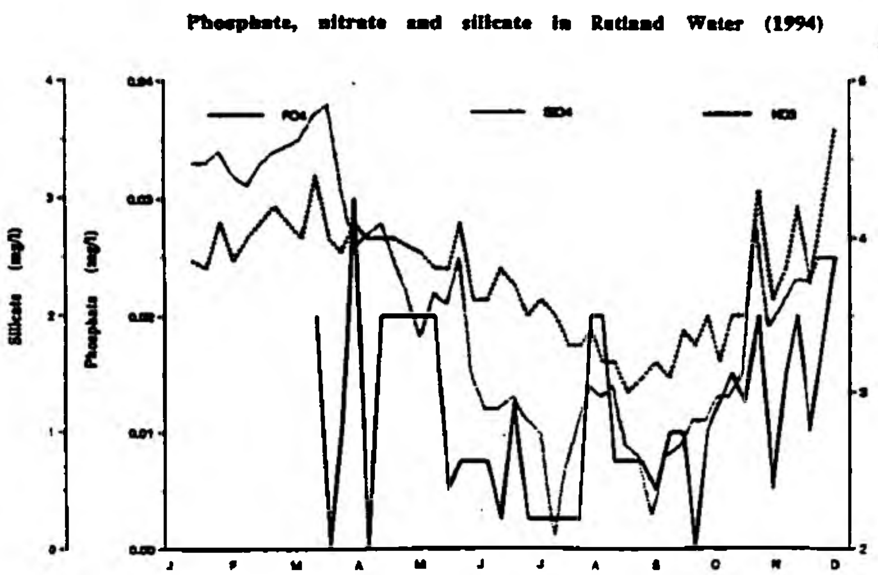


Figure 4.8 Phytoplankton (as chlorophyll *a*) and Secchi transparency at Covenham reservoir

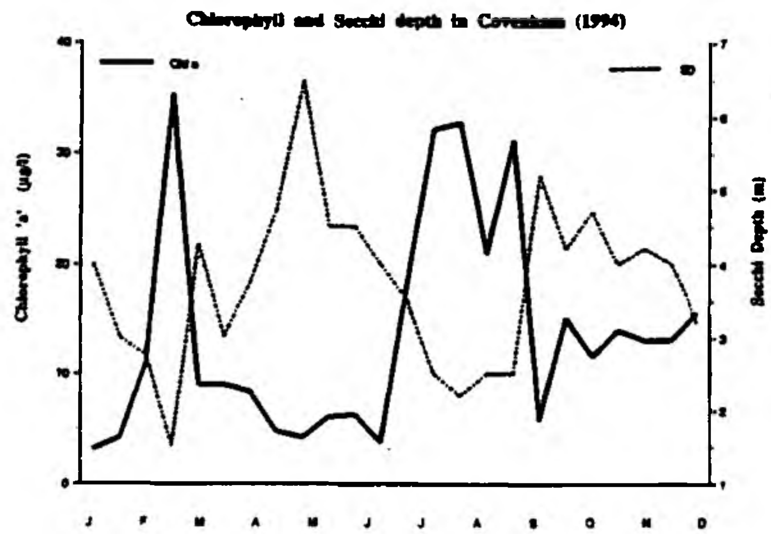
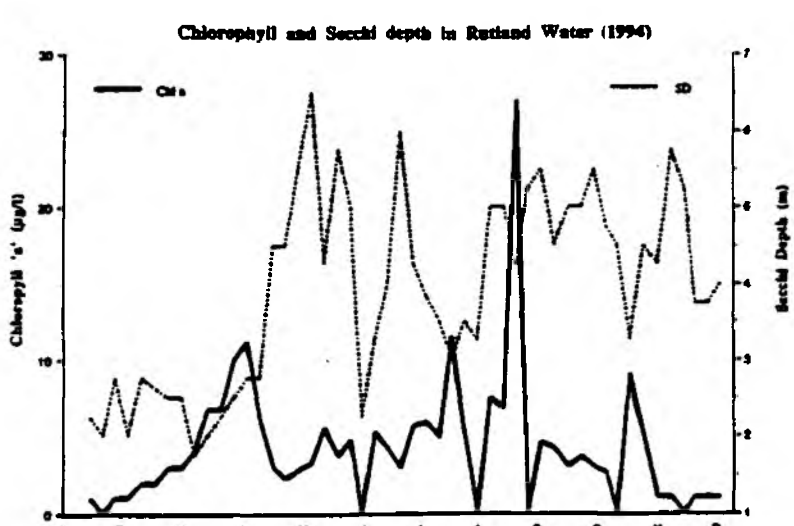


Figure 4.9 Phytoplankton (as chlorophyll *a*) and Secchi transparency at Rutland Water



In both reservoirs however cyanobacteria still form important components of the summer maxima: in Rutland there appears to have been less effect of phosphorus control upon cyanobacteria than upon other groups (Fig 4.10).

4.8 Factors controlling zooplankton

Three main factors may affect zooplankton populations – the physical environment (mainly temperature), the food supply (primarily phytoplankton but also seston in cases such as highly mixed river-supplied reservoirs) and predation (mainly by fish).

4.8.1 Temperature

An examination of the temperature records of the reservoirs was carried out to see whether spring temperature controls the onset of zooplankton growth and hence sets the pattern for the year (suggested by Harper and Ferguson, 1982). Water temperature directly affects the developmental rates of cladoceran populations. High temperatures shorten the egg development time, the time taken to reach maturity, and the moult time once mature, which increases the reproductive potential of parthenogenetic females. Temperature may also have a less direct but similarly important role as species may exhibit optimum growth and competitive ability within a certain range of temperatures. The development of the water temperature through the year may therefore be an important factor regulating the successful development of competing species. Egg development in daphnids is proportional to ambient temperature. At temperatures below 7°C more than 10 days are required to hatch (Bottrell *et al.*, 1976). This temperature can be taken as a reference for the start of cladoceran development in the spring.

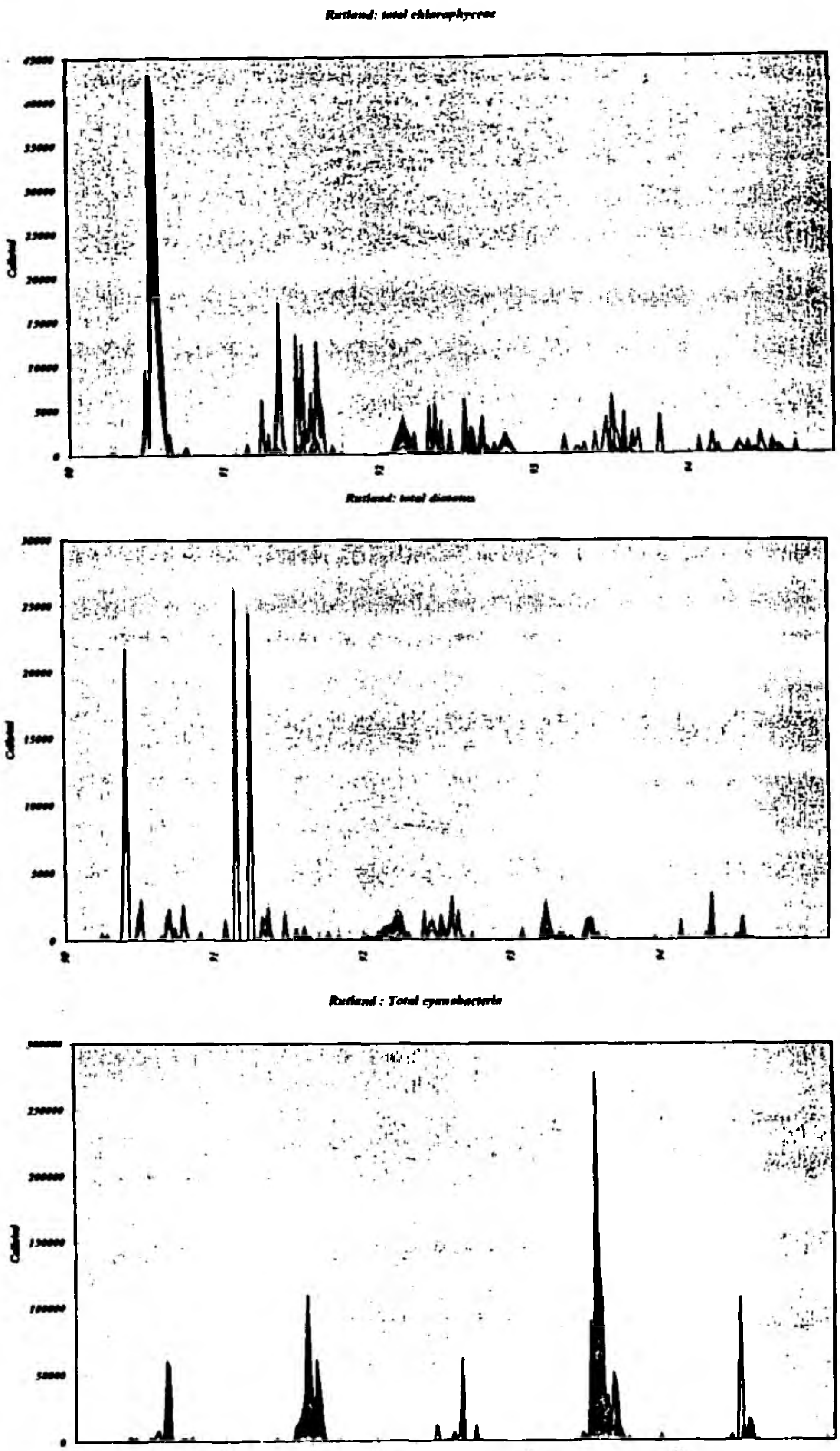
The degree days prior to population development were calculated for Rutland Water and Covenham Reservoir. The calculation of degree days was performed on an average temperature for the whole water column, assuming total circulation during the spring period. The cumulative degree days above 7°C were calculated for each year until the 31st May.

Strict comparisons cannot be made because of the difference of the thermal regimes of the two water bodies but general annual trends may be inferred from the comparison in Table 4.5.

Table 4.5 Degree days above 7°C in each reservoir in Spring (until 31.5).

Year	Rutland	Covenham
1991	549	no data - inferred c. 540
1992	748	735
1993	609	594

Fig 4.10 Algal taxonomic composition at Rutland Water



Covenham Reservoir

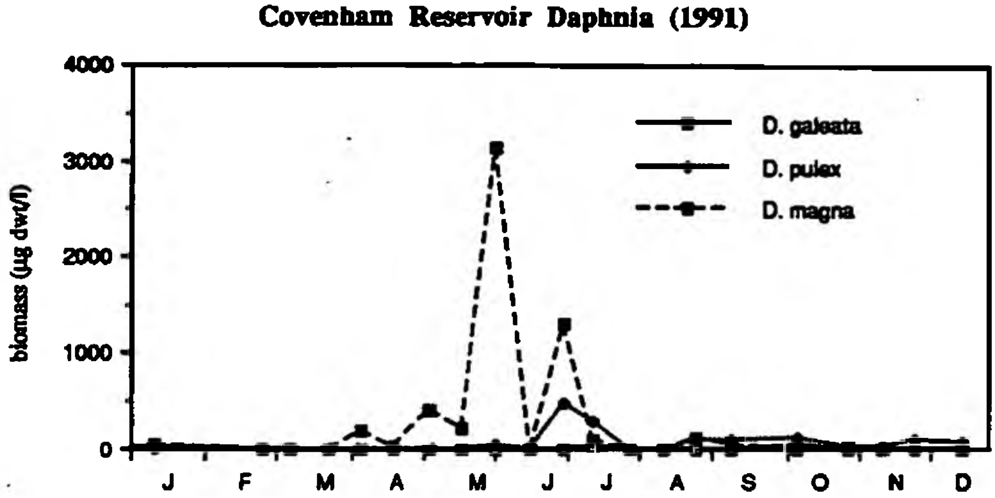
1991 probably had a lower cumulative degree day than 1992 or 1993 (see similarity between Rutland and Covenham in 1992 and 1993). This may have had an effect on the development of the zooplankton. The first cladoceran to develop in appreciable numbers in 1991 was *Daphnia magna* during April (Fig 4.11, Fig 4.12). The initial increase was not supported by increased egg production and may therefore have been partly from the hatching of resting eggs. *D. pulex* numbers increased in July and persisted during the winter period of 1991-1992. The timing of the development of biomass in 1991 was delayed substantially until the end of May, when chlorophyll a levels had already declined. The high biomass was sustained for a short period of time only. The lower spring cumulative water temperatures may have had some effect on the late timing of the *Daphnia* peak, but the lack of an earlier development of *D. galeata* may have been the product of early competition with *D. magna*. The fact that *D. magna* was dominant in this year but not 1992 may indicate a lower degree day requirement of this species. In 1992 however, an early spring peak of *D. magna* was not produced even though chlorophyll a levels were suitably high. There are two possible reasons for this: selective predation by planktivorous fish, the presence of cyanobacteria which are known to interfere with feeding of larger species and the more rapid increase in temperature which might have created unsuitable conditions for ephippial hatching.

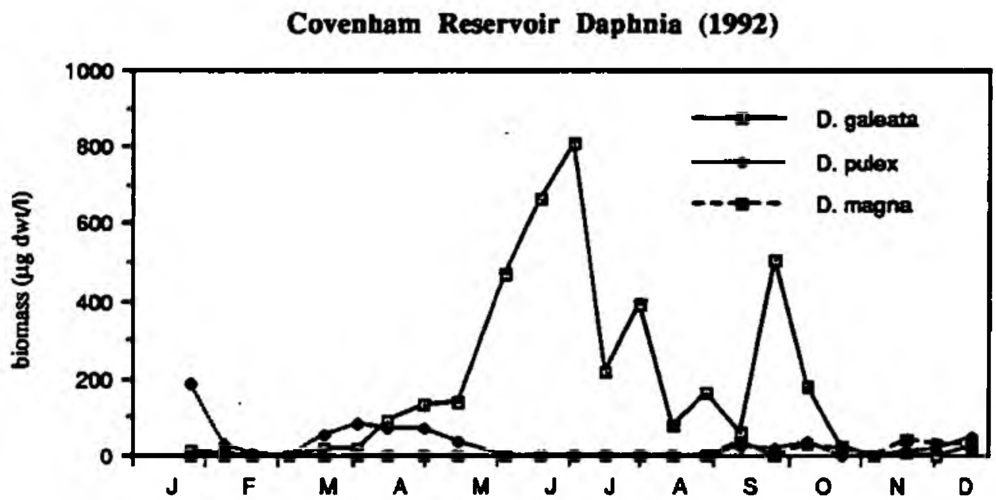
The initial peak of *D. pulex* in the spring of 1992 was accompanied by elevated egg ratios indicating the reproduction of over wintering adults was the prime source of the peak. *D. galeata* then became the dominant cladoceran in 1992 from April until November associated with increased egg production during the early spring. The population density peaked in summer and in autumn before declining to the winter low density.

D. galeata remained at very low levels during the early part of 1993. *D. pulex* peaked early in the year which was again associated with an increased egg production. This species remained the dominant form in terms of biomass throughout most of the summer although *D. magna* reappeared during August along with *D. galeata*. This was the only year when no single species was clearly dominant throughout the spring / summer months.

It is possible that the slightly lower cumulative degree day values of 1991 allowed the development of *D. magna* in Covenham in preference to *D. galeata*, a trend that was reversed in 1992 but the completeness of the switch in species abundance indicates that increased fish planktivory may also be the cue. This could have come about by high recruitment of cyprinids during 1992, a warmer year. *D. magna* appeared again in 1993, a colder spring. This type of cyclic relationship is one possibility of top down control that could explain the cycles seen in the cladoceran zooplankton .

Figure 4.11 Species development of *Daphnia* in Covenham reservoir





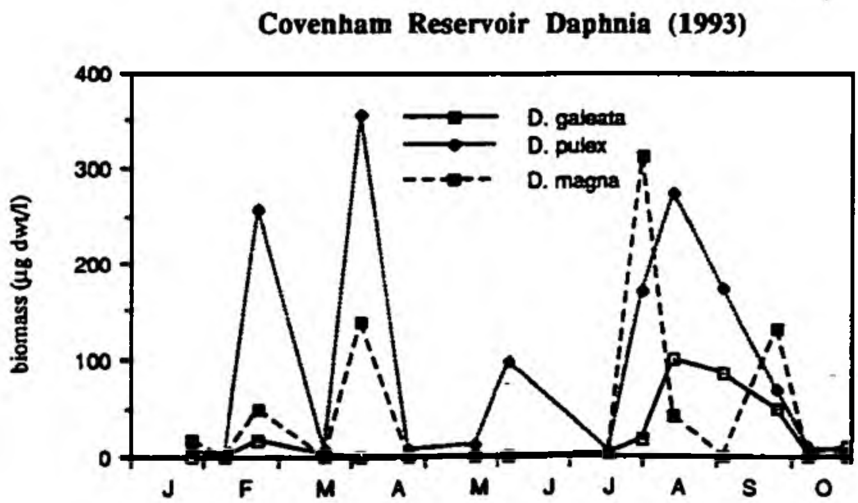
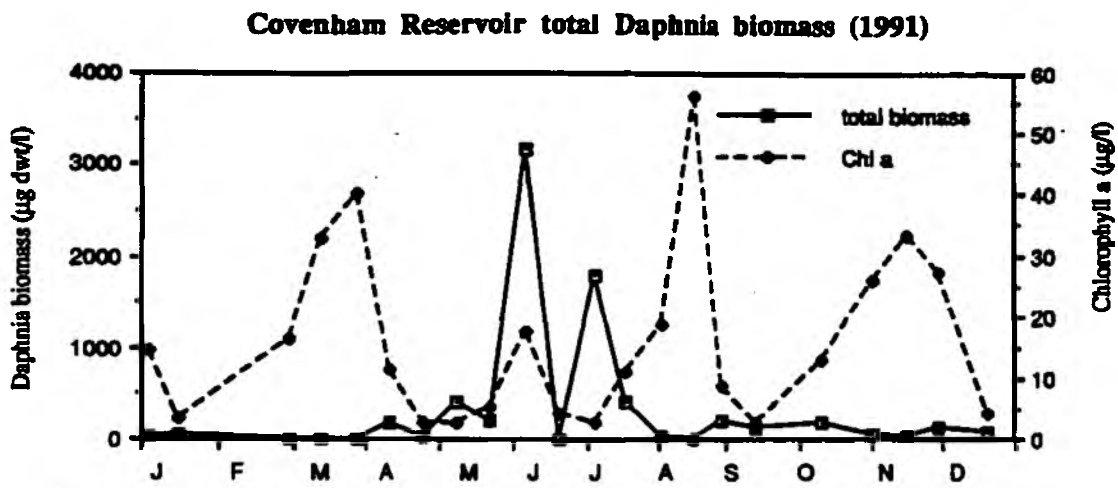
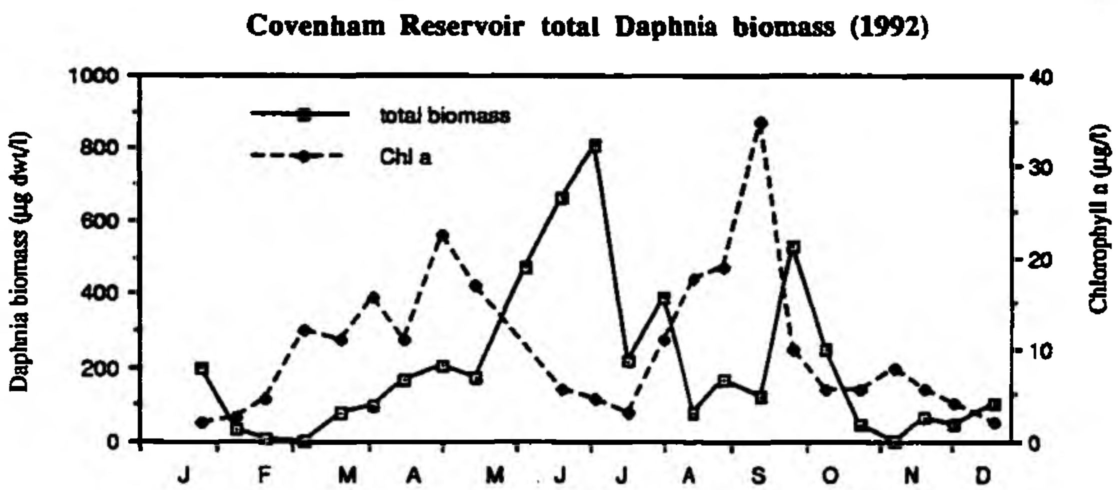
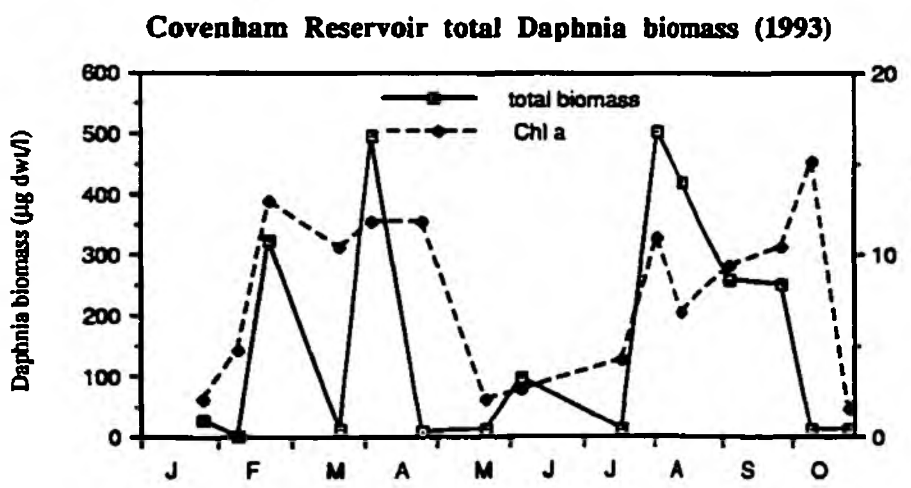


Figure 4.12 Biomass of *Daphnia* and chlorophyll *a* in Covenham reservoir







Rutland Water

Rutland Water experienced a spring development of *D. galeata* in each year (1991 and 1992 are shown, Fig.4.13). The start of the development was relatively synchronous in both years although the biomass attained differed. The cumulative degree days were lower during the spring of 1991 than 1992. The cumulative biomass of the spring population peak of *Daphnia* was also lower in 1991, indicating the possible role of temperature. The chlorophyll *a* levels in the reservoir during the spring prior to the *Daphnia* increase were higher in 1991. This may indicate that temperature has more control over *Daphnia* development than does food levels. The spring peaks of both years coincided with reduced chlorophyll *a* levels. This reduction, although not necessarily due to grazing, was more pronounced in 1991. The biomass of *Daphnia* during 1992 was maintained above 500 µg dry weight l^{-1} until mid June and chlorophyll *a* levels seemed to be little affected by this elevated biomass.

The effect of degree days on the timing and size of *Daphnia* development in Rutland cannot be easily defined from a two year period. If any patterns do emerge it is that slightly larger spring biomass was attained during 1992, when degree days above 7°C were higher, and the peak was more long-lived than 1991. In both years spring development seemed relatively synchronous with the phytoplankton bloom. High spring development in 1992 was accompanied by high chlorophyll, indicating little impact of grazing on the phytoplankton standing crop.

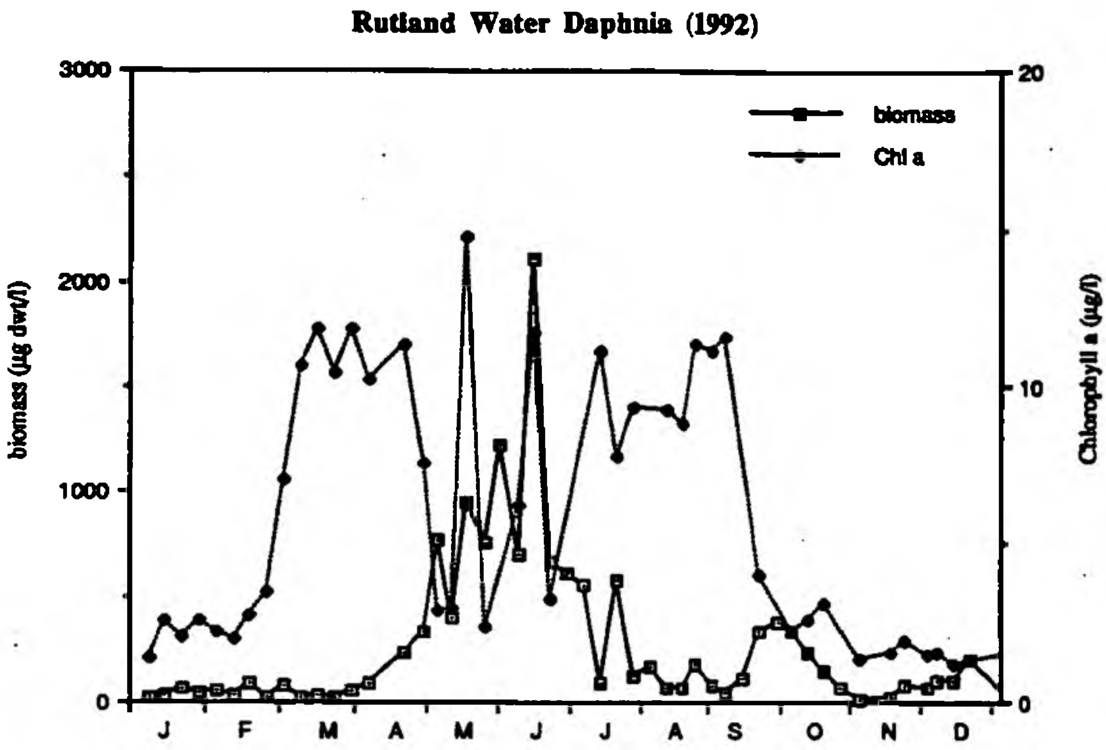
4.8.2 Phytoplankton

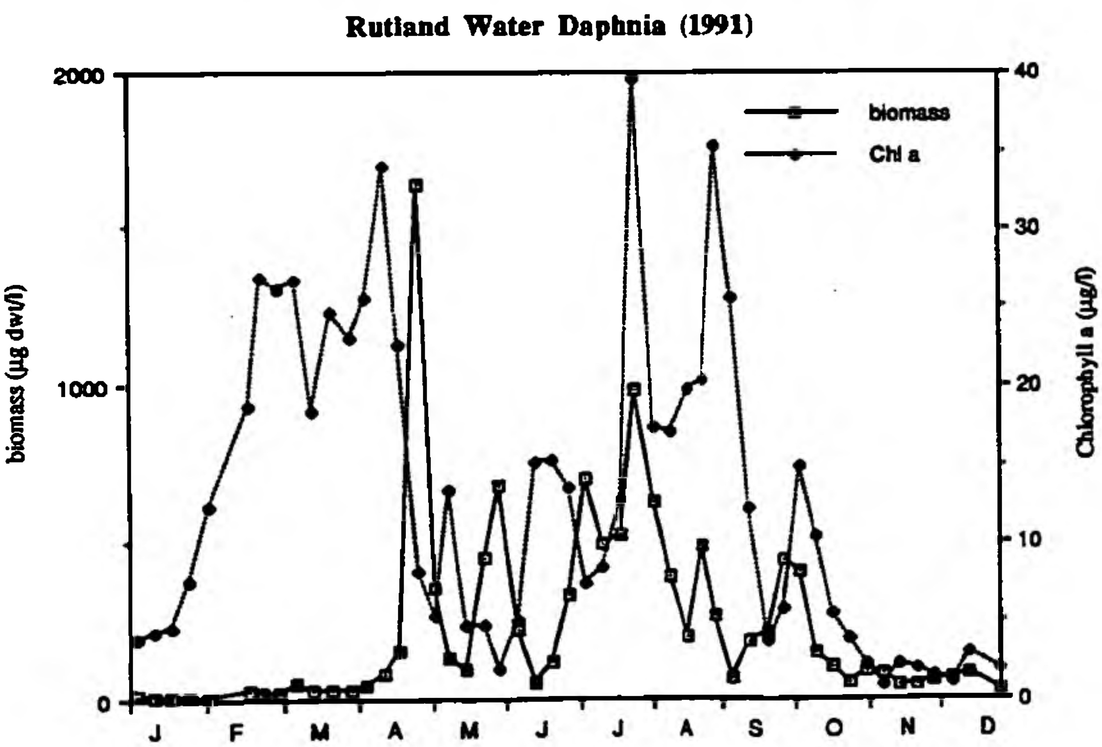
Covenham

The general pattern of cyanobacteria in the three years 1991-93 was similar in each reservoir, with lower biomass in 1992 than the other two years. The pattern of daphnid development was different, as three species were involved (Figure 4.11) whose proportions were determined by planktivory (see below) and in addition other phytoplankton taxa waxed and waned in different sequences.

In 1991 the *D. magna* population started developing moderately late (Figure 4.11, 4.12) after the crash of early spring algae dominated by centric diatoms. This could have been due to a colder spring, since even though temperature data for this year are not available, the degree days in Covenham and Rutland were similar in two years out of three (Table 4.5) *D. magna* populations therefore developed when chlorophyll a levels were low and this may thus reflect the longer development time of *D. magna* at reduced food levels. Grazing control exerted by the population of *D. magna* that was maintained during June-July (under possibly low planktivory because of the cold spring) suppressed cyanobacterial competitors, permitting blooms to occur in August and October.

Fig 4.13 Biomass of *Daphnia* and chlorophyll *a* in Rutland Water





D. magna was not present in any numbers during the spring of 1992. The most likely cause is a change in the annual pattern of recruitment of planktivorous fish in the reservoir, which could itself have been a result of the warmer spring (Table 4.5). Several possible alternative explanations however make interpretation difficult:

a. predation on animals in summer 1991 may have reduced the effective stock of ephippia produced.

b. the presence of cyanobacteria, an unsuitable food, in the spring of 1992.

During 1992 *D. galeata* started to increase in biomass during April. This may have been because planktivory restrained the larger species. The peak biomass coincided with reduced levels of chlorophyll a during June and July and probably caused them, since edible species dominated the algal composition. The late summer phytoplankton peak in August through to October was not cyanobacteria-dominated, possibly due to low phosphorus concentrations (the effect of ferric dosing) coupled with a reduced grazing pressure; faster growing, more mesotrophic species dominated.

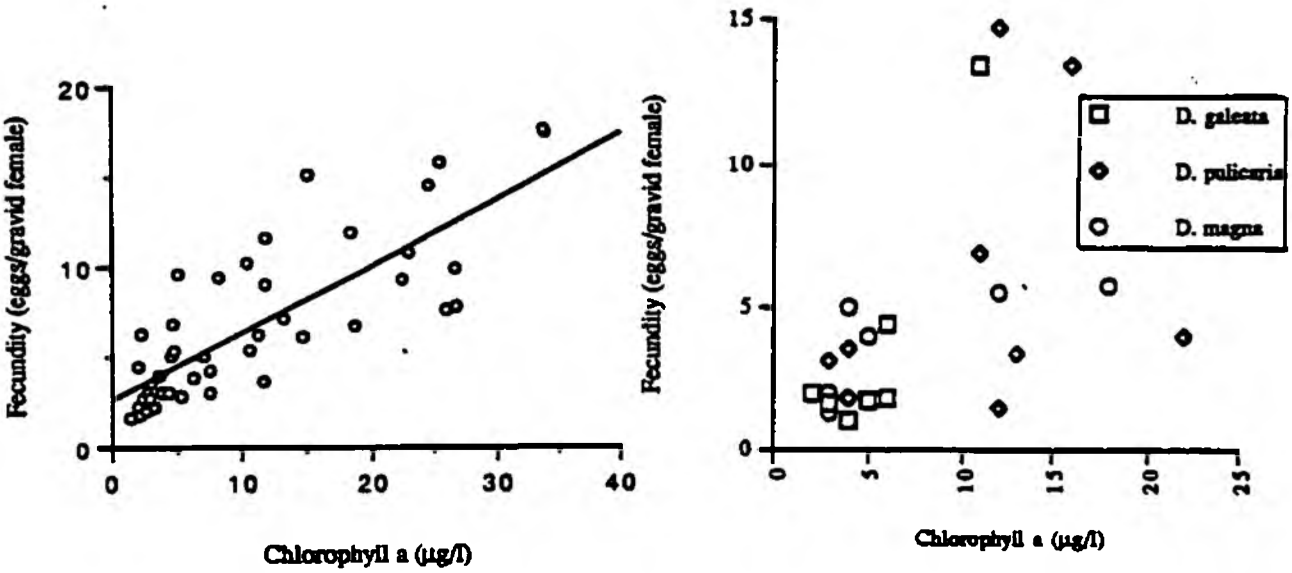
The *Daphnia* of 1993 were reduced in biomass, but dominated once again by the larger species *D. pulex* and *D. magna*; *D. pulex* early in the spring and *D. magna* briefly in the summer. Spring development of *D. pulex* seemed to be ephippial hatching because it was quite erratic, but in a colder year was less suppressed by planktivory. The spring phytoplankton was dominated by cyanobacteria with little diatom growth. A decline of the cyanobacteria in May through to July was not followed by any typical summer algae, and little daphnid biomass, which was quite atypical. Eventually in late summer a mixture of mesotrophic algae developed, with little cyanobacteria, followed by populations of the two larger daphnids.

Rutland

The fecundity of *Daphnia* in the first half of both years was generally related to total chlorophyll a levels in the reservoir (Figures 4.13, 4.14). The higher fecundity in spring 1991 (possibly due to ephippial hatching which was not sustained) led to a short lived increase in biomass, even though temperatures were low. The initial spring peak of 1991 reached a level of >1600 µg dry wt/l and coincided with a sharp drop in chlorophyll a levels. The dominant spring algae were diatoms. In the summer a strong development of cyanobacteria occurred. The reasons for this may include reduced early grazing pressure allowing the spring diatom populations to sequester nutrients encouraging the competitive superiority of phosphorus-scavenging cyanobacteria. The cyanobacteria (mainly *Aphanizomenon*) thus built up through July and August in 1991 and the grazing pressure of daphnids reduced potentially competing, more edible species. The summer daphnids might have persisted at moderate but fluctuating biomass due to reduced planktivory as a result of poor recruitment in a colder spring.

Spring of 1992 had a more reduced diatom development than 1991. An earlier rate of increase of *Daphnia* due to higher temperatures was sustained for a greater period of time, with a maximum of >2000 μg dry wt/l in late June. Chlorophyll a levels fluctuated rapidly during this period, possibly due to the instability created by a daphnid biomass whose own fluctuations might have been caused by planktivory from new cyprinid fry. Daphnid biomass in the summer fell to low levels about two months earlier than in the equivalent period of 1991, which could have been the result of better fry recruitment in a warmer spring. This lower biomass of *Daphnia* through July and August might have had a reduced grazing effect upon the nutrient-competitors of cyanobacteria, allowing such faster-growing species to dominate (diatoms and chlorophyceae dominated this period).

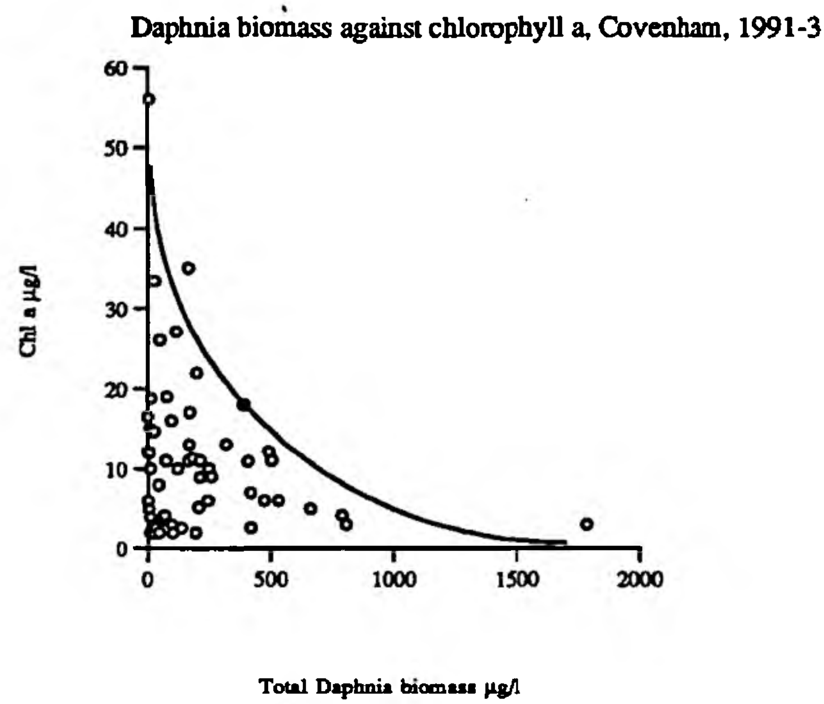
Figure 4.14 Daphnia fecundity and chlorophyll relationships in Rutland Water (left) and Covenham Reservoir (right). No statistical relationship exists for Covenham because the graph is derived from three species, each with too few data points.



In both reservoirs overall, daphnid biomass and phytoplankton biomass are negatively related (Figure 4.15) although a large number of joint low biomasses obscures a statistical relationship.

Studies on the population dynamics of the zooplankton in Covenham from 1990-93 were reported in interim in 1994 (Sanderson 1994) and will be completed by late 1995, which will enable the remaining hypotheses to be fully evaluated with two more years' data. Nevertheless, we feel that a tentative model for the fish-zooplankton-phytoplankton relationships can be proposed which explains the zooplankton-phytoplankton part in five years oout of six so far (Figures 4.16, 4.17). This explains biotic relationships controlling biomass achieved driven by the early consequences of spring temperatures, against a background of stability and nutrient control (and nutrient ratio control) of phytoplankton taxonomic composition.

Figure 4.15 Daphnia biomass - chlorophyll a relationships in the two reservoirs.



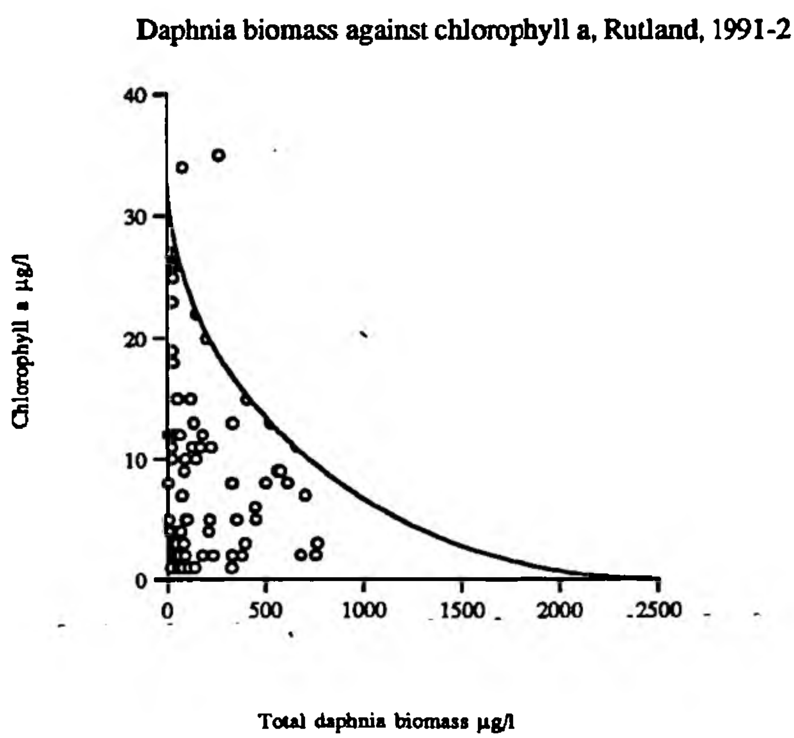


Figure 4.16. A model for fish-zooplankton-phytoplankton relationships in cold spring years

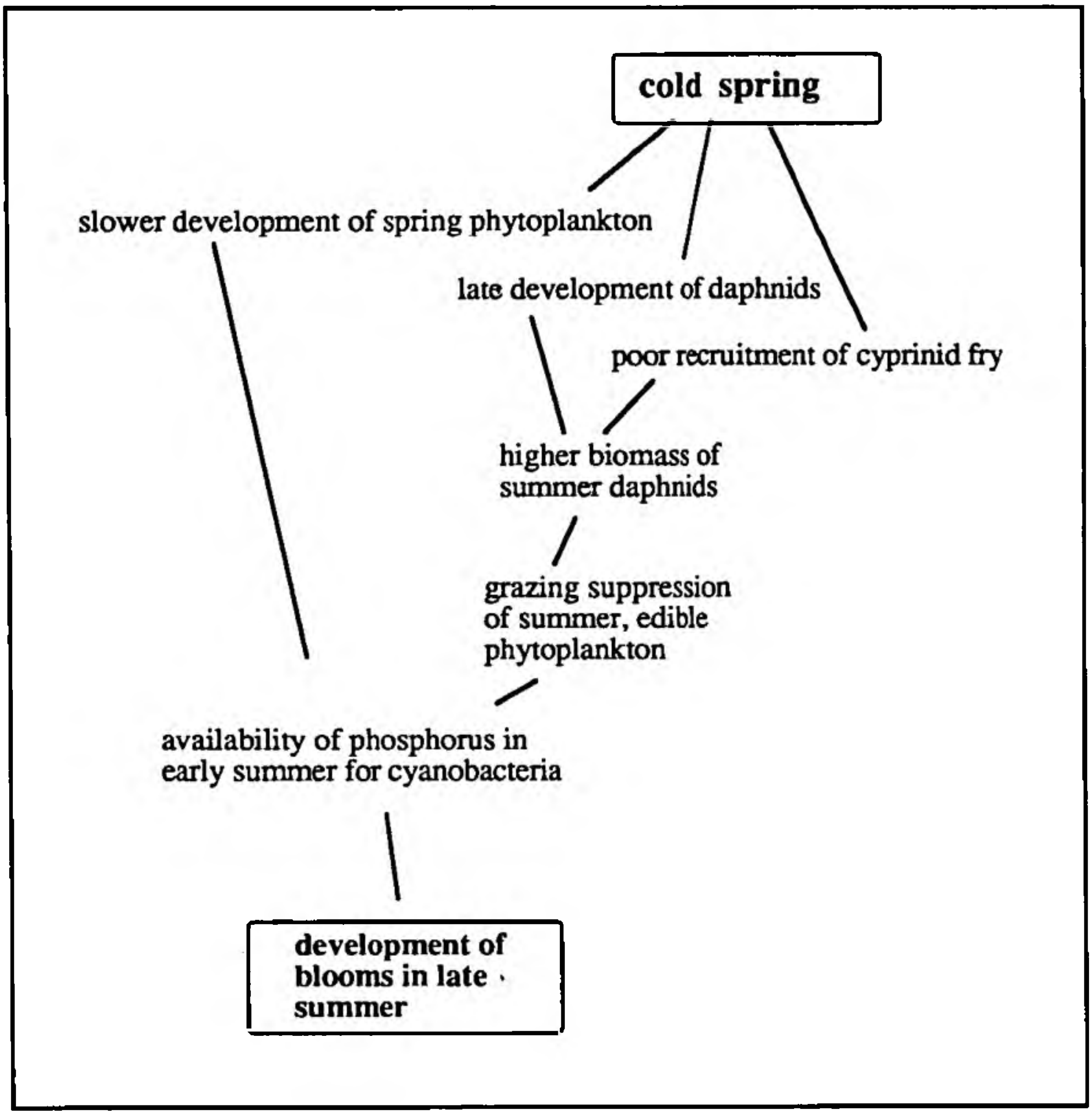
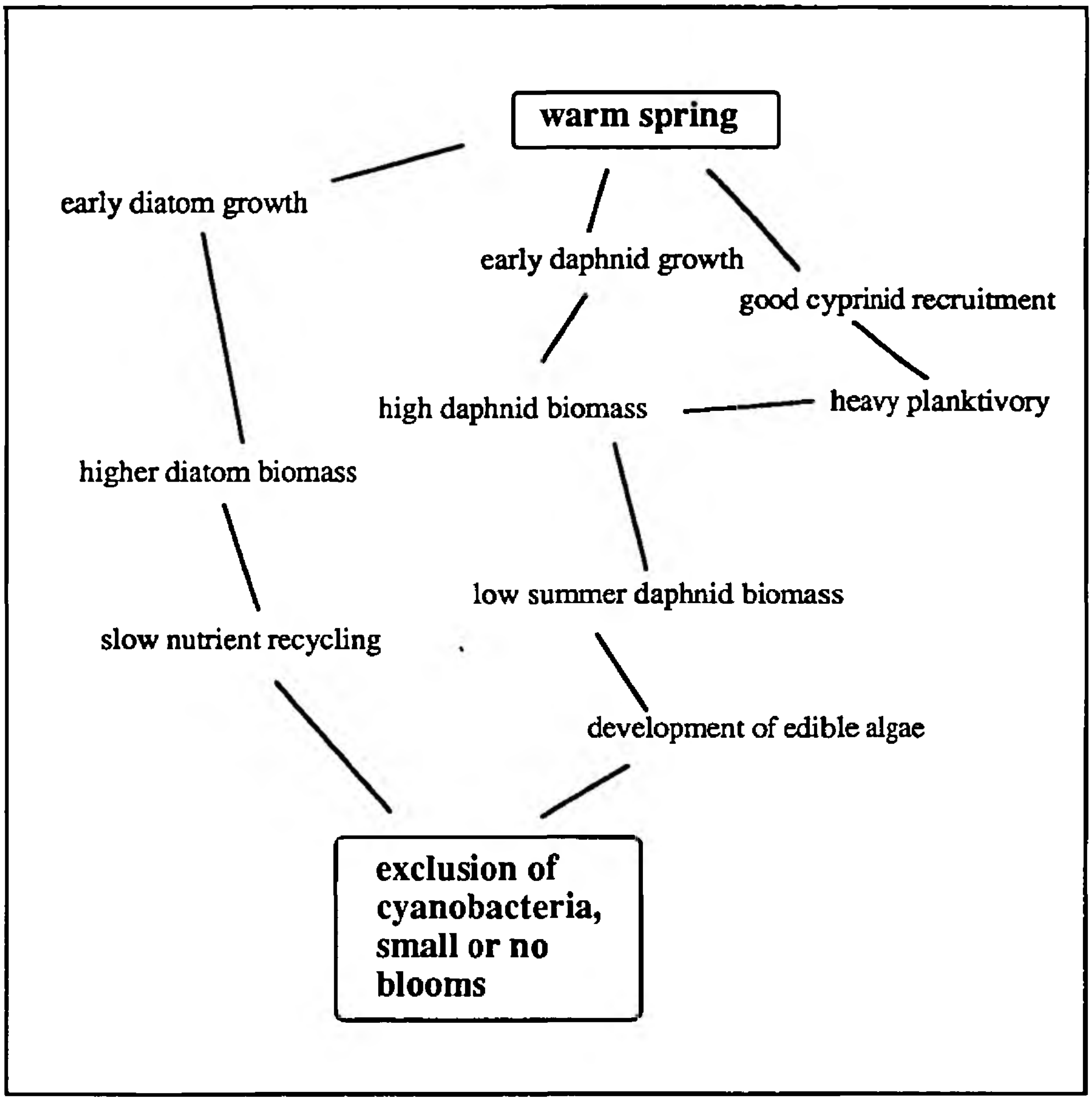


Figure 4.17. A model for fish-zooplankton-phytoplankton relationships in warm spring years

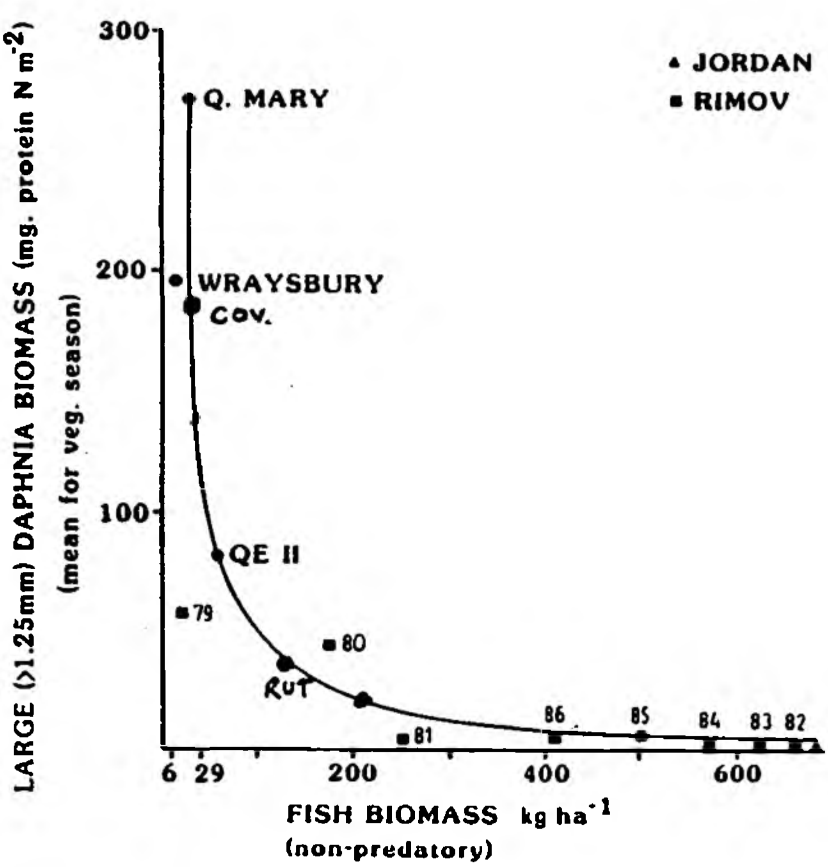


4.8.3 Fish biomass and predation upon zooplankton in the two reservoirs

The only knowledge currently available about fish predation comes from the unpublished information summarised in the earlier section of this report, combined with the literature syntheses about the relationship between fish biomass and zooplankton size composition (Kubecka and Duncan 1994), (Figure 4.18). Calculation from the relationship published by these authors between large daphnid biomass and fish biomass in a number of reservoirs suggests that Rutland Water, with a mean zooplankton biomass as protein N mg m^{-2} of 47, contains a non-predatory fish biomass of around 200 kg ha^{-1}. Covenham reservoir, with a mean of 190 protein N mg m^{-2}, has a predicted fish biomass of around 30 kg ha^{-1}. A 1995 acoustic survey of the Covenham fish fauna has been undertaken but not yet reported.

It is probable that the zooplankton of Covenham Reservoir therefore, are lighly predated, that those of Rutland are moderately predated (and those of Pitsford are predicted to be more heavily predated from rotifer biomass comparisons alone).

Figure 4.18 Fish biomass - large cladoceran relationships in reservoirs (from Kubecka and Duncan (1994) with Rutland Water and Covenham reservoir added)



4.9 Assessment of the possible effects of food-web management at Covenham Reservoir and Rutland Water

4.9.1 Covenham Reservoir

Two large species of *Daphnia* are present and dominant for most of the time. The dynamics of the three species must be more fully understood if conditions are to be controlled for the successful maintenance of annual *D. magna* populations, because the maintenance of high standing crops throughout each growing season is essential for effective control of algal biomass, rather than the spasmodic cycling of daphnids out of sequence with phytoplankton often typical of highly eutrophic shallow lakes. It is probable, from the limited data available, that the higher grazing rate of larger *Daphnia* is reducing algal abundance.

The possibilities to biomanipulate Covenham are real as it is not managed as a viable fishery (although it is used as a supply of fish for restocking programmes). The options include:

a. large scale removal of cpyrinids on a continuous basis regardless of the need for restocking elsewhere as a deliberate policy for biomass reduction,

b. artificial draw-down in the spring to destroy spawning in the littoral zone,

c. use of artificial substrates (removing roach eggs, leaving in perch),

d. stocking of perch to try to create an even-aged population structure which will contain piscivorous older individuals.

A complementary option which should be explored is the extent to which pumping of inlet water is currently continuous. If, as at Rutland, it is intermittent, then the extent to which reduced-scale continuous pumping would provide an allochthonous carbon seston source for zooplankton to sustain populations over periods of low autochthonous food supply could be investigated.

The application of any one of these options has little implication for the management of the reservoir as a water supply source, except that b) can only be applied if there is an adequate water supply and this has economic implications. The others all require that reliance on the reservoir as a fish stock source by Anglian Water be reduced, and that time and manpower need be expended by the NRA and/or Anglian Water in fish population management.

4.9.2 Rutland Water

Rutland Water is dominated by small *Daphnia*, which are middle-sized cladoceran filter feeders. This is typical of many eutrophic reservoirs studied in the UK over the past few decades (Grafham, Farmoor, Bough Beech). Larger species were initially present after filling but their absence now indicates abundant planktivory. The possibilities for whole-reservoir biomanipulation are limited by scale and existing management. This means that they may be realistically confined to small areas of the reservoir as experimental analyses. The reservoir is a trout fishery with an international reputation. The following management options could be evaluated:

a. the introduction of large piscivores (pike). If a pike population was artificially maintained it might provide an additional (regulated) sport fishery without excessive impact on the trout fishery,

b. The large-scale removal of cyprinids. The existing licence could in theory be extended so that continuous effort was expended to deplete the coarse fish population, with acceptance of the need for destruction of fish which could not be immediately utilised. Swedish experience shows however that realistic removal of cyprinids might be necessary using intensive trawling carried out by experienced fishermen. Additional methods might be netting out fry from the littoral zone during April/May/June (during the night is most effective elsewhere) or by seine netting the deep water during winter. The extensive use of artificial substrates may reduce the recruitment of roach populations. Physical destruction of littoral zone submerged plants beds might be necessary during April each year.

Draw-down is not a viable option due to economic costs of pumping and the limited capacity of the downstream river Gwash (itself a resource of high value for trout fishing and conservation).

The current mixing of the reservoir may not be sufficient to reduce cyanobacteria growth even with the reduction of phosphorus. Increasing the power of the mixing equipment may be a viable option.

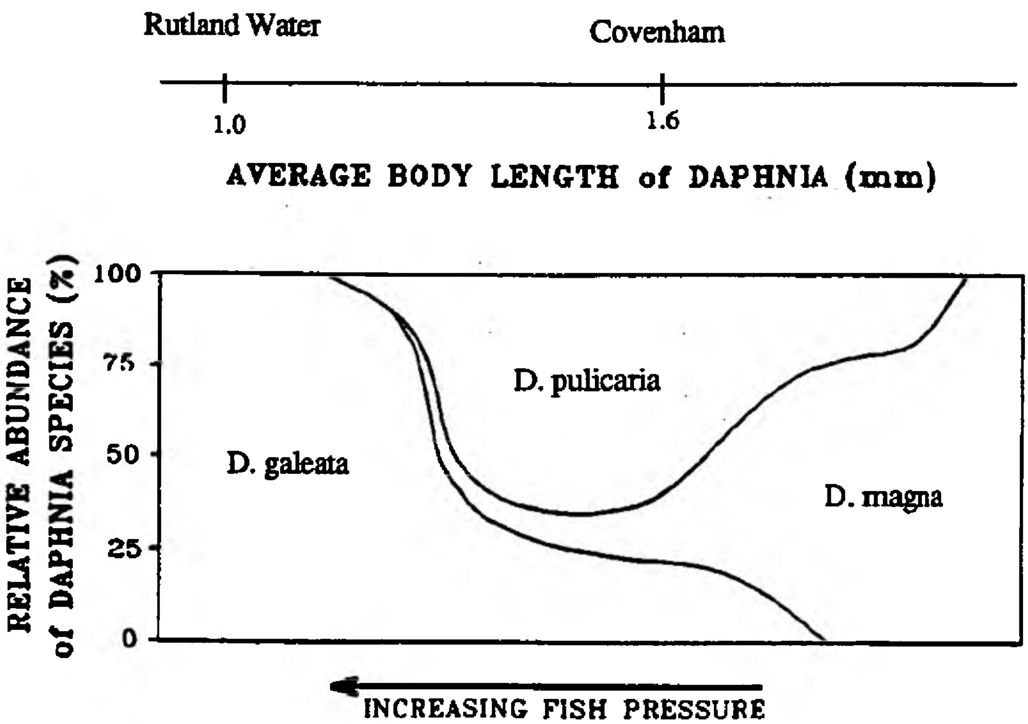
Thus far, the *Daphnia* community grazing alone is not managing to prevent cyanobacterial blooms. A return to larger species of *Daphnia* will provide a more effective control in conjunction with mixing and continued phopsphorus removal at sources.

4.9.3 Conclusion

The proportion of large cladocerans to the total zooplankton biomass is significantly greater in Covenham than in Rutland. This is consistent with the occurrence of a larger average body length in Covenham than Rutland and with the presence of three species of *Daphnia*. These population structure indices indicate the difference between the intensity of fish predation. Covenham is similar to the London reservoirs in this respect (Figure 4.19).

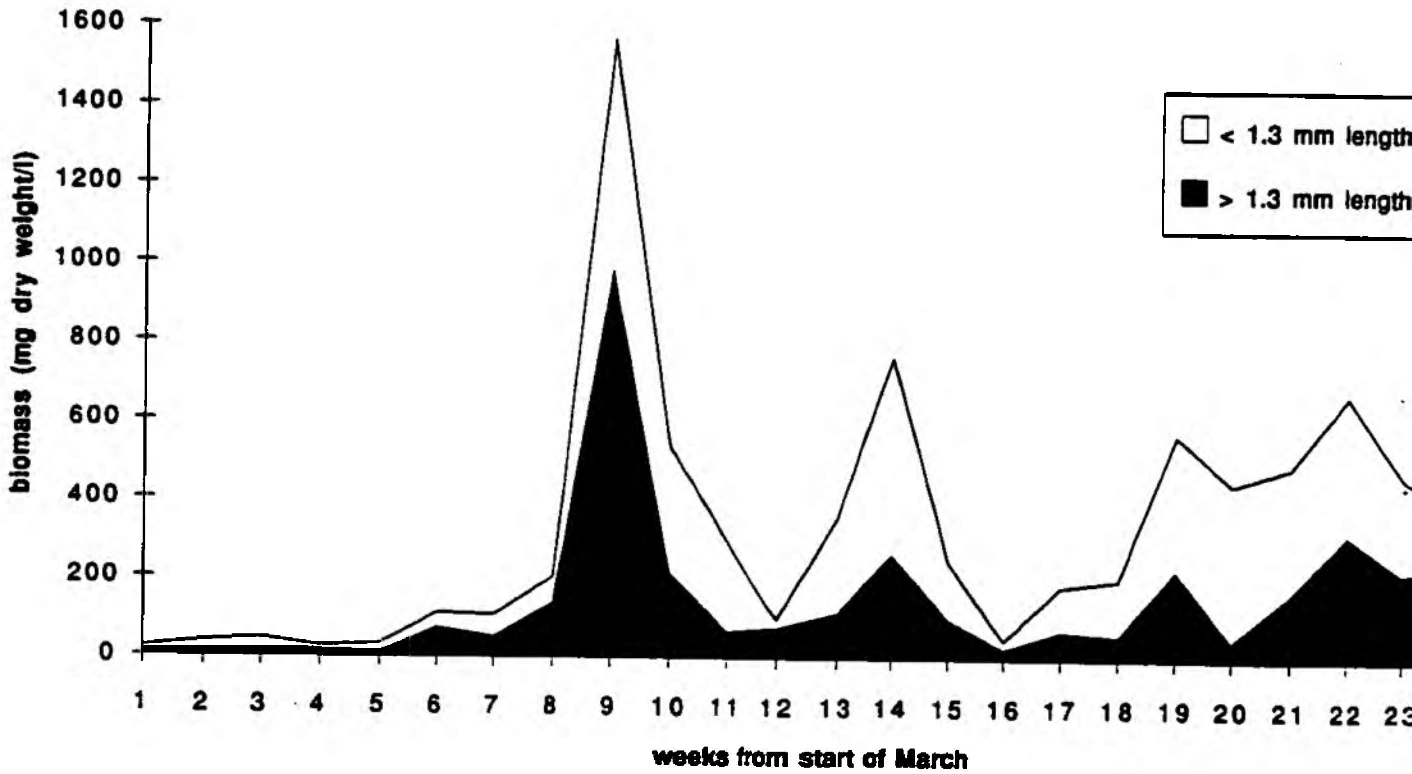
The timing of the start of cladoceran population development is largely under the influence of spring temperature. Calculation of cumulative degree days indicated a relationship between *Daphnia* biomass and cumulative temperature. The fecundity of *Daphnia* during early spring is then related to phytoplankton biomass. High population growth rates are realised in the absence of fish predation. Between May and June the total biomass of *Daphnia* shows wide variations, which probably correspond to the emergence of the young of the year fish and their impact upon the zooplankton. The analysed data thus show the stongest grazing control of phytoplankton in late spring through into summer, supporting the possibility that biomanipulation could further improve control of late summer cyanobacteria.

Figure 4.19 Seda's model of Daphnia size and species composition in relation to fish predation pressure (modified from Seda and Duncan, 1995)

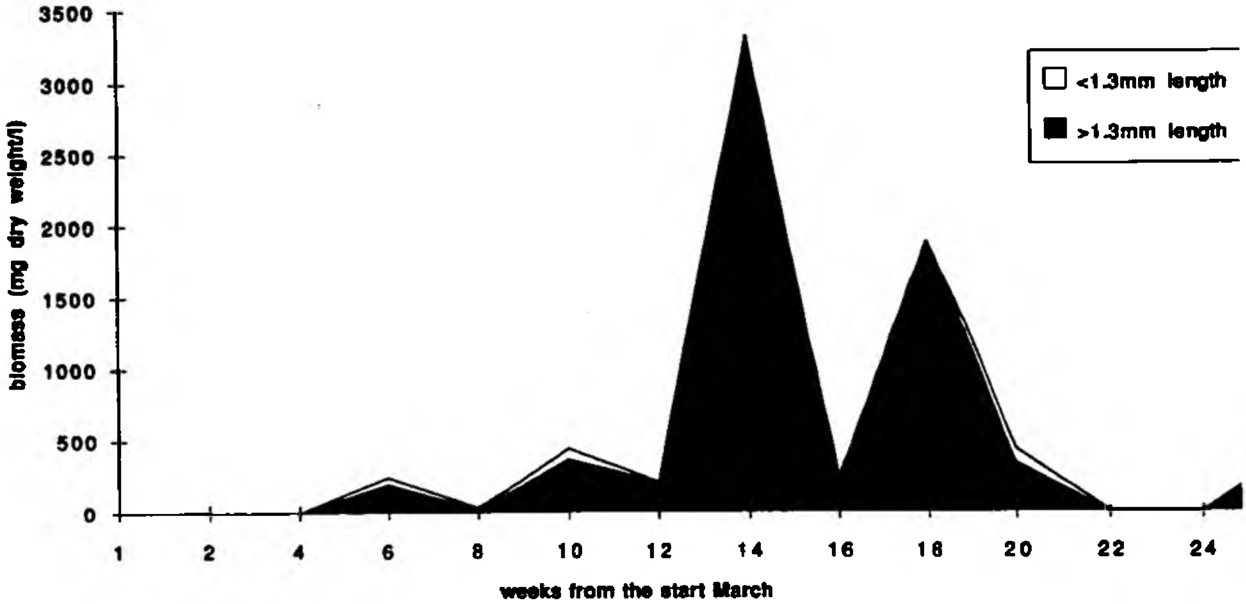


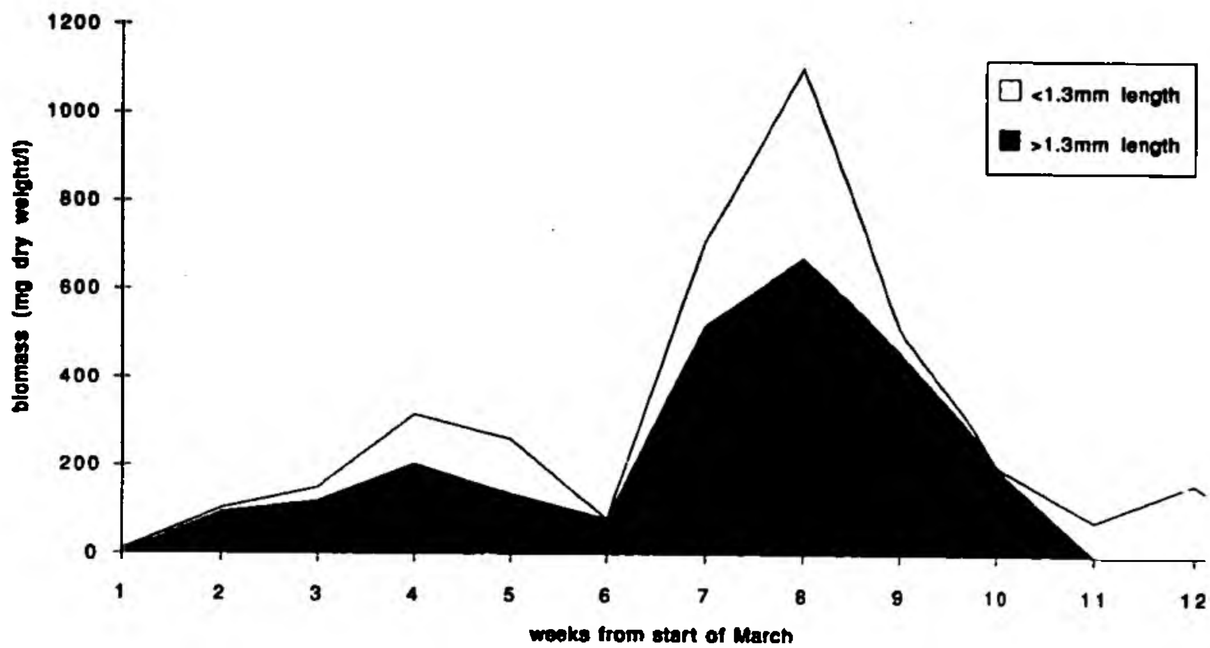
Figures 4.20-22 illustrate the differences in size structure through the year for Rutland and the two contrasting years in Covenham. There is evidence from the comparative analyses of Randall (1995) that the mean size of the population of *D. galeata* in Rutland Water has declined slightly from 1985 to present, suggesting a slight increase in planktivore predation pressure. Nevertheless, there is still a substantial proportion of large-bodied Daphnia in Rutland, confirming moderate rather than severe predation pressure.

Figure 4.20 Size structure of *Daphnia* at Rutland Water, 1991



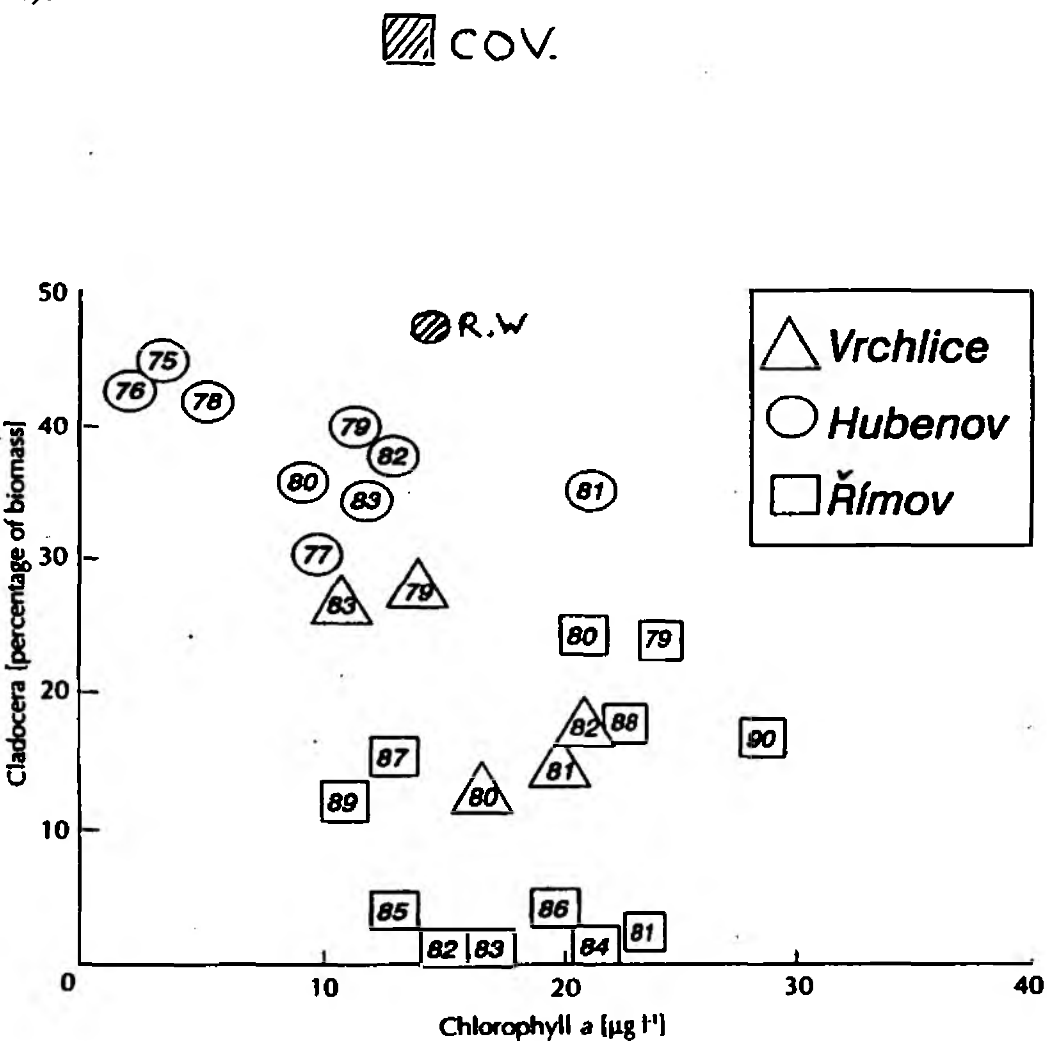
Figures 4.21 and 4.22 Size structure of *Daphnia* at Covenham reservoir, 1991/2





The proportions of large-bodied *Daphnia* in each reservoir may be compared with other valley reservoirs for which data are available. Figure 4.23 shows these comparisons for Covenham Reservoir and Rutland Water, and three Czech reservoirs taken from from Hrbacek *et al.*, (1994).

Figure 4.23 The relationship between the mean percentage of large-bodied cladocerans and mean chlorophyll a concentrations in Czech and Anglian reservoirs. From Hrbacek (1994).



5 PROSPECTS FOR THE DEVELOPMENT OF BIOMANIPULATION IN COVENHAM RESERVOIR, RUTLAND WATER AND PITSFORD RESERVOIR

5.1 <u>The information base</u>

5.1.1 Further information needed by the National Rivers Authority

The NRA at present only has information in enough detail for this initial consideration of biomanipulation at two reservoirs. This is because the traditional view of monitoring from the 'bottom-up' – physical/chemical parameters, to nutrients and to phytoplankton – has historically been the important means of providing information for water quality management. In the past fifteen years this attitude to monitoring has been widened for the important reservoirs in the region, most notably Rutland Water, Grafham Reservoir and now Covenham Reservoir, with the analysis of zooplankton populations. Scientific publications on the zooplankton of Rutland Water and Grafham Water have, for example, shown their basic similarity. Outside the northern and central areas, the reservoirs of Essex - such as Ardleigh and Alton may also have a reasonable data base as a consequence of studies by the NRA, water undertakings and Essex University.

The possibilities of biomanipulation extend this view further. In order to understand biomanipulation, it is essential that certain basic information about zooplankton and fish populations be continuously analysed alongside the other water quality parameters. Such information needs to continue up to the implementation of propsed biomanaipulation (see below) – as the variability of Covenham Reservoir's *Daphnia* species composition demonstrates the difficulty of interpreting one or two years' events.

The nature of additional information required in the three reservoirs is as follows:

- The zooplankton community of Pitsford reservoir. At present nothing is known, beyond a limited run of rotifer data, but the zooplankton community appears to be more heavily predated than the other two main reservoirs and this provides a valuable comparison.

- The size structure of the zooplankton, at its simplest the proportion of the community made up by *Daphnia* >1.3mm, which is an important indicator of the degree of predation pressure it experiences (Hrbacek *et al.*, 1986).

- The size and species structure of phytoplankton to establish the proportions of 'grazable' algae.

- Some quantitative estimates of the fish community and population structure, together with annual recruitment success, are needed in each reservoir. Accurate estimates of the population can be produced using recently developed echo-sounding techniques (Kubecka and Duncan 1994) as well as by conventional netting techniques.

- A study of fish preference in selecting spawning substrates in the reservoirs is necessary since the availability of spawning sites is a determining factor for the natural regulation of the fish community in the London reservoirs (Kubecka and Duncan 1994).

- The inter-annual variation in spawning successes should be monitored, if necessary by artificial sites and related to environmental factors such as temperature and littoral zone status (substrate, drawdown, macrophyte development). Even if these monitoring details cannot be achieved because of manpower and economic restrictions, all anectodal observations could be recorded. For example, the progress of spawning and fry development could be formally recorded on every limnological/water quality sample occasion, details of the removal of coarse fish for any reason could be recorded and basic semi-quantitative parameters of the littoral zone and its vegetation also monitored.

- The diet selectivity of coarse fish fry would be useful information, as this could then be analysed to show the extent of selective feeding on zooplankton.

An additional perspective on the possibilities for reservoir biomanipulation would be provided by a comparative analysis of the full suite of reservoirs within the Anglian Region using data from NRA areas, Anglian water and Essex Water Company. These provide a contrast in characteristics, with a range of phosphorus levels; and contrasting fisheries management. For example, Grafham (Cambridgeshire), Ravensthorpe (Northamptonshire) and Ardleigh (Essex) as well as Rutland and Pitsford are trout fisheries, while Hollowell (Northamptonshire) and Alton (Suffolk) are coarse fisheries. A number of other smaller reservoirs and artificial lakes (e.g. large gravel pits) operated by British Waterways or County Councils where fisheries policy was recorded, could be included in the comparison by a one-off analysis of zooplankton size structure, making a database large enough for multivariate analyses to find out whether any relationship existed between fish species composition, fisheries type and zooplankton structure. Such a database, once started, could be extended by inclusion of published and unpublished data where they exist for other lowland reservoirs such as Bough Beech (Southern Region).

5.1.2 Current studies at Leicester

Two projects relating to the impact of predation on zooplankton are currently underway; one laboratory and one field.

Simulation of predation pressure upon the two large *Daphnia* species

A laboratory study was undertaken to test the hypothesis that predation pressure can shift the balance between different sized *Daphnia* species through differential reproduction, under conditions of equal food availability. This is important to reduce the effects of internal competition and allow the effects of predation alone to be apparent (Greulich 1995).

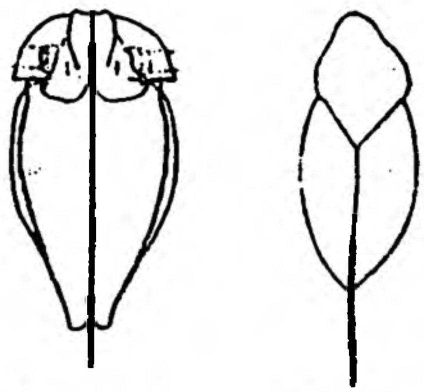
Observations of Covenham and the London reservoirs indicate that *D. magna* and *D. galeata* tend to exclude each other. In years during which *D. galeata* is abundant *D. magna* is virtually absent, and *vice versa*. One of the two species always seems to prevail over the other. *D. pulex* is placed at an intermediate position among the two species, but it is usually associated with *D. magna*.

A study of the competition between *D. magna* and *D.pulex* cannot be carried out unless the effect of predation, the main determinant factor explaining the occurrence of different species of zooplankton in eutrophic reservoirs, is accounted for. An innovative experimental set–up was designed to reproduce the effects of predation in the laboratory by the gentle filtering of zooplankton cultures through sieves of different mesh sizes representing different intensities of predation. The effect of the treatement on the structure of the population was observed and compared with untreated "test" populations. The three species of *Daphnia* commonly found in the Region's reservoirs; *D. magna, D. pulex, D. galeata* were initially cultured. Ten individuals of each species were reared under non-limiting food conditions *(Chlorella vulgaris* culture changed every day or dried algal fish food). Food concentration in the jars was monitored and adjusted according to the population size.

Repeated trials showed a significantly different response of *D.magna* and *D.pulex* to the simulated predation resulting in marked changes in their population structure consistent with what is known about the different development strategies adopted by the two species. These have been described by Romanovsky (1984) who classified cladoceran survival strategies into 'violent', 'explerent' and 'patient' modes. *D. magna*, belonging to the 'violent' competitors, is described as being characterised by high fertility and rapid growth rates which enable this species to rapidly exploit resources present in the environment and achieve large biomass sooner than other daphnids. *D. pulex* applies a more 'patient' strategy characterised by a slower growth rate and the achievement of reprouctive maturity at a lower size.

The experiments proved that, beyond a certain predation intensity, *D. magna* was not able to compensate for losses due to predation through its faster growth potential as individuals were large enough to be selectively removed by the filters before achieving fertility. Conversely *D. pulex* was able to reproduce under high predation pressure because it could achieve a sustainable population of small individuals. This effect is due primarily to the average size of the two species, *D. magna* being on average significantly longer, larger and thicker. Thickness appeared to be a very important factor. Under the experimental conditions the slender and streamlined shape of *D. pulex* was much more successful in avoiding the meshes of the sieve. *D. magna* was significantly thicker in particular at the level of the head capsule (Flossner 1984, Figure 5.1).

Figure 5.1 Body shape of D. magna and D. pulex to illustrate feeding efficiencies. From Flossner (1984)



D.magna *D.pulex*

The results of these experiments carried out on single–species cultures, treated by artificial size–selective predation, cannot be directly translated to complex situations found in the field. However they provide strong support for the hypothesis that size–selective predation is a major element in structuring zooplankton communities by establishing the dominance ranking of species. A similar conclusion was reached by Seda and Duncan (1994) in their analysis of field data on zooplankton structure in reservoirs characterised by different fish predation pressures.

Analysis of zooplankton

An interim report (Sanderson 1994) of the analysis of rotifer and crustacean zooplankton from Rutland Water, Covenham Reservoir (and a small number of samples from Pitsford) which is being carried out in the Ecology Unit has formed the basis of the evaluation presented here. A final report dealing with all the data except Covenham Reservoir for 1994-5 will be submitted by the end of 1995, and the supplementary report of the most recent Covenham samples submitted in January 1996. Early indications of the data (for example, the dominance of large-bodied *Daphnia* in Covenham in 1994 and 1995) suggest that these reports will extend the information presented here and strengthen the conclusions rather than cause any changes to the conclusions and recommendations.

5.1.3 Further analysis of existing data

This present report was commissioned as a feasibility study of the possibility for developing biomanipulation in Northern Area's reservoirs. It has reviewed the case studies which indicate the successes of biomanipulation and examined the body of limnological data which is held on them for clues about biomanipulation. It has not been possible to complete a detailed statistical analysis of the full run of data. Such analyses will be caried out once the full data are available for both Rutland and Covenham for the past five years (see above) which will, for example, show whether periods of large *Daphnia* dominance are significantly associated with particular algal taxa or with lower algal biomass. Such analyses form part of the PhD thesis of R. Sanderson which will be completed in March 1996.

5.2. Practical aspects of biomanipulation in Anglian Region reservoirs

5.2.1 Introduction

The previous section referred to information required for effective decisions about biomanipulation to be taken. This pre-supposes that time exists for the information-gathering stage. There can be no doubt that the implementation of biomanipulation will be a difficult task, which will inevitably proceed in small stages until all parties to the process have been able to see the benefits.

The NRA will not be able to implement biomanipulation in reservoirs on its own, and negotiation of partnership will be time-consuming. The first step, which can be taken alone initially, should be to implement a data-gathering programme effective for biomanipulation rather than effective just for water quality management as we currently understand it. It is unlikely that an investigation of the possibilities for biomanipulation can take place at more than two or three reservoirs, because of the cost, and effort should therefore be directed at those for which the maximum body of information already exists -- Rutland and Covenham, with the addition of Pitsford if resources permit because of those features which indicate it to be a more extreme example of a lake under planktivore control than the others. The first management step therefore, should be the development of a programme of research whose goals are to quantify fish population sizes, impact on zooplankton, and zooplankton grazing on phytoplankton.

The next stage is to drawn up a 'biomanipulation action plan', examining the feasibility in detail for each possible fish biomass control technique. It is clear that, for both biological and political reasons, biomanipulation will be most effective where some evidence for its natural occurrence already exists (Covenham) and there is limited commercial or recreational interest in the fish stock (also Covenham). Consequently Covenham should be considered as suitable for a whole-lake experiment in biomanipulation and plans developed for the implementation and the monitoring of such an experiment, in conjunction with Anglian Water Services who own the reservoir and whose positive co-operation is essential.

Rutland Water should not be excluded from consideration for full biomanipulation, but further studies of the fish stock and its feeding behaviour indicated above should enable a realistic assessment to be made of whether, for the first time ever, a lake biomanipulation in the presence of a dominant trout population is possible. Arguments in support of the possibility centre on the degree of piscivory of trout; arguments against centre on the degree of planktivory of trout and the need for continuous suppression of piscivorous pike and perch in order to maintain healthy trout populations. These considerations suggest that steps should be taken to justify and then plan an experimental biomanipulation of an enclosed arm, within which cyprinid populations are intensively managed but trout fishing remains unaltered, and the consequences carefully monitored.

5.2.2 Biomanipulation action plan

Detailed plans for experimental biomanipulation over a six year period, with advance provision made for the costs and time of all fish management and scientific monitoring effort, are recommended. Joint sources of funding should be explored; both the NRA and Anglian Water could approach NERC with a proposal which fell within the framework of the proposed new Special Topic on shallow lake management for example if the plans fit the Topic timescale.

The basic requirements of such a plan are as follows:

- Choose sites and scales
- Set goals and timescales
- Establish project management structure
- Determine technical methods
- Decide upon additional eutrophication management requirements
- Determine research and monitoring requirements
- Establish project costs and determine funding sources
- Develop positive public relations
- Start biomanipulation

It is possible to consider both Rutland and Covenham as candidates for biomanipulation, using different approaches in each one. The characteristics of the two suggest that Covenham should be a 'whole lake' biomanipulation experiment with maximum fish stock removal attempted, whereas Rutland should be a 'lake section' experiment with fish stock manipulation. These two approaches are explained below

1. Sites and scales. Covenham should be the site for a whole-lake experiment because it displays the most advanced indications of 'natural' biomanipulation. These are the presence of large bodied *Daphnia* in some years as well as their absence in some years which indicate possible variations in fish recruitment. It also has the potential for effective fish management because it is not currently a fishery of any kind, and also because the economic value of the coarse fish used for stocking by Anglian Water is low and in any case might not necessarily be lost if more intensive fish removal effort is required. The only drawback of this reservoir is that it is less typical of the Anglian Region's reservoirs because it is an artificial bowl reservoir.

Rutland cannot be treated thus because of its dominant trout fishery and the near impossibility of total removal of fish stock due to spawning opportunities in its littoral zone. There is no knowledge however, about the extent to which biomanipulation of the cyprinid fish community can co-exist with a partly-piscivorous trout population, but such coexistence is possible. Rutland therefore, should be considered for an experiment in one of the creeks, Barnsdale is the most suitable, which would be separated from the rest of the reservoir by a substantial, weather-proof, mesh curtain (but passable by fishing boats at a single location). This would enable it to be managed in the same way as the main reservoir with the exception of the biomanipulation techniques. An alternative to a Rutland enclosure might be one in another reservoir, such as Eye Brook (upper quarter) or Pitsford (an advantage here might be that more than one of the upper arms could be used and thus replicate the experiment), but the drawback of both these two, or any other small valley reservoir is a paucity of limnological back data.

2. Goals and timescales. The goals should be both scientific and managerial. That is to say, the scientific goals should be statistically significant changes to the zooplankton community and to phytoplankton biomass or species composition. The managerial goals should be cost effectiveness and so relate the scientifically-measured improvements to the costs, both economic and political (in recreational and public relations terms) in a cost-benefit analysis. The timescale should be six years, because the experiment needs to be in two halves and for each half short term changes (1-2 years) could be either positive or negative and not be sustained over a longer-term. The two halves, in each reservoir are (i) maximum possible removal of coarse fish stock followed by (ii) re-structuring of coarse fish stock with addition of predators pike, eel and large perch, the exact species composition to be determined by the end of the first three years.

3. Project management structure. An advisory committee should be established which consists of the widest representation: at Lake Finjasjön for example the municipality

established an international advisory board. This project should at least be national, and include that expertise within the NRA which is of international quality (e.g. Phillips, Hickley), with if possible such limnologists as Moss and Duncan, and equivalent fish scientists such as Giles. The management level of both the NRA and Anglian Water should also be represented, so that the project does not become marginalised a mere scientific experiment. The advisory committee should direct a project management team which is responsible for the day-to-day implementation and smooth running of the project. It is essential that the management team and those people answerable to it are in frequent and direct contact, so that fish removal, and all aspects of scientific monitoring are continuously communicating.

4. Technical methods for fish management. The Covenham experiment should seek to use all acceptable methods for total removal of fish and maintain cyprinid stock at the lowest achievable level for the duration of the first phase of the experiment. The most effective are likely to be trawling, seine- and fyke-netting with trapping for any eels. All fish caught at each removal operation should be identified, weighed and measured. If technically possible, spring draw-down should be evaluated as a means of removing any spawning opportunity, and the efficiency of intake screens should be investigated and if necessary, they should be improved to prevent the ingress of young-of-the-year fish hatched outside the waterbody. Evaluation and debate of all possible options for predator enhancement should precede the second phase where the chosen species composition is added, and this should include the possibilities of using a non-reproducing population (genetically modified or single sex) pikeperch, since Covenham Reservoir has no outlet to river systems.

The Rutland experiment should remove cyprinids by small-scale netting and trawling. All fish caught at each removal operation should be identified, weighed and measured. Trout fishing should be maintained, with stocking exactly the same as in the main reservoir, and monitoring of stomach contents from a proportion of angler-caught fish carried out. Angler catch returns should be compared with other reservoir sections to detect any changes in catch per unit effort or caught fish characteristics. Cyprinid fry deposition should be monitored and controlled by the use of artificial substrates each year following littoral zone plant removal (conventional weed-cutting or harrowing) in late March-early April. Re-stocking with, at minimum, an even age population of perch and eel should follow in the second phase. The possibilities of restocking with pike should be evaluated and debated if it proves impossible to effectively lower cyprinid biomass through repeated removal operations.

5. Additional eutrophication management. Covenham should be maintained as a fully-mixed reservoir, as its technical capacity appears able to achive this. The Rutland enclosure should itself be mixed by a simple compressor/hosepipe system (as Brierley 1985) capable of fully mixing the volume of water enclosed (Reynolds *et al.*, 1984). This would provide the opportunity of experimentally maintaining the near-mixed state of Rutland or of providing total mixing.

6. Research and monitoring. All the normal water quality parameters of each reservoir need to be monitored continuously (at least weekly duration) and replicated in the enclosure.

The zooplankton species composition and size structure needs to be analysed in each location, together with details of the structure of the littoral zone, particularly macrophyte species composition, biomass and growth forms. Additional effects such as possible waterfowl grazing on macrophytes, possible sediment chemistry changes should be covered.

7. Costs and sources of funding. The costs of the fish removal and the costs of redeployment/additional appointment of staff need to be carefully calculated so that once in operation, the project is not trimmed, since a reduced effort is likely to create failure through either inadequate fish removal or inadequate recording and analysis of the consequent changes. The benefits which could be anticipated from a successful biomanipulation should encourage the NRA and Anglian Water and ensure that the two organisations are willing to provide initial support, such that the project management team, once established can, particularly with the help of the project advisory group, seek wider financial assistance from NERC/EC sources.

8. Public relations. Biomanipulation is likely to generate considerable public interest because of the central role of fish and coarse fish removal in its operation. Attitudes to ish removal could therefore be negative if not carefully managed. It is therefore essential that positive public relations be established early in the programme, using the positive image that can be generated for removal of the scourge of toxic cyanobacteria using "eco-technical" means.

6. CONCLUSIONS

Biomanipulation could be established on an experimental basis in the reservoirs of Anglian Region. It is a new tool for waters other than shallow lakes, and for the United Kingdom it has the potential drawback that it requires deliberate management of the fish community for purposes other than angling improvement. Initially therefore, it is likely to be viewed with suspicion by the angling community, which is a fairly conservative community.

The greatest changes have to be made to coarse fish populations, therefore the logical places to start are those where coarse fish anglers do not have an influence. Covenham reservoir, which is not fished for safety reasons is one and a section of Rutland Water, a trout fishery, is another.

The greatest problem with all biomanipulation experiments has been the creation of a new self-perpetuating sustainable state of quasi-oligotrophy, maintained without continuous fish removal effort. There is no clear gurantee from the literature or the available information that such a 'nirvana' can be achieved, but there are strong lines of evidence available from the data and the literature to indicate the possibility of success, such that large-scale experiments can now be justified.

This document is a feasibility study. The conclusion demonstrated here is that such management options are feasible, and that the NRA procede from a feasibility study to a detailed project planning stage herewith. The outline of the plans have been presented above.

7 ASPECTS OF FISH BIOLOGY RELEVANT TO BIOMANIPULATION

Outside the angling community and professional fisheries staff, there is often limited knowledge about the biology of freshwater fish. This stems from limited field-based science and a lack of available publications. Two excellent books which have recently appeared are Maitland and Campbell (1994) and Giles (1994). The following information is taken from these two, together with the literature on the case studies cited in chapter 1.

7.1 Bream *(Abramis brama* Linnaeus 1758)

These fish are characteristic inhabitants of lentic waters devoid of vegetation. They are highly adapted to turbid lakes, reservoirs, large slow-flowing rivers and canals. In their sixth year bream are able to reproduce; egg deposition takes place on the littoral vegetation from the end of May to July as the temperature exceeds 15° C (Maitland and Campbell, 1992). Depending on the temperature bream can deposit their eggs two or three times during the spawning period for a total of 250,000 eggs per kilo body weight.

Bream feed mostly on zooplankton, insect larvae, worms and soft-shelled molluscs but do not take invertebrate predators such as *Neomysis integer*. After the second year they switch from eating only zooplankton to benthic invertebrates. They adapt to low oxygen conditions and are said often to dig 10 cm deep in the mud searching for chironomid larvae (Hosper *et al.*, 1992). The growth potential of bream can be directly related to the abundance of chironomid larvae in the sediments: less than 5 grammes wet weight per square metre is poor, more than 20 grammes is very good (Giles 1994). Their pattern of feeding at the bottom of lakes causes high sediment resuspension with a consequent significant loss of transparency and increase in the rate of internal phosphorus loading. Like other bottom feeding cyprinids their mouths can be extended to suck in mud; food items are separated from sediment particles in the buccal cavity. Sediments pass the pharyngeal sieve while food organisms are retained (Breukelaar *et al.*, 1994). An efficient filtration mechanism allows bream to feed on zooplankton as well as on larger invertebrates. Large bream can consume large amounts of zooplankton in conditions of high zooplankton density. Bream are the most efficient filter–feeders of european continental waters but their feeding mechanism is inhibted in presence of coarse substrates which do not pass the filtering apparatus. In the pelagic region of lakes where zooplankters are small as a consequence of size–selective predation in the absence of any refuge (macrophytes) and substrate particles are very fine, bream is more successful than other filter–feeders such as white bream *(Blicca björkna)* and roach. Conversely they may be out-competed in the littoral zone of lakes.

Gut content analyses have revealed zooplankton (*Daphnia)* sizes taken by fish from 1 to 1.5 mm. The preferred prey size changes with the size of the fish but not continuously as fish change their feeding strategy during their growth. Specimens smaller than 20 cm employ particulate feeding when feeding on *Daphnia hyalina* as do those smaller than 10 cm when feeding on *Bosmina coregoni* (Lammens 1986). Young bream experience a gradual switch from particulate to filter feeding with a consequent progressive decrease in the size of the average food organism. Beyond 20 cm bream are exclusively filter–feeding. The length of food organisms becomes larger again as the filter apparatus becomes coarser proportionally to the size of the fish. At a size between 20 and 25 cm, bream are particularly efficient in feeding on small zooplankters (<1 mm). A bream population characterised by a high proportion of individuals of this size would induce a dramatic shift in zooplankton population structure as most daphnids become fertile only when larger than 1 mm.

Bream are very abundant in shallow turbid lakes where they often form more than 80% of the fish stock. Fish densities can reach as much as 1000 kg ha^{-1} (Hosper *et al.*, 1992). In 1985 in Honderd en Dertig (the second reservoir of the Biesbosch chain) bream reached 75% of the biomass of coarse fish (Visser, 1993). Populations are often dominated by year classes corresponding to years warmer than average. Observation at the Great Linford Wildfowl Reserve showed that the adult bream stock was dominated by 1973 and 1976 fish (Giles 1994).

In clear water bream are preyed upon by perch and pike, in turbid water by pikeperch. However clear water is critical for its control by predatory fish. Bream are said to be favoured by biomanipulation due to the removal of food competition by roach and carp which are easier prey of pike and pikeperch. There is indication that the introduction of pikeperch may actually cause an increase of bream that can be resolved only by active fishing (Eddy Lammens, pers. comm.). Techniques for the capture of bream include fyke nets, traps (large fish) and seine nets during the spawning period. Only intensive fish removal can reduce the population of bream which is relatively sheltered from predation as most predatory fish require relatively high transparency. Benthic foraging habits confer additional protection as few predators will venture in deep waters to attack it. In such conditions bream can live for more than 20 years and achieve a weight of more than 3 kg.

By generating turbidity, increasing internal nutrient loading, depressing transparency and macrophyte biomass, the presence of bream has a far reaching impact on the structure of the lake food chain and the creation of a stable eutrophic system. In such cases only biomanipulation by reduction of the fish biomass can change environmental conditions towards a sustainable improvement. When the bulk of the bream (about 3 tonnes, plus 2.5 tonnes of roach) was removed from the lakes of the Great Linford Wildfowl Reserve (Bedfordshire), the water cleared, algal blooms diminished and submerged weedbeds sprouted across a 30–acre lake which had been devoid of macrophytes while the fish were present. The invertebrate supply of ducks increased substantially and the survival rate of tufted ducklings improved (Giles 1994).

7.2 Perch (*Perca fluviatilis* Linnaeus 1758)

Perch are found in lakes and slow flowing rivers throughout most of Europe. They are widespread throughout the British Isles.

The size of perch varies greatly. Some individuals may never exceed 15 cm. Such stunted size is usually the product of a strong year class depleting the common food base rather than an adaptation to high predation levels. Strong year classes may dominate the whole population for a number of years, suppressing the development of subsequent year classes by decreasing food supply and eventually cannibalism as the dominant class becomes large enough.

Spawning occurs late in the spring (mid March-June) when water temperatures are between 10 - 15°C. Eggs are laid in ribbons up to one metre long draped over submerged objects in shallow water, although waterlogged tree trunks and branches along with weeds are the favoured spawning substrate. They use submerged terrestrial vegetation in the shallow littoral area but also deposit eggs even down to a depth of 20 m provided adequate oxygenation persists during the spawning period and the temperature remains between 8 and 12° C. Over a 4-year investigation period in Rímov reservoir the appearance of the first ribbons coincided with the onset of thermal stratification (Kubecka, 1992).

Perch are considered to be non-selective spawners as they have the ability to lay eggs on bare sand or concrete bottoms in reservoirs. However, when present, any available natural stone/gravel substrate is highly preferred and the presence of different substrates greatly influences the intensity of egg deposition (Kubecka, 1992). Females lay up to 45,000 eggs per kg body weight. The eggs, which are between 1.5 - 2.5 mm in diameter, hatch after 120 - 160 degree days (usually equivalent to 8 - 16 days).

The fry are approximately 6.4 mm long after hatching and immediately swim to the surface to inflate their swim bladders. They remain planktonic for a short time where they suffer massive mortality due to predation. Once the fins have fully developed they move inshore in shoals and adopt a more benthic habit. In so doing perch switch to a more nutritious food source; this stage is critical for their development to the piscivorous stage which is achieved as the fish reach >15 cm. If conditions prevent perch from feeding on invertebrates fish will remain stunted as they are outcompeted by cyprinids who can consume small zooplankton more efficiently by filter-feeding. Perch feed during the daytime in shoals. Feeding activity is controlled primarily by water temperature.

As autumn approaches, they move into deeper water (10 - 15m depth). Growth and survival is dependant on temperature. A warm summer will often produce a very strong year class. Individuals mature after 2 - 4 years. Growth is not halted in older animals and an increase in food availability can produce a spurt of growth in even old individuals. Several studies indicate the existence of in-shore and off-shore sub-populations. In Klícava reservoir (Czech Republic) 3 separate groups were identified (Kubecka and Svátora, 1993). Older perch were found to spend more time in the pelagic region while young of the year were in the littoral zone. Perch are easily captured by fyke nets (Kubecka, 1992).

Due to their specific ability to adapt to a large variety of food items perch play a key role in the stabilisation of biomanipulated lakes (Mehner *et al.*, 1994). Perch hunt by sight and are known to pursue their prey tenaciously. Due to the lack of pikeperch in British waters, larger perch represent the only predatory fish active in the pelagic region of larger water bodies. Pike instead remain concealed at the edge of the littoral zone. Perch often move in loose shoals within which each fish searches independently for food. As one strikes many others quickly join in the attack. A single prey may be struck by several before being eaten by one. A single roach may be able to avoid one perch, but when several attack the effort to escape from one quickly puts the roach into the attack zone of another. The success of predation of perch on cyprinids is density dependent. Experiments proved that when hunting other fish, perch predator attack success diminished with increasing prey density as the schooling of prey caused target switching which confuses the predator. Therefore after reaching a certain prey concentration perch predatory success rates decreased with increasing prey density.

Practitioners of biomanipulation are divided about the utility of supporting perch populations. Hosper *et al.*, (1992) recommend the introduction of large perch >15 cm particularly because of their capacity to control invertebrate predators such as *Neomysis integer*. At the same time it is known that adult perch have a high preference for large daphnids. In Rímov reservoir *Daphnia galeata* constituted a considerable part of the diet of perch fry, but the impact of the fry on the *Daphnia* population was less than the impact of adult perch (Kubecka, 1991). Despite this, the presence of large daphnids in the London reservoir and in Covenham confirms that their presence is not incompatible with perch-dominated fish assemblages. An explanation of this can be the lower fish biomass reached in perch dominated waterbodies and the selection against zooplanktivorous habits among individual perch because higher condition may be achieved through feeding on invertebrates and fish.

In a review of the fish stock composition of central and eastern European reservoirs, Kubecka found that 61% of them had cyprinids as their main fish assemblage. Indeed the change in fish stock composition from salmonids to percids and to cyprinids is seen as a classical succession of the fish community after changes due to impoundment. Such changes are caused by the interplay of 5 factors (Kubecka, 1993b):

- the time-course of reservoir productivity after filling,
- nutrient enrichment processes in the catchment,
- the development of complex feeding interactions within the reservoir,
- the hydrological regime,
- reservoir management.

Along the successional gradient of water bodies progressively coming under domination of cyprinids, reservoirs represent intermediate situations. Frequent changes of water level that limit the development of a large littoral zone and the presence of concrete banks are 'anti-fish' features that can *rejuvenate* the successional stage of the fish stock by preventing the establishment of cyprinids. The presence of artificial mixing that provides good conditions for spawning at greater depth and for the development of a high biomass of benthic invertebrates make reservoirs potentially ideal water bodies for perch-dominated fish assemblages.

7.3 Pikeperch or zander (*Stizostedion lucioperca* Linnaeus 1758)

The pikeperch is established in some southern English waters having been introduced from Central and Eastern Europe where it inhabits slow flowing rivers and productive lowland lakes. It is considered a noxious species and has been reported to have caused damages to riverine fish communities in the south of the country. Pikeperch is considered an exotic fish and as such introduction is not permitted by English Nature.

Spawning takes place in the littoral zone among vegetation or over stones and gravel from April - June when the water temperature is between 12 - 15 °C. Eggs, of between 1 - 1.5 mm diameter, are laid singularly and adhere to underwater structures. The eggs are guarded by the parents and hatch between 5 - 10 days after being laid (160,000 - 200,000 eggs per kg body weight). Adult fish usually reach a length of approximately 40 - 50 cm. Newly hatched fry are typically 5 - 6 mm long and form shoals initially feeding on invertebrates and zooplankton although they soon become more solitary in their habits. Growth is initially rapid with individuals reaching an average length of 15 cm. Animals become mature after 2 - 5 years.

Adult pikeperch are principally piscivorous, feeding in the open water at dawn and dusk. Common prey items include roach, bream, ruffe and most other small fish. They consume perch but will tend to prefer cyprinids when given the option due to their softer rays. They will readily prey on their own young if abundant. Feeding seems not to be affected by turbidity as pikeperch eyes are adapted to cope with poor visibility and the fish is able to detect water movement by its lateral line. Their efficiency in predating upon roach is said to cause an increase of bream in biomanipulated lakes that have had pikeperch addition.

Pikeperch play a determinant role in the control of fish stock assemblages in temperate mesotrophic lakes and reservoirs. A bi-modal distribution distribution of the pikeperch population was recently described in Sulejów reservoir (Frankiewicz *et al.*, 1995). Part of the young fish left the littoral zone to the open water to avoid predation and was able to adapt to a shift towards filter-feeding of zooplankton. In so doing however they achieved lower condition than their conspecifics who remained in the littoral zone and reached the piscivorous phase earlier. In Bautzen reservoir pikeperch cannibalism was judged less important than predation by perch (Schultz *et al.*, 1992).

7.4 Pike (*Esox lucius* Linnaeus 1758)

Pike adults typically attain an adult length of 40 - 100 cm. They are widely distributed through Europe, Asia and North America in lakes and slow flowing rivers. They are indigenous to south-east England and have spread throughout much of Great Britain from this point (Maitland and Campbell, 1992).

Spawning typically occurs between February and May when water temperature rises from 4°C to 11°C. Favoured sites include shallow water with thick vegetation cover, marshy edges of river and lakes and flooded terrestrial sites. Spawning begins as the male gently rubs its snout against the head and body of the female. The couple starts to move with an undulating movement until the male strikes the female with a lateral tailbeat. After this signal the fish unite their genital pores; the eggs are fertilised and sink to the bottom. Eggs are 2-3 mm in diameter, scattered at random and adhere to vegetation. Between 9,000 and 20,000 eggs are produced per kg body weight. Eggs hatch after 150 -155 degree days which is usually equivalent to 10-30 days depending on temperature.

Once hatched, the larvae of between 6-8 mm length remain attached to the vegetation for up to 10 days. They become planktonic after leaving the vegetation and feed primarily on zooplankton and insects. Growth is initially rapid, the larvae can increase by 4 mm within the first month. Massive mortality is usual during the early stages of development. Surviving fry become piscivorous after one year and mature within 3 - 4 years. Pikelets become piscivorous from a length of 4 cm.

Adults inhabit shallow water and tend to become more piscivorous with age. They are solitary animals which adopt ambush tactics to capture prey which they will take all year round. They spend much of their time within weed beds and will not venture out to follow prey for long distances. Typically pike hunt by stalking with a slow, stealthy approach to within striking distance. Here they slowly orient towards it, pause briefly, flex their tail and body together into an 'S' shape and suddenly leap forward with a single flick of the tail. The prey is attacked and swallowed immediately. Large prey may be turned around before being swallowed head first. Strong posteriorly pointing teeth prevent the escape of the prey during this brief handling.

Prey items are located by vision and mechanical detection. Pike will eat any suitably sized animal whether alive or dead. They have been known to take small mammals, wading birds and will even attack hands that are left trailing in the water from boats. They are principally piscivorous however, especially animals above 50 cm long. They are known to hunt for larger fish, a strategy termed *size–biased feeding* (Gerkin 1994). In one Irish lough it is estimated that 51.5 tonnes of brown trout were destroyed by 1170 pike. Populations of char *(Salvelinus alpinus)* and brown trout in Lake Windermere did not recover until local fishermen carried out a drastic reduction of the pike population. Little wonder that pike are often considered as a nuisance and removed from trout and salmon fisheries. The diet of larger pike, in rivers and lakes, will depend on the composition of the local fish community. Perch are favoured almost in all lakes where they occur, while in english rivers the main food organism is roach (Gerkin 1994).

Pike have been extensively used for the successful biomanipulation of small, shallow and macrophyte-dominated lakes. Their decrease in surface waters is a direct consequence of eutrophication due to the disappearance of macrophytes. Pike spend most of their time at the edge of the macrophyte beds. The development of this ecotonal frontier can be directly related to pike abundance. The parallel presence of pike and macrophytes is also a result of the existence of a common limiting factor, water transparency, as pike cannot reach high condition in turbid waters. This characteristic limits the option of introduction of pike at the beginning of biomanipulation projects.

A high density of small pike is a prerequisite for the control of small bream (Hosper *et al.*, 1992).

7.5 Roach (*Rutilus rutilus* Linnaeus 1758)

Roach are widely distributed over Europe and are found throughout most of England. They inhabit a variety of water bodies in lowland areas from small pools to clear lakes and from small streams to large rivers. They form an important part of the diet of pike and pikeperch. Year class instability is a common feature of roach populations. Good conditions lead to a strong year class with a high number of stunted individuals. Strong year classes may account for half the population present. Adults typically reach a length of 20 - 25 cm.

Spawning occurs from April - June when the water temperature rises above 12°C. Eggs of 1 - 1.5 mm diameter are laid in weed beds in the shallows where they attach to the vegetation, or on trailing structures such as tree roots. Each female may lay between 5000 and 200,000 eggs which hatch after 5 - 10 days depending on the temperature. The fry, which are typically 4.5 - 6.5 mm long, remain attached to the vegetation for a few days after hatching. Roach fry grow rapidly under favourable conditions. The number of days above 14°C seems to be an important determinant of growth rate. The young fry feed on small zooplankton (rotifers) and some vegetable matter (periphyton) initially but switch to larger invertebrates, such as large crustacean zooplankton and molluscs, and to a minor extent chironomid larvae and pupae, as they reach 20–30 cm. Zooplankters are eaten by a form of filter–feeding requiring rapid suction movements not directed towards any particular prey alternated to chewing movements. A similar technique is employed during the benthivorous feeding mode when the substratum is sieved through the gill rakers and nutritious particles are chewed. Inorganic particles larger than 0.25–0.35 cm are spat out as they cannot pass through. Mouth protrusion allows a closer contact with the substrate, such that the fish can explore the top sediment by gentle suction while swimming. While filter feeding does not depend on sight, particulate feeding does. Under this mode of feeding organisms are picked individually or a few at a time by biting or sucking movements. Particulate feeding is commonly observed with young roach predating on relatively large food organisms, such as zooplankters (Lammens 1986). Roach is not a highly efficent filter feeder due to its relatively restricted filtering area. They are however expert particulate feeders and are provided by very strong pharyngeal teeth which allow them to feed on gastropds such as *Valvata* and *Bithnia* and bivalves such as *Dreissena*.. The hard shells of Dreissena can be cracked by roach at a size of 16 cm approx. Energy requirements for this operation suggest that the fish concentrate on larger more nutritious specimens while abundant small molluscs (<10mm) are not fed upon (Lampert and Sommer 1993). The feeding mode of roach is dependent on vision as demonstrated by the high proportion of chironomid pupae and large larvae in roach guts and by its feeding on molluscs. Its capability to switch between two different modes of feeding enable roach to respond promptly to changes in the proportion of available resources.

Roach typically reach maturity after 2–4 years. Higher densities of roach are found in the littoral environments during the day; at night however, often most of the population migrates to the pelagic environment.

7.6 Eel *(Anguilla anguilla* Linnaeus 1758)

Eel are widely distributed throughout Europe, the southern Mediterranean up to the Black Sea and the western coasts of North Africa as far south as 25°N. The full breeding cycle of the European eel and the location of the spawning grounds in the Atlantic Ocean were investigated by intensive research expeditions during the turn of the century and are regarded still today as one of the world's wonders. It is only relatively recently that scientists have reached an agreement in locating the spawning grounds of the European eel in the central and deeper part of the Sargasso Sea at a depth of 100–200 m between the 16°C and 17°C isotherm (Sinha and Jones 1975). A one year journey, following the Gulf Stream, brings the larvae (conventionally named "leptocephali") to the coasts of western Europe. During this migration leptocephali–larvae drift almost passively, aided by their laterally compressed, leaf–like shape which enables them to remain bouyant in the current. Divers working in the Western Approaches have reported eels drifting passively towards the coast in a vertical position, with their heads upwards (Maitland and Campbell 1992). Soon after entering the strait of Gibraltar and the North Sea, eel start metamorphosing into *glass eels*, develop a swim bladder, become elongate, slim and cylindrical and enter freshwater streams. In the freshwater environment eels spend 7–12 years in the case of males achieving a length of 0.5 m (36 cm on average), while the females tend to stay longer, 9–19 years, and may attain 1.5 m in length (46 cm on average) for a weight of 7 kg.

Eel migrations take place on moonless stormy nights towards the end of summer. Most migrant eels tend to move together and the whole yearly migration can be over within few days. It has been observed that movement of eels is triggered by rises in discharge; some support the idea that eels would respond to microseisms generated by depression over the English Channel or the North Sea. The largest eel catches are made by unbaited gear during such massive migration. The means of navigation of the silver eel during its return journey to the Sargasso Sea is still a matter of controversy.

Eel inhabit lakes, streams and brackish waters but tend to avoid swiftly flowing waters. Both freshwater stages, the yellow and the silver eel, are actively fished and their flesh is highly priced. Silver eels are particularly sought because they are larger, fatter and ideal for smoking, smoked eels are considered a delicacy in most of central and northern Europe. Stocking with eels is common practice in most countries in Europe. Eels are relatively slow growing fish, sensitive to overcrowding and to low temperatures. These factors explain the poor growth attained by eels in British stocking ponds. Most activities stop as the temperature decreases below 10°C. Eels are warm–water species and their feeding activities show a seasonal rhythm related to temperature. In Britain their feeding shows a peak between April and July and very little feeding during autumn and winter. In winter eels spend a lot of time immobile at the sediment bottom and are known sometimes to bury in the sediment itself. This burrowing behaviour protects eels from predation by pikeperch and ducks.

The principal food of eels is benthic invertebrates, mainly crustaceans, molluscs and insects. They will select preferentially isopods, trichopterans and ephemeropterans if present. Chironomids, however, are often selected because they are generally more abundant. In lakes and reservoirs foraging eels swim with slow zig–zag movements, closely observing the sediment surface. Due to this habit they tend to notice chironomid pupae first of all that are hence highly selected while the larvae buried in the sediment are not seen. Eel sight–dependent predation restricts its action to the upper sediment layer. Their eyes are adapted to low irradiances due to the high content of rhodopsin (a pigment characteristic of deep–sea fish) in their rod cells (Maitland and Campbell 1992). Electrofishing evidence, however, proves that eel are also feeding during the day. Their sense of smell is very acute and they respond readily to baited traps which constitute one of the methods of choice for their capture.

Fish constitute often an important part of the eel's diet as they increase in size. In East Anglia loach, bullhead, gudgeon and lampreys have been reported in eels stomachs (Hartley, 1948). When caught in estuaries eel show evidence of feeding on flounder. A study in the Willow Brook, Northamptonshire, reported that fish constituted as much as 75% of eels' stomach content (Cragg–Hine, 1964). Only relatively large eel seem to be able to feed on fish other than fry due to their relatively narrow mouth gap. Often they attack other fish caught in gill nets, they tend to take small cyprinids but avoid perch. In the spring eel are told to be feeding actively on fish spawn. Eel catches in the De Gijster reservoir (Biesbosch, the Netherlands) showed that eels were strongly attracted by the presence of spawning fish. This factor and the phase of the moon were the mean determinants of eel catches in the reservoir (Visser 1993). Only one observer from Germany reported eel feeding on cladocera, this has not been reported since (Sinha and Jones 1975). In general eel are opportunistic feeders highly adaptable to the food available; there are reports of eel found feeding on terrestrial insects and on carrion. On warm summer nights they have been seen to come to the water surface to catch emerging caddis flies with a sucking action called "chirping".

In contrast to other fish such as perch or trout, eel maintain their feeding preferences even when increasing in size without significant changes. Fears of damage to salmonid stocks by eels are not supported by consistent scientific evidence. Although small trout and salmon have been found in eel stomachs this has never built up to significant proportions. The spawn of salmonids occurs at times when temperatures are too low for eels to feed actively. The salmonid spawn is buried deep into the gravel and stands little chances of being damaged by eels. In fact eels are more often cannibalistic and tend to feed on elvers and small eels. Competition between salmonids and eels seems to be in partly determined by the scarce activity of eels at low water temperatures. Times of dietary overlap occur mainly in June–July when both eels and salmonids feed on mayfly nymphs and caddis fly larvae. In contrast to salmonids, eels rarely consume surface food items of terrestrial origin.

Eels are important components of the food chain of temperate lakes. Their presence should be encouraged as they do not feed on zooplankton and have an impact in reducing the recruitment of cyprinids by damaging their spawn and predating on their young. Although eel are considered a warm-water species and one relatively resistant to organic pollution, they do not benefit from highly eutrophic conditions as they find themselves under strengthened competition with cyprinids, in particular resource partitioning occurs between bream and eel since both are active benthic feeders.

A decrease in the average size of zooplankton due to an increase in smelt *(Osmerus eperlanus)* populations in Lake Tjeukemeer (the Netherlands) caused a shift of the bream from planktivorous to benthivorous diet. In so doing bream came into competition with eel forcing it to switch its diet from chironomids, gammarids and molluscs to fish (Lammens *et al.* 1985). Bream are better adapted to feed on chironomids as they sieve the substrate in depth gaining access to larvae buried in the sediment that are not predated upon by eels. The equilibrium reverted the year after when the smelt, which had been inadvertedly introduced during pumping operations, was heavily reduced by pikeperch predation. During the year of diet overlap the condition of large eels did not suffer as these were able to handle small smelt easily, small eels, however, showed a loss in condition.

In recent years the distribution of eels has become progressively under stress because of pollution, reduction in water resources, and the building of dams. Eels can overcome physical obstacles and are known to be able to avoid dams by moving overland during rainstorms. Both juvenile eels on their upward migrations and adult eels moving downstream to sea can by–pass waterfalls and dams. During their travel on land eels perform exaggerate undulations of their body and tail, often embracing rocks and other objects on the substrate. Virtually no barrier can totally prevent their occurrence in a given waterbody. However, due to the increasing number of obstacles, their numbers would be naturally reducing if eels were not intensively restocked in most European countries.

7.9 Ruffe (*Gymnocaphalus cernua* (Linnaeus 1758))

A member of the perch family, ruffe is characterised by a developed dorsal fin bearing 11–16 hard and sharply pointed spines at the front that make it unpalatable for predators. In ruffe this part of the dorsal fin is directly connected to the soft–rayed part while in perch the two are separated. The body is covered in tough ctenoid scales and even the head is well–armoured bearing 10–12 spines on the pre–operculum. Like perch, ruffe are highly adaptable to a wide range of aquatic environments and are able to spawn under difficult conditions such as in the absence of suitable substrata. Ruffe are smaller than perch and have lower oxygen requirements. They are able to colonise brackish waters achieving good condition and large sizes (e.g. up to 50 cm in the Baltic Sea). Spawning takes place between March and May; eggs are laid forming sticky strands and hatch at a temperature between 10 and 15°C. They tend to grow slowly, reaching only 10 cm in four years. However they often achieve early sexual maturity (within 2 years) such that the population can respond rapidly to favourable conditions. Their food habits are very similar to those of perch apart from the fact that the ruffe has a distinct habit of feeding and hunting head–down. Ruffe may particularly feed on fish spawn and by doing this they can control other fish populations. In the large lakes of Russia where they occur together with whitefish *(Coregonus)*, it has been shown that the whitefish was significantly affected. They seem to have the ability to penetrate deep into the mud to catch burrowing invertebrates, such that their benthic feeding might be more efficient than that of perch. They are also active predators on small fish.

Ruffe are common in the Broads of Norfolk and Suffolk where they form large gregarious shoals.

Lack of further information on ruffe prevents us from establishing its position in regards to biomanipulation. Its impact could favour a general decrease in cyprinids due to the damage ruffe could cause to fish spawn and young of the year. Data on stomach contents of ruffe caught in the Norfolk Broads and in Lake Vänern (Sweden) shows that in both cases zooplankters accounted for less than 15% of stomach contents (cited in Maitland and Campbell 1992). Midge larvae and water louse were the preferred food items in the Norfolk Broads and in Lake Vänern respectively.

7.10 Brown trout (*Salmo trutta* (Linnaeus 1758))

Despite the great morphological variation found within this species only 2 sub–species are recognised by scientists. These are *S. trutta trutta* and *S. trutta fario*, the anadromous (sea trout) and the non anadromous (brown trout) respectively. The two varieties are difficult to distinguish, particularly because of frequent interbreeding. The distinction between the two is not directly relevant to this document.

In Britain brown trout spawn mainly from mid–October to mid–December. Time of spawning is subject to the rise in water levels necessary for the parents to reach their spawning grounds. Runs to the spawning ground usually take place when a spate is declining and are usually followed by high mortality. While the closely related salmon die after spawning, trout often spawn several times in successive years.

Spawning in salmonids occurs mostly on silt–free, gravel substrates in fast flowing shallow rivers and streams. Lake trout deposit their spawn near river inlets, often at sites of subterranean springs. Two main criteria determine the success of the spawn:

- the presence of sufficient current through the gravel to provide oxygen for the eggs and to remove metabolic wastes,
- the presence of gravel of such a depth and size composition that the buried eggs are protected against the scouring action of floods, desiccation during periods of low water, sudden vibrations and direct sunlight.

Nest digging is carried out by the female. She turns on one side and beats the gravel several times with the caudal fin. She then presses her extended anal fin down among the stones to "probe" the quality of the gravel, and finally deposes the eggs that are immediately fertilised by the male. After the first batch is laid she excavates immediately upstream partially covering the deposited spawn. At the end of these operations the nest or *redd* is abandoned.

Lake dwelling salmonids typically live in schools. In streams instead they lead a solitary life in separate individual territories. The size of each given territory is inversely related to the abundance of prey. However, adults and juveniles of brown trout often share the same regions of the stream. In such situations the territorial mosaic is replaced by dominance ranking.

Activity takes place at dusk and at night particularly for sea trout. In lakes, however, they are active during the day as well, particularly during autumn. It has been shown that feeding activity can be accommodated to suit times of higher food availability. Several studies report a strong positive correlation between trout feeding activity and the time of invertebrate drift in streams. Bisson (1978) found the same correlation, although in his experimental stream channel in the Kalama river, Washington, drift and feeding activity are both greater during midday than at other times.

Trout are strictly carnivorous and are known to be voracious predators. They are highly adaptable to a large variety of prey available. After an early stage devoted to feeding on small invertebrates such as small mayflies and midge larvae, trout start catching larger invertebrates such as stoneflies, caddisflies, chironomids. After a few years fish may become an important part of their diet and indeed some populations, popularly named "ferox", specialise in making fish their main food item. These populations are characteristic in Scottish lochs. In other populations the proportion of fish taken increases generally with the size of the trout. In Windermere trout less than 30 cm seldom eat fish, while fish form a large part of the diet of larger trout (Frost and Brown 1967). Cannibalism is common, but more often trout prey on sticklebacks and perch fry, undeterred by the strong spines that make these organisms unpalatable to other predatory fish, and sometimes pike fingerlings. Perch, sticklebacks and minnows are commonly selected species as they occur in shoals, conversely solitary fish are seldom attacked. In large rivers cyprinids are not hunted, however in Eye Brook reservoir (Northants/Leicestershire), where roach are very abundant trout feed on roach fry (Frost and Brown 1967).

In small streams trout may specialise in aerial feeding and become expert in capturing flying or even terrestrial insects such as ants by jumping out of the water to capture them. Such prey items may become predominant in late summer and autumn. This habit distinguish trout from salmon that never have a large number of such food organisms in their stomachs. Trout catch their prey individually, typically different fish may gain experience in hunting for a particular food organisms, its stomach may be bulging with it while no other trout in the same environment might have eaten it. The relative longevity of trout is a factor that tends to strengthen this tendency towards acquired habits.

The diet of trout in lakes includes planktonic crustaceans. These are caught individually, not by filter feeding, which must represent quite an effort for trout. Large organisms such as the cladocerans *Bythotrephes, Leptodora, Daphnia* and *Bosmina* are strongly preferred to the smaller copepods that form only a minor proportion of the food taken. *Eurycercus* is also a highly selected food organism due to its relatively low mobility, compared to *Daphnia* and *Bosmina* that are more difficult to capture, and to its habit of remaining confined to the littoral zone. Zooplanktivorous habits are only characteristic of a particular stage in the life of the lake trout; there are indications that beyond a certain size (>400g) trout stop feeding on zooplankton to concentrate on larger food organisms. Average trout growth is higher in lakes and reservoirs than in rivers despite benthic organisms being less abundant in deep lakes than in rivers. This is probably related to higher yearly temperatures and to the availability of zooplankton.

In lakes trout spend most of their time in the littoral zone which offers a higher variety of organisms. The growth rate and condition of a lake trout population will be highly dependent on the presence of a developed shallow area (<10 m). The highest growth rates occur in shallow, hard–water lakes colonised by abundant aquatic vegetation such as Blagdon reservoir (Avon) where trout reach an average length of 36 cm by the end of their third year (Frost and Brown 1967).

The highest short-term growth rates occur in reservoirs soon after impoundment when trout can exploit freshly inundated terrain. During the first three years after the impoundment of Rutland Water trout invaded newly flooded land, mainly during water rises in autumn and winter, such that terrestrial organisms (mainly earthworms), sometimes composed 80% of their stomach content. The feeding on terrestrial invertebrates alternated with catches of littoral amphipods, molluscs and zooplanktivory during summer (Harper 1982).

Evidence shows that fish size development can be limited by the availability of large and nutritious food organisms. In lakes devoid of intermediate size food organisms, trout may never achieve large sizes which would allow them to attack large food organisms such as frogs, toads, newts and crayfish that remain therefore unexploited. Sometimes small rodents and young birds can be also eaten when washed into rivers during spates. A wide range and variety of food organisms is necessary for trout to achieve full condition (Maitland and Campbell 1992). In lakes trout patrol in search of food while in streams they tend to hide behind obstacles and ambush drifting invertebrates. In general they hunt by sight. In conditions of low light penetration they can rely on a powerful sense of smell and on the ability shared by many fish, to detect turbulence caused by moving objects.

In rich lakes, in presence of a large variety of small fish and invertebrate hosts trout tend to accumulate large numbers of parasites such as cestode tapeworms and nematode round worms. Evidence suggest that this may be one of the main mechanisms reducing trout longevity in eutrophic lakes (Maitland and Campbell 1992).

Predation on trout occurs by other predatory fish such as older trout, pike and eel, but more importantly by piscivorous birds such,as herons and divers.

7.11 Rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) (formerly*Salmo gairnderi* (Richardson))

This Pacific cousin of the european brown trout was introduced to Britain towards the end of last century. It is known to achieve higher growth rates than indigenous trout, be easier to catch by anglers and offer flesh of better flavour. Most populations are sustained by continuous reintroductions; only very few are self-sustaining. Part of the reason may be due to competition with the brown trout which are able to hatch earlier and occupy spawning grounds damaging successive spawns of rainbow trout which in Britain occur typically between March and April.

Three forms are generally recognised: the rainbow trout which typically inhabits small streams, the kamloops which lives in moderately deep to deep, cool lakes and the steelhead which migrates to sea. In lakes rainbows will thrive successfully on a diet of zooplankton.

Food habits are in general common for the rainbow and brown trout, however when the two species are found in the same waterbody, some form of resource partitioning might occur. In Rutland water, a study of the relationships between chironomids in the trout diet and those in the reservoir substrate (Brown *et al.* 1979) showed differences in the diet of the two species of trout indicating spatial separation, brown trout feeding in deeper water and rainbow trout closer to the surface (Warlow and Oldham 1982).

The role of either species of trout in biomanipulation has not been studied, largely because many of the the shallow lakes and bowl reservoirs which have been the subject of biomanipulation research have not lent themselves to trout fisheries for other reasons. It is likely that the main determinant of the importance of these species will be their mean size at stocking, since many reservoirs are put-and-take fisheries with a relatively short average survival time from stocking to capture.

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