# FISH COMMUNITIES IN SOUTH-FINNISH LAKES AND THEIR RESPONSES TO BIOMANIPULATION ASSESSED BY EXPERIMENTAL GILLNETTING

## Mikko Olin

Department of Biological and Environmental Sciences,
Aquatic Sciences,
Biocenter 3, P.O. Box 65, FI-00014 University of Helsinki, Finland

**Academic dissertation in Fishery Science**

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Author's address:   Aquatic Sciences, Department of Biological and Environmental Sciences
                    Biocenter 3, P.O. Box 65, FI-00014 University of Helsinki, Finland
                    E-mail: mikko.olin@helsinki.fi

Supervisors:        Dr. Martti Rask
                    Evo Fisheries Research Station
                    Finnish Game and Fisheries Research Institute, FI-16970 Evo, Finland
                    E-mail: martti.rask@rktl.fi

                    Dr. Jukka Horppila
                    Aquatic Sciences, Department of Biological and Environmental Sciences
                    Biocenter 3, P.O. Box 65, FI-00014 University of Helsinki, Finland
                    E-mail: jukka.horppila@helsinki.fi

Reviewers:          Prof. Erik Jeppesen
                    Department of Freshwater Ecology
                    National Environmental Research Institute, Denmark
                    E-mail: ej@dmu.dk

                    Dr. Thomas Mehner
                    Department of Biology and Ecology of Fishes
                    Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Germany
                    E-mail: mehner@igb-berlin.de

Opponent:           Prof. Jouko Sarvala
                    Department of Biology, Section of Ecology
                    University of Turku, Finland
                    E-mail: jouko.sarvala@utu.fi

Quite a polka!

# Contents

## 1. List of papers

The thesis is based on the following articles (I-VI in the text):

I      Olin, M., Rask, M., Ruuhijärvi, J., Kurkilahti, M., Ala-Opas, P. & Ylönen, O. 2002: Fish community structure in mesotrophic and eutrophic lakes of southern Finland: the relative abundances of percids and cyprinids along a trophic gradient. Journal of Fish Biology 60: 593-612.

II     Rask, M., Olin, M., Horppila, J., Lehtovaara, A., Väisänen, A., Ruuhijärvi, J. & Sammalkorpi, I. 2002: Zooplankton and fish communities in Finnish lakes of different trophic status: responses to eutrophication. Verhandlungen der Internationalen Vereinigung für Limnologie 28: 396-401.

III    Olin, M. & Malinen, T. 2003: Comparison of gillnet and trawl in diurnal fish community sampling. Hydrobiologia 506–509: 443–449.

IV    Olin M., Kurkilahti M., Peitola P. & Ruuhijärvi J. 2004. The effects of fish accumulation on the catchability of multimesh gillnet. Fisheries Research 68: 135-147.

V     Rask M., Olin, M., Keskitalo, J., Lehtovaara, A., Ruuhijärvi, J. & Vesala, S. 2003: Responses of plankton and fish communities to mass removal of planktivorous fish in a two-basin lake in southern Finland. Hydrobiologia 506–509: 451–457.

VI    Olin, M., Rask, M., Ruuhijärvi, J., Keskitalo, J., Horppila, J., Tallberg, P., Taponen, T., Lehtovaara A. & Sammalkorpi, I. Effects of biomanipulation on fish and plankton communities in ten eutrophic lakes of southern Finland. Hydrobiologia, in press.

## 2. Author's contribution

I      MO, MR and JR planned the article. MO, PA-O and OY participated in the fishing, and entered and pre-analysed the data. MO and MK did the statistical analyses. MO wrote the paper.

II     MR designed the paper. MO contributed to fish sampling. JH, AL and AV participated in sampling and counting of the zooplankton data. MR and MO did the data analyses. MR wrote the paper.

III    Both authors designed the study. MO participated in the sampling and analysed the gillnet data. TM analysed the trawl data. MO wrote and TM commented on the text.

IV    MO and JR planned the study. MO and PP partook in the gillnetting. MO, MK and PP analysed the data. MO wrote the article.

V     MR, MO and JR planned the paper. MO and SV shared in fish sampling. JK counted the phytoplankton and AL the zooplankton data. SV aged the fish. MR and MO did the statistical analyses. MR wrote the paper.

VI    MO, JR and MR designed the study. JK and PT counted the phytoplankton data and JH and AL the zooplankton data. MO took part in the fish sampling and did the statistical analyses of the combined data. MO wrote the paper.

# 3. Abstract

Biomanipulation, by removing planktivorous and benthivorous fish, has proved to be an effective method for restoration of eutrophicated lakes. Despite the increasing knowledge of complex food webs in lakes, problems and uncertainty still remain. Some of the main questions are related to fish and their role in attaining the objectives or sustaining the improvements.

In Finnish eutrophicated lakes, biomanipulation is among the most common restoration measures. Problems and neglects have, however, often appeared in obtaining the foreknowledge and studying the responses of fish community. This thesis is based on the results of a research program related to the effects of biomanipulation in different kind of lakes and the applicability of gillnet test fishing as a research tool. The specific objectives of this thesis were to (1) explore the factors regulating the fish biomass and community structure in south-Finnish lakes; (2) study how the characteristics of lake affect the target catch and the outcome of biomanipulation; and (3) evaluate the applicability of experimental gillnetting especially in estimating the catch-need of biomanipulation and the consequent changes in the fish biomass and community structure.

In the study of 36 lake basins, the total fish biomass as well as the number of species increased with the nutrient concentration. The shift from percid to cyprinid domination from mesotrophic to eutrophic lakes was not supported since cyprinids already dominated in mesotrophic lakes. Bream and white bream had a biomass peak in more eutrophic lakes compared to bleak and roach. Large lake size and high transparency enabled high biomass of perch in spite of abundant cyprinids. Thus, in Finnish lakes, fish biomass and community structure can depend, besides on the nutrient concentration, also on the lake area and depth, and turbidity.

The methodological studies revealed that, when fish accumulate in the gillnet, the catching efficiency decreases noticeably at a relatively low catch level. The reliability of gillnetting results could be, however, improved by reducing the set time of gillnets. When comparing the trawl CPUE and the gillnet CPUE of 4 h, the CPUE of Nordic multimesh gillnet as an index of fish abundance was quite reliable for ≥6 cm fish. As a conclusion, experimental gillnetting can be used to roughly estimate the target catch of biomanipulation, and to follow the responses in fish community.

In the study of 14 biomanipulated lake basins, the general shifts in the fish assemblage of effectively (> 200 kg ha$^{-1}$ 3yr$^{-1}$) biomanipulated lakes were: 1) the reduction of large cyprinids, 2) the expansion of juvenile cyprinids and, to the lesser extent, percids, and 3) the increase in the proportion of piscivores. Cladocerans responded positively in most of the basins. In the basins with effective cyprinid-removal , the biomass of cyanobacteria decreased, and the duration of the blooms shortened and shifted towards the autumn. Successful and sustainable biomanipulation is more likely if the external loading is low, clay-turbidity is modest and the juvenile expansion of cyprinids is prevented.

# 4. Introduction

## 4.1. Starting point for the study

Since the successful restoration of Lake Vesijärvi (see Horppila et al. 1998), biomanipulation has been one of the most common restoration methods in Finnish lakes. By the end of the century, dozens of biomanipulation projects had been started (Äystö 1997, Penttilä 2002). Often however, the mass removal of fish has been conducted without foreknowledge of the characteristics of fish community or the adequate target catch, and even without appropriate study of the responses. In 1997, Finnish Game and Fisheries Research Institute, together with Finnish Environment Institute, University of Helsinki and local water authorities, initiated a 5-year research project called HOKA (Effects of biomanipulation in Finnish lakes). The aim was to explore the effects of biomanipulation in different kind of lakes and study whether the gillnet test fishing would be a suitable method for estimating the sufficient target catch and responses in fish community. This thesis is based on the results of the HOKA project.

## 4.2. Biomanipulation

### 4.2.1. Theory

Biomanipulation is a restoration method in which the lake's water quality is improved by modifying the food web (Shapiro et al. 1975, Lammens et al. 1990, Carpenter & Kitchell 1993, Reynolds 1994, Perrow et al. 1997, Hansson et al. 1998, Drenner & Hambright 1999, Meijer et al. 1999, Mehner et al. 2002). Usually, the biomanipulation is conducted by mass removal of planktivorous and benthivorous fish (Drenner & Hambright 1999). According to the trophic cascade hypothesis (Carpenter et al. 1985), the impacts at the top trophic level cascade down to the lower trophic levels, and thus the top-down forces can regulate algal biomass. When the abundance of planktivorous fish is reduced, the density and size of cladocerans increase, which results in increased grazing pressure on phytoplankton. This in turn leads to lower algal biomass and higher water transparency. The potential of planktivores to reduce zooplankton biomass is evident (Brooks & Dodson 1965, Shapiro & Wright 1984, Hambright 1994). The ability of zooplankton to control phytoplankton biomass in lakes has found to be more variable (Brooks & Dodson 1965, McQueen et al. 1986, 1989, Kerfoot et al. 1988, de Bernardi & Giussani 1990, Lammens et al. 1990, Sarvala et al. 2000a). According to some authors (McQueen et al. 1986), the top-down forces attenuate when moving down several trophic levels, and the bottom-up forces have stronger effect on phytoplankton than on the higher levels of the lake food web.

Importantly, fish can affect the bottom-up forces and regulate phytoplankton directly by increasing the amount of suitable nutrients. Cyprinids are the most abundant fish group in eutrophicated north temperate lakes, and many cyprinid species are omnivorous feeding on zooplankton, detritus, algae, macrophytes and benthic invertebrates (Niederholzer & Hofer 1980, Persson 1983, Prejs 1984, Lammens et al. 1987, Vinni et al. 2000). Cyprinids release nutrients from the bottom sediment when foraging food and keep the uppermost sediment layer loose and vulnerable to wind resuspension further accelerating nutrient escape from the sediments (Shapiro & Carlson 1982, Tatrai & Istvanovics 1986, Lammens et al. 1990, Horppila & Kairesalo 1992, Breukelaar et al. 1994, Karjalainen et al. 1997, Scheffer 1998). Cyprinids perform diurnal migrations from littoral to pelagial or from hypolimnion to epilimnion (Bohl 1980, Helfman 1981). During these migrations, fish transfer nutrients from one habitat to another (Lamarra 1975, Brabrand et al. 1990, Tatrai & Istvanovics 1986). The nutrients excreted by cyprinids are in suitable form for the nutrient uptake of phytoplankton (Brabrand et al. 1990).

With the increasing knowledge of the complex interactions in lake food webs, the biomanipulation research has proceeded towards a more holistic view compared to original biomanipulation concept (Shapiro et al. 1975). Marten Scheffer has developed a hypothesis of alternative stable states in eutrophic shallow lakes (Scheffer 1989, 1990, 1998, Scheffer et al. 1993). A shallow lake can be either turbid with

high algal and cyprinid biomass or clear and dominated by macrophytes, cladocerans and piscivores. With high nutrient loading the previous state is the only option, and with low loading the latter state is valid. In the middle ground, either one can be possible. Both states have self reinforcing mechanisms. For example, high algal biomass reduces the amount of light inducing decreased macrophytes vegetation, which increases the availability of nutrients enabling high algal biomass. The high biomass of macrophytes stabilizes the bottom sediment and provides refuge for zooplankton, thus reducing the nutrients for algae and increasing the grazing pressure. The water stays clear and macrophytes can colonise the lake. Due to high resistance, the shift from one state to another requires a shock event e.g. storm, changes in water level or biomanipulation. According to Hansson et al. (1998), biomanipulation can act as a trigger to several secondary processes including recovering of submerged macrophytes, and reduction of resuspension and internal loading.

In relation to fish community, the practical target of biomanipulation is usually to reduce the cyprinid density and to increase the proportion of percids and pike. Compared to cyprinids, percids are less harmful in nutrient circulating (Andersson et al. 1988) and have a higher economic value (Moilanen 2004). Mass removal of cyprinids should increase perch biomass and the individual growth rate in two ways: 1) in short-term, food competition with roach decreases with decreasing roach density (Persson 1986), 2) in long-term, with increasing water transparency and colonisation of submerged vegetation, the changed environment favours perch more than roach (Winfield 1986, Diehl 1988, Persson et al. 1991). Pikeperch, adapted to turbid waters, may not have positive responses to biomanipulation. Higher water transparency could make the fry more vulnerable to predation (Neuman et al. 1996) and the adults less effective piscivores (Ali et al. 1977, Disler & Smirnov 1977). In the response to increased transparency by pikeperch, the lake size can be important: in deep waters of large lakes there will probably be enough suitable habitat for pikeperch (**I**). Further, abundance of humic substances in Finnish lake waters (see Henriksen et al. 1998) may also support light

conditions favourable for pikeperch. The possible juvenile expansion of cyprinid fishes after mass removal (Brabrand et al. 1986, Romare & Bergman 1999) should benefit pikeperch due to increased prey availability. This type of slightly positive response in pikeperch growth has been recorded also in one of the recent study lakes (Rask et al. in print). The response of ruffe to biomanipulation can be twofold, as well. If occurrence of anoxia is reduced in the hypolimnion and zoobenthos recovers, ruffe profits from biomanipulation. If the predation by perch is increased, however, the response can be negative. As a visual predator ambushing from the cover of vegetation (see Bry 1996), pike should benefit from biomanipulation.

Once established, pikeperch, large perch and small pike prey on juvenile fish thus hindering the expansion of cyprinids and shifting the size structure of prey species towards larger size classes (Persson et al. 1991, Prejs et al. 1994, Berg et al. 1997). Large pike can consume adult cyprinids as well (Skov et al. 2002). Decreasing abundance of juvenile cyprinids should release cladocerans from high predation pressure especially during spring before the recruitment of young-of-the-year (YOY) fish (Temte et al. 1988, Vanni et al. 1990, Rudstam et al. 1993). The grazing-induced clear water phase in spring is essential for the development of submerged macrophytes (Scheffer 1998). Besides direct effects on mortality, piscivores may change the behavior of cyprinids, restricting them to refuges thus reducing the transfer of nutrients (Brabrand & Faafeng 1993).

## 4.2.2. Potential and problems

Biomanipulation has proved to be an effective lake restoration method according to several reviews since 1990 (e.g. Benndorf 1990, Lammens et al. 1990, Perrow et al. 1997, Hansson et al. 1998, Drenner & Hambright 1999, Mehner et al. 2002). According to Mehner et al. (2002), ca. 60% of the biomanipulations have achieved to improve water quality. Prerequisites for successful biomanipulation are potential for intensive fish reduction (> 75%, see Hansson et al. 1998) and bearable external loading (see Mehner et

al. 2002). Still, some problems and confusion remain after two decades of research including (1) deteriorating effect of juvenile expansion (i.e. effective reproduction of remaining fish, e.g. Romare & Bergman 1999), (2) complexity of food-web interactions (e.g. different time and size scales of organisms and ontogenetic niche shifts, see Mehner et al. 2002), (3) applicability to deep lakes (Hansson et al. 1998, Mehner et al. 2002), (4) sustainability of effects (Hansson et al. 1998, Mehner et al. 2002), and (5) required proportion of piscivores after the biomanipulation (Mehner et al. 2002). To answer these open questions, it is essential to increase the understanding of the interactions between fish species in eutrophic lakes.

## 4.3. Fish communities in eutrophic lakes

According to Tammi et al. (1999), eutrophication is one of the main environmental problems in lakes of Finland affecting the fish community of more than 2000 lakes. The mechanisms through which eutrophication shapes fish communities are changes in the habitats and modifications in inter- and intraspecific competition and predation. The primary changes in habitats are reduced water transparency (Scheffer 1998), poor oxygen concentration in the hypolimnion (Harper 1992) and decreased structural complexity, that is, the diminished area of submerged macrophytes (Persson et al. 1991, Scheffer 1998). Eutrophication increases the importance of competition as a mechanism regulating fish community structure (Lodge et al. 1988, Persson et al. 1988, Persson 1994). At the same time, the importance of predation is reduced.

Eutrophication-induced alterations in fish assemblages are documented in many studies since early 1970s. According to a theory of Hartmann & Nümann (1977), (see also Svärdson 1976, Kitchell et al. 1977, Leach et al. 1977, Persson et al. 1991, Jeppesen et al. 2000) the fish communities from oligotrophic to eutrophic lakes undergo several dominance shifts: Salmoniformes is often the dominant fish group in oligotrophic lakes, percids in mesotrophic lakes and cyprinids in eutrophic lakes. The restriction of Salmoniformes to the low and medium pro-

ductive lake is due to their high oxygen demand and adaptation to relatively cold water (Colby et al. 1972, Nümann 1972). At a species level there are certain exceptions to this general rule so that coregonids (whitefish, *Coregonus lavaretus* and vendace, *Coregonus albula*) may have their biomass peak in mesotrophic lakes (Persson et al. 1991) and smelt (*Osmerus eperlanus*) can form a dense stock even in eutrophic lakes (Keto & Sammalkorpi 1988).

The dominance of percids in mesotrophic lakes is related to clear water and structural complexity, which favours especially perch (*Perca fluviatilis*) (Winfield 1986, Diehl 1988, Persson 1991). Ruffe (*Gymnocephalus cernuus*) and pikeperch (*Sander lucioperca*) can feed effectively in turbid waters, and their biomass peak is at a higher productivity level (Bergman 1988, Persson 1994).

Cyprinids are generally well adapted to eutrophic conditions. Roach (*Rutilus rutilus*), bream (*Abramis brama*), white bream (*Abramis bjoerkna*) and bleak (*Alburnus alburnus*) are species that have been documented to profit from eutrophication (Svärdson 1976, Lammens et al. 1987, Persson et al. 1991). This is due to their effective feeding in turbid waters (Townsend & Risebrow 1982, Lessmark 1983, Lammens et al. 1987, Persson 1987, Diehl 1988), generalist feeding behaviour including ability to utilise plant material (Niederholzer & Hofer 1980, Lessmark 1983, Persson 1983, Prejs 1984, Vinni et al. 2000), and large capacity and flexibility in reproduction (Barthelmes, 1983).

Moreover in eutrophic lakes, the predatory pressure on cyprinids is lowered because the abundance of predatory fish species or stages is often reduced. The decrease of predatory fishes is related to asymmetric competition/predation interactions and size-structured interactions (Werner & Hall 1979, Persson et al. 1988). Many predatory species undergo several ontogenetic niche shifts before a piscivorous stage. Competition of prey species can reduce the growth and survival of young piscivores, leading to a juvenile competitive bottleneck. In turbid conditions with poor submerged vegetation, perch, as a visual predator (Bergman 1988), is an inferior competitor compared to roach (Winfield 1986, Diehl 1988). The adult population of a predator

can in turn regulate the biomass of their prey, as described between perch and roach by Lennart Persson and co-workers (Persson 1986, 1987, 1988, Persson & Greenberg 1990).

Eutrophication changes the fish community but a cyprinid-dominated fish community can also maintain and even increase the eutrophication problems (e.g. Tatrai & Istvanovics 1986, Horppila & Kairesalo 1990, Brabrand et al. 1990). So also from the lake management point of view, understanding the mechanisms leading to conditions that favour cyprinids is important.

## 4.4. Challenges in fish sampling

### 4.4.1. Significance of and difficulties in fish stock assessment

Successful management or biomanipulation of fish stocks requires estimates of fish abundance, community structure and size distributions. This information is essential when deciding the target species and the fishing effort. Unfortunately, especially the fish abundance can be difficult to evaluate particularly in large and deep lakes. As the 75% reduction in fish biomass has been the rule of thumb in several biomanipulation projects (e.g. Jeppesen et al. 1990, Meijer et al. 1999), the knowing of original fish biomass is essential before these measures.

The major problem is that all sampling methods are, more or less, dependent on the catchability or perceptivity of fish, which vary greatly due to number of factors (Backiel & Welcomme, 1980). Gillnet is a passive and selective gear, catching only fish that swim to and retain in the net (Hamley 1975, Backiel & Welcomme 1980, Kurkilahti 1999). A trawl, as an active gear, is less selective but the catch depends on how large proportion of the total fish population is in the trawling area (Backiel & Welcomme 1980) and on the amount of fish that avoid the gear (Richardson 1956, Bethke et al. 1999, Hjellvik et al. 2001).

Further to the catchability problems, the distribution and activity of fish community undergoes drastic diurnal changes. Many species have diurnal vertical or horizontal migrations (Bohl 1980, Helfman 1981). This produces diurnally deviating samples even from the same site within the same day.

### 4.4.2. Gillnet as a sampling gear

The gillnet catch is the result of a complex process having several stages. Fish have to (1) encounter, (2) contact and (3) retain in the net (Hamley 1975, Kurkilahti 1999). The first, encounter factor relies on the swimming activity and speed. Thus, the encounter factor varies due to species, size, time of year, time of day, water temperature, weather conditions etc. Once the fish encounters the net it can avoid it (visually or due to other senses) swim through it or get caught in it. In this stage, the catch depends on the size and morphology of the fish but also on the perceptiveness and saturation of the gillnet (Kennedy 1951, Hamley 1975, Minns & Hurley 1988, Hansen et al. 1998, **IV**). If the fish girth is close to the mesh size or the fish has projections (e.g. percids), the fish has high catchability. The perceptiveness and saturation (amount of occupied meshes) increase as the fish accumulate in the gillnet thus decreasing the catching efficiency. In the last stage, the fish can retain in the net or escape from it. Fish size and morphology as well as gillnet properties (e.g. hanging ratio, twine diameter, saturation) interact at this stage (Hamley 1975, Kurkilahti 1999).

Due to passiveness, selectivity, perceptiveness and saturation, the reliability of gillnet CPUE as an index of fish abundance is very variable. Both studies where the gillnet CPUE correlated with the fish abundance estimated by an active gear or echo sounder (Borgstrøm 1992, **III**), and studies without the correlation (Enderlein & Appelberg 1992, Hansson & Rudstam 1995, Peltonen et al. 1999) have been published. Nevertheless, gillnet CPUE has been used as an index of fish abundance in several ecological (e.g. Forney 1977, Svärdson & Molin 1981, Tonn et al. 1990, Persson et al. 1991, Jeppesen et al. 2000, **I**) and fisheries studies (e.g. Hubert 1983, Hyvärinen & Salojärvi 1991). The bias in the deductions concerning the size of fish populations can result in over- or under-exploitation.

Gillnet characteristics induce flaws to the fish species structure and species' size structure. For
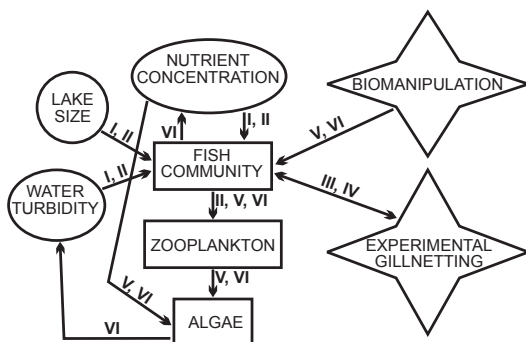
**Fig. 1.** Interactions between abiotic (ellipses), biotic (boxes) and human impacts (stars) that are studied or discussed in this thesis. Note that only a small fraction of all possible factors and interactions are drawn.

example, percids can be overestimated compared to cyprinids (Prchalová & Kubečka 2004, **III**) or smaller size classes are underestimated compared to large ones (Hamley 1975, Kurkilahti 1999, **III**). Thus, the gillnet catch may overvalue the condition of a fish community.

Given the shortcomings, the characteristics of gillnets have to be known in order to make right decisions on the basis of the gillnet catch. Numerous studies concerning the mechanical selectivity of gillnets have been published (e.g. Hamley 1975, Kurkilahti 1999). The catchability-effects of fish activity or fish accumulation are less studied (**IV**). Studies concerning simultaneous fish sampling with different gears are also rare (Peltonen et al. 1999, Pierce et al. 2001). However, best results in fish monitoring can be obtained by standardising gears and fishing time, and by combining different methods (Backiel & Welcomme 1980).

# 5. Study objectives

From the starting point of demands, three general goals were appointed to produce more information for assessing the need and the results of biomanipulation in Finnish lakes:

1. to increase the information concerning the fish communities in different types of Finnish lakes,
2. to explore the effects of biomanipulation on

fish communities, and further on zooplankton and phytoplankton in these lakes, and
3. to test the suitability of sampling fish with Nordic gillnets for the purposes above.

More specifically (see Fig. 1), the objectives were to:

1. explore how nutrient concentration, size and turbidity of a lake affect the total fish biomass and the fish species (cyprinids vs. percids) interactions,
2. study how the characteristics of lakes affect the target catch and outcome of biomanipulation, and
3. evaluate the applicability of experimental gillnetting as a research tool especially in estimating the target catch of biomanipulation and the consequent changes in the fish biomass and community structure.

# 6. Material and methods

## 6.1. Study and control lakes

### 6.1.1. Summarized characteristics

The whole set of lakes in this thesis includes 54 lakes or basins (Table 1). In Table 1, the lakes are divided into three groups that are sorted according to area. The first group contains the most studied and biomanipulated lakes. The second group includes the non-biomanipulated lakes that have fishery and water quality information. The third group consists of the water quality reference lakes from the data basis (Hertta) of the Finnish Environment Institute.

The size of the lakes ranged between 8 and 4018 ha and mean and maximum depths between 0.3 and 11.2 m, and 1 and 39.5 m, respectively. According to the classification by Wetzel (1983), the trophic state of the lakes varied from mesotrophic to eutrophic (average value in the growing season in 1 m depth: 12–130 $\mu$g TP l$^{-1}$). According to the algal biomass, the trophic state of the lake set ranges from oligotrophic to hypereutrophic (2–107 $\mu$g chlorophyll *a* l$^{-1}$). Some of the lakes were turbid while other had clear water (Secchi depth: 0.5–4.3 m). The average

**Table 1.** Characteristics of study lakes.

| Lake | Year | Area | $z$ | $z_m$ | C. a. | TP | TN | chl $a$ | $S_d$ | Fishes | $T_{BPUE}$ | Cyp% | Article |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Takajärvi | 1997–2001 | 15 | 2.1 | 3.8 | 2.46 | 38 | 700 | 41 | 1.4 | 6 | 2.06 | 50.7 | I, II, VI |
| Etujärvi | 1997–2001 | 16 | 3.2 | 5.1 | 3.52 | 38 | 690 | 45 | 1.4 | 5 | 1.46 | 44.0 | I, II, VI |
| Otalampi | 1997–2001 | 31 | 3.3 | 6.8 | 1.44 | 24 | 524 | 30 | 2.3 | 6 | 1.15 | 57.7 | I, II, IV, VI |
| Rusutjärvi | 1997–2001 | 133 | 2.0 | 3.5 | 9.6 | 50 | 1066 | 44 | 0.8 | 10 | 3.20 | 76.6 | I, II, VI |
| Pusulanjärvi | 1997–2001 | 207 | 4.5 | 9.5 | 226 | 47 | 853 | 24 | 1.1 | 13 | 2.23 | 61.1 | I, II, VI |
| Enäjärvi | 1997–2001 | 492 | 3.4 | 10 | 34 | 102 | 1019 | 57 | 0.7 | 10 | 2.80 | 63.2 | VI |
| Tuusulanjärvi | 1997–2001 | 592 | 3.2 | 10 | 92 | 93 | 1176 | 49 | 0.6 | 12 | 3.48 | 74.5 | I, II, VI |
| Lehijärvi | 1997–2001 | 704 | 6.0 | 18 | 83 | 37 | 592 | 15 | 2.0 | 13 | 1.78 | 53.4 | I, II, VI |
| Äimäjärvi | 1997–2001 | 852 | 2.6 | 10 | 93 | 58 | 835 | 30 | 1.2 | 12 | 3.34 | 68.4 | I, II, VI |
| Ä1 | 1997–2001 | 370 | 2.0 | 4 | 53 | 71 | 1002 | 40 | 0.9 | 12 | 4.59 | 75.7 | I, II, V, VI |
| Ä2 | 1997–2001 | 480 | 3.0 | 10 | 40 | 44 | 668 | 20 | 1.5 | 10 | 2.09 | 61.2 | I, II, V, VI |
| Hiidenvesi# | 1997–2001 | 2910 | 6.6 | 33 | 934 | 66 | 1097 | 31 | 0.7 | 15 | 2.71 | 66.5 | I, II, VI |
| H1 | 1997–2001 | 160 | 0.9 | 4 | – | 88 | 1159 | 39 | 0.5 | 12 | 3.31 | 72.7 | I, II, IV, VI |
| H2 | 1997–2001 | 260 | 2.0 | 4.5 | – | 87 | 1152 | 46 | 0.5 | 10 | 3.39 | 76.3 | I, II, III, VI |
| H3 | 1997–2001 | 360 | 2.6 | 6 | – | 52 | 1065 | 26 | 0.7 | 12 | 2.69 | 58.2 | I, II, VI |
| H4 | 1997–2001 | 970 | 11.2 | 33 | – | 37 | 1011 | 14 | 1.0 | 13 | 1.43 | 58.8 | I, II, VI |
| R. Valkjärvi | 1999 | 8 | 4.5 | 9 | 0.36 | 14 | 353 | 6 | 2.5 | 4 | 0.53 | 12.2 | I |
| Hervonjärvi | 1998 | 8 | 3.5 | 13 | 0.29 | 30 | 649 | 8 | 3.0 | 2 | 1.75 | 11.5 | I |
| Gallträsk | 1999 | 11 | 1.0 | 1.7 | 0.82 | 45 | 760 | 13 | 1.7 | 3 | 6.31 | 74.6 | I |
| Pakkaselanjärvi | 1999 | 12 | 4.7 | 14 | 5.00 | 18 | 776 | 9 | 1.6 | 5 | 0.48 | 65.1 | I |
| Kaukasenjärvi | 1999 | 13 | 3.6 | 6 | 5.68 | 30 | 855 | 11 | 1.6 | 5 | 1.26 | 69.7 | I |
| Kyynäröjärvi | 1998 | 24 | 1.3 | 3 | 29.16 | 61 | 2115 | 26 | 0.7 | 7 | 0.59 | 55.4 | I |
| Iso Vehkajärvi | 1998 | 32 | – | 4 | 7.08 | 30 | 773 | 13 | 1.0 | 5 | 0.97 | 62.8 | I |
| Kastanajärvi | 1998 | 33 | 3.5 | 9 | 2.85 | 17 | 365 | 2 | 4.2 | 4 | 0.79 | 32.1 | I |
| Pannujärvi | 1998 | 36 | 3.8 | 10 | 2.36 | 27 | 442 | 13 | 2.2 | 2 | 1.15 | 67.3 | I |
| Harasjärvi | 1999 | 41 | 2.4 | 5 | 2.50 | 24 | 544 | 20 | 2.0 | 5 | 1.17 | 77.4 | I |
| Lippajärvi | 1999 | 57 | 2.2 | 4.5 | 6.46 | 130 | 1100 | 33 | 0.6 | 10 | 3.66 | 60.7 | I |
| Ekojärvi | 1998 | 73 | 2.5 | 7 | 114.20 | 24 | 733 | 12 | 1.3 | 8 | 0.50 | 53.3 | I |
| Lehee | 1998 | 104 | 1.5 | 2 | 8.44 | 31 | 660 | 17 | 1.3 | 8 | 1.80 | 70.0 | I |
| Kataloistenjärvi | 1999 | 107 | 1.2 | 1.9 | 10.68 | 31 | 735 | 20 | 1.3 | 6 | 4.55 | 75.7 | I |
| Teuronjärvi | 1998 | 132 | 1.8 | 5 | 27.77 | 55 | 914 | 46 | 1.4 | 6 | 1.62 | 64.3 | I |
| N. Valkjärvi | 1999 | 152 | 6.8 | 12 | 6.51 | 28 | 640 | 24 | 1.6 | 8 | 1.89 | 60.7 | I |
| Pitkäjärvi | 1999 | 171 | 2.3 | 5.6 | 65.81 | 110 | 590 | 22 | 0.7 | 11 | 4.22 | 91.2 | I |
| Tevänti | 1999 | 194 | – | 9 | 14.07 | 22 | 471 | 6 | 2.4 | 4 | 0.58 | 60.1 | I |
| Suolijärvi | 1998 | 203 | 4.7 | 10.4 | 56.81 | 27 | 778 | 23 | 1.7 | 8 | 0.71 | 65.7 | I |
| Ormajärvi | 1998 | 653 | 10.7 | 30 | 79.52 | 28 | 726 | 11 | 2.3 | 13 | 1.05 | 57.9 | I |
| H. Pyhäjärvi | 1998 | 949 | 10.1 | 35 | 78.00 | 18 | 517 | 10 | 3.0 | 10 | 0.60 | 60.0 | I |
| Enonselkä* | 1998 | 2600 | 6.8 | 33 | 84 | 27 | 509 | 9 | 2.3 | 12 | 1.23 | 40.1 | I |
| K. Vesijärvi | 1999 | 4018 | 6.2 | 39.5 | 221 | 20 | 375 | 12 | 1.9 | 13 | 1.50 | 55.0 | I |
| V1 | 1999 | 1553 | 3.6 | 22 | 160.9 | 27 | 400 | 17 | 1.4 | 13 | 1.05 | 56.2 | I |
| V2 | 1999 | 2465 | 7.9 | 39.5 | 60.1 | 12 | 350 | 6 | 2.3 | 11 | 1.95 | 53.7 | I |
| Stora Lonoks | 1997–2001 | 48 | – | – | 48.2 | 82 | 864 | – | 0.5 | – | – | – | VI |
| Valkjärvi Vitsjön | 1997–2001 | 72 | 3.4 | 12.1 | 2.94 | 23 | 458 | 7 | 1.8 | – | – | – | VI |
| Vuorenselkä | 1997–2001 | 92 | – | – | – | 79 | 1054 | 107 | 0.8 | – | – | – | VI |
| Källträsket | 1997–2001 | 105 | – | – | – | 36 | 436 | 25 | 1.9 | – | – | – | VI |
| Tjusträsk | 1997–2001 | 114 | 4.4 | 9.8 | 410.7 | 74 | 1000 | 33 | 0.7 | – | – | – | VI |
| Averia | 1997–2001 | 138 | 3.2 | 6.5 | 232.1 | 80 | 1016 | – | 0.8 | – | – | – | VI |
| K. Pyhäjärvi | 1997–2001 | 138 | 0.3 | 1 | – | 22 | 570 | – | 1.4 | – | – | – | VI |
| Vikträsk | 1997–2001 | 187 | 4.4 | 15 | 477.5 | 59 | 985 | 31 | 0.8 | – | – | – | VI |
| Tiiläänjärvi | 1997–2001 | 213 | 4.4 | 10.3 | 38.1 | 53 | 950 | 29 | 0.5 | – | – | – | VI |
| Sakara | 1997–2001 | 231 | – | – | 132.3 | 22 | 340 | 6 | 2.8 | – | – | – | VI |
| Kytäjärvi | 1997–2001 | 267 | 4.5 | – | 138.7 | 48 | 846 | 22 | 0.9 | – | – | – | VI |
| Humaljärvi | 1997–2001 | 429 | 4.0 | – | 11.7 | 32 | 404 | 13 | 0.9 | – | – | – | VI |
| Kernaalanjärvi | 1997–2001 | 446 | – | – | – | 45 | 978 | 25 | 1.1 | – | – | – | VI |
| Nuijamaanjärvi | 1997–2001 | 528 | – | – | – | 26 | 666 | 9 | 1.5 | – | – | – | VI |
| Punelia | 1997–2001 | 819 | – | – | 101.8 | 21 | 240 | 4 | 4.3 | – | – | – | VI |
| Vanajavesi# | 1997–2001 | 1030 | – | – | – | 58 | 1484 | 36 | 0.9 | – | – | – | VI |

Year = study year, Area = lake area (ha), $z$ = mean depth (m), $z_m$ = maximum depth (m), C. a. = catchment area (km²), TP = total phosphorus (µg l⁻¹), TN = total nitrogen (µg l⁻¹), chl $a$ = chlorophyll $a$ (µg l⁻¹), $S_d$ = Secchi depth (m), Fishes = number of fish species caught by gillnetting, $T_{BPUE}$ = total biomass per gillnet, Cyp% = percentage of cyprinids from $T_{BPUE}$. Article refers to the **I–VI** articles of this thesis. – = missing data. * = basin of L. Vesijärvi of Lahti, # = the whole area of the lake is not included in the study.
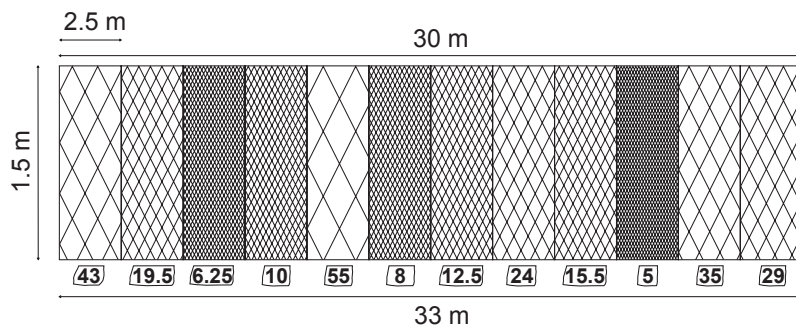
**Fig. 2.** Schematic illustration of Nordic multimesh gillnet. Length of upper and bottom rope, and width and height of panel are shown. Small tags below panels indicate mesh size.

total biomass per unit effort (BPUE, arithmetic mean) ranged between 0.5–6.3 kg net$^{-1}$. The fish community varied from 2 species lakes to multispecies lakes (15 species) and from percid to cyprinid domination.

### 6.1.2. Selection criteria

In the fish community study (**I**), the lakes consisted of 36 lake basins that were part of several simultaneous projects, using similar fish sampling methods.

In the zooplankton and fish communities study (**II**), all nine lakes had more or less severe eutrophication problems and had an extensive research programme.

In the methodological gillnetting studies (**III**, **IV**), Lake Hiidenvesi was selected due to its suitability for trawling and due to its high fish biomass. Lake Otalampi had clearly lower fish biomass and higher transparency compared to Hiidenvesi. Both lakes had been monitored for several years.

In the biomanipulation studies (**V**, **VI**), the ten study lakes, including 14 basins, were selected due to their eutrophication problems and because of the high cyprinid biomass. In addition, the lakes had background information and the mass removal of fish was considered possible. The control lake-group of 16 lakes was selected from the database (Hertta) of the Finnish Environment Institute for comparison in water quality responses with the biomanipulated lakes. The size and nutrient concentration in the control lakes was within the ranges of the study lakes.

### 6.2. Mass removal

During the study years 1997–2001, mass removal was conducted in 10 lakes including 14 basins (Table 1, first lake group, **V**, **VI**). The fishing methods were mainly motorised seining in the autumn or in the winter and fyke netting during the spring spawning time. The seining based on the localisation of shoals by echosounder (Turunen et al. 1997, Sammalkorpi 2000). Usually, the people of local lake protection associations conducted fyke netting, whereas a professional team was hired for seining.

The target catch was set for 200 kg ha$^{-1}$ in three years based on the successful biomanipulation of Vesijärvi (Horppila et al. 1998). In each fishing day, the weight of the mass removal catch (MRC) was estimated from the volume of the catch. The species composition was estimated from subsamples of ca. 30 kg.

### 6.3. Fish sampling

#### 6.3.1. Experimental gillnetting and trawling

The fish samples were taken mostly in July–August between years 1997 and 2001 by test fishing with NORDIC multimesh gillnets (**I–VI**). The gillnet (Fig. 2) consists of twelve $1.5 \times 2.5$ m panels having mesh sizes 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm (from knot to knot) (Appelberg et al. 1995, Kurkilahti 1999, **IV**). The mesh sizes of the panels followed a geometric series (Baranov 1914) the adjacent mesh sizes ratio being on average 1.24 in order to reduce size selectivity (Kurkilahti 1999).

The sampling procedure was stratified and random (Kurkilahti 1999). The lakes were divided into depth zones from which the net sites were chosen randomly (Fig. 3). In the shallowest zone only bottom gillnets were used. Depending on the water depth, surface and 1–2 mid-water gillnets were used in addition to bottom nets. In **I**, **II**, **V** and **VI**, fishing time was one night (12 h). The sampling effort varied between 10–80 gillnets per lake per year, and it was adjusted to the size of the lake or depth zone (Table 2). Every lake and depth zone was sampled 2–5 times per year. In the methodological studies **III** and **IV**, the gillnetting was conducted diurnally. In **III**, the set time was 4 hours and the fishing effort was $6 \times 12$ gillnets. In **IV**, continuous 12 h and 4 h set time was compared to three consecutive 4 h or four consecutive 1 h set time, respectively. In the previous experiment, the sampling effort was 24 continuous (12 h) and $3 \times 24$ consecutive (4 h) gillnets within one lake. In the latter experiment, the corresponding effort was 12 continuous and $4 \times 12$ consecutive gillnets.

Each gillnet and panel was treated individually. The catch was assorted to species and then counted and weighed. For length distributions,
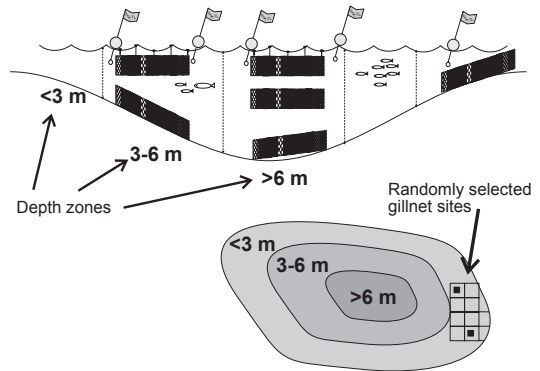


**Fig. 3.** Schematic illustration of stratified random sampling.

every fish was measured (TL, 1 cm size-classes), or a random sample of at least 50 individuals was taken on every fishing day.

Trawl was used for fish sampling in addition to gillnets in **III**. A small pelagic pair-trawl (theoretical opening $1.5 \text{ m} \times 5 \text{ m}$, cod-end 3 mm) was towed (mean: 1.34 m s⁻¹) diurnally in 4 h periods in two depth layers (0–1.5 m and 3–4.5 m). Total fishing effort was 19 trawl hauls. Subsample of ca. 30 kg was taken from every trawl

**Table 2.** Stratified sampling procedure of biomanipulated lakes.

| | Area | $z_m$ | < 3 m tot. | 3–6 m | | | 6–12 m | | | | 12–20 m | | | | | Total FE | FE:ha |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | sur | bot | tot. | sur | mid1 | bot | tot. | sur | mid1 | mid2 | bot | tot. | | |
| Takajärvi | 15 | 3.8 | 6 | 2 | 2 | 4 | – | – | – | – | – | – | – | – | – | 10 | 0.67 |
| Etujärvi | 16 | 5.1 | 4 | 3 | 3 | 6 | – | – | – | – | – | – | – | – | – | 10 | 0.63 |
| Otalampi | 31 | 6.8 | 6 | 3 | 3 | 6 | – | – | – | – | – | – | – | – | – | 12 | 0.39 |
| Rusutjärvi | 133 | 3.5 | 20 | – | – | – | – | – | – | – | – | – | – | – | – | 20 | 0.15 |
| Pusulanjärvi | 207 | 9.5 | 12 | 5 | 5 | 10 | 6 | 6 | 6 | 18 | – | – | – | – | – | 40 | 0.19 |
| Enäjärvi | 492 | 10 | 18 | 16 | 16 | 32 | – | – | – | – | – | – | – | – | – | 50 | 0.10 |
| Tuusulanjärvi | 592 | 10 | 30 | 5 | 5 | 10 | 5 | 5 | 5 | 15 | – | – | – | – | – | 55 | 0.09 |
| Lehijärvi | 704 | 18 | 16 | 7 | 7 | 14 | 8 | 7 | 7 | 22 | 2 | 2 | 2 | 2 | 8 | 60 | 0.09 |
| Äimäjärvi | 852 | 10 | 34 | 6 | 6 | 12 | 5 | 5 | 4 | 14 | – | – | – | – | – | 60 | 0.07 |
| Ä1 | 370 | 4 | 24 | – | – | – | – | – | – | – | – | – | – | – | – | 24 | 0.06 |
| Ä2 | 480 | 10 | 10 | 6 | 6 | 12 | 5 | 5 | 4 | 14 | – | – | – | – | – | 36 | 0.08 |
| Hiidenvesi* | 2910 | 33 | 40 | 9 | 9 | 18 | 4 | 4 | 4 | 12 | 3 | 3 | 2 | 2 | 10 | 80 | 0.05 |
| H1 | 160 | 4 | 4 | – | 2 | 2 | – | – | – | – | – | – | – | – | – | 6 | 0.04 |
| H2 | 260 | 4.5 | 5 | – | 5 | 5 | – | – | – | – | – | – | – | – | – | 10 | 0.04 |
| H3 | 360 | 6 | 10 | 4 | 4 | 8 | – | – | – | – | – | – | – | – | – | 18 | 0.05 |
| H4 | 970 | 33 | 14 | 5 | 5 | 10 | 4 | 4 | 4 | 12 | 3 | 3 | 2 | 2 | 10 | 46 | 0.05 |

sur, bot, mid1 and mid2 = gillnets in the surface, bottom, mid–water 3 m and mid-water 6 m, respectively. * = whole area of the lake is not included in the study. In the deeper basins (H3 and H4) of Hiidenvesi, the depth zones were < 5, 5–10, 10–20 and > 20 m; mid1 was in 6 m and mid2 in 12 m depth. FE = fishing effort, FE:ha = fishing effort in relation to the lake area.

haul and assorted to species before counting and weighing. At least 50 individuals of each species in one haul were measured (total length, 1 mm accuracy). The trawl data were transformed to number ha$^{-1}$ and kg ha$^{-1}$ estimates.

### 6.2.3. Age and growth

The age of roach was determined from scales and the age of perch from opercular bones (**V**). The growth was backcalculated with the Fraser-Lee procedure for roach and with the Monastyrsky procedure for perch (Bagenal & Tesch, 1978).

### 6.3. Water chemistry and plankton studies

Samples for water quality (surface water 0–2 m) were taken during the growing season at the deepest part of each basin (**I–VI**). The analyses of TP, TN and chlorophyll *a* (chl *a*) were conducted according to the Finnish standard methods (Niemi & Heinonen 2003). The number of observations per growing season ranged from 5 to 17 in the first lake group (Table 1), between 2–4 in the second group and between 1–12 in the third group.

The zooplankton and phytoplankton samples were taken only from the biomanipulated lakes and from the deepest part of each basin (Tallberg et al. 1999, **II**, **V**, **VI**). Phytoplankton samples (5–10 per basin per year) were taken during the growing season from 0–2 m depth with a tube sampler and preserved with Lugol solution. Phytoplankton taxa were identified and cells counted by using an inverted microscope technique (modified from Utermöhl 1958, see e.g. Tikkanen & Willén 1992). The results were converted to wet weight (Edler 1979, Tikkanen & Willén 1992).

Zooplankton samples (3–6 per basin each year) were collected mainly in July–August. The samples (28–105 l) were taken with tube samplers from the whole water column in shallow lakes or from surface water (0–4 m) in deeper basins (see Tallberg et al. 1999, **II**, **V** for details). After filtration (50-$\mu$m net) and preservation

(formaldehyde 4%), the crustacean zooplankton were identified, calculated and measured. The results were transformed into carbon contents according to Luokkanen (1995). The potential grazing pressure (PGP) was estimated according to Jeppesen et al. (1994).

### 6.4. Statistical analyses

In article **I**, the effects of trophic state (TP concentration) and basin morphology (area, mean depth) on different variables of gillnet catch (species no, total BPUE, BPUEs of fishes and cyprinids:percids biomass ratio) were studied with mixed linear models (PROC MIXED in SAS version 8.01). In **II**, linear regression was used to explain the relations between basin area, water quality, zooplankton density and size, and gillnet catch.

In **III** and **V**, the between-hours or years differences in the gillnet CPUE were tested with ANOVA. Non-parametric sign test was used to test the between-gear differences in species composition and size distribution in **III**. In articles **I–III** and **V**, variables were ln($x$ + 1)-transformed when necessary.

In **IV** and **VI**, the differences between gill-netting method or years were analysed with generalized linear model (PROC GENMOD, SAS, 1999) with the assumption of Poisson or negative binomial distribution (McCullach & Nelder, 1989).

The reduction of gillnet catchability in relation to catch rate (**IV**), measured as share of occupied meshes, was modelled by fitting a segmented nonlinear model (PROC NLMIXED, SAS, 1999) in the data of consecutive and continuous gillnetting.

The responses to biomanipulation in the characters of fish groups, zooplankton, phytoplankton, nutrients and transparency were tested with Kruskal-Wallis non-parametric rank test (**VI**). Before testing the basins were divided into two groups (loC and hiC) according to the attained or unattained mass removal target catch (200 kg ha$^{-1}$ in three years). Control lakes were included as the third lake group in the statistical analyses concerning nutrients, chl *a* and Secchi depth. The relations between the cyprinid BPUE and

the cladoceran biomass, between the cladoceran and phytoplankton biomass, and between MRC and *G. semen* biomass were studied with linear regression. Correlation analyses was used for explaining Secchi depth with chl *a*.

In the summary, principal component analysis (PCA) was used to arrange the gillnet BPUE of different species and species groups on two main components. To normalize the variances, all variables were ln-transformed. The relation between $\log_{10}$-transformed gillnet catch and the following catch in autumn seining was analyzed with mixed linear model (PROC MIXED in SAS version 8.01) including basin and year as explaining variables. Kruskal-Wallis non-parametric rank test was used to test the dependence between relative mass removal efficiency and proportion of improved variables in the biomanipulated lakes.

# 7. Results and discussion

## 7.1. Differences in fish communities in Finnish lakes in relation to different nutrient concentration and lake size

### 7.1.1. Species number

According to the gillnet dataset of 36 lake basins, the number of fish species is positively related to lake area and trophic status (**I**). This was in accordance with the earlier studies (e.g. Tonn et al. 1990, Helminen et al. 2000, Jeppesen et al. 2000). The increasing size of a lake increases the diversity (Matuszek & Beggs 1988) and stability (Tonn et al. 1990) of habitats, thus enabling the survival of number of species with different habitat demands. The high trophic status correlates with the high availability of energy, which is thought to be related to the variety of resource types (Wright 1983). In our study (**I**), the higher species number in eutrophic lakes was mainly due to cyprinids, such as rudd, white bream and blue bream (*Abramis ballerus*), all favouring a eutrophic environment. In general, the most common species in the lakes were perch, roach, ruffe and bream (**I**, **II**), which was congruent with earlier results in Finland (Tonn et al. 1990, Tammi et al. 1999, Helminen et al. 2000).

### 7.1.2. Total BPUE and cyprinids:percids dominance

Both total BPUE and cyprinid BPUE increased with TP concentration (**I**) as found in earlier studies (Persson et al. 1991, Helminen et al. 2000, Jeppesen et al. 2000). Contrary to expectations (Hartmann & Nümann 1977, Svärdson 1976, Kitchell et al. 1977, Leach et al. 1977, Persson et al. 1991, Jeppesen et al. 2000), cyprinids dominated the gillnet catch from mesotrophic to highly eutrophic lakes (**I**, **II**). Thus, no actual shift from percid to cyprinid dominance occurred, although the biomass ratio of cyprinids to percids increased with the phosphorus concentration. As gillnets catch percids more effectively than cyprinids (Prchalová & Kubečka 2004, **III**), the actual domination of cyprinids in the lakes might have been even more pronounced. The reason for the high dominance of cyprinids in Finnish lakes, when comparing to e.g. Swedish lakes (Persson et al. 1991) of same trophic state, is unclear. It could be possible, that the active and selective recreational fishing (Moilanen 2004), as well as the prevalence of low water transparency (SYKE unpublished) favour cyprinids over percids in Finnish lakes.

Lake size may also affect the cyprinids:percids dominance due to lower competition between percids and cyprinids in large lakes. In small eutrophic lakes, perch and roach can severely compete with each other (Persson 1983). In eutrophic, large Lake Vesijärvi (Horppila et al. 2000), both cyprinids and percids were simultaneously abundant. Congruently, we found positive effect of lake area on percid BPUE (**I**). In older studies (Tonn et al. 1990, Ranta et al. 1992), percids dominated fish biomass in small, oligo-mesotrophic forest lakes with few fish species including perch. The acidity of small forest lakes may have contributed to the low biomass of roach (Tammi et al. 2004). Thus in Finland, percids may dominate only in small lakes with few species and low trophic state and in meso-eutrophic large lakes with plenty of different habitats. If the negative effects of cyprinids on perch are more likely in small lakes, the relatively small average size of Finnish lakes (Eloranta 2004) can promote the cyprinids dominance if the lakes are eutrophicated.
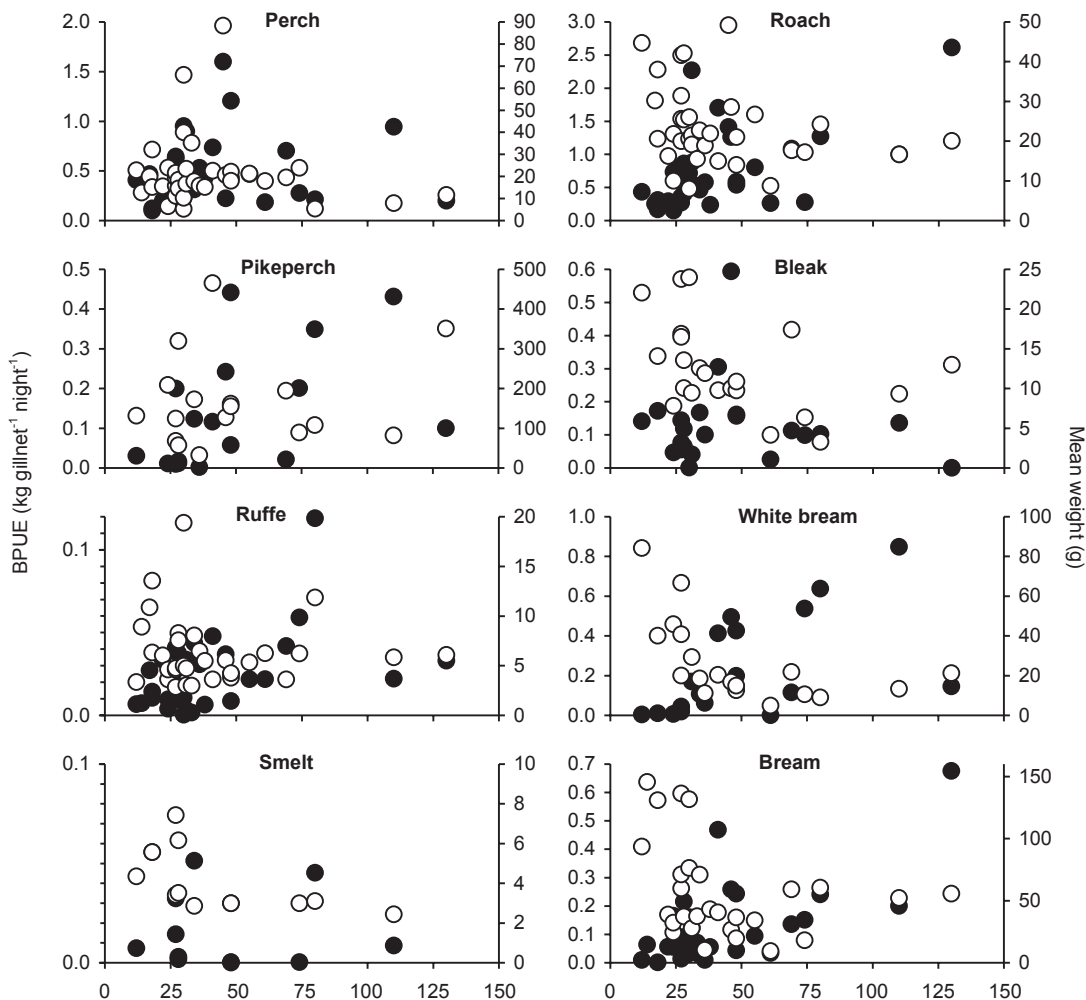
**Fig. 4.** The arithmetic mean BPUE (filled circle) and mean weight (open circle) of fish species in lakes with different TP concentration. Outlier in mean weight of bream (617 g in 28 TP μg l$^{-1}$) is not shown in the picture.

### 7.1.3. Species relations to abiotic and biotic factors

In the species level, cyprinids were not a homogenous group responding similarly to trophic state (**I**). Bream, and especially white bream, seemed to benefit more from strong eutrophication than roach and bleak, which was previously found by Svärdson & Molin (1981) (Fig. 4). This can be explained by interspecific competition. Bream and white bream can feed effectively in turbid waters (Lammens et al. 1987), whereas bleak and roach are adapted to less turbid waters (Lammens et al. 1987, 1992, Winkler & Orellana 1992). However, the ability of roach to feed on

plant material enables it to build high biomass even in very eutrophic conditions (Persson et al. 1991). The low mean size of roach (**II**) and other cyprinids (Fig. 4) in eutrophic lakes support the ability of cyprinids to reproduce effectively and probably also reflect the slow growth rate in dense populations indicating severe food competition. As expected, the dense cyprinid fish stock seemed to strongly change the zooplankton community towards smaller species and lower mean size (**II**). This may also indicate high food competition of fish in eutrophic lakes.

No separate biomass peaks for perch and other percids, pikeperch and ruffe, were detected (**I**) as in the study of Persson et al. (1991) and

Jeppesen et al. (2000). This was partly due to lower nutrient levels of lakes compared to Jeppesen et al. (2000). In addition, high perch biomass was observed in two highly eutrophic lakes. Perch seemed to be related to biotic rather than to abiotic factors. This could be due to the asymmetric competition-predation interaction between perch and roach (Persson 1986, 1987, Persson & Greenberg 1990). Our results support that a dense roach stock has a negative effect on perch biomass in eutrophic lakes (**I**). In addition, water transparency seemed to have a positive effect on perch biomass. We found some evidence that the predation of perch might affect the roach population in mesotrophic lakes but not in eutrophic lakes (**I**). Likewise, the competition effect of roach on perch seems to be valid in mesotrophic lakes but not in higher nutrient concentration. It could be that in eutrophic lakes with a higher number of abundant species, the relations between perch and roach may be hidden behind more complex interactions.

The catch of pikeperch was related both to nutrient content and water turbidity, but the turbidity seemed to have a more significant effect (**I**). The importance of turbidity is likely related to effective feeding in low light (Ali et al. 1977, Disler & Smirnov 1977) and the survival of yearlings (Neuman et al. 1996).

The biomass of ruffe seemed to be dependent on lake size, depth relations and trophic state (**I**). High nutrient concentration had a negative effect in small and deep lakes but a positive effect in large and shallow lakes. This could be due to the higher possibility of eutrophication-induced oxygen depletion in small and deep lakes (Wetzel 1983) that greatly affects this strict benthivore (Bergman 1988, 1991). In large and shallow lakes, eutrophication may increase suitable habitats and food availability for ruffe without severely reducing the oxygen content.

As analysed with the PCA, the gillnet data deviated into several components of which the first two explained 65% of the total variation. The first factor (explaining 44% of total variation) was regarded as "the eutrophication component" and it had a high score for white bream, bream, total BPUE, cyprinids, pikeperch and ruffe (in this order) (Fig. 5). Burbot (*Lota lota*), vendace, bullhead (*Cottus gobio*), salmonids,
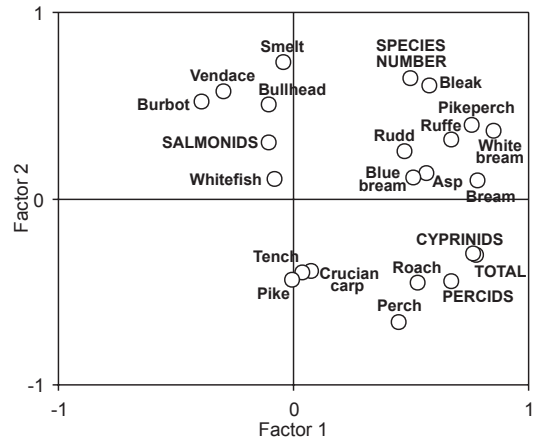


**Fig. 5.** Values of total BPUE, species BPUEs and species number along first two factors, "the eutrophication component" and "lake volume component", in PCA analysis. SALMONIDS include coregonids and smelt.

and whitefish had negative values for this factor. The second factor was "the lake volume component". It explained 21% of the variation and had a high score for smelt, species number, bleak, vendace and burbot. The above-mentioned species are pelagic or demand cool and well-oxygenated water (Colby et al. 1972, Nümann 1972, Tammi et al. 1999, Vinni et al. 2000). The high score of species number can be explained by the linkage between lake size and habitat stability (Matuszek & Beggs 1988) and diversity (Tonn et al. 1990), as explained above. Perch, roach, pike, tench and crucian carp had high negative scores for "the lake volume component". This group of species included littoral-oriented or general species. Both the mixed linear model (see above) as well as the PCA indicated that white bream and bream favour higher nutrient concentrations than roach and bleak. Congruently, pikeperch and ruffe seem to be better adapted to eutrophic conditions compared to perch.

## 7.2. Experimental gillnetting as a fish sampling method

### 7.2.1. Gillnet CPUE as an index of fish abundance

The factors affecting the reliability of gillnet CPUE as an index of fish abundance include activ-

ity, selectivity, avoidance, and saturation (Hamley 1975, Minns & Hurley 1988, Borgstrøm 1992, Enderlein & Appelberg 1992, Hansson & Rudstam 1995, Hansen et al. 1998). Activity, and thus CPUE, is largely dependent on water temperature and weather conditions. In our studies, CPUE was considerably lower in cold and rainy summers in 1998 and 2000 compared to warm summers of 1997, 1999 and 2001 (**VI**). Part of this might be due to lower fry production, slower growth and later recruitment of 0+ fish to Nordic nets, but lower activity may also have affected. The effects of varying fish activity on gillnet CPUE can be levelled down to some extent by sampling several times within the season and by keeping a few days gap between samplings. The activity of fishes varies a lot also during a short time scale (Helfman 1981), resulting in a considerable diurnal variation in gillnet CPUE (**III**, **IV**).

Due to selectivity, the reliability of gillnet CPUE index can largely depend on the structure of the fish community. As compared to the trawl catch, gillnets considerably underestimated the relative abundance of small (< 5 cm) fish (**III**, Fig. 6). Thus, the higher the proportion of small fish, the more unreliable is the CPUE index. For fish ≥ 6 cm, however, the CPUE index of abundance can be quite reliable (**III** and Fig. 7).

The catching efficiency of a gillnet strongly declines as the fish accumulate in it during the 12 h set time (**IV** and Fig. 8). This results in relatively lower CPUEs in high than in low fish density. Avoidance, rather than space limitation, seemed to be the main reason for decreasing efficiency because the reduction in catching efficiency was relatively higher in a clear water lake and during daytime.

When considering a biomanipulated lake and a possible positive response in transparency, the gillnet CPUE can decline besides due to lowered fish density also due to increased visual avoidance in clear water conditions (**IV**). It is also possible that the increased proportion of piscivores after biomanipulation reduces catchability of cyprinids due to declining migration from littoral to pelagial (Brabrand & Faafeng 1993). If the original fish density before biomanipulation is very high and thus the catching efficiency of gillnet decreases noticeably during 12 h set time, the responses for fish removal in gillnet CPUE can be minor due to increased catching efficiency after reduced fish abundance. The latter may have been the situation in our biomanipulation experiments, as the original CPUE was often high and decreases in the cyprinid CPUEs were mainly modest (**VI**).

Despite the varying reliability of gillnet CPUE as an index of fish abundance, is it possible to predict a mass removal catch on the grounds of gillnet results? According to our results, there is a relation between gillnet BPUE and the corresponding BPUE in autumn seining (Fig. 9). Roughly it can be estimated that gillnet BPUEs of 1, 2 and 4 kg predicts seine BPUEs of 500, 900 and 1300 kg, respectively. However, the between-year variation is high (Table 3), and the relation is not linear but becomes gentler as the gillnet BPUE increases. This is not expectable, as the reduced efficiency of gillnets in high fish densities should affect vice versa: steeper relation with higher gillnet BPUE. The numerous factors affecting the fish aggregation and the seine catch, including lake size and depth relations, size of seine, biological interactions, weather conditions and turbidity (see Sammalkorpi 2000 and the references therein), should have effects on the relation, as well.

## 7.2.2. Gillnet catch in reflecting fish community structure

The consistency of gillnet CPUE in reflecting fish community structure is dependent on the factors that affect the fish activity and gillnet efficiency (Hamley 1975). More active species tend to have higher proportions compared to stationary species. In our study, this was seen as a low proportion of pike compared to actively swimming percids and cyprinids (**I**, **III**). The diurnal changes in species activity reverberated to the gillnet catch composition (**III**, **IV**). White bream and pikeperch had relatively high catches during night and perch during daytime.

The mechanical selectivity of gillnets strongly affects the species and size structure of the catch (Hamley 1975). According our comparison of gillnet and trawl (**III**), gillnets gave unreliable estimates of small individuals and species with low catchability due to smooth body outline, e.g. smelt. In addition, the proportion of large speci-
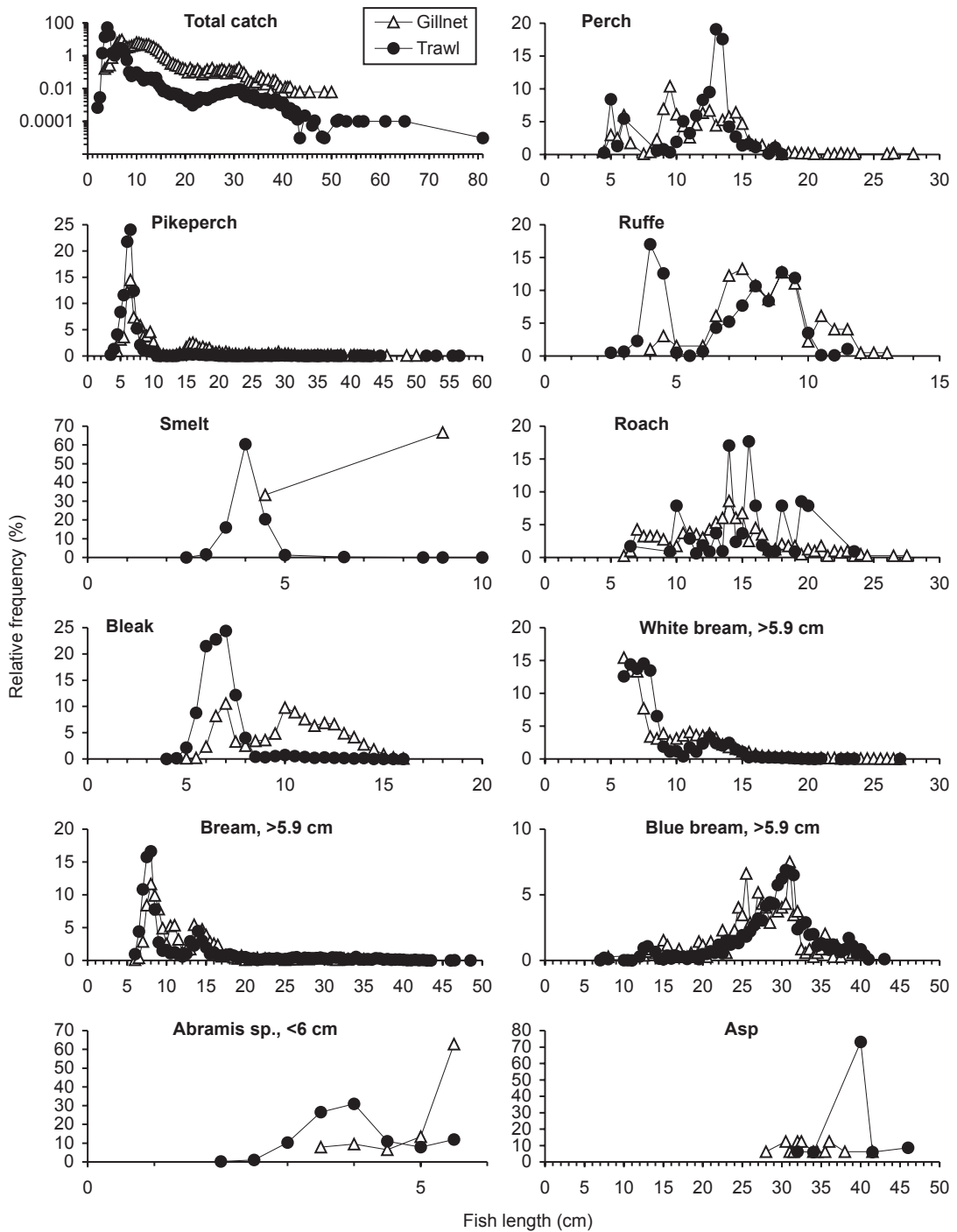
**Fig. 6.** Length distributions of individual species and total catch in gillnet (open triangles) and trawl (closed circles) catch in August. Note the logarithmic scale for total catch. Combined data of two years 2001 and 2002 (only data of 2001 was presented in **III**).
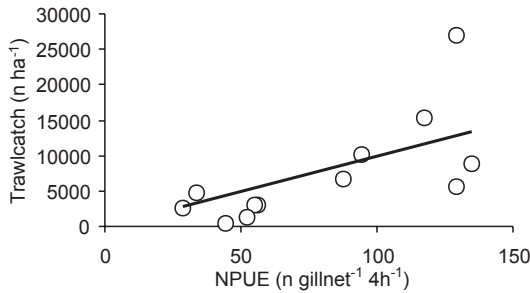
**Fig. 7.** Relation between gillnet NPUE and fish density estimated by trawl catch. Trawl catch ($n$ ha$^{-1}$) = 99.3 × gillnet catch ($n$ gillnet$^{-1}$ 4h$^{-1}$), $r^2$ = 0.451, $F$ = 9.032, $P$ = 0.013. Combined data of two years 2001 and 2002 (only data of 2001 was presented in **III**). Only fish ≥ 6 cm are included.
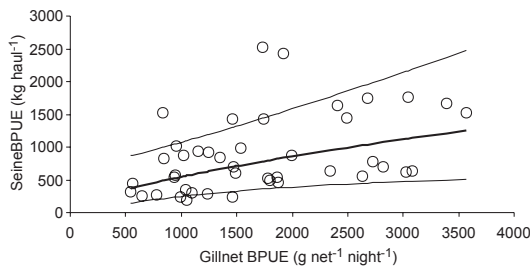


**Fig. 9.** Relation between gillnet BPUE and BPUE in seining in the following autumn. Each circle represents a lake-year. Predicted values and 95% confidence limits of mixed linear model (Table 3) are shown.



**Fig. 8.** Curve of decreasing catching efficiency for Nordic multimesh gillnet (nlin) in turbid (**a**) and clear water lake (**b**) (**IV**). In relation to fish accumulation, consecutive gillnetting represents the catch of constant efficiency and continuous gillnetting is the catch of declined efficiency. Accumulation % is the mean number catch in a panel of a given mesh size divided by number of meshes in the same panel. Each mesh size (5–55 mm) is marked with a different symbol. Hypothetical curve for stable efficiency (lin) is also shown.

composition in the catch (**IV**). This was probably due to quite similar diurnal rhythm of the main species resulting in comparable possibility to encounter an empty gillnet. However, if the activity pattern of fishes is highly different the accumulation likely affects the species proportions in gillnets (see Minns & Hurley 1988).

### 7.3. Varying responses to biomanipulation

#### 7.3.1. Fish

In the biomanipulation study of 14 basins, the target mass removal catch (200 kg ha$^{-1}$ 3 year$^{-1}$) was attained in seven basins (Fig. 10, **VI**). According to the achieved or non-achieved target MRC, the basins were respectively divided into two groups hiC and loC both including 7 basins. The proportion of cyprinids in the MRC varied between 63% and 97% in the basins. Roach and bream were usually the most important removed species. Besides roach, small perch

mens (ca. > 30 cm) of *Abramis* sp. was low compared to the trawl catch. Some piscivores probably avoided or escaped from the trawl. For other fish species and size classes, the gillnet CPUE was quite congruent with the trawl estimate.

The decrease of gillnet catchability due to fish accumulation had minor effect on species

**Table 3.** Results of the general linear model predicting seine BPUE (log$_{10}$ kg haul$^{-1}$) from gillnet BPUE (log$_{10}$ grams of cyprinids net$^{-1}$ night$^{-1}$) and year. Model: d.f. = 42, $r^2$ = 0.418, $P$ < 0.001.

| Parameter | Estimate | S.E. | $P$ |
|---|---|---|---|
| Intercept | 0.595 | 0.570 | 0.303 |
| log$_{10}$ cyprinids | 0.653 | 0.178 | 0.001 |
| 1997 | 0.283 | 0.125 | 0.030 |
| 1998 | 0.089 | 0.113 | 0.438 |
| 1999 | 0.296 | 0.108 | 0.010 |
| 2000 | 0.247 | 0.110 | 0.030 |
| 2001 | 0.000 | | |

**Fig. 10.** Total mass removal catch (MRC) and species' MRCs from autumn 1997 to spring 2001 in study basins. Weight of catch is presented as columns and the total number catch as open squares. Basins are divided into two categories (loC: target catch 200 kg ha$^{-1}$ 3 yr.$^{-1}$ not achieved and hiC: target catch achieved).



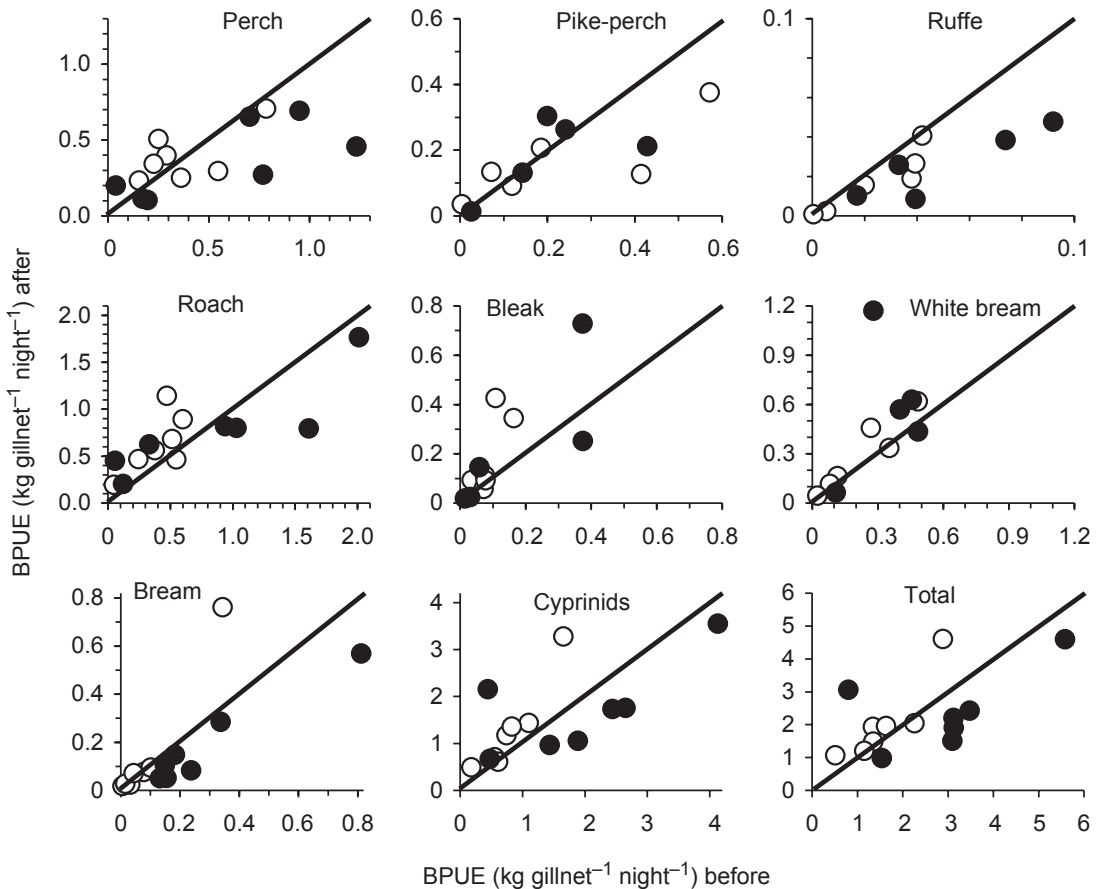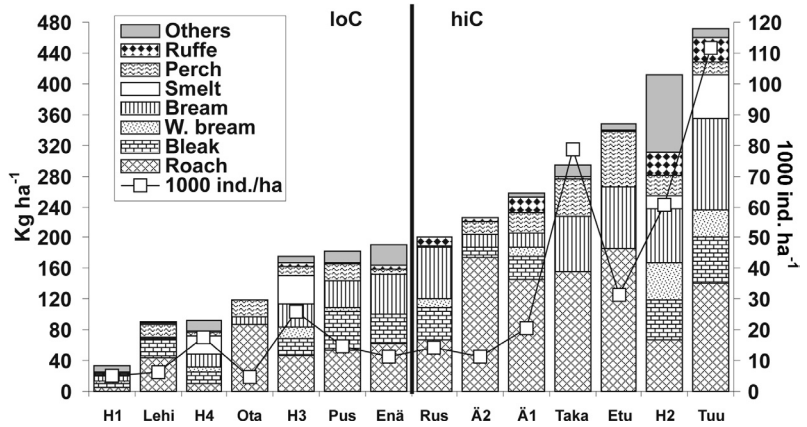**Fig. 11.** BPUEs of fish species before (*x*-axis) and after (*y*-axis) biomanipulation in loC (open circles) and hiC basins (closed circles). Below the black line BPUEs decreased and above the line BPUEs increased.

and bleak were among the major species in less eutrophic lakes. In Hiidenvesi, blue bream, bream and smelt had similar MRC with roach.

The total gillnet BPUE decreased in most of the hiC basins but increased in almost all of the loC basins (**VI**, Fig. 11). This could indicate that a moderate mass removal effort can affect negatively and increase the fish biomass due to

responses in reproduction and growth rate. Even in the hiC basins, the magnitude of responses in the total gillnet BPUE was moderate (**VI**), and no 75% reductions (Meijer et al. 1999) were observed. This can be due to several reasons. Firstly, the fishing effort was too low to induce severe reduction in the fish biomass. However, in the most efficiently fished lakes, the effort should have been high enough in relation to the target catch estimated by the equation of Jeppesen & Sammalkorpi (2002) (**V**, **VI**). Secondly, the fish production may have compensated the fished biomass. Evidence for this was found from many lakes as the reproduction and the fish growth increased considerably (Rask et al. in print, **V**, **VI**). Thirdly, the catching efficiency of gillnets may have increased as the fish density reduced, as mentioned above.

Besides the changes in the total biomass, the responses in the fish community structure have likely had wide-ranging effects in the lake eco-system. The general shifts in the fish assemblage were (1) the reduction of large cyprinids, (2) the expansion of the cyprinid fry and, to the lesser extent, percid juveniles, and (3) the increase in the proportion of piscivores (**VI**). The shifts likely have depressed the internal loading and nutrient recycling due to fish. The reduction in the large cyprinids and the increment in juveniles result in less individuals disturbing the bottom sediment and releasing nutrients, and more specimens eating zooplankton but not adding "new" nutrients from the sediment (Shapiro & Carlson 1982, Tatrai & Istvanovics 1986, Lammens et al. 1990, Horppila & Kairesalo 1992, Breukelaar et al. 1994, Vinni et al. 2000). The smaller average size of cyprinids enables better top-down control by piscivores (Lammens 1999). In addition, the observed higher proportion of piscivores can alter the behaviour of prey, reducing the migration from shelter to the open water (Brabrand & Faafeng 1993). With the diminishing littoral-pelagic coupling, the nutrients recycling from the littoral to the pelagial (Schindler et al. 1996) and the predatory pressure on pelagic zooplankton (Gliwicz & Dawidowicz 2001) decrease. The direct effect of nutrient removal due to fish bound nutrients might also have contributed as TP concentration decreased most evidently in the basins where the fish removal was highest in

relation to the water volume (**VI**). Moreover, it seems reasonable, that part of the nutrients that otherwise could be used to algal production, are absorbed to fast growing fish biomass, even though especially YOY fish mobilize and excrete nutrients as well (e.g. Post et al. 1997). However, as the water P concentration and P storage in the sediment of shallow lakes are in balance (Søndergaard et al. 2001), the water P concentration may not reduce until the sediment is impoverished or the P flux is otherwise restricted.

As to the individual fish species, roach and bream decreased as a result of the biomanipulation (Fig. 11). In 1997, the average BPUEs of roach and bream were higher in the hiC basins compared to loC basins (Tukey, $P < 0.1$ and $P < 0.05$, respectively). Until 2001, roach and bream decreased in most of the hiC basins but increased or remained the same in almost all loC basins so that the lake groups differed no more. The reason for the clear response of these species could be high catchability. The BPUEs of white bream and bleak increased in almost every basin. For white bream, the increment was higher in the hiC lakes, yet not significantly. The response might reflect the low catchability of this species, and the higher production due to released resources. The response of bleak was negative soon after the biomanipulation started (Olin & Ruuhijärvi 2000), but the BPUE increased in many lakes during the last year of this study possibly reflecting the decreased intensity of biomanipulation.

In many basins, perch did not respond positively to the biomanipulation contrary to expected. For two basins, Etujärvi and Takajärvi, the obvious reason for the negative response is the relatively high by-catch of perch in the mass removal catch (Fig. 10). It could be that the high pressure of recreational fishing in Finland (Moilanen 2004) makes perch vulnerable for even a low by-catch in biomanipulation. Pike-perch BPUE increased in other cases except in the basins of Hiidenvesi. Pikeperch might have gained from the increased abundance of juvenile fish but also from the warm summers (**VI**). The reason for the exceptional negative trend in Hiidenvesi is unclear. Ruffe responded clearly negatively in all basins even though the catch of ruffe in biomanipulation was fairly low (Fig. 10 and

11). It could be that the increased biomass and predation of pikeperch together with the moderate removal catch had induced the collapse of ruffe BPUE.

## 7.3.2. Zooplankton

The responses in zooplankton biomass and in the potential grazing pressure were moderately positive in most of the biomanipulated basins (**V**, **VI**). As the median size of herbivorous cladocerans did not respond, however, the positive response in cladoceran biomass was due to the increase in numbers not in size. Likely, the reason for the modest response in cladocerans was the high recruitment of YOY fish (**VI**), which are strict and effective zooplanktivores (e.g. Post et al. 1992). Nevertheless, increased grazing might have contributed to the decreased phytoplankton biomass (**V**, **VI**, Rask et al. in print). The reduction of chl-*a*:TP ratio in several effectively biomanipulated basins can indicate increased herbivore control (Mazumder 1994; Meijer et al. 1999, Sarvala et al. 2000b). The potential grazing pressure (Jeppesen et al. 1994), increased in many basins (**VI**) indicating higher herbivorous control after biomanipulation. In addition, the role of grazing became more important as the phytoplankton communities shifted towards more edible algae than cyanobacteria (Mazumder 1994). It should be also noted that since the samples were collected from the deepest point of the basin (**VI**), the responses in the littoral zone were not detected.

Changes in zooplankton might have effects on the nutrient balance, as large cladocerans store more nutrients than smaller ones (Carpenter et al. 1992). Though we did not find positive response in cladoceran size, the higher total biomass of cladocerans should contain more nutrients that are temporary withdrawn from the circulation.

## 7.3.3. Phytoplankton

The biomass of cyanobacteria decreased, and the duration of the blooms shortened and shifted towards the autumn in effectively biomanipu-

lated lakes (**V**, **VI**). As we found decreased nutrient concentrations in some basins, nutrient shortage might be one reason for the decline of cyanobacteria. In the fall turnover, the nutrient storage in the water column replenishes and a delayed peak of cyanobacteria can occur. Besides the nutrient concentrations, the speed of nutrient cycling might also have changed. The reduction of chl-*a*:TP ratio in almost all effectively biomanipulated basins (**VI**) indicates that with a certain level of phosphorus, algae can not build up as high a biomass as before biomanipulation. Besides increased grazing, this can be due to changed nutrient availability (Meijer et al. 1999, Sarvala et al. 2000b). The effects of fish and zooplankton on the changed nutrient cycling were discussed in 7.3.1 and 7.3.2. In addition, the colonisation of macrophytes, benthic algae and macroinvertebrates can be other reasons for the changes in nutrient cycling increasing the nitrogen retention (Van Donk et al. 1993, Jeppesen et al. 1998, Scheffer 1998, Meijer et al. 1999, Svensson et al. 1999). A direct observation of macrophytes, benthic algae and macroinvertebrates we have only from Tuusulanjärvi, where all three increased substantially (Venetvaara et al. 2003 and unpublished), probably inducing the observed reduction in TN concentration (**VI**). Two other effectively fished basins had decreased TN concentrations (Table 4), but those lakes lacked the corresponding data.

## 7.3.4. Transparency

Only minor increments in Secchi depth occurred in the biomanipulated basins, likely due to high fraction of non-algal turbidity caused by clay and humic substances (**VI**). This may suggest that the positive effects of biomanipulation are transient. According to Scheffer (1998), the alternative stable state with low algal and fish biomass and high zooplankton and macrophyte biomass is attained only with substantial increase in water clarity. In a shallow lake, however, even a minor increase in the transparency substantially extends the euphotic bottom area. In Tuusulanjärvi, rather moderate enhancement in the Secchi depth in 2000 induced a notable expansion of the submerged vegetation (Venetvaara et al. 2003).

### 7.3.5. Success-failure review

When considering the overall success or failure of biomanipulation in our study lakes, the judgement was based on the improvement (≥ 15%) in the essential variables from 1997 to 2001 (Table 4). The boundary of 15% was the same as Hansson et al. (1998) used in their review. No general agreement of the correct definition for the successful biomanipulation exists. Drenner & Hambright (1999) judged simply by the direction, not the amount, of a change, in water quality variables, and Meijer et al. (1999) by "lake bottom view" i.e. the bottom of the lake became visible.

In our study, eight basins had the success% of ≥ 50 i.e. at least 50% of the essential variables improved until 2001 (Table 4). In the hiC basins, only one basin had ≤ 50 success% compared to five basins in the loC basins. Of the single objectives, increment in cladoceran biomass and in the Secchi depth, and the reduction in biomass of cyanobacteria (or *G. semen*) were most often attained. The reduction in nutrient concentrations or in cyprinid biomass failed most often.

High mass removal catch in relation to trophic state was likely the reason for success in six basins

(Table 5). These included two lakes, Otalampi and Lehijärvi where the target catch was not achieved but the original cyprinid biomass seemed to be low enough to enable successful biomanipulation with a lower catch. In spite of the attained target catch, mass removal catch seemed to be too low in two highly eutrophic basins Rusutjärvi and Ä1 and was likely one reason for partial failure of biomanipulation. It seems reasonable to set the target catch according to an original cyprinid biomass if possible. The mass removal target catch can be roughly estimated from the BPUE of the Nordic gillnet. Based on the mass removal catch in the lakes where cyprinids decreased and the original gillnet BPUE of cyprinids in 1997, each kg of cyprinid BPUE should mean the target catch of at least 100 kg ha$^{-1}$ in 2–3 years. If the original fish biomass cannot be estimated, as often is the case, the target catch can be estimated from TP concentration according to Jeppesen & Sammalkorpi (2002): catch-need (kg ha$^{-1}$) = $16.9 \times TP^{0.52}$. When proportioning this catch-need to the attained catch from our study lakes and comparing it to the succession%, the proportion of improved variables was higher in the basins where the attained catch was close to the catch-

**Table 4.** Summary of changes in the essential variables in biomanipulated basins. Basins are sorted according to the increasing mass removal catch (**VI**), which was lower or higher than 200 kg ha$^{-1}$ 3yr$^{-1}$ in loC or hiC basins, respectively. The signs +, – or 0 denote ≥ 15% increase, ≥ 15% decrease or < 15% change from 1997 to 2001 (in July–August). MRC, mass removal catch (kg ha$^{-1}$ 4y$^{-1}$), %c-n = proportion of the calculated catch need (Jeppesen & Sammalkorpi 2002, see text) after the best fishing season, Cyprin. = BPUE of >10 cm cyprinids, Clad. = cladoceran biomass, TP = total phosphorus, TN = total nitrogen, Phytop. = total phytoplankton biomass, Cyanob. = cyanobacterial biomass, except for *Gonyostomum semen* (G) in Otalampi, Takajärvi and Etujärvi, chl:TP = chlorophyll-*a*:TP ratio, Secchi = Secchi depth, Succ% = proportion of the improved variables (Clad. and Secchi should increase, other variables should decrease).

|  | Basin | MRC | %c-n | Cyprin. | Clad. | TP | TN | Phytop. | Cyanob. | chl:TP | Secchi | Succ% |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| loC | H1 | 44 | 13 | + | + | 0 | + | 0 | – | 0 | + | 25 |
|  | Lehi | 90 | 59 | + | + | – | 0 | – | – | + | 0 | 50 |
|  | Ota | 119 | 67 | 0 | + | 0 | 0 | – | –$^G$ | – | + | 63 |
|  | H4 | 121 | 33 | + | + | + | + | 0 | + | 0 | – | 13 |
|  | H3 | 153 | 43 | + | 0 | – | 0 | 0 | 0 | 0 | 0 | 13 |
|  | Pus | 182 | 43 | + | + | + | + | + | – | – | – | 38 |
|  | Enä | 190 | 36 | + | ? | + | + | + | 0 | + | 0 | 0 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |
| hiC | Rus | 201 | 90 | – | + | + | 0 | – | – | – | – | 63 |
|  | Ä2 | 226 | 84 | – | + | + | – | – | – | – | + | 88 |
|  | Ä1 | 257 | 58 | – | + | 0 | 0 | – | – | – | 0 | 63 |
|  | Taka | 295 | 81 | – | – | – | 0 | – | –$^G$ | 0 | + | 63 |
|  | Etu | 348 | 68 | 0 | – | + | 0 | 0 | +$^G$ | 0 | + | 13 |
|  | H2 | 411 | 80 | – | – | – | – | + | + | + | + | 50 |
|  | Tuu | 472 | 99 | + | + | – | – | – | – | – | + | 88 |

need (Fig. 12). Thus, the equation of Jeppesen & Sammalkorpi (2002) seems to predict the target catch relatively well. In addition, the observed dependence between the succession% and the relative mass removal efficiency indicates that the intensity of biomanipulation was among the main factors inducing the positive changes in the lake basins.

According to Hansson et al. (1998), high production of YOY fish after the biomanipulation is probably the main reason for biomanipulation failure. This was also supported in our study, as in ten basins the juvenile expansion was one of the causes of failure restricting the cladoceran response (Table 5). As the proportion of piscivores was lower (≤ 20% in all basins in 2001, **VI**) than recommended (30%–40%, Benndorf & Kamjunke 1999), the relatively low predation pressure might contributed to the juvenile expansion of cyprinids. However, Otalampi, Lehijärvi and Ä2 which lacked the juvenile expansion, had even lower percentage of piscivores compared to the other basins. It could be that, the relatively low trophic state has affected the weakness of cyprinid reproduction in Otalampi and Lehijärvi.

A low or moderate external loading is generally argued to be a prerequisite for success in biomanipulation (e.g. Scheffer 1998, Hansson et al. 1988, Benndorf et al. 2002). This is also supported by our results. Of the eight cases with succession% at least 50, five had an external loading lower than or close to the critical level, as defined by Vollenweider (1976). In the other basins Takajärvi, Tuusulanjärvi and H2, high
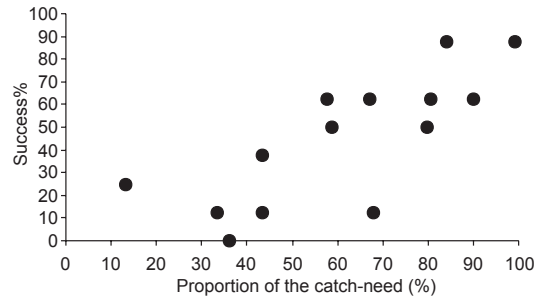


**Fig. 12.** Percentage of improved variables in relation to attained proportion of the catch-need in study basins. See Table 4 for the variables. Proportion of the catch-need is calculated as mass removal catch of the best fishing season divided by the catch-need of Jeppesen & Sammalkorpi (2002, see text). Spearman rank correlation: $r_s = 0.774$, $P < 0.01$.

external loading was one possible reason maintaining high nutrient concentration and algal biomass or enabling high fish production after restoration measures. It should be noticed, however, that in our study, the rates of external loading, as well as the nutrient concentrations, were generally much lower compared to biomanipulated lakes in Denmark (Jeppesen et al. 1999) and in The Netherlands (Gulati & van Donk 2002).

According to Scheffer (1998) high background turbidity may reduce the potential for successful biomanipulation. Thus, low background turbidity might have enabled the positive responses in five study basins (Tables 4 and 5). However, only Otalampi and Ä2 of these basins had ≥ 15% improvement in the transparency. On the other hand, of nine basins with high

**Table 5.** Probable explanations for success (upper) or failure (lower) in biomanipulation of the study lakes.

| | |
|---|---|
| Reasons for success | Basin |
|     High MRC (in relation to trophic state) | Taka, Ota, Tuu, Lehi, Ä2, H2 |
|     No juvenile expansion | Ota, Lehi, Ä2 |
|     Low external loading | Ota, Lehi, Ä1, Ä2 |
|     Low background turbidity | Ota, Rus, Lehi, Ä1, Ä2 |
|     Artificial mixing during summer | Tuu |
| Reasons for failure | |
|     Low MRC (in relation to trophic state) | Pus, Rus, Ä1, H1, H3, H4 |
|     Short fishing period (< 3 yr) | Rus, Lehi |
|     Effective Cyprinid compensation | Taka, Etu, Rus, Pus, Tuu, Ä1, H1, H2, H3, H4 |
|     *Gonyostomum semen* | Taka, Etu, Ota |
|     High external loading | Taka, Etu, Pus, Tuu, H1, H2, H3, H4 |
|     High wind resuspension | Enä, H1, Ä1, H2 |
|     High background turbidity | Taka, Etu, Pus, Tuu, Enä, H1, H2, H3, H4 |
|     Artificial mixing during summer | Enä, Tuu |

non-algal turbidity only three basins, Takajärvi, H2 and Tuusulanjärvi, had succession% ≥ 50. Clay turbidity in particular might be crucial for effective biomanipulation, because clay has extended effects on the ecosystem functioning (see the review by Lind 2003). Clay turbidity reduces the feeding efficiency of visual predators (Benfield & Minello 1996) and the filtration rate of large cladocerans (McCabe & O'Brien 1983, Hart 1987). In addition, clay turbidity might contribute to cyanobacterial blooms, as they are adapted to shady conditions (Scheffer 1998). Loose clay sediment is readily disturbed by fish and wind thus preventing the invasion of submerged vegetation due to light limitation and up-rooting (Scheffer 1998, Meijer et al. 1999, Nurminen 2003). In our study, wind induced resuspension may have prevented or reduced the positive responses in four shallow basins having a long fetch in the prevailing wind direction (Table 5), as was also found by Meijer et al. (1999). The potential of biomanipulation in clay turbid lakes may depend on depth. In deep lakes, clay turbidity favours the larvae of invertebrate predator *Chaoborus* sp. that effectively consume zooplankton (Cuker 1993, Horppila et al. 2000, Liljendahl-Nurminen et al. 2003). It also seems reasonable, that in shallow lakes, where fish may directly affect the clay turbidity by disturbing the sediment, the decreased fish biomass induces more obvious response in the transparency compared to deep lakes. In this study, the only clay turbid lake having a highly successful biomanipulation was shallow Tuusulanjärvi.

Artificial mixing during summer stagnation may have affected the responses in three lakes. The mixing was most efficient in Tuusulanjärvi, preventing the thermal stratification during the growing season. This might have averted the blooms of *Microcystis* sp. (Gulati & van Donk, 2002) and favoured other cyanobacteria as the blooms diminished and consisted of several genera. The mixing also kept the bottom sediment oxygenated, restraining the mobilisation of phosphorus. However, the mixing also increases the shear stress, temperature and pH near the bottom sediment which all can increase the release of phosphorus from the sediment (see Scheffer, 1998). Thus, artificial mixing might have had both positive and negative effects on

the water quality in Tuusulanjärvi. In Pusulanjärvi and Enäjärvi, the artificial mixing was less effective in order to keep only the hypolimnion oxygenated without breaking the summer stratification. However, in both lakes hypolimnetic water was concentrated with nutrients, and the stratification was weakened, resulting in high internal loading during wind turbulence. This may explain the high phytoplankton biomass in Enäjärvi in 1999. After the summer artificial mixing had ceased, the lake returned to the previous better condition.

## 8. Concluding remarks

According to the results of the present study, the fish biomass and species interactions in Finnish lakes depend on, besides the nutrient concentrations, also on lake area and depth, and turbidity. The shift from percid to cyprinid dominance from mesotrophic to eutrophic lakes was not recorded as cyprinids dominated already in the mesotrophic lakes. Large lake size and / or low turbidity can enable a high biomass of perch in spite of abundant cyprinids.

Experimental gillnetting can be used to roughly estimate the target catch of biomanipulation and the CPUE in seining, as well as the following responses in fish community. The validity of gillnet CPUE as an index of fish density is fairly good for mid-sized (6–30 cm) fish and active species, and when the set time is short enough to diminish the effects of the lowering catching efficiency.

The results of the biomanipulation experiments indicated that in meso- and eutrophic Finnish lakes the blooms of cyanobacteria can be decreased considerably by effective cyprinid removal (200–400 kg ha$^{-1}$ 3 yr.$^{-1}$). Successful and sustainable biomanipulation is more likely if the external loading is low, clay-turbidity is modest and the juvenile expansion of cyprinids is hindered.

## 9. Future aims

When considering the fish communities in Finnish lakes, more information is needed on the

interactions of species in different environments. Also, the role of recreational fishing and high frequency of turbid lakes need more attention as potential reasons of the unexpectedly common cyprinid dominance.

The dependence between fish abundance and community structure and gillnet CPUE should be examined further. Some questions in need of further investigation are: how is the catching efficiency affected by different fish density and water turbidity, what is the role of weather conditions, and how should the gillnet sampling of fish be performed in a most cost-effective way?

Concerning the biomanipulation, we still need more information on the restoration possibilities in humic or clay turbid-lakes, and about the possibilities of reaching alternative stable states of lake ecosystems in Finland.

# 10. Acknowledgements

# 11. References

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