

# Ecosystem change in the large and shallow Lake Säkylän Pyhäjärvi, Finland, during the past ~400 years: implications for management

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**Abstract** Lake Säkylän Pyhäjärvi has been an important fishing site and drinking water source for the local population for centuries. The lake has undergone significant changes: (1) the water level was lowered in the 1600s and in the 1850s; (2) planktivorous coregonid fish were successfully introduced in the early 1900s; (3) nutrient input from intensified agriculture has increased since the 1950s and (4) the effects of the current variable climate on the lake and its catchment have become more evident since the 1990s. We determined the phases of oligotrophication, eutrophication and recovery and elucidated the ecosystem changes by combining palaeolimnological records with detailed neolimnological data. The sedimentary diatom and cladoceran assemblages first showed a relatively eutrophic period

followed by oligotrophic periods, linked with the artificial changes in water level and consequent shifts in macrophyte abundance. The oligotrophic period in the early 1900s is thought to represent the target trophic state for the lake. After the 1950s, introduction of vendace resulted in higher planktivory reflected by an increased relative abundance of small-bodied pelagic cladocerans. Signs of eutrophication occurred due to increased nutrient load. During the last 10 years, signs of recovery have been recorded. A complex history such as that of Lake Pyhäjärvi illustrates the difficulties in selecting management targets, and the risk of setting false targets, for lakes based solely on monitoring data—both neolimnological and palaeolimnological approach are needed.

**Keywords** Eutrophication · Palaeolimnology · Diatoms · Cladoceran subfossils · Monitoring · Lake recovery · Restoration targets · Climate change adaptation

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## Introduction

Lakes around the globe have undergone increasing eutrophication due to sewage loading, input of diffuse nutrients from agricultural activities, fish stockings and other pressures related to human activities (Millennium Ecosystem Assessment, 2005). It is expected that the pressure on lakes and their ecological state will increase in the future due to both an increasing world population, demanding a higher food production and to climate change (Millennium Ecosystem Assessment, 2005). Such changes will further challenge the protection and use of ecosystem services of the lakes such as water supply, industry, recreation and fisheries, not least because nutrient loading and climate warming can have a synergistic effect (Jeppesen et al., 2010; Moss et al., 2011; Jeppesen et al., 2014). Thus, adaptation and management actions are often needed. Predicting future climate change is, however, difficult due to the high uncertainty regarding large-scale dynamics, mechanisms and timing of the changes (IPCC, 2014; Refsgaard et al., 2014). It is moreover expected that the frequency and magnitude of extreme weather events will increase (Knutti & Sedláček, 2013; IPCC, 2014), which will further challenge the function and quality of lake ecosystems (Jeppesen et al., 2015). Detailed analyses of the long-term dynamics of lake ecosystems as well as key factors and interactions affecting water quality and ecosystem services are, therefore, required to allow implementation of mitigating management measures including climate change adaptation tools.

Although many lakes have been intensively monitored for multiple years, the existing long-term records usually cover only the recent 40–50 years or often less. If longer records are needed, palaeolimnological studies may help to extend the time series (Smol, 1985, 1991; Battarbee et al., 2005; Sayer et al., 2010). Analyses of cladoceran subfossils and of diatoms have been used to reconstruct long-term changes in lake ecosystems and their response to, for instance, eutrophication (summarised in Davidson & Jeppesen, 2013). Cladocerans are functionally adapted to different microhabitats (pelagic, macrophyte-associated, benthic). Changes in the contribution of key cladoceran taxa may therefore yield information about habitat alterations and changes in lake trophic structure (Frey & Pamini, 1986; Jeppesen et al., 2001). In addition, cladoceran subfossils are useful indicators of

changes in predation by planktivorous fish and fish stockings (Amsinck et al., 2007), the latter being reflected in changes in the size of *Daphnia* ephippia (Verschuren & Marnell, 1997; Jeppesen et al., 2002) and the contribution of *Daphnia* to the total sum of *Daphnia* and *Bosmina* ephippia (Leavitt et al., 1994; Jeppesen et al., 2003). Changes in cladoceran community can also be caused by climate change (Smol et al., 2005; Thienpoint et al., 2015) though such effects may be difficult to separate from those of other factors. Also, the climate change effect may be indirect and for example channelled through food webs. Fossil diatom assemblages have, among other purposes, been extensively used for creating quantitative inference models for, for example, total phosphorus (e.g. Anderson, 1993; Bennion et al., 2001; Hall & Smol, 2010), but although qualitatively diatoms can be very good at tracking nutrients, no matter how carefully the quantitative inference is done—it cannot be trusted alone (Davidson & Jeppesen, 2013). Also, for both neolimnological and palaeolimnological approaches, reduction of the detailed species level data to annual or decadal scale or indexes may potentially lead to loss of valuable ecological information on species' seasonality, habitat structure and food web interactions (Sayer et al., 2010).

Restoration of eutrophicated lakes in Europe aims to maintain or restore good ecological status according to EU's Water Framework Directive where 'good ecological status' is defined for all lake types based on a set of variables to be compared to reference systems (European Union, 2000; Phillips, 2014). The current status is evaluated relative to past 'pristine status', i.e. the time when the aquatic system was not influenced by human activities. 'Pristine status' may be difficult to define or quantify as aquatic systems in rather densely populated Europe have been influenced by various anthropogenic pressures for thousands of years (Battarbee & Bennion, 2010; Bouleau & Pont, 2015) and are constantly changing in reaction to new pressures such as those related to the ongoing climate change.

Lake Säkylän Pyhäjärvi (61°00'N, 22°18'E, 45 m.a.s.l) in Southern Finland (hereafter "Pyhäjärvi") is an example of a large shallow lake affected by human activities in its catchment and by lake fishery for centuries. The Pyhäjärvi Restoration Programme was voluntarily established 20 years ago by

local municipalities, companies and associations after the lake had shown visible symptoms of eutrophication and monitoring data had indicated that the external nutrient load was too high to maintain an oligotrophic state (Sarvala & Jumppanen, 1988; Malve et al., 1994; Ekholm et al., 1997). In recent years, climate change-related alteration of both nutrient loading (Ventelä et al., 2011) and the fish community (Jeppesen et al., 2012) has affected the lake.

In this paper, we describe the aquatic ecosystem history and water quality of Pyhäjärvi during the past ~400 years using a combination of palaeolimnological and neolimnological records. We further aim to define a target ecological status for use in lake management processes.

## Materials and methods

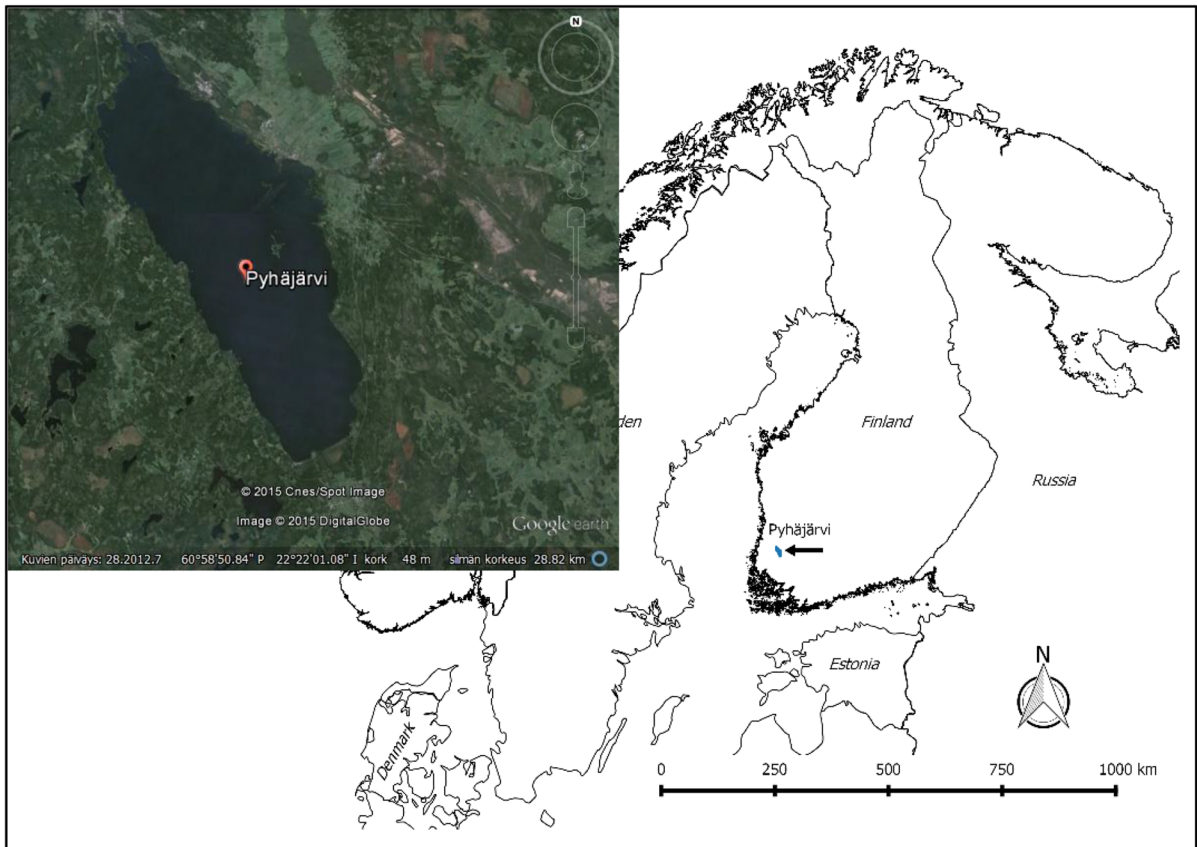
### Study lake

Pyhäjärvi is a lowland lake in SW Finland (Fig. 1). It is one of Finland's most extensively studied lakes due to its important role in supporting local ecosystem services. The lake is shallow both in absolute terms (mean depth 5.5 m, maximum depth 26 m), and especially relative to its large surface area (155 km<sup>2</sup>); moreover, the openness of the basin enhances water movements and wave action. The total catchment area including the lake is 615 km<sup>2</sup>, the main rivers entering the lake are River Yläneenjoki from the south and River Pyhäjoki from the east (catchment areas 234 and 78 km<sup>2</sup>, respectively). Nowadays, most of the lake bottom is subjected to either erosion or sediment transport, and permanent deposition is limited to a narrow depression on the western side of the lake. Cultivated fields cover 22% of the catchment area, the rest comprising forests (50%), peatlands (20%) and built-up areas. The long-term (1959–2009) average annual precipitation in the area is 590 mm. During the period 1970–2000, the annual mean temperature in the study area was 4.8°C. The wintertime mean air temperature in the area is –2.1°C and the lake is, on average, covered by ice for 140 days. The catchment is usually covered by snow in winter. The warmest month is generally July when the average temperature was 16.5°C during the period 1980–2009.

### History of the lake

Pyhäjärvi was isolated from the Litorina Sea (one of the former phases of the Baltic Sea) about 5600 years B.P. (Eronen et al., 1982). Archaeological findings (Lehtomäki-Hilander, 2000) suggest that the lake catchment was already then colonised by humans and used as a fishery. There are also indications of pre-industrial production of iron from the lake ore (Uotila, 2011), which is formed when dissolved iron hydroxide in the groundwater moves through the sediment and precipitates around the oxic-anoxic interface. The outflow, River Eurajoki, was modified for the first time for industrial use in the late 1600s when an iron works was established at the outflow in the northern part of the lake (Korvenmaa, 1989). There are indications that this increased river outflow may have resulted in a lowering of the water level, but no quantitative data are available (Uotila, 2011; G. Haggren, personal communication). Increased use of firewood for iron production may have impacted the land use characteristics of the catchment area (Laitakari, 1965). A major lowering of the water level by 2 m occurred during 1852–1854 in connection with reclamation of arable land (Laitakari, 1925; Veira, 1974). The pre-lowering mean depth was ~7.5–8 m. Further modifications of the outflow were officially permitted in 1910, but the first real regulation permit was given in 1936. The upper and lower limits of the permit were, however, often exceeded during extreme flood and drought events. Therefore, new regulations were established by the Water Court in 1975. The present regulation amplitude between the permitted lower and upper water levels is rather narrow, 58 cm, but continuous monitoring of river flows and improved hydrological forecasts have made it possible to mostly fulfil the authorised water level targets (Marttunen et al., 2000). The lake's current mean depth is 5.5 m.

The lake and its fishery have both been strongly influenced by a long history of stocking events. Three commercially important species, whitefish (*Coregonus lavaretus*), vendace (*Coregonus albula*) and signal crayfish (*Pacifastacus leniusculus*), were introduced. Whitefish was stocked in 1908–1909 and soon after it became the most important species for the commercial fishery (Sarvala et al., 1998a). Vendace was introduced for the first time in 1925, but extensive stocking of the species in 1948–1952 resulted in the



**Fig. 1** Location and satellite image (from Google Earth) of Lake Pyhäjärvi

establishment of a permanent population (Helminen et al., 1993). The third commercially significant introduced species was signal crayfish, which was imported from Sweden to replace the plague-ravaged noble crayfish (*Astacus astacus*). In the beginning, the population developed slowly, but since the 2000s the catches have increased (Karjalainen et al., 2015) and crayfish catch has become an economically important income source of fishermen.

Shifts have also occurred in the nutrient loading to the lake. South-western Finland is an important food production area. After the Second World War, the efficiency of the agriculture increased and so did soil fertilisation. In addition, the municipalities developed sewage systems, and flush toilets became increasingly common from the 1950s and onwards. Currently, industrial and municipal waste waters are treated in waste-water treatment plants and diverted from the drainage area of Pyhäjärvi, i.e. they are led to the outlet below the lake.

Pyhäjärvi has been subjected to a large-scale restoration programme since 1995 (Ventelä & Lathrop, 2005; Kirkkala, 2014). A multitude of measures have been implemented in the catchment in order to reduce the external load (Kirkkala et al., 2012; Kirkkala, 2014). Pyhäjärvi has also been intensively biomanipulated for decades in the form of removal of planktivorous fish by commercial fishery. Fish removal has traditionally been undertaken in winter and the annual harvest rate of vendace has approached the total production (Sarvala et al., 1998a). Since 2013, an increasing proportion of fish removal by biomanipulation consisted of the natural planktivore smelt (*Osmerus eperlanus*), which was fished in late autumn with open-water seine nets. The restoration project has also subsidised the harvest of commercially unwanted fish since 1995. In 2002–2006, the EU provided funds for this fishing, which was especially intensive in 2002–2004 and was partly, together with lower external nutrient load,

responsible for the observed water quality improvement (Ventelä et al., 2007). The annual biomanipulation effort varied in 1995–2014 from 50 kg/ha (in 2002) to 8 kg/ha (in 2008) (A-M. Ventelä, unpublished data).

### Limnological monitoring

The data used in this study originate from national, areal and project-funded monitoring programmes; yet, the monitoring protocol and methods are comparable. The water chemistry and hydrology of Pyhäjärvi have been monitored since the 1960s as part of a national programme. Since 1971, monitoring has been more intensive and involves use of automatic meters continuously measuring the river flows (Ekholm et al., 1997). The nutrient concentrations in the water of Pyhäjärvi and the main rivers Yläneenjoki and Pyhäjoki have been measured since 1980, first as part of a statutory monitoring programme (Sarvala & Jumppanen, 1988) and since 1992 by the regional authorities approximately at a 2–3 week interval during the open-water season. The water chemistry and hydrology data used in this study are derived from the Finnish Environment Institute's Oiva data service ([www.ymparisto.fi/oiva](http://www.ymparisto.fi/oiva)).

Water samples for nutrient and chlorophyll *a* analyses were taken from the surface to the bottom at a single sampling point situated in the deepest area of the lake. In our study, we used average open-water season (May–October) values for the 0–5 m layer, representing >80% of the total lake volume. The methods of analyses followed Finnish standard laboratory procedures (Ekholm et al., 1997) and are accepted by Finnish Accreditation Service (FINAS).

The annual total phosphorus (TP) and total nitrogen (TN) loads from the major rivers were calculated based on TP and TN concentrations in water samples and continuously measured stream flow data (Ekholm et al., 1997). We used the sums of the TP and TN loads of River Yläneenjoki and River Pyhäjoki as total external nutrient load.

### Sediment coring, subsampling, dating and core correlation

Two sediment cores were taken through the ice from the deepest part of the lake in March 2004 using a HON-Kajak-type corer (Renberg, 1991) for the most

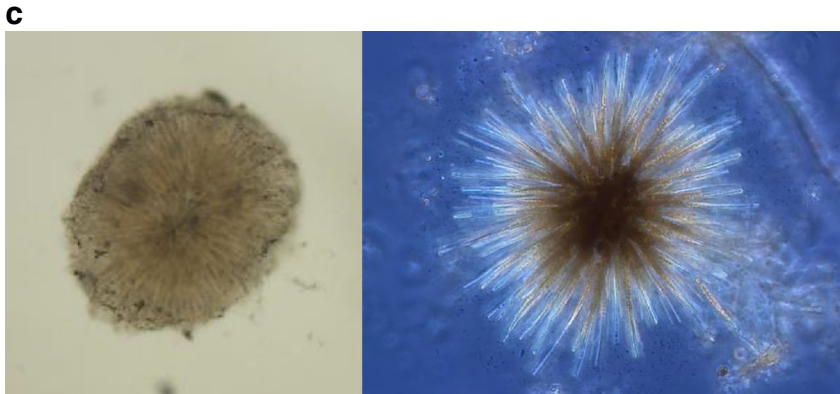
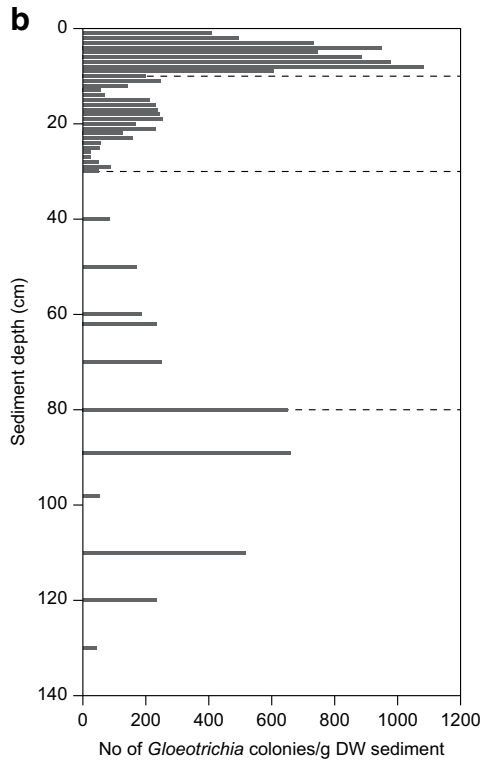
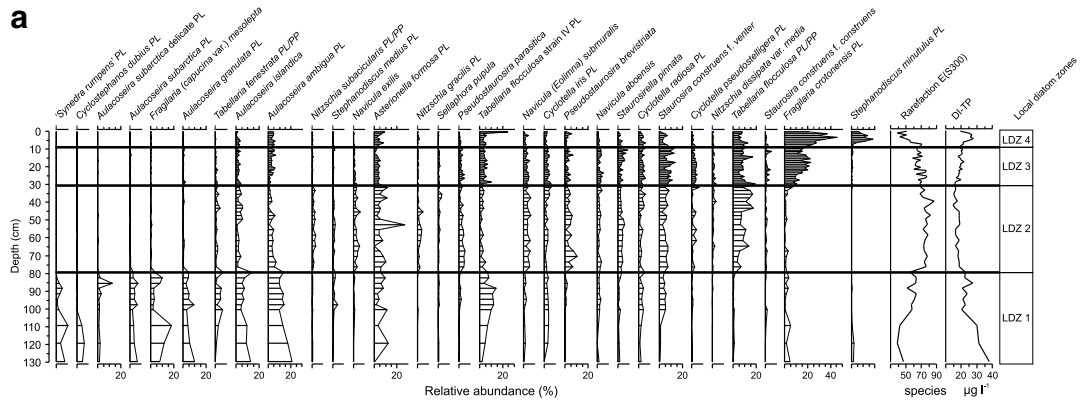
recent sediments (0–30 cm) and a modified Kullenberg corer (PP corer; Putkinen & Saarelainen, 1998) for the deeper Sections (0–687 cm, of which the uppermost 130 cm were used here). The Kajak core was sectioned into 1 cm slices for all analyses, whereas subsamples from the PP core were taken at different intervals for diatom and cladoceran analyses (see below).

Sediment samples from the HON-Kajak corer (0–30 cm) and the topmost sediment (0–15 cm) from the PP cores were analysed for  $^{137}\text{Cs}$  activity using an Ortec gamma spectrometer equipped with a four-inch NaI(Tl) crystal, two amplifiers and a 2048-channel pulse height analyser at the Geological Survey of Finland. The HON-Kajak and the PP cores were correlated based on their  $^{137}\text{Cs}$  activity profiles using the 1986 Chernobyl nuclear fallout peaks as reference point. The resulting composite core was analysed for  $^{210}\text{Pb}$  activity using an ORTEC OCTETE PC alpha spectrometer (Äikäs et al., 1994) at the Institute of Geological Sciences, Polish Academy of Sciences, Warsaw, Poland. Radiometric dates were calculated using the Constant Rate of Supply (CRS) model of dating (Appleby, 2001) and applying the  $^{137}\text{Cs}$  date of 1986 as reference point.

### Sedimentary diatom, cladoceran and *Gloeotrichia* analyses

Diatoms were analysed from 60 samples with varying frequency (each 1 cm slice down to 30 cm, every other slice down to 50 cm, every third slice down to 101 cm and every tenth slice below that) (Fig. 2a). The samples were prepared using  $\text{H}_2\text{O}_2$  digestion and a mixture of  $\text{HNO}_3$  and  $\text{H}_2\text{SO}_4$ . The cleaned diatoms were mounted in Naphrax<sup>®</sup>. A minimum of 300 diatom valves were identified from each sample using a Leitz Diaplan light microscope at 1250 $\times$  final magnification with phase contrast optics. Diatom identification was based mainly on Krammer & Lange-Bertalot (1986, 1988, 1991a, b). The diatom counts were converted into relative percentages and plotted as a stratigraphical frequency diagram (Fig. 2a) using the program C2 (version 1.4 beta; Juggins, 2003).

Cladoceran and *Gloeotrichia* remains were analysed from 41 subsamples with varying frequency (each 1 cm slice down to 30 cm and approximately



◀ **Fig. 2 a** Diatom stratigraphy and diatom-inferred TP of Lake Pyhäjärvi (combined core). Zonation according to constrained clustering of diatom data. *PL* planktonic taxa, *PL/PP* planktonic/periphytic taxa. **b** *Gloeotrichia* profiles of the combined core. **c** *Gloeotrichia* fossil (left, photo by Liselotte Sander Johansson) and preserved sample (right, photo by Kristiina Vuorio)

every tenth below that) (Figs. 2b, c, 4). Each sample was homogenised, and subsamples of approximately 5 g wet sediment were boiled in 30 ml 10% KOH and kept cold (4°C) until all taxonomic analyses had been performed. All subfossils larger than 80 µm were identified using an Olympus SZX12 stereomicroscope with 100× magnification and a Leitz Labovert FS inverted light microscope with 320× magnification. The subfossils were divided into two size fractions: >140 µm and 80–140 µm. *Daphnia* spp. ephippia and *Gloeotrichia* colonies were counted from the entire sample, whereas the remaining Cladocera taxa were subsampled due to high densities. As several different subfossil parts (e.g. carapace, headshield, postabdomen, postabdominal claw) of each taxon were counted, only the most abundant and most representative subfossil part was used for data analysis. Whenever possible, all taxa were identified to species level. In addition, the dorsal length of all enumerated *Daphnia* spp. ephippia was measured. Cladocerans were identified using standard keys such as Frey (1959), Margaritora (1985), Hann (1990) and Flössner (2000) and *Gloeotrichia* using Tikkanen & Willén (1992). The cladoceran assemblages were expressed as percentage abundance. Classification of cladoceran habitat preferences was based on Hann (1990) and Røen (1995). The Palaeolimnological Predation Index (PPI) is based on a relationship between the ephippia ratio of *Daphnia*(*Daphnia* + *Bosmina*) and fish abundance (catch per unit effort in gillnets) (Jeppesen et al., 2003). The macrophyte indices are Chydoridae/(Chydoridae + *Bosmina*) carapaces excluding *C. sphaericus* (Jeppesen et al., unpubl.; Bjerring et al., 2008) and the sum of the relative abundance of the macrophyte-associated species.

#### Numerical methods

In order to explore possible shifts in diatom assemblages and to identify zones with similar species

compositions, constrained cluster analyses with the paired group method were conducted using Euclidean, Bray–Curtis and chord distance similarity measures. Changes in species richness were analysed through rarefaction analysis (Birks & Line, 1992), which produces realistic estimates of richness without any bias associated with the variability of individual sample count size. Cluster analyses and rarefaction analyses were performed using the software PAST (Hammer et al., 2001).

Past lake water TP concentrations were inferred using a quantitative diatom-based TP inference model comprising 68 southern Finnish lakes with a TP range from 3 to 89 µg TP/l (Kauppila et al., 2002).

#### Neolimnological plankton

For phytoplankton analyses, composite samples have been collected from 0 to 5 m depth six to 24 times during May–October each year since 1980. Two sites were sampled in the first decade, and samples from ten locations have been bulked since the early 1990s. Additional phytoplankton data collected as part of a national monitoring programme were available from the years 1963–1965, 1968, 1971 and 1977. Phytoplankton was counted using the Utermöhl technique (Utermöhl, 1958) and biomass was estimated separately for each cell using standard methodology (Tikkanen & Willén, 1992).

Zooplankton has been sampled weekly or at 2–3 week intervals during the open-water season (May–October) since 1987, and less complete data were available for 1977, 1982 and 1986. Samples were taken during day from 0 to 5 m depth with a 0.5- or 1-m-high tube sampler (volume 3.4 or 6.8 l) at ten locations selected using a stratified random design. The samples were concentrated with a 50-µm mesh net and combined in the lab to one composite sample per date. In the lab, subsamples were enumerated until 50–200 individuals of the dominant crustacean species had been counted and measured. Zooplankton counts and measurements were converted to zooplankton biomass using carbon-length regressions (Sarvala et al., 1998b).

The weight of 0<sup>+</sup> vendace in autumn (S0<sup>+</sup>) was used as a neolimnological index for planktivory (NPI) (transformed as: NPI = 100–S0<sup>+</sup>) (Ventelä et al., 2011).

## Results

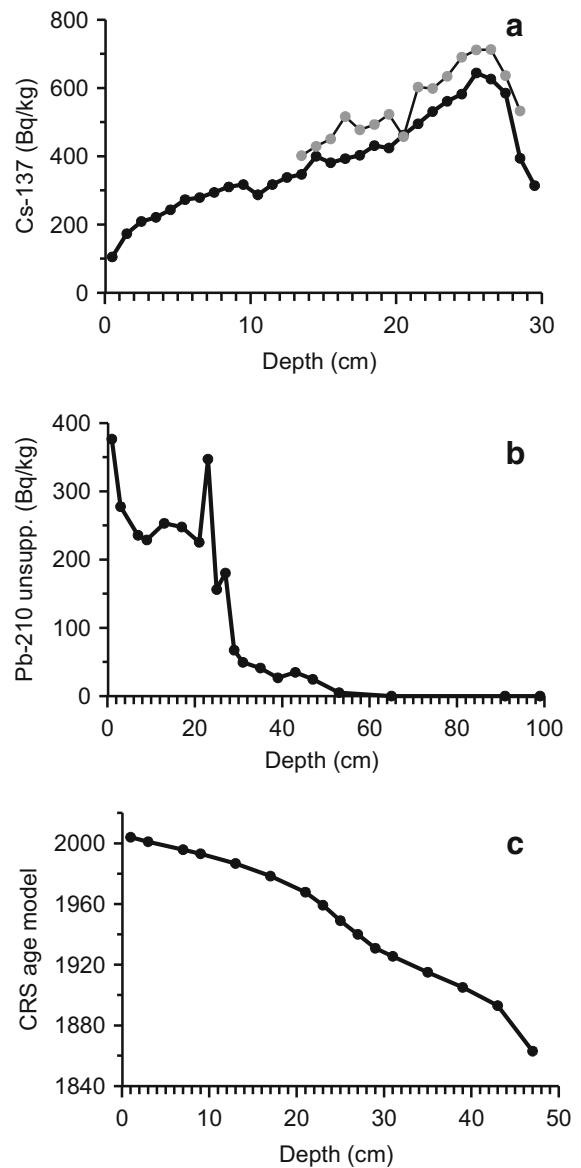
### Sediment dating and core correlation

The  $^{137}\text{Cs}$  profiles of the HON-Kajak and the PP cores showed similar activity profiles with peaks of 629 and 720 Bq/kg at ca. 26 cm (HON-Kajak) and ca. 13 cm (PP) sediment depths, respectively (Fig. 3a).  $^{210}\text{Pb}/^{226}\text{Ra}$  equilibrium was recorded at ca. 47-cm depth (AD  $1863 \pm 6$ ) of the composite core. The  $^{210}\text{Pb}$  activity profile (Fig. 3b) deviated from an ideal curve and suggested heterogeneous sedimentation through time as the  $^{210}\text{Pb}$  activity decreased rapidly in the upper part of the core, followed by a relatively flat plateau between 7 and 21 cm and a peak of  $^{210}\text{Pb}$  activity (total activity 0.388 Bq/kg) at 23 cm. Despite the irregularities in sedimentation, the Pb-210 age-depth model (Fig. 3c) was here used as a basis for dating the composite core and ages for sediments below 47 cm were estimated by rough linear extrapolation of the age-depth model.

### Biological indicators

The distributions of the most abundant diatom taxa in the composite core are displayed together with the rarefaction-estimated number of species at 300 counted valves and the diatom-inferred past lake water TP concentrations (Fig. 2a). Four distinctive local diatom zones (Z1–Z4; Fig. 2a) were identified based on the clustering results (not shown).

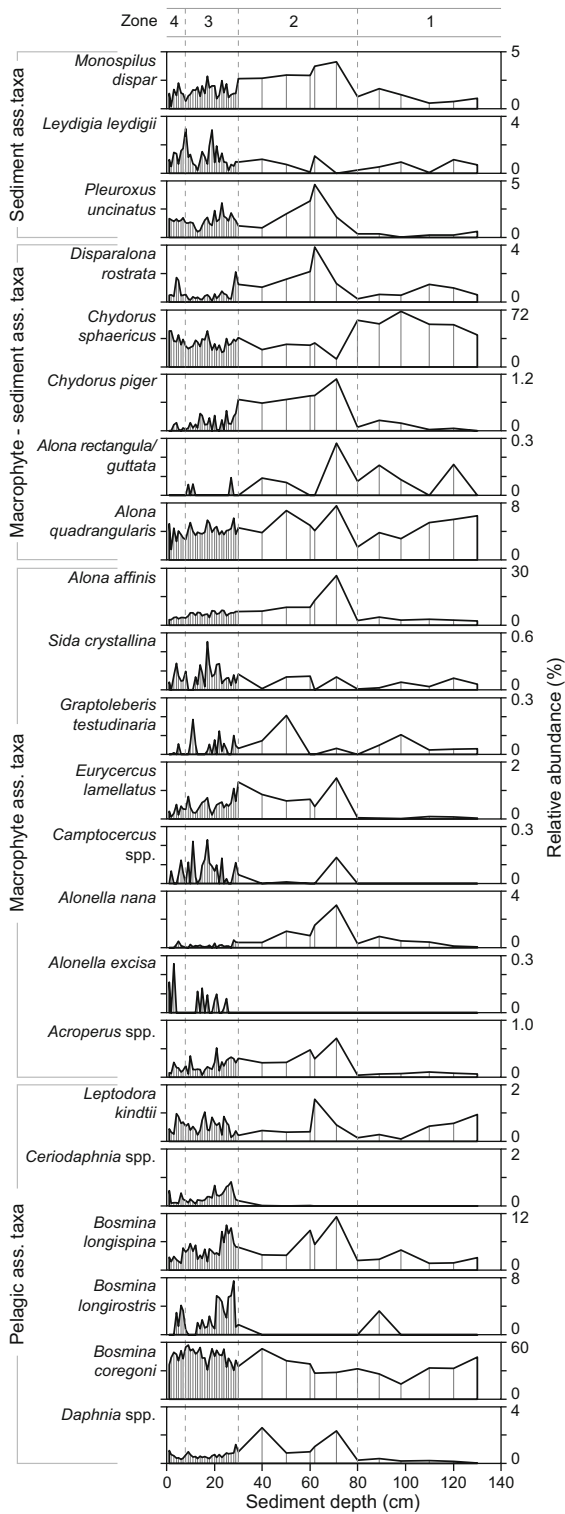
Z1 (80–130 cm; AD ~1600–1700): This zone was not dated in our study, and based on the available data only estimates can be given for the presented time period, which extrapolating from the sedimentation rates in the surface sequences could be the period from the 1600s to about 1700. The zone was characterised by planktonic and meroplanktonic diatoms (*Aulacoseira ambigua* and ‘*Synedra rumpens*’-type) as well as species occurring commonly in eutrophic waters (*Cyclostephanos dubius*, *Aulacoseira granulata*, *Fragilaria crotonensis* and *Stephanodiscus minutulus*) and mesotrophic waters (*Aulacoseira subarctica*, *Tabellaria fenestrata*, *Fragilaria capucina* var. *mesolepta* and *A. islandica*) (Fig. 2a). Also *Tabellaria flocculosa* (Roth) Kützing var. *flocculosa* ‘Strain IV’ sensu Koppen (1975) occurred frequently (Fig. 2a), as did *Gloeotrichia* (Fig. 2b). The diatom-inferred TP (DI-TP) concentrations were relatively high (range



**Fig. 3** Dating of sediment cores. **a**  $^{137}\text{Cs}$  activity profiles of Kajak core (black) and PP core (grey), **b**  $^{210}\text{Pb}$  activity profile versus depth of Kajak core, **c**  $^{210}\text{Pb}$  estimated age versus depth of the upper part of the composite core (CRS model). Note the varying depth scale of the diagrams

20–38  $\mu\text{g TP/l}$ ), and the rarefaction-estimated numbers of diatom species were low (39–64 taxa). As for zooplankton, the number of *Chydorus sphaericus* was high, but the abundances of large-bodied *Daphnia* spp. and *Bosmina* were low (Fig. 4). The palaeolimnological predation pressure index indicated an overall low pressure and, accordingly, the median ephippial size of *Daphnia* spp. was relatively large (613  $\mu\text{m}$ )



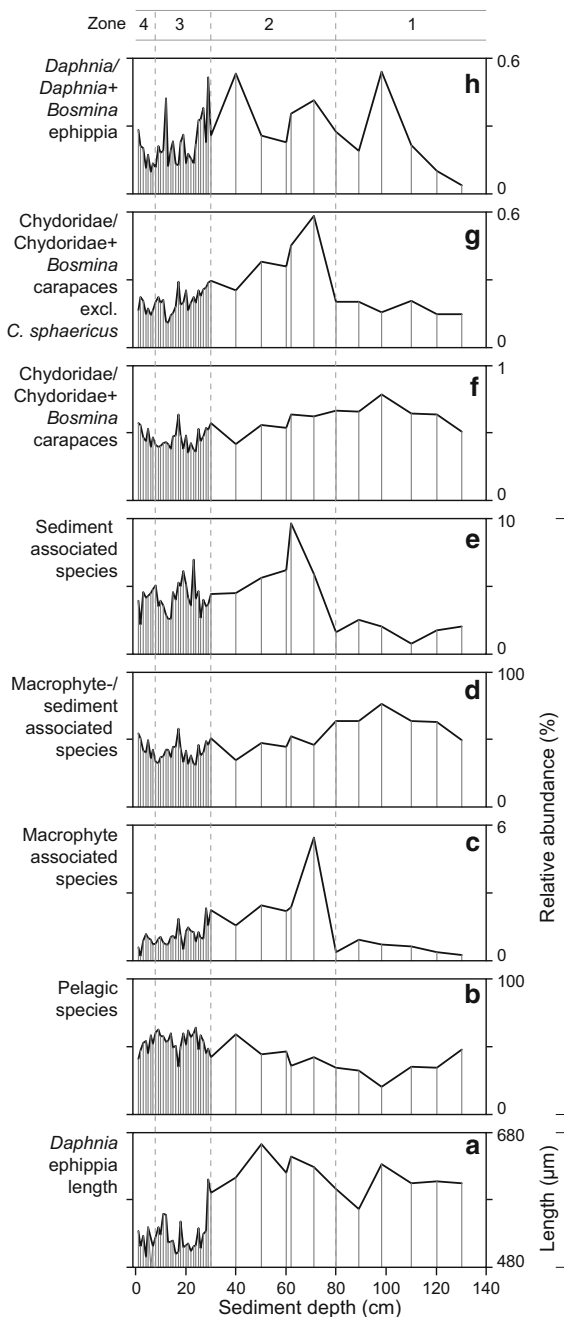


**Fig. 4** Cladoceran stratigraphy of Lake Pyhäjärvi (Kajak core). Classification into habitat preferences according to Hann (1990) and Røen (1995). Zonation as in Fig. 2a

(Fig. 5a). Macrophyte abundance was presumably low based on the low number of truly macrophyte-associated cladoceran taxa (Fig. 5c) (*C. sphaericus* is also found in the pelagic and is therefore a poor indicator of plants) and the low macrophyte abundance index (Fig. 5g). Also the number of sediment-associated taxa was low (Fig. 5e).

Z2 (30–80 cm; ~1700–1930): In this zone, the amount of periphytic diatoms such as *T. flocculosa*, *Pseudostaurosira brevistriata*, *Navicula exilis*, *Nitzschia subacicularis*, *N. gracilis* and *N. dissipata* var. *media* increased (Fig. 2a). The diatom-inferred TP concentrations decreased to 15–20 µg TP/l, and the number of diatom taxa increased to 70–80. *Gloeotrichia* abundance decreased (Fig. 2b). Large-bodied *Daphnia* and *Bosmina* increased, especially *Bosmina longispina*. The abundance of the predatory *Leptodora kindtii* decreased (Fig. 4). The palaeolimnological predation pressure index indicated an overall low predation pressure and the ephippial size of *Daphnia* spp. was large (Fig. 5a). Both the number of macrophyte-associated taxa (Fig. 5c) and the macrophyte abundance index (Fig. 5g) showed an abrupt increase at the onset of zone 2 followed by a declining trend from mid-zone 2. The major artificial lowering of the lake water level was undertaken in the later part of this period.

Z3 (8–30 cm; ~AD 1930–1994): *F. crotonensis* increased. *T. flocculosa* and *Staurosira construens* f. *venter* maintained high abundances in the now shallower lake despite the increase in planktonic algae, reflecting the influence of habitat availability on algae (Fig. 2a). DI-TP increased to 20–25 µg TP/l, but the overall diatom species diversity declined. Neolimnological data showed a mean TP in 1980–1994 of  $16.5 \pm 2.4$  µg/l. Also *Gloeotrichia* started to increase again in this zone (Fig. 2b). In the neolimnological samples, *Gloeotrichia* was first observed in 1963 and again in the 1990s (Fig. 6a), but the sediment record shows that it has been present at least since the 1600s. In the neolimnological monitoring, annual total phytoplankton and cyanobacteria biomasses were low in the 1980s, except in 1982 when the cyanobacteria *Planktothrix agardhii* (previous *Oscillatoria agardhii*) was abundant (Fig. 6b). In the 1990s, the abundance of cyanobacteria (e.g. *Anabaena* spp.) (Fig. 6c) and diatoms (e.g. *Tabellaria* spp., *Aulacoseira* spp.) increased (Fig. 6d, e). In the palaeolimnological records, the numbers of large *Daphnia* and *Bosmina* declined distinctly (Fig. 4). The palaeolimnological

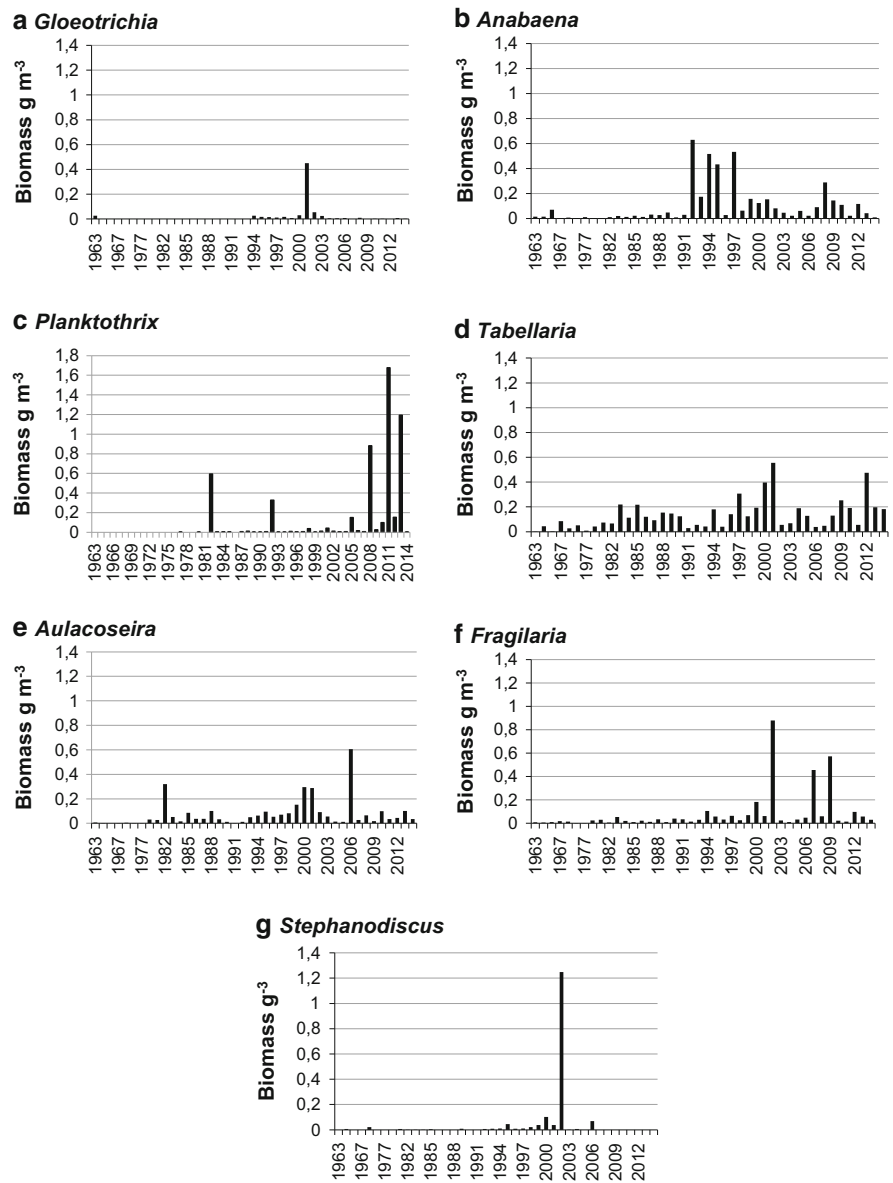


**Fig. 5** Stratigraphic cladoceran summary curves of Lake Pyhäjärvi (Kajak core). **a** *Daphnia* ephippia length, **b** relative abundance of pelagic species, **c** relative abundance of macrophyte-associated species, **d** relative abundance of macrophyte-/sediment-associated species, **e** relative abundance of sediment-associated species, **f** *Chydoridae/Chydoridae* + *Bosmina* carapaces, **g** *Chydoridae/Chydoridae* + *Bosmina* carapaces excluding *C. sphaericus*, **h** *Daphnia/Daphnia* + *Bosmina* ephippia. Zonation as in Fig. 2a

predation pressure index decreased, indicating enhanced predation in this zone and ephippia concurrently became smaller in size. The number of macrophyte-associated zooplankton (Fig. 5c) and the macrophyte abundance index (Fig. 5g) were both low. *Camptocercus* spp., *Sida crystallina* and *Alonella excisa* predominated (Fig. 5). In the neolimnological zooplankton, which has been monitored in the pelagic zone since 1977, small-bodied *Bosmina longirostris* and *Ceriodaphnia* spp. appeared (Fig. 7a, c). The large-bodied *B. longispina* was scarce but occurred regularly in the 1980s and the early 1990s (Fig. 7a). The abundance of *D. galeata* exhibited large variations following the variation in the neolimnological fish predation pressure index (Fig. 7b). Also the mean carapace lengths of *Daphnia* and *Bosmina* and the ratio (in terms of total numbers) of *Daphnia* spp. to the sum of *Daphnia* spp. and *Bosmina* spp. (ranging between 0.2 and 0.8) were inversely related to the contemporary planktivory index (Fig. 8e;  $R^2 = 0.15$ ,  $P = 0.037$ ), showing that this ratio can be used as a rough indicator of planktivorous fish predation pressure.

Z4 (0–8 cm; ~AD 1995–2004): The diatoms *S. minutulus* and *F. crotonensis* increased markedly and became dominant, but their relative abundance decreased again in the topmost layers (Fig. 2a). During this period the diatom-based DI-TP increased to 25–30 µg TP/l, the average of the 1995–2004 monitoring data being  $19.9 \pm 2.2$  µg/l. Diatom species diversity declined even more. *Gloetrichia* was abundant in both the palaeo- and neolimnological samples (Figs. 2b, 7a). The neolimnological data showed a clear phytoplankton biomass increase between 1995 and 2002 (Fig. 9). During the 2000s, both total phytoplankton and cyanobacteria biomasses varied markedly. Diatom biomass was more stable, but species dominance varied. The relative proportion and biomass of diatoms were high in 2002, the dominant taxa being *F. crotonensis* (Fig. 7f) and, uncommonly, *Stephanodiscus hantzschii* (Fig. 7g), both species typical of eutrophic waters. The biomass of cyanobacteria was also high in 2002 but rather low in 2003 and 2004. The biomass and proportion of Chrysophyceae, common in waters with lower phosphorus content (Smol, 1985), were high in 2003 as were those of Dinophyceae in 2002 and 2003 (Fig. 9). In the palaeolimnological samples, the abundances of large *Daphnia* and *Bosmina* species were low, but *B.*

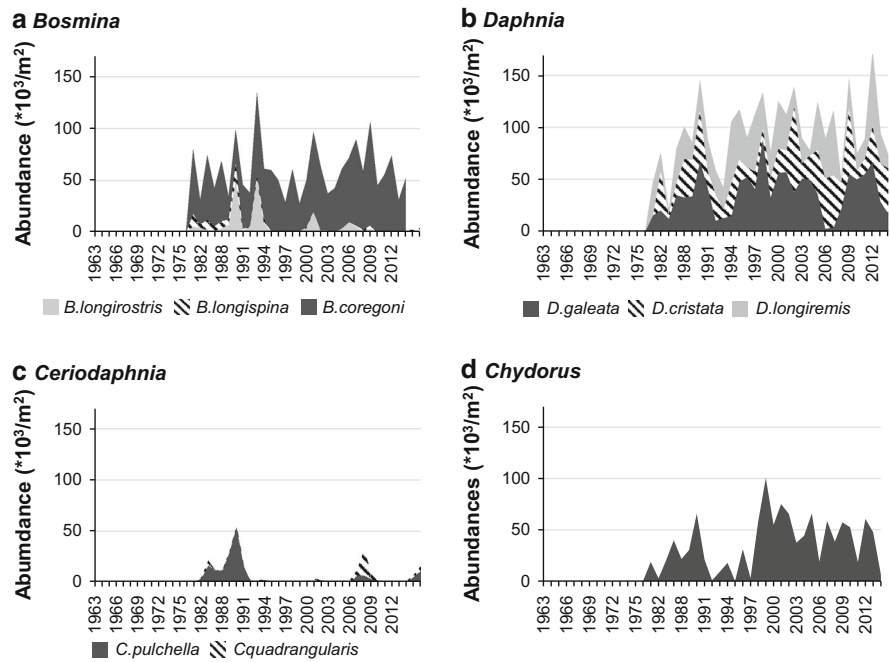
**Fig. 6** Annual means as biomass (wet weight,  $\text{g m}^{-3}$ ) of phytoplankton genera **a** *Gloeotrichia*, **b** *Anabaena*, **c** *Planktothrix*, **d** *Tabellaria*, **e** *Aulacoseira*, **f** *Fragilaria*, **g** *Stephanodiscus* in 1963–2014



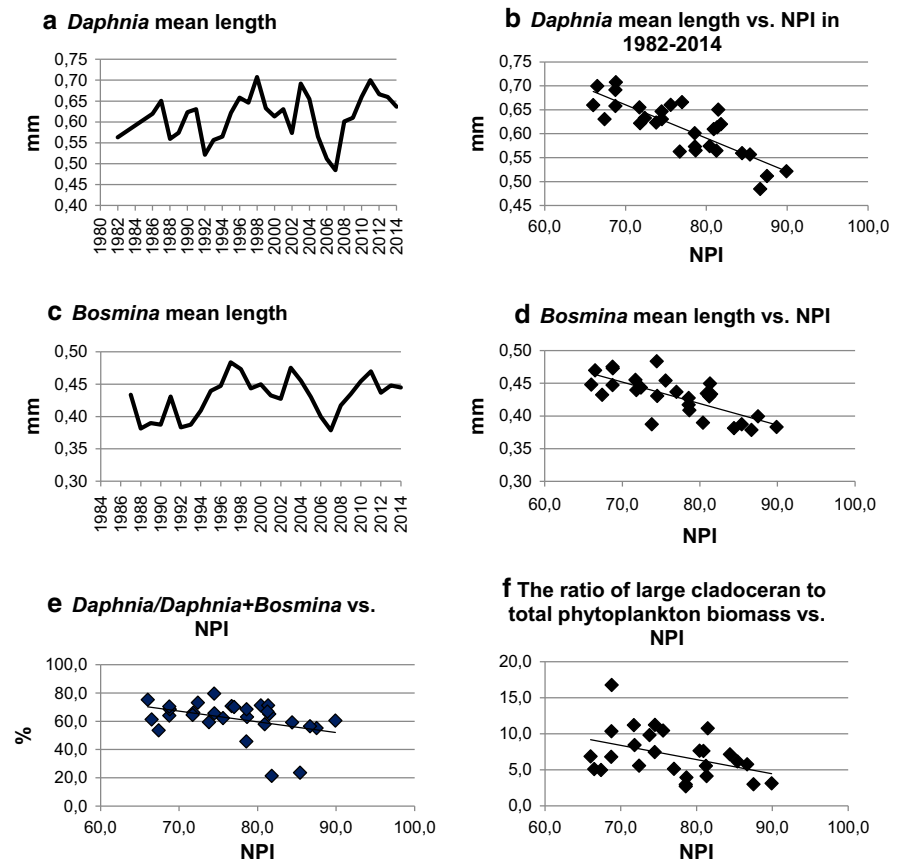
*coregoni* abundance was higher here than in the other zones (Fig. 4). The small-bodied *B. longirostris* and *Ceriodaphnia* spp. were abundant, *Camptocercus* spp., *S. crystallina* and *A. excisa* being predominant. Sediment-associated taxa were also found (Fig. 4). In the neolimnological data the mean abundance of *C. sphaericus* was low in the 1990 s, peaking in 1999 after which the numbers remained at a higher, although gradually decreasing, level (Fig. 7d). Both *Ceriodaphnia pulchella* and *C. quadrangula* were generally scarce but appeared occasionally (Fig. 7c). The same applies to *Limnospira frontosa* and

*Holopedium gibberum*, which never occurred in high numbers, however. *Diaphanosoma brachyurum* was regularly recorded in the samples during the 2000s. As the sampling was undertaken in the pelagic area, macrophyte-associated species such as *S. crystallina* were only occasionally represented in the contemporary samplings. The ratio of *Daphnia* spp to the sum of *Daphnia* spp and *Bosmina* spp was inversely related to the planktivory index, as in zone 3 (Fig. 8e). The ratio of the biomass of large cladocerans to total phytoplankton biomass varied widely between years (1987–2014) and was negatively related to the

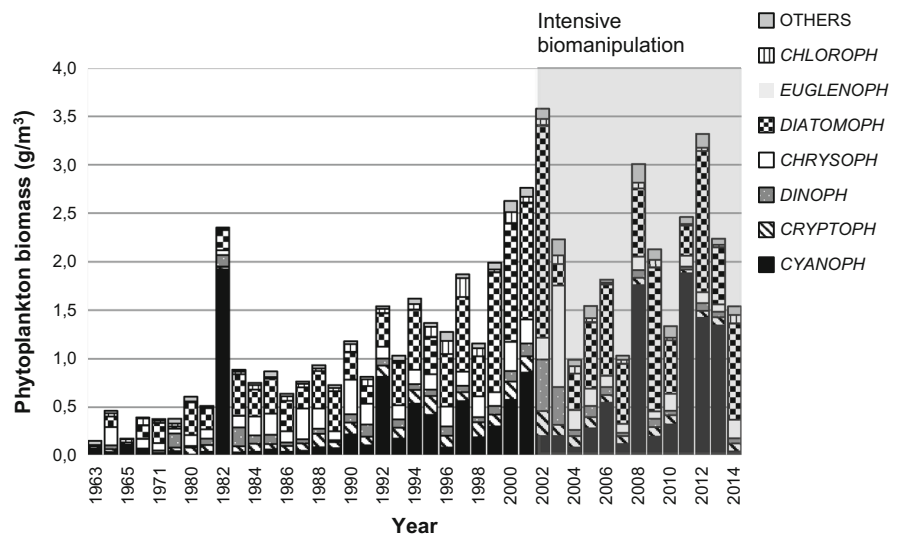
**Fig. 7** Annual means as abundances ( $\times 10^3/m^2$ ) of cladocerans **a** *Bosmina*, **b** *Daphnia*, **c** *Ceriodaphnia* and **d** *Chydorus*



**Fig. 8** **a** *Daphnia* spp. mean length (mm), **b** correlation between *Daphnia* spp. mean length and neolimnological planktivore index (NPI) in 1982–2014, **c** *Bosmina* spp. mean length (mm), **d** correlation between *Bosmina* spp. mean length and NPI in 1987–2014, **e** correlation between the ratio of *Daphnia* spp to the sum of *Daphnia* and *Bosmina* and NPI, **f** correlation between the ratio of large cladocerans to total phytoplankton biomass and NPI



**Fig. 9** Annual mean phytoplankton biomass ( $\text{g}/\text{m}^3$ ) in May–October 1963–2014. The period of intensive biomanipulation is indicated in grey



planktivory index (Fig. 8f;  $R^2 = 0.17$ ,  $P = 0.034$ ), indicating that the lowest grazing pressure on phytoplankton occurred in years when planktivorous fish were abundant.

2004–2014: The mean TP concentration in the lake during 2004–2014 was  $19.6 \pm 2.0 \mu\text{g}/\text{l}$ , decreasing from the previous period. Total phytoplankton biomass decreased since 2003; in 2011–2013 the cyanobacteria species *P. agardhii* constituted relatively high proportions of the total biomass (Fig. 9). In 2004 and 2014, cyanobacteria annual biomass means were exceptionally low. *Bosmina* spp. and *Daphnia* spp numbers were high (Fig. 7a, b), but as in Z3–Z4 their size was closely linked to the level of planktivory (Fig. 8b;  $R^2 = 0.68$ ,  $P < 0.0001$ , Fig. 8d;  $R^2 = 0.53$ ,  $P < 0.0001$ ).

#### External load and water quality

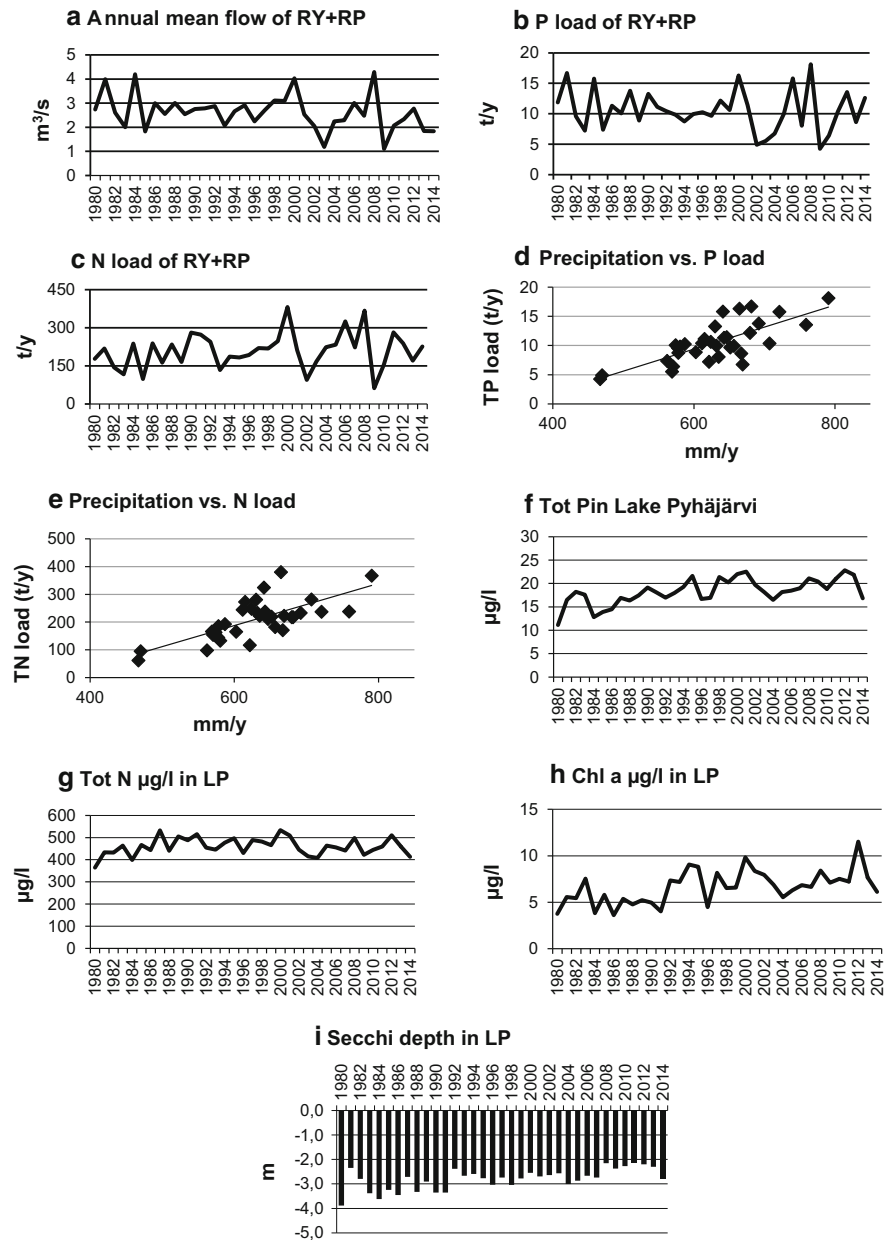
The combined annual mean flow and annual mean TP and TN loads from River Yläneenjoki and River Pyhäjoki were estimated for the periods 1980–1994, 1995–2003 and 2004–2014, referring to zones in palaeolimnological data. The flow was  $2.8 \pm 0.6$ ,  $2.7 \pm 0.8$  and  $2.4 \pm 0.8 \text{ m}^3/\text{s}$ , respectively (Fig. 10a), the TP load was  $11.0 \pm 2.8$ ,  $10.1 \pm 3.4$  and  $10.4 \pm 4.2 \text{ t}/\text{year}$ , respectively (Fig. 10b), and the TN load was  $193 \pm 57$ ,  $213 \pm 77$  and  $228 \pm 83 \text{ t}/\text{year}$ , respectively (Fig. 10c). The annual nutrient loads from agricultural and forest areas were strongly correlated with annual precipitation (Fig. 10d,  $R^2 = 0.56$ ;  $P < 0.0001$ ; Fig. 10e, nitrogen:  $R^2 = 0.52$ ,  $P < 0.0001$ ).

The annual mean concentration of TP in the lake increased in the 1980s and the early 1990s. The highest mean concentration ( $22 \mu\text{g}/\text{l}$ ) was observed in 1994. The variation increased during the 2000s ( $17\text{--}23 \mu\text{g}/\text{l}$ ) (Fig. 10f). The annual mean concentration of TN remained rather stable ( $400\text{--}500 \mu\text{g}/\text{l}$ ). The means of TN for the periods 1980–1994 (Z3), 1995–2003 (Z4) and 2004–2014 were  $457.4 \pm 43.6$ ,  $474.2 \pm 38.4$  and  $452.4 \pm 32.0 \mu\text{g}/\text{l}$  (Fig. 10g), respectively. The average annual chlorophyll *a* concentration varied, but in the 1990s and 2000s the level was higher than in the 1980s. The means of chlorophyll *a* for 1980–1994, 1995–2003 and 2004–2014 were  $5.6 \pm 1.6$ ,  $7.5 \pm 1.6$  and  $7.35 \pm 1.59 \mu\text{g}/\text{l}$ , respectively (Fig. 10h). Secchi depth decreased during the monitoring period 1980–2014. Average Secchi depth for the periods 1980–1994, 1995–2003 and 2004–2014 were  $3.1 \pm 0.5$ ,  $2.8 \pm 0.2$  and  $2.5 \pm 0.3 \text{ m}$ , respectively (Fig. 10i). In 2014, the water quality parameters indicated more oligotrophic conditions than in the previous years. TP, TN and chlorophyll *a* concentrations were low, and in July 2014 exceptionally high Secchi depths (up to 4.8 m) were recorded, and also the annual mean Secchi depth was relatively high.

#### Discussion

The results from Z1 (AD  $\sim 1600\text{--}\sim 1700$ ), the period before the major water level drawdown, suggest that the lake was meso-eutrophic. The diatom assemblages

**Fig. 10** Monitoring data 1980–2014: **a** combined annual mean flow ( $\text{m}^3/\text{s}$ ) of River Yläneenjoki and River Pyhäjoki (RY + RP), **b** annual mean phosphorus load (t/year) of RY + RP, **c** annual mean nitrogen load (t/year) of RY + RP, **d** correlation between precipitation and phosphorus load, **e** correlation between precipitation and nitrogen load, **f** annual mean total phosphorus concentration ( $\mu\text{g}/\text{l}$ ) in Lake Pyhäjärvi (LP), **g** annual mean total nitrogen concentration ( $\mu\text{g}/\text{l}$ ) in LP, **h** annual mean chlorophyll *a* concentration ( $\mu\text{g}/\text{l}$ ) in LP, **i** annual mean Secchi depth (m) in LP



were dominated by planktonic and meroplanktonic species, and based on the low macrophyte abundance index and the low number of truly macrophyte-associated cladoceran taxa macrophyte abundance was presumably low. Judging from the size of *Daphnia* and the paleolimnological predation index, the predation pressure on cladocerans was moderate to low. This concurs with the fact that there was no specialised planktivore among the native fish species (Sarvala et al., 1998a).

The human-induced water level decrease apparently had a profound effect on the aquatic ecosystem of Pyhäjärvi during Z2 (~1700–~1930). A major shift in the diatom and cladoceran communities, indicating an increase in macrophytes and improved water quality, occurred at 80-cm sediment depth. This corresponds to a change in sediment properties as the magnetic susceptibility increased from ~1.5 to ~4 SI units between 90 and 80 cm (data not shown; magnetic susceptibility was measured at 1 cm

intervals directly from unopened core tubes using a Bartington MS2 magnetic susceptibility meter and the MS2C Core Logging Sensor), indicating that the sediment became permanently more mineral-rich. It is quite likely that this was a result of lake water lowering, changing the system into one that constantly transports more mineral matter to the deep than before. However, it is unclear whether the oligotrophication was caused by the possible lowering in the late 1600s or by the lowering in the 1850s. The  $^{210}\text{Pb}$  dating of the core covered only part of this period (>1863 AD) and partly contradicts the earlier study by Räsänen et al. (1992) who ascribed the oligotrophication to the 1852–1854 water level lowering undertaken to develop by then still traditional and low-intensive agriculture. However, dating uncertainties occurred also in Räsänen et al. (1992) for sediment depths below 53 cm. The possible early water level modification in connection with the establishment of the Eurajoki iron mill in the late 1600s is based not on data but on qualitative archaeological and historical evidence and it is thus difficult to estimate its role in oligotrophication.

Notwithstanding uncertainty over the timing of oligotrophication (biotic community changes and lowering of DI-TP), it likely occurred in this period as a response to the water level drawdown. This is supported by an increase in macrophyte abundance as evidenced by the enhanced proportion of periphytic diatoms and of both macrophyte- and sediment-associated cladocerans, with potential positive feedback on water clarity via reduced phytoplankton development, as seen in other studies (e.g. Coops et al., 2003; Bucak et al., 2012; Jeppesen et al., 2015). Accordingly, a decline in the proportion of planktonic diatom forms suggests a reduction in phytoplankton production and improved water clarity. The increase in littoral taxa may also reflect a change in sedimentation patterns, associated with the lower water level, which would increase the share of littoral diatoms and cladocerans at the deep water coring site. The cladoceran record suggests continued low planktivory, a typical response to oligotrophication (Persson et al., 1988; Jeppesen et al., 2000). All these results suggest that during Z2 Pyhäjärvi was in a meso-oligotrophic clear-water state with relatively high abundance of macrophytes and relatively low fish planktivory, this being consistent with early limnological observations in the mid-1910s (e.g. Secchi depth 4.0–4.3 m;

Järnefelt, 1927). The connection of Pyhäjärvi with an aquifer (Rautio & Korkka-Niemi, 2011, 2015) might also have contributed to the oligotrophication. Planktivorous whitefish were successfully introduced in 1908, but our study did not find any clear effects of this introduction on the cladoceran community in the Z2 sediment record. Salo et al. (1989) and Räsänen et al. (1992), however, found a reduction in *B. coregoni* mean body size in sediment samples representing year ~1921, which they ascribed to whitefish stocking.

During Z3 (~AD 1930–1994), some major changes occurred in the catchment and the lake: the introduction of vendace in the 1950s, resulting in high vendace abundances since the 1960s (Sarvala et al., 1998a), intensification of agriculture and increased use of chemical fertilisers after the Second World War (Valkama et al., 2009). Finally, in the early 1990s, the effect of climate change on the lake and its catchment became more evident, including changes in winter precipitation and nutrient load (Ventelä et al., 2011) and in lake temperature (Jeppesen et al., 2012). These changes apparently had a pronounced impact on the lake ecosystem. DI-TP increased to 20–25  $\mu\text{g/l}$ . Similarly, the monitoring TP record increased from 11  $\mu\text{g/l}$  (in 1980) to 19.3  $\mu\text{g/l}$  (in 1994). The eutrophication can also be seen as a rapid increase of *F. crotonensis*, a species indicative of eutrophic waters, and as a clear increase in cyanobacteria and diatoms. Algal blooms were observed, arousing public concern (Kirkkala, 2014). *Anabaena* akinetes were also recorded in the entire 30-cm core in a separate study by Räsänen et al. (2006), but the akinete record does not allow estimates of past *Anabaena* abundances. Similar problems are not likely with *Gloeotrichia*, which were counted as whole colonies.

A marked decline of large-bodied *Daphnia* and *B. longispina* is evidenced by both palaeolimnological and neolimnological samples. The abundance of the macrophyte-associated species of cladocerans decreased, also indicating more eutrophic conditions with higher phytoplankton growth, further facilitated by low grazing of phytoplankton by the small-bodied zooplankton (Jeppesen et al., 1997). The fish stockings, especially of vendace, had a strong effect on the zooplankton through increased planktivory, clearly reflected as changes in cladoceran body sizes (Fig. 5a) (see also Sarvala et al., 1998b).

The large-scale restoration of Pyhäjärvi started in 1995 (the beginning of Z4) (Ventelä & Lathrop, 2005; Kirkkala, 2014). The most important activities have been

the nutrient load reduction measures in the catchment and the intensive long-term biomanipulation conducted by local professional fishermen. The biomanipulation effort was intensified after 2002 (Ventelä et al., 2007). In this zone, the diatoms associated with eutrophic conditions dominated but decreased in the topmost layers, showing detectable recovery of the lake after restoration. The neolimnological monitoring data show that total phytoplankton biomass more than doubled from 1995 to 2002 but then declined steeply, which is consistent with the TP changes and the initiation of restoration measures. The phytoplankton changes were mainly due to variations in biomass and species dominance of cyanobacteria (e.g. *Anabaena* spp.) and diatoms (e.g. *Tabellaria* spp., *Aulacoseira* spp.). The highest *Gloeotrichia* biomass recorded by monitoring data was in 2001 with highly visible blooms in shore areas, which attracted great public attention and concern, and the users of the lake were dissatisfied with the water quality (Stedman et al., 2007). Both *Gloeotrichia* and *Anabaena* spp had lower biomasses later in the 2000s.

Both palaeo- and neolimnological results reveal a high predation pressure: small-sized ephippia dominated in the palaeo data, and the mean carapace length of *Daphnia* and *Bosmina* was inversely related to the fish predation pressure in the neolimnological data. Our results suggest that it took some time before the intensive lake management efforts started to take effect, but the deterioration trend finally ceased in the 2000s.

For the most recent period, 2004–2014, only neolimnological data are available. High latitude lakes have been shown to be sensitive to climatic forcing (Itkonen et al., 1999; Sorvari et al., 2002), and the impact of climate-related environmental variables clearly increased also in Pyhäjärvi: the length of the ice cover period decreased (Ventelä et al., 2011) and the maximum lake temperature increased at the same time as the vendace stock declined (Jeppesen et al., 2012). Also the external phosphorus load varied strongly; the highest (wet 2008) and lowest (dry 2009) annual loads during the monitoring period were observed in consecutive years. From 2004 to 2014, the mean TP concentration was similar to that in 1995–2004, which likely reflects the loading reduction in the catchment and the successful biomanipulation.

After 2002, phytoplankton biomass and composition varied strongly but are indicative of lake recovery. The proportion and biomasses of species and taxa indicative of eutrophic conditions were lower than in the 1990s.

*Gloeotrichia* biomass was low and the cyanobacteria community was dominated by *P. agardhii*, a species that does not form visible blooms disturbing the recreational use of the lake, and which is mainly concentrated in the deeper parts of the water column. In 2014, the phytoplankton composition and biomass reflected a, perhaps temporary, improvement in ecological status. The increase in zooplankton abundance was connected with the low abundance of planktivores resulting from sufficiently large biomanipulation catches.

Based on our study results, we conclude that the external nutrient load is closely linked with precipitation, indicating that the current catchment measures are not sufficiently able to reduce the nutrient load peaks derived from an increased water flow. More detailed studies and new practical tools, in particular better buffering of the system to hydrological extremes, are needed to compensate for the climate change-induced higher nutrient loading, as highlighted also in other studies (Trolle et al., 2011; Jeppesen et al., 2014). Controlling the nutrient load during very rainy periods and extreme weather events may turn out to be a strongly demanding and almost impossible task.

Biomanipulation may be an effective in-lake management tool also in a variable climate. The current trend of increasing temperatures and a decreasing planktivore biomass (Jeppesen et al., 2012) indicates a change towards a food web structure with high numbers of large cladocerans and of other herbivorous zooplankton, with a resulting positive effect on water quality, a development that may be furthered by fish manipulation. However, the phytoplankton community is also strongly affected by climate change (Adrian et al., 2009; Pätynen et al., 2014) and may, as indicated by the development in recent years in Pyhäjärvi, become dominated by cyanobacterial species like *Planktothrix*, which are less edible to zooplankton (Rücker et al., 1997). This may diminish the trophic cascade effect of the biomanipulation (Søndergaard et al., 2007; Ger et al. 2014).

## Conclusions

Climate-related changes will challenge the protection and use of ecosystem services such as water supply, industry, recreation and fisheries, not least because nutrient loading and climate warming effects act in synergy (Jeppesen et al., 2010; Moss et al., 2011;



**Table 1** Summary

Time (AD)	Diatoms	Cladocera	<i>Gloeotrichia</i>	Plant macrofossils	Fish predation	Human activities	Interpretation
2014–2004	Decrease in eutrophic taxa	Increase in abundance and size	Decrease in biomass		Varying, but relatively low (biomanipulation, low stock of planktivores)	Increase in climate-related effects	Recovery
2004–1995	Both eutrophic and benthic taxa	Varying, affected by planktivory	Abundant, highest biomass in 2001		High Variation in planktivore stocks	Initiation of Pyhäjärvi restoration programme	Elevated nutrient levels
~ 1995–1930	Increase in eutrophic taxa, high abundance of periphytic taxa	Decrease in <i>Daphnia</i> and <i>Bosmina</i> , dominance of pelagic taxa	Observed	Decrease in macrophyte abundance	Stocking and consequent high abundance of whitefish and vendace, enhanced planktivory	Increased nutrient input	Increase in TP concentration
~ 1930– ~ 1700	Oligotrophic and periphytic taxa	Sediment- and macrophyte-associated taxa, significant increase in <i>Daphnia</i> and <i>Bosmina</i>	Observed	Increase in macrophytes to relatively high abundance	Introduction of whitefish since 1908, but low level of planktivory	Lowering of water level	Decrease in TP concentration, meso-oligotrophic clear-water state
~ >1600–1700	Planktonic and meroplanktonic diatoms, mesotrophic taxa	Low abundance of <i>Daphnia</i> and <i>Bosmina</i> , high abundance of pelagial <i>Chydorus</i>	Relatively abundant		Low	Modifying outflow	Natural meso-eutrophic lake

Jeppesen et al., 2014). Adaptation and management actions are needed, but to be sufficiently efficient they should be based on the knowledge of the key functions of the ecosystem.

In this study, the ecosystem history of Pyhäjärvi was determined by combining palaeolimnological records with detailed neolimnological data. Distinctive phases of oligotrophication, eutrophication and recovery were found (Table 1), and the key processes in ecosystem changes were elucidated. The sedimentary diatom and cladoceran assemblages revealed a period of elevated nutrient concentrations between AD ~1600 and ~1700, which may be considered the original natural and pristine state of the lake. However, it cannot be used as a target point for the restoration of Pyhäjärvi as the lake had a different structure than today (water level, catchment). The oligotrophication period between AD ~1700 and 1930 linked with artificial changes in water level resulted in lower phytoplankton abundance and higher macrophyte abundance. Those features are also currently highly valued, as the policy and social studies made in the Pyhäjärvi catchment (Stedman et al., 2003; Kuoppa, 2006; Stedman et al., 2007) indicate that the clear water and the high recreational usability of the lake are the most important factors for the local tourism, industry and the community, who also fund the restoration work. Thus, this oligotrophic period up to the early 1900s can be used as the target trophic state for lake restoration purposes. Also the lake's boundary conditions then were similar to those existing today.

In spite of the current climate-driven challenges to restoration of Pyhäjärvi, some signs of recovery emerged in both the palaeo- and neolimnological records following the initiation of restoration. Particularly, the clearly improved water quality recorded in 2014 offers hope that the target state of the meso-oligotrophic period of the early 1900s may be reached. However, if the challenges induced by the climate change become too difficult to meet in the future, the restoration target should be the best possible adaptation and mitigation of the negative effects. A similar revision of targets may be necessary in other similar lake restoration projects irrespective of whether the current targets are set by the local communities or, for example, the European Union.

Our case study shows that long-term data records are needed to understand the realistic management targets. Together the palaeo- and neolimnological

records provide a more detailed insight into the recent changes as well as a more reliable hindcast of the changes occurring before initiation of monitoring than monitoring data alone, as highlighted also by Battarbee et al. (2005). Also, neolimnological data are needed to complement the information given by palaeolimnological methods (Davidson & Jeppesen, 2013). A complex history such as that of Lake Pyhäjärvi illustrates the difficulties in selecting management targets, and the risk of setting false targets, for lakes based solely on monitoring data.

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