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REVIEW PAPER

Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes

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Abstract Fish play a key role in the trophic dynamics of lakes. With climate warming, complex changes in fish assemblage structure may be expected owing to direct effects of temperature and indirect effects operating through eutrophication, water level changes, stratification and salinisation. We reviewed published and new long-term (10–100 years) fish data series from 24 European lakes (area: 0.04–5,648 km^2; mean depth: 1–177 m; a north–south gradient from Sweden to Spain). Along with an annual temperature increase of about 0.15–0.3°C per decade profound changes have occurred in either fish assemblage composition, body size and/or age structure during recent decades and a shift towards higher dominance of eurythermal species. These shifts have occurred despite a reduction in nutrient loading in many of the lakes that should have benefited the larger-sized individuals and the fish species typically inhabiting cold-water, low-nutrient lakes. The cold-stenothermic Arctic charr has been particularly affected and its abundance has decreased in the majority of the lakes where its presence was recorded. The harvest of cool-stenothermal brown trout has decreased

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We dedicate this paper to the late Prof. Jürgen Benndorf, a true pioneer and mentor in lake and reservoir management oriented research, who inspired a number of us to initiate long-term comprehensive experimental ecological studies on lakes and reservoirs.

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substantially in two southern lakes. Vendace, whitefish and smelt show a different response depending on lake depth and latitude. Perch has apparently been stimulated in the north, with stronger year classes in warm years, but its abundance has declined in the southern Lake Maggiore, Italy. Where introduced, roach seems to take advantage of the higher temperature after years of low population densities. Eurythermal species such as common bream, pike–perch and/or shad are apparently on the increase in several of the lakes. The response of fish to the warming has been surprisingly strong and fast in recent decades, making them ideal sentinels for detecting and documenting climate-induced modifications of freshwater ecosystems.

Keywords Climate change · Fish assemblages · Functional traits · Long-term data series · Europe

Introduction

Climate change is acknowledged to be one of the principal threats to biodiversity (IPCC, 2007), with many of its effects being related specifically to global warming (Root et al., 2003). There are two types of thermal shifts to which populations have to respond: geographic shifts of isotherms over time and temporal shifts in the seasonal development of temperatures (Burrows et al., 2011). The consequences of global warming for biodiversity and biogeography are relatively well documented in terrestrial and marine ecosystems and encompass range shifts along latitudinal and altitudinal thermal gradients or increasing frequencies of temporal mismatch between predator and prey population dynamics (Parmesan & Yohe, 2003; Perry et al., 2005; Durant et al., 2007). An even more pronounced response to global warming is expected for freshwater ecosystems, in part because geographic range shifts compensating for higher temperatures are prevented when habitats and ecosystems are effectively spatially isolated as is the case for many lakes (Hickling et al., 2006; Heino et al., 2009).

Aquatic animals will be differentially affected by warming depending on their body size and thermal biology (Olalla-Tárraga, 2011). Freshwater fish are directly affected by changes in temperature. As ectotherms, fish cannot thermoregulate physiologically, but only behaviourally by moving to areas with appropriate temperatures. Therefore, if they are able to do so, the population ranges of cold-stenothermal species (e.g. Arctic charr, *Salvelinus alpinus*) will likely shift towards higher latitudes or altitudes, while such species may become locally extinct at the warmest edge of their current distribution ranges (Lappalainen & Lehtonen, 1997; Wrona et al., 2006; Graham & Harrod, 2009). In contrast, eurythermal species exhibiting wide thermal tolerance (e.g. common carp, *Cyprinus carpio*) may be able to cope with the new thermal regimes and so experience no loss and potentially even an increase in thermal habitat (Lappalainen & Lehtonen, 1997). By contrast, tropical

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species typically experience mean temperatures that are close to their physiological optima, and even a small increase in temperature may thus put them at high risk of extinction (Tewksbury et al., 2008). Many fish species are also adapted to low oxygen concentrations, specifically at either low or high temperatures (Holopainen et al., 1997; Soares et al., 2006). When temperature increases, oxygen may drop to critical levels as warm water holds less oxygen and the respiration rates increase. Global warming may therefore create novel fish assemblages by effectively favouring species which have responded to range shifts in addition to those already locally present within their native range, thereby potentially increasing competition for space and food. As fish species richness is currently higher in warmer climates (Griffiths, 1997; Amarasinghe & Welcomme, 2002; Zhao et al., 2006; Meerhoff et al., 2007a; Teixeira-de Mello et al., 2009), richness may increase in present-day cold lakes in a future warmer climate, depending on local conditions, original assemblages and physical barriers to colonisation.

In addition to effects on fish assemblage composition, life history traits will also be affected by warmer temperatures. Cross-comparisons of fish populations in similar systems in South America and Europe (Teixeira-de Mello et al., 2009) and within Europe have shown that lower-latitude fish species are often not only individually smaller (Griffiths, 1997; Jeppesen et al., 2010a), but also grow faster, mature earlier, have shorter life spans and allocate less energy to reproduction (measured as the gonadosomatic index) than species at higher latitudes (Blanck & Lammouroux, 2007). Similar patterns were found in a very comprehensive study of North American fishes (Mims et al., 2010). Such changes are evident within species along a latitudinal gradient in numerous studies (Mills, 1988; Venne & Magnan, 1989; Malmquist, 2004; Blanck & Lammouroux, 2007; Lappalainen et al., 2008). The general pattern also seems to be common for fishes in marine habitats (Vila-Gispert et al., 2002).

In a recent review, Jeppesen et al. (2010a) showed that climate warming will probably generate changes in lake fish assemblage structure, life history traits, feeding modes, habitat use and winter survival. Their conclusions were mainly based on space-for-time-substitution studies comparing lake fish assemblages and cross-latitude experiments from different climate zones and, thus, different mean temperatures. The strength of this approach is that the fish assemblages per se have had time to evolve and adapt to the climate in which they live, but a potential weakness is that they may not yet have reached a mature state. This is especially true in the cold regions where speciation is currently occurring, for instance among the dominant species there: Arctic charr, three-spined stickleback (*Gasterosteus aculeatus*) and whitefish (*Coregonus* spp.) (Robinson & Schluter, 2000; Snorrason & Skúlason, 2004; Klemetsen, 2010; Hudson et al., 2011). Moreover, regional biogeographical constraints are not taken into account. Current patterns in species richness and assemblage composition of fish are strongly influenced by past glaciations, their present distance from the refuges available during these periods, and the dispersal barriers that appeared following deglaciation, such as the mountains of Europe (Griffiths, 2006; Abell et al., 2008; Volta et al., 2011). Finally, although the differences in life history traits between populations at varying latitudes may reflect long-term evolution, they do not indicate how local populations might respond to accelerated climate warming at decadal to centurial scales. Rapid micro-evolution of life history traits, for example survival and aspects of individual performance (e.g. age at reproduction and number of offspring), was recorded for the freshwater cladoceran *Simocephalus* by Van Doorslaer et al. (2007), suggesting that populations may buffer changes in community structure and persist locally under the conditions of the predicted climate warming. Such a response, however, has not yet been demonstrated for fishes.

An obvious alternative, or complementary method, to space-for-time comparisons is to analyse time series from a given lake or region under the influence of climate variability and recent climate change. This approach has been successfully used to demonstrate strong responses of lake ecosystems to warming over the last 30–50 years (Straile et al., 2003; Blenckner et al., 2007; Adrian et al., 2009). However, in the great majority of the case studies summarised so far, the response of lake fish assemblages to changes in temperature and thermal stratification has been neglected. Analyses of long-term data from fish assemblages (as well as other biotic communities) in lakes are frequently hampered by the combined effects of increases in nutrient load and (for fish specifically) fisheries intensity which have occurred over recent decades in different regions of the globe, not least in

Europe (Thomas et al., 2009; Anneville et al., 2009). With respect to fish in European lakes, eutrophication generates a dominance shift from salmonids to percids and then from percids to cyprinids (Hartmann, 1977; Persson et al., 1991; Jeppesen et al., 2000), and particularly to low-oxygen-tolerant cyprinids in stratified lakes (Mehner et al., 2005).

In the present review, we focus on the response of fish assemblages to climate change and climate variability by discussing trends in long-term data series from 24 European shallow and deep lakes (Table 1). Lakes that had >9 years of paired data on at least one fish metric and one climate metric were included. European lakes constitute an appropriate and tractable sample of the world's lakes since many of them have been monitored more intensively and for a longer period of time than have most lakes elsewhere. Where possible, we seek to disentangle the effects of climate from those of other anthropogenic factors such as local changes in nutrient loading and fisheries. Overall, we argue that lake fish assemblages are sensitive to even subtle changes in temperatures, making them ideal sentinels for detecting and documenting climate-induced modifications of freshwater ecosystems.

Materials and methods

We aim to extract patterns of change by analysing specific case studies at different locations and, thus, different climates within Europe. For the majority of the studies, the methods used are described in detail in published papers to which we refer. Accordingly, we give below only a brief overview of the lake characteristics, methods and add specific information when unpublished data are used, with lakes ordered by decreasing latitude. Some basic information on location, morphometry and physical and chemical variables is given in Table 1 and Figs. 1, 2A, 3A, 4A, 5A, 6A, 7A, 8A, 9A, 10A, 11A, 12A, 13A.

Lake Elliðavatn, Iceland

Lake Elliðavatn is a small, clear water oligo-mesotrophic shallow lake within the metropolitan area of the capital city Reykjavík. The lake is largely (~50%) fed by cold (3–6°C) subsurface spring water with a high natural pH (≥7.5 all year round and pH 9.0–10.0 for several weeks in July–August) due to neo-volcanic bedrock in the catchment area (270 km^2). The lake and its inlet rivers have been subjected to various impacts following urbanisation in the catchment area, including damming of the outlet river Elliðaár in 1924–1925 and regulation of the water levels (ca. ~0.4 m), phytoplankton biomass is low (chlorophyll (chl) *a*: 1.7–2.8 $\mu g\ l^{-1}$, annual mean in the last decade) and the water clarity and abundance of submerged macrophytes are high (Thórðarson, 2003; Malmquist et al., 2009, 2010).

The fish assemblage consists of a few species, dominated by Arctic charr and brown trout (*Salmo trutta*). Charr spawn primarily within the lake and trout mainly in the tributaries. Three-spined stickleback are also abundant in the lake, while Atlantic salmon (*Salmo salar*) and European eel (*Anguilla anguilla*) are less common.

The lake has one of the best long-term data series in Iceland on the relationship between climate warming and freshwater fish (Malmquist et al., 2009). The published fish data cover the period 1974–2006, but in the present paper we use annual data from 1987 to 2010 based on a common sampling protocol described by Malmquist et al. (2009). The fish data were extracted from annual reports published by the Institute of Freshwater Fisheries, Iceland (Antonsson & Árnason, 2011). In short, sampling was conducted in late September/early October with two gill-net series, each comprising 10 nets with different mesh sizes (16.5–60 mm, knot to knot). In 1993, a 12.0-mm mesh-sized net was added to the net series. Nets were set overnight (~12 h) in one of two main basins of the lake.

Data on lake temperature were provided by the Icelandic Meteorological Institute and temperature has been measured at the lake outlet since August 1988 (1–4 records h^{-1}). Nutrients, including total phosphorus (TP), were measured in 2001–2002 in a few samples ($n = 18$) taken at ~0.4 m depth in both basins (Thórðarson, 2003).

Lake Valkea-Kotinen, Finland

Lake Valkea-Kotinen is a small, mesotrophic shallow brown-water lake located in a small headwater catchment (0.3 km^2) in a remote protected forest area in southern Finland, only affected by pollution from airborne sources (for details see Ukonmaanaho et al.,

Table 1 Information about lake locations, morphometry and fish data series

Lake	Country	Position	Altitude (m.a.s.l.)	Lake area (km^2)	Mean depth (m)	Maximum depth (m)	Mean total phosphorus in surface waters (μg P l^{-1})
Lake Elliðavatn	Iceland	64°05′N, 21°48′W	75	2.02	1.0	2.3	Mean 13 (Jan–Dec, 2000–2002) Maximum: 18 (2001)
Lake Valkea-Kotinen	Finland	61°15′N, 25°04′E	156	0.041	2.5	6	Mean 17 (Jan–Dec, 1989–2009) Maximum 21 (in 2009)
11 lakes	Sweden	56–64°N, 12–18°E	35–268	0.18–4.89	4–14	9–42	Mean 5–12 (Feb–Oct 1993–2010) Maximum 12–16 (in different years)
Lake Säkylän Pyhäjärvi	Finland	61°0′N, 22°15′E	45	155	5.5	26	Mean 18 (May–Sep, 1980–2011) Maximum 23 (in 2000)
Lake Peipsi	Estonia/Russia	57°8′N, 27°5′E	30	3,555	7.1	15.5	Mean 42 (May–Sep, 1985–2010) Maximum: 78 (1992)
Lake Vänern	Sweden	58.5	44	5,648	27	106	Mean 6 (May–Sep, 1995–2010) Maximum 8 (in 1995)
Lake Vättern	Sweden	57.5	89	1,939	40	126	Mean 5 (May–Sep, 1995–2010) Max 7 (in 1989)
Lake Søbygaard	Denmark	56°15′N, 9°48′E	49	0.4	1	1.2	Mean 507 (May–Sep, 1989–2010) Maximum: 997 (1996)
Windermere	UK	54°22′N, 2°56′W	39	14.8	25	64	Mean 13 in North basin, 21 in South basin (Jan–Dec, 1970–2010) Maximum 17 in North Basin (1981), 31 in South Basin (1990)
Lake Stechlin	Germany	53°10′N, 13°02′E	72	4.3	22.8	69	Mean 12 (Jan–Dec, 2000–2010) Maximum: 16 (2007)
Lake Constance, Upper Lake	Austria/ Germany/ Switzerland	47°39′N, 9°18′E	395	473	101	254	Mean 36 (Winter mixing, 1951–2010) Maximum: 87 (1979)
Lake Geneva	France/ Switzerland	46°27′N, 6°32′E	372	582	153	309	Mean 42 (Jan–Dec, 1986–2010) Maximum: 71 (1986)
Lake Maggiore	Italy/ Switzerland	45°57′N, 8°33′W	193	212.5	177	377	Mean 13 (1979–2008) Maximum: 23 (1981)
Lake Albufera	Spain	39°20′N, 0°21′W	0	23.2	1.2	3	Mean 280 (Jan–Dec, 1988–2007) Maximum: 483 (1988)

1998). Steep thermal and oxygen stratification is typical for the lake, resulting in a 2-m thick warm and oxygenated epilimnion and a cold and anoxic hypolimnion during the growing season (Forsius et al., 2010).

Perch (*Perca fluviatilis*) and pike (*Esox lucius*) are the only fish species present in the lake. The size and structure of the perch population have been monitored since 1991 (Rask et al., 1998). Annual abundance estimates were obtained from 2 weeks of continuous marking and recapturing without fish removal (modified Schnabel estimate, Krebs, 1989). The fish were caught in wire traps with a 1-cm^2 mesh retaining perch ≥8 cm in length, which corresponds to ≥2 years in age. The fish were subsequently measured to record total length, after which they were fin-clipped and released. Samples for age determination were taken after the mark-recapturing, with opercular bones being used to determine age and to back-calculate growth (Raitaniemi et al., 1988).

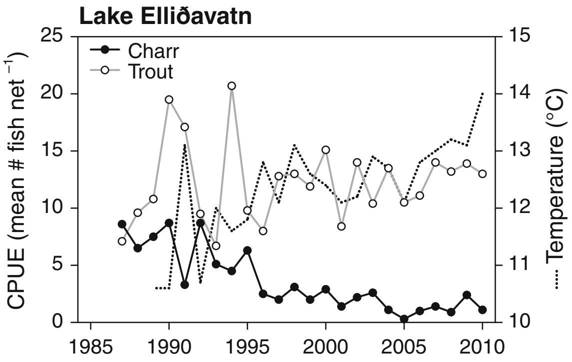


Fig. 1 Lake Elliðavatn. Catch per unit effort (CPUE, average number of fish caught per net) of Arctic charr and brown trout together with June–September mean temperatures (modified from Malmquist et al., 2009; Antonsson & Árnason, 2011; IMO, 2011)

Regular monitoring of water quality and hydrobiology has been carried out since 1990 (Keskitalo et al., 1998; Rask et al., 1998).

Eleven forest lakes, Sweden

The 11 lakes are situated at low to mid altitudes (35–268 m a.s.l.) and vary in area and depth. The lakes range from oligo- to mesotrophic and total organic carbon (TOC) varies from 4 to 11 mg l^{-1}.

Total fish species richness per lake was 4–8, and a total of 14 fish species was observed at least once in one lake (Holmgren, 2009). The following species were caught each year: perch and roach (*Rutilus rutilus*) (all lakes), ruffe (*Gymnocephalus cernuus*) (6 lakes), rudd (*Scardinius erythrophthalmus*) (3 lakes), vendace (*Coregonus albula*) (3 lakes), whitefish (3 lakes), smelt (*Osmerus eperlanus*) (2 lakes), bleak (*Alburnus alburnus*, 2 lakes) and common bream (*Abramis brama*) (1 lake).

Fish were monitored annually in July or August using multi-mesh gill nets (CEN, 2005; Holmgren, 1999). To ensure a set of lakes with similar fish assemblages, only circum-neutral lakes (annual mean pH >6) inhabited by perch, roach and pike were included. Age of perch was determined using operculum bones and sagittal otoliths, and length was, after the first year, back-calculated according to Holmgren & Appelberg (2001). Mean length at 0^{+} was used as a measure of first year growth for each of the perch cohorts hatched in 1993–2009.

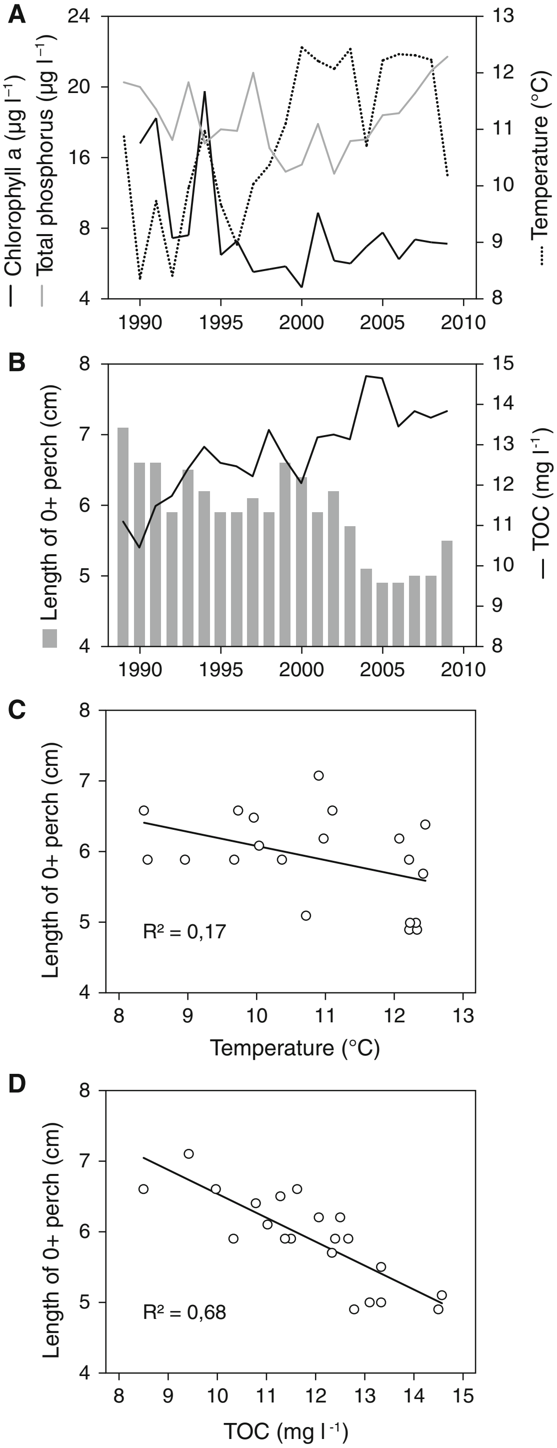


Fig. 2 Lake Valkea-Kotinen. **A** Annual mean total phosphorus concentration, chlorophyll *a* and water temperature (1 m depth). **B** Mean length of 0^{+} perch and annual mean concentration of total organic carbon (TOC, 1 m depth). **C**, **D** Relationship between mean length of 0^{+} perch, water temperature and TOC

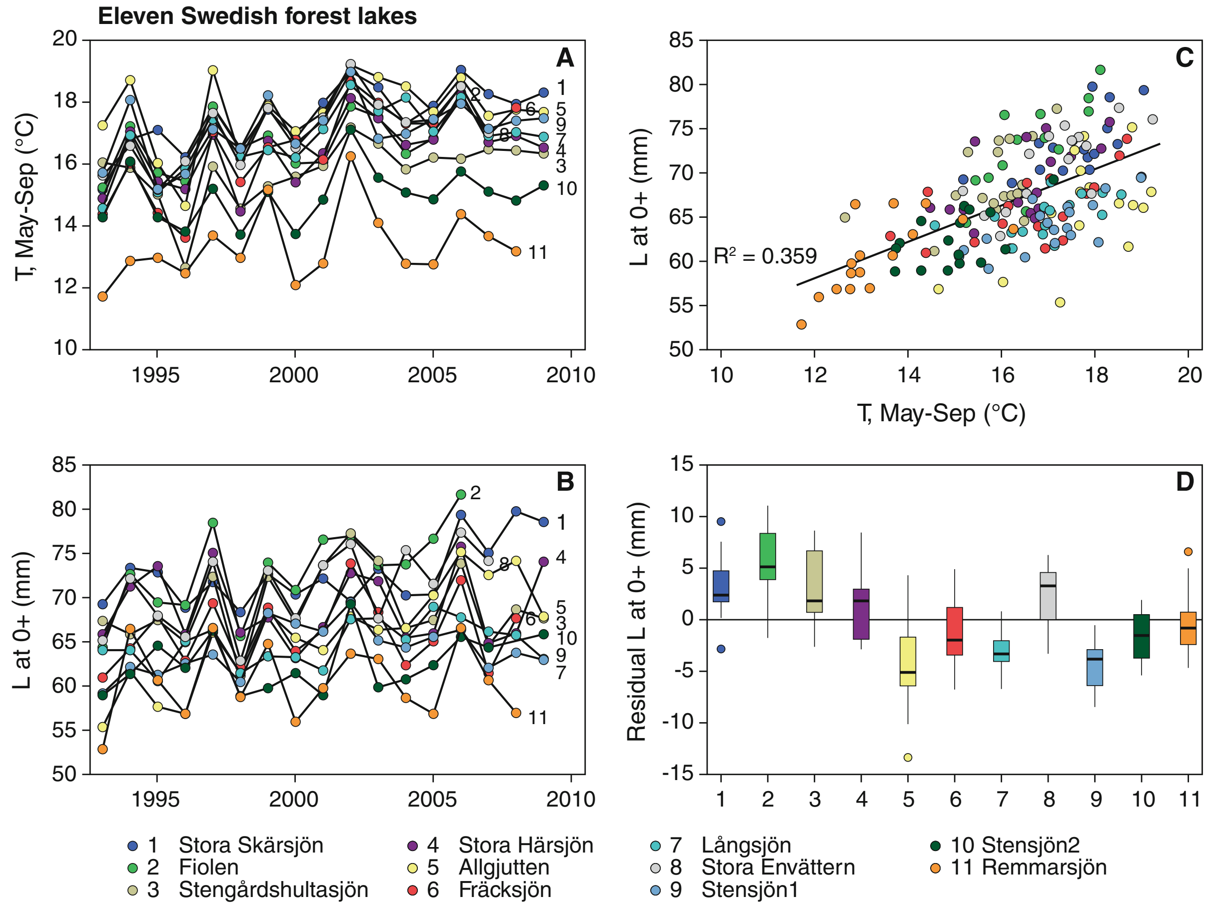


Fig. 3 Eleven Swedish forest lakes. **A** Mean surface water temperature in May to September. **B** Mean length of perch after the first year. **C** Linear relationship between summer temperature and 0^+ perch length. **D** Lake-specific residual variation in the linear relationship between temperature and 0^+ perch length. Lakes in **D** are ordered from south to north, and the *same colour codes* are used in all panels

Water temperature during the first growth season has been expressed as annual mean values at 1–1.5 m depth during May–September. Concentrations of TP, TOC and sulphate are means of 7–8 samples per lake and year, sampled at 0.5 m depth at a mid-lake station.

Lake Säkylän Pyhäjärvi, Finland

Säkylän Pyhäjärvi is a large, polymictic, meso-eutrophic shallow lake with a hydraulic retention time of about 4–5 years. The catchment area is 615 km^2 (including the lake surface). Two incoming rivers with a strong agricultural nutrient load impact account for more than 70% of the annual TP load. The lake is located in the boreal temperate zone (cold climate type) and is, on average, ice covered for 141 days.

The fish assemblage consists of 18 species, dominated by perch, ruffe, roach and vendace. The most important commercial catch species is vendace, which is the main planktivore in the lake (Sarvala et al., 1998). The annual harvest rate approaches the total production of vendace. In addition to this self-supporting biomanipulation, a restoration project has subsidised the harvest of commercially unwanted fish since 1995. The fishing was especially intensive in 2002–2004 and apparently resulted in improved water quality (Ventelä et al., 2007).

Data on fish assemblage composition were obtained from extensive test fishing with gill nets in 1984 (non-standard series) and in 2000, 2004, 2006 and 2009 (Nordic gill nets; CEN, 2005), as well as from catch samples and surveys (Sarvala

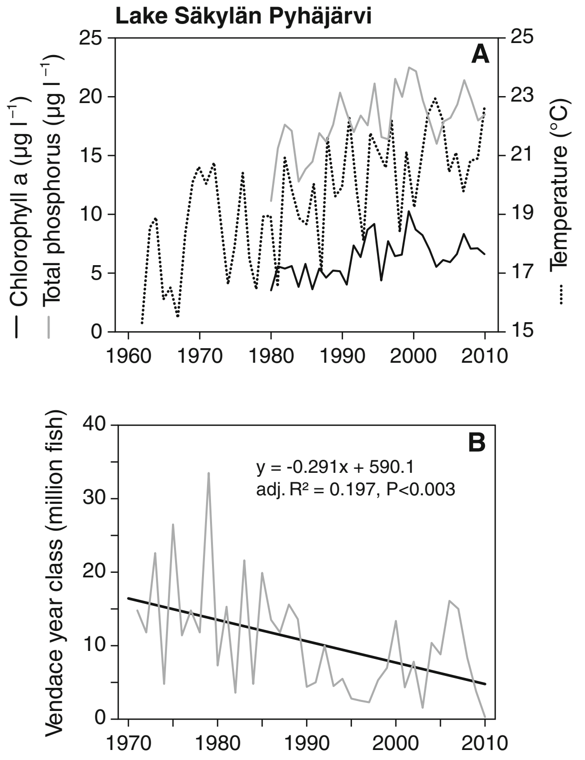


Fig. 4 Lake Säkylän Pyhäjärvi. **A** Mean total phosphorus, chlorophyll *a* (0–5 m; May–September) and annual maximum water temperature. **B** Year class size of vendace (in millions)

et al., 1998; Ventelä et al., 2011 and unpublished). The majority of the annual fish catch is taken in winter by seining through holes in the ice. In addition, fyke nets are applied by professional fishermen in the open-water season. Samples for vendace and whitefish have been collected since 1971 and the winter seine catch of all species has been sampled from 1989 to 2011. Subsamples of each species for individual weight and length and age determination were obtained from the fishermen's catches; at least thirty 0^+ vendace individuals were measured each time. Daily seine catch records for vendace (age 0^+ and older fish separately) were obtained for the winters 1980–2011 from each seine crew and/or the most important wholesale fish agent. For most years, the 0^+ year class size of vendace in autumn could then be calculated from the decrease in catch per unit effort (CPUE) during winter (Helminen et al., 1993). For other years, year class size was estimated utilising the strong density dependence of first-summer growth of vendace.

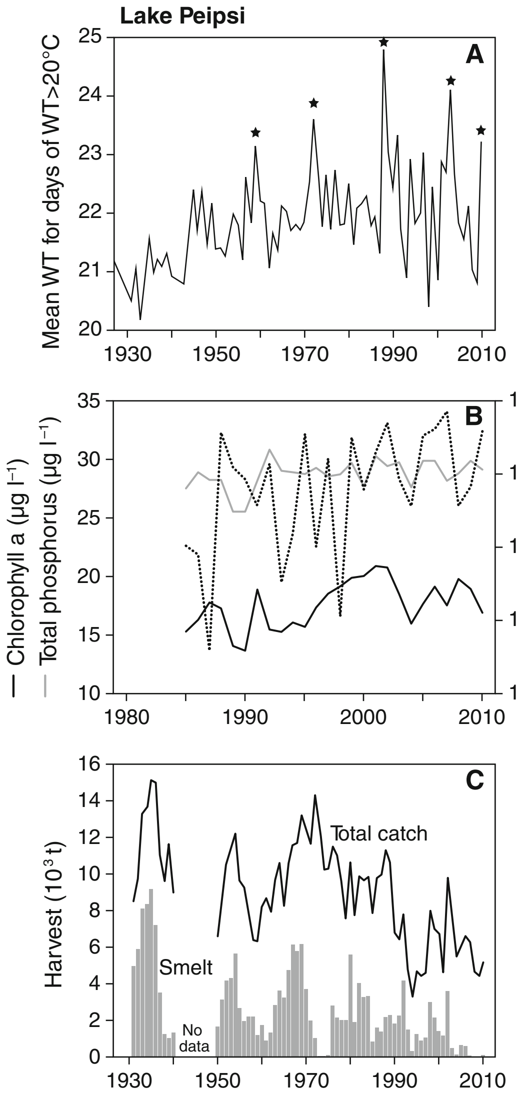


Fig. 5 Lake Peipsi. **A** Mean water temperature (WT) for days with temperature >20°C from 1925 to 2010. The occurrences of fish kills during the hottest summers are marked with *asterisks*. **B** Mean water temperature, total phosphorus and chlorophyll *a* for the ice-off period. **C** Annual catches of smelt and total fish

The water chemistry and hydrology of the lake have been monitored since the 1960s, and in 1980 monitoring was extended to cover biotic components such as phyto- and zooplankton (Ventelä et al., 2007, 2011), chl *a* and nutrients. Ice data for 1958–2010 were recorded by local observers and the Finnish Environment Institute's Oiva data service (www.ymparisto.fi/oiva); which also provided water temperature and water quality data.

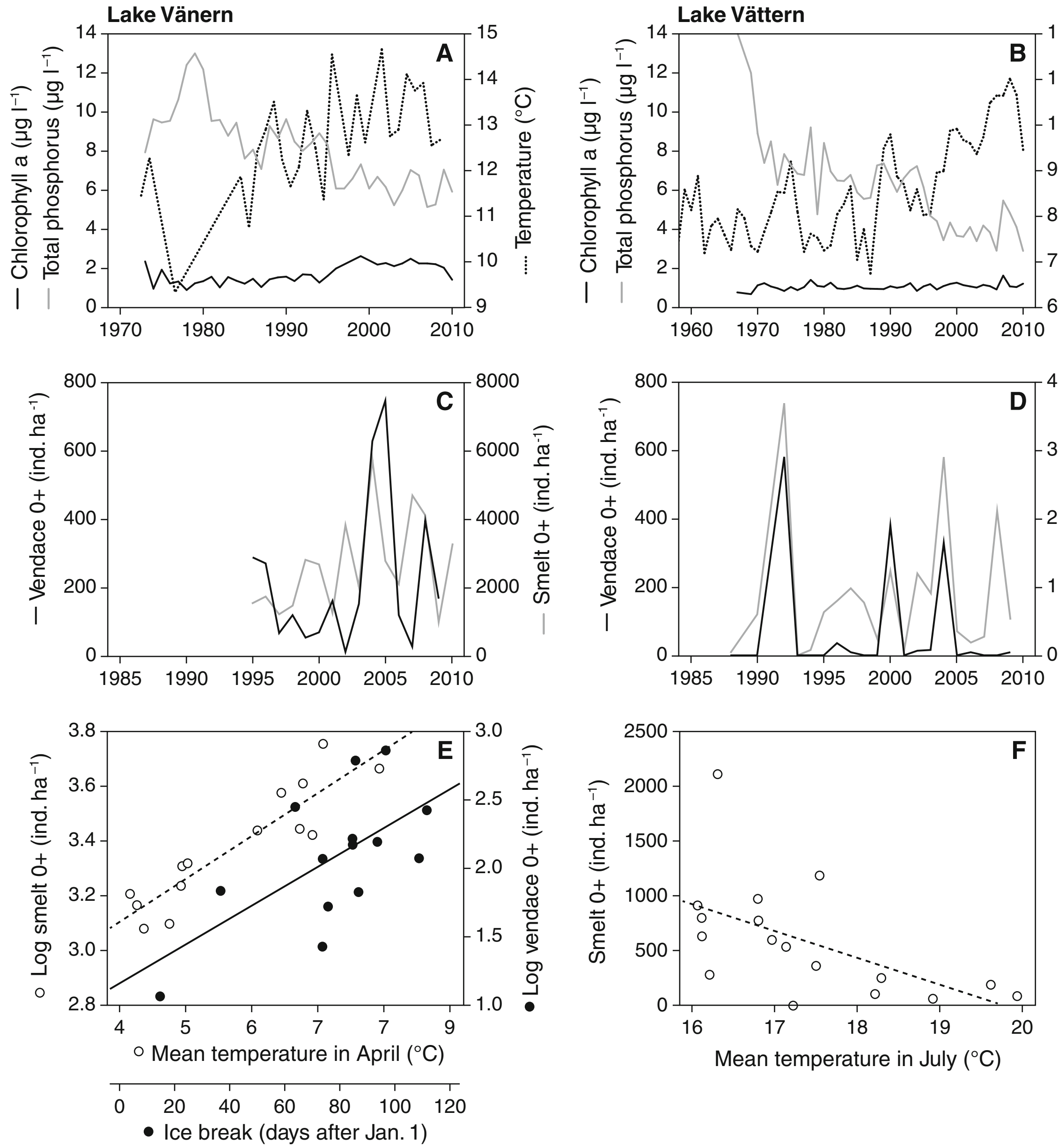


Fig. 6 Lake Vänern and Lake Vättern. **A**, **B** Annual mean water temperature, chlorophyll *a* and total phosphorus (0–10 m). **C**, **D** Annual variation in abundance (ind. ha^{-1}) of young-of-the-year smelt and vendace. **E** Relationship between abundance of young-of-the-year smelt and temperature in April and between abundance of young-of-the-year vendace and the date of ice break in the sheltered basin of Brandsfjorden in the south-eastern part of the lake. **F** Relationship between abundance of young-of-the-year smelt and July water temperature (only years without strong pulses of vendace recruitment). Note that the year 2009 is an extreme outlier and was not included in the regression line. In 2009 smelt recruitment in Lake Vänern collapsed despite optimal temperature conditions. The reason for this collapse is under investigation

Lake Peipsi, Estonia/Russia

Lake Peipsi, situated on the Estonian/Russian border, is large, eutrophic, polymictic and shallow with a hydraulic retention time of about 2 years. TP is higher in the southern parts of the lake due to higher and increasing P loading from the catchment (Kangur & Möls, 2008).

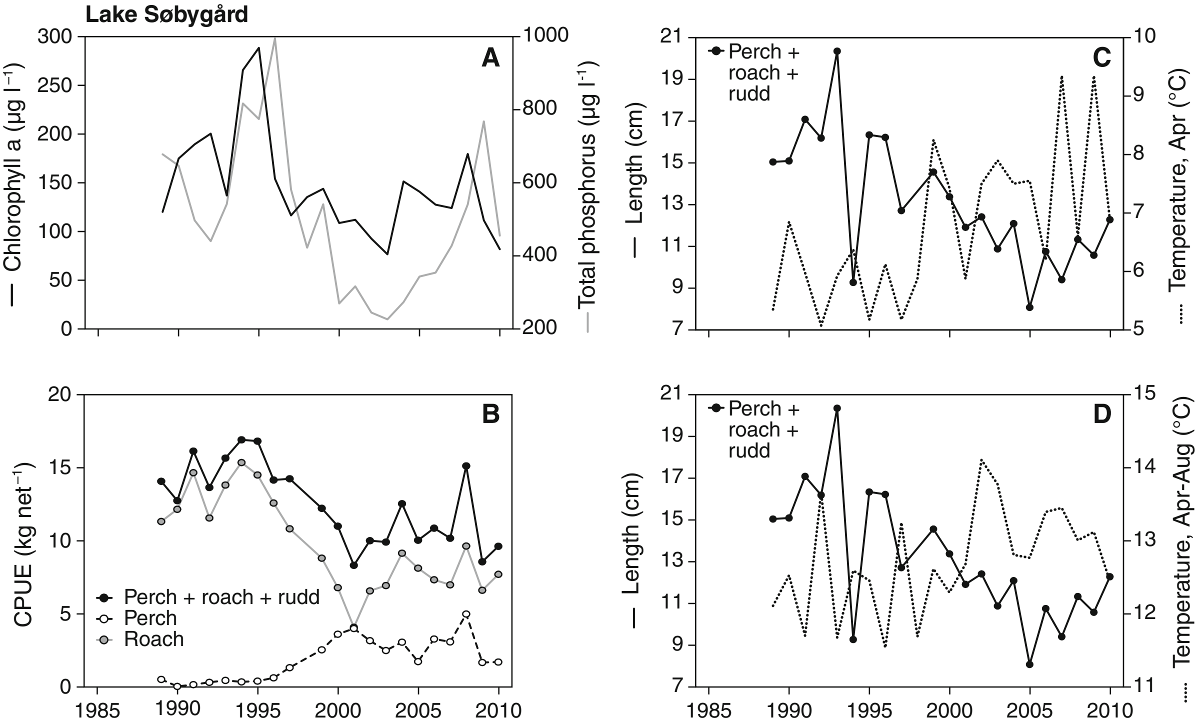


Fig. 7 Lake Søbygård. **A** Summer mean total phosphorus and chlorophyll *a*. **B** CPUE by weight of various key fish species. **C**, **D** Mean per capita biomass of roach, rudd and perch (pooled together) and average air temperature in April and summer (Apr. 1 to Sept. 1)

The lake is inhabited by 37 fish species (Kangur et al., 2008). Lake (dwarf) smelt (*Osmerus eperlanus eperlanus* m. *spirinchus*), vendace and pike–perch (*Sander lucioperca*) have been the main commercial species in the lake at different times.

Commercial fisheries statistics for the lake, collected from fishermen by the state authorities (former Soviet Union, Russian and Estonian), are available for the periods 1931–1940 and 1950–2010. Fish data come from a variety of fishing gears used during different time periods and localities. The basic fishing gear used represents local modifications of fence traps for smelt and perch as well as gill nets for pikeperch, pike and bream. Bottom seining is used mostly for pikeperch and perch. A limited experimental trawling data set was used to control the reliability of commercial fishery statistics. Test trawling was carried out in central and northern parts of the lake in autumn 1986 and 1998–2010. Methods of test trawling are described in detail by Kangur et al. (2003).

Surface water temperature data were available for the period 1924–2010, mainly from the Mustvee weather station (58°50′N, 26°57′E). The data were collected by the Estonian Institute of Hydrology and Meteorology. Basic water quality parameters have been recorded as far back as the 1950s, and regular biota monitoring has been conducted since 1962. Although most studies since 1992 have been made in the Estonian part of the lake, joint Estonian–Russian expeditions over the whole lake have been arranged regularly since 2001 (Kangur & Möls, 2008).

Lake Vänern and Lake Vättern, Sweden

Lakes Vänern and Vättern are oligotrophic, large and deep lakes. Both were affected by eutrophication in the 1960s and 1970s, but following improved water treatment facilities TP has declined substantially and is currently close to the historical reference levels (Renberg et al., 2003). However, eutrophication is still observed locally, in enclosed inlets and archipelago areas.

Lake Vänern holds 38 and Lake Vättern 31 fish species. In both lakes, the fish assemblages are markedly influenced by fisheries. Traditionally, the most important species for the fisheries have been

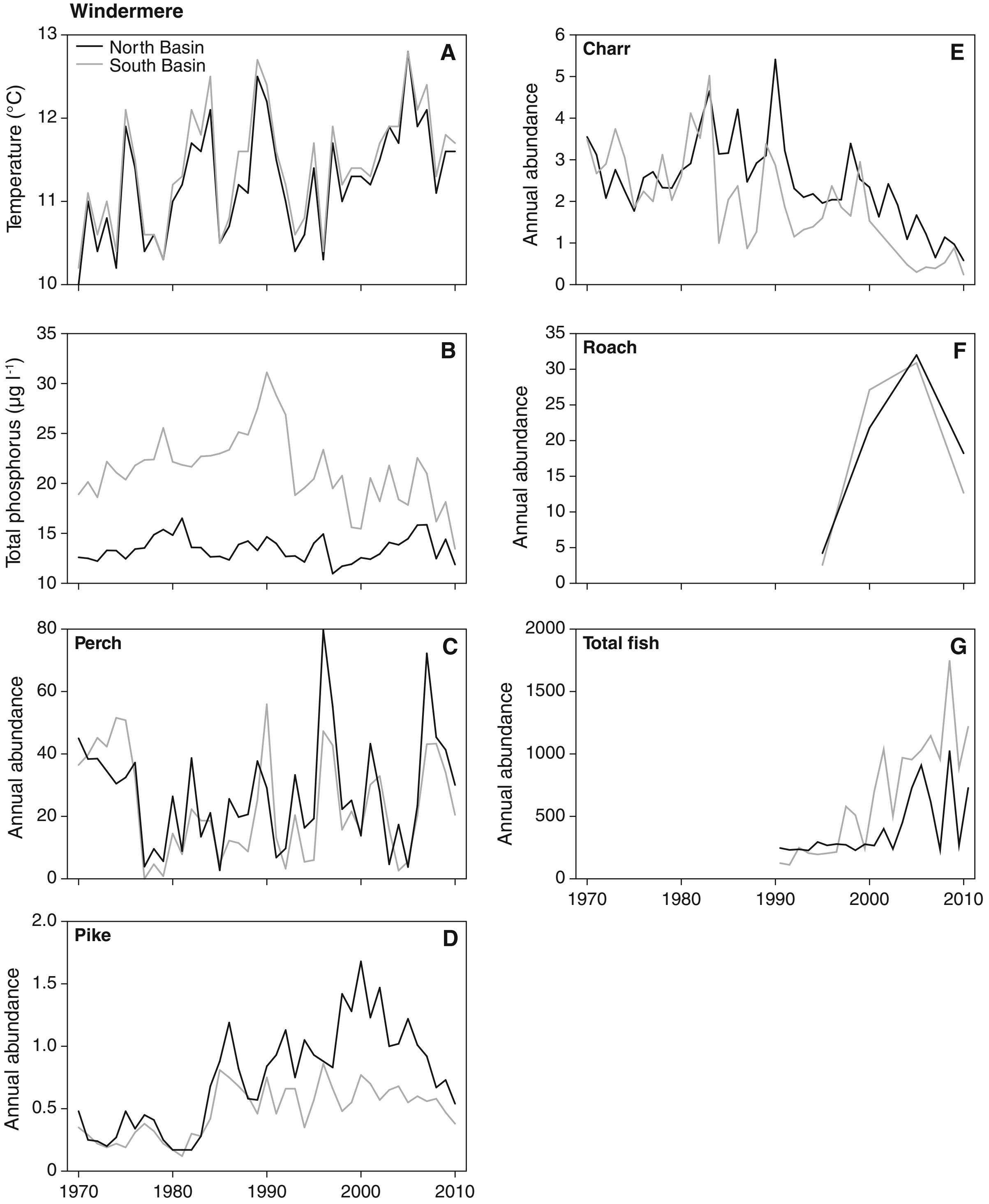


Fig. 8 Windermere. **A** Annual mean surface water temperature in the north and south basins. **B** Annual mean total phosphorus in the north and south basins. **C**–**F** Annual abundance of perch (fish trap^{-1} week^{-1}), pike (fish net^{-1} day^{-1}), Arctic charr (fish angler^{-1} h^{-1}), and roach (fish 100 m^2 net^{-1} day^{-1}), data are only available from 1995, 2000, 2005 and 2010). **G** Annual abundance (fish ha^{-1}) of all fish species as recorded by hydroacoustics

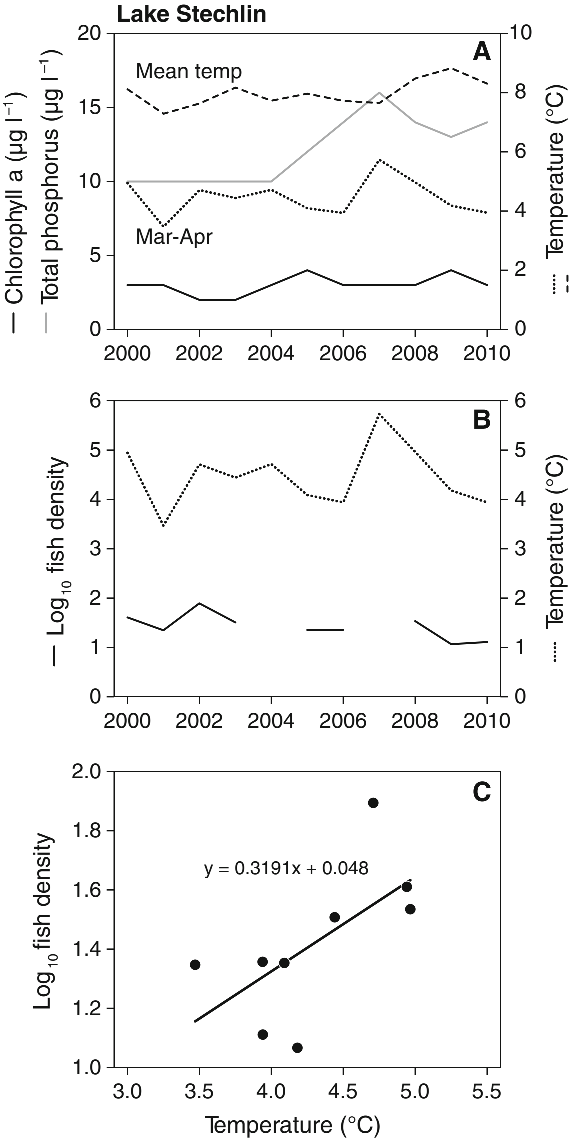
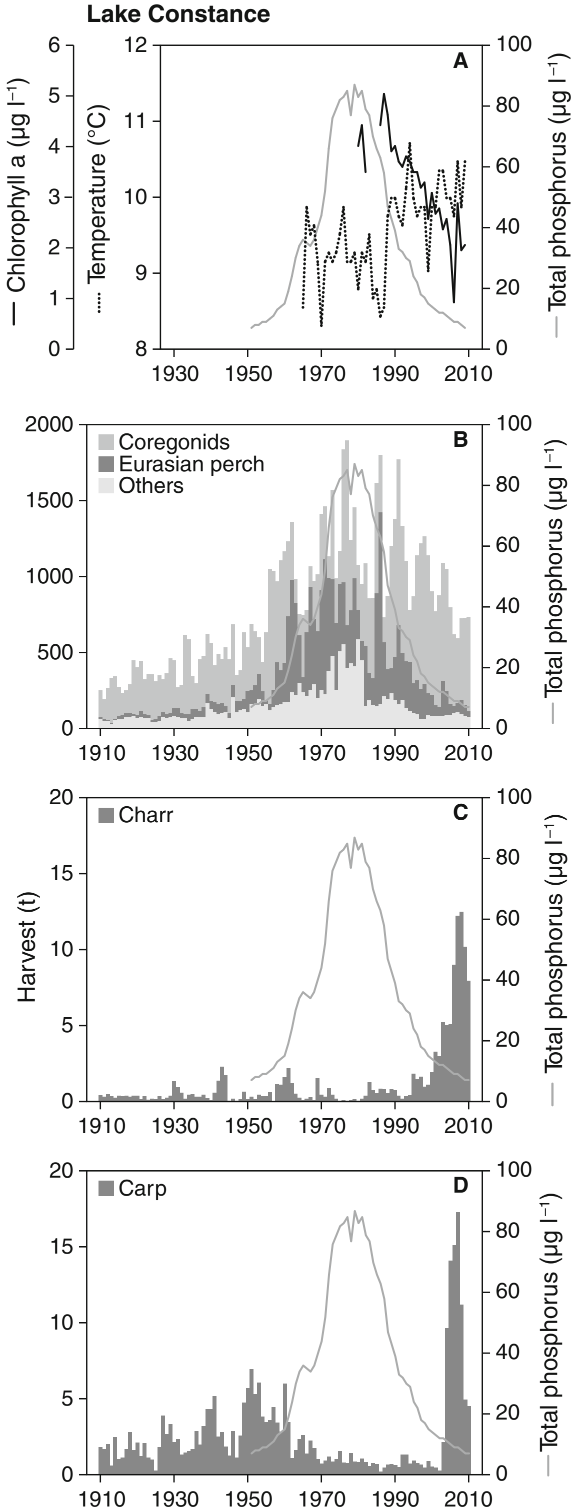


Fig. 9 Lake Stechlin. **A** Annual mean concentrations of total phosphorus (µg l^{-1}) and chlorophyll *a* (µg l^{-1}), and annual mean and spring (March–April) temperatures (°C) measured at 2 m depth intervals from the surface to 20 m depth. **B** Time series of spring (March–April) water temperatures and total density of pelagic coregonids ($\log_{10}$ ind. (1000 m^{-3})) as obtained by hydroacoustics in June. **C** Scatter plot and linear regression line of spring temperature and hydroacoustic fish densities in June



whitefish, Arctic charr and vendace in Lake Vättern and vendace, whitefish and pike–perch in Lake Vänern (Degerman et al., 2001). In recent years, the

◀**Fig. 10** Lake Constance. **A** Total phosphorus concentration during winter mixing, yearly average temperature from 0 to 20 m depth, and yearly average chlorophyll *a* concentration from 0 to 20 m. **B–D** Commercial fish, Arctic charr and carp harvests (in tonnes), respectively, from Upper Lake Constance and total phosphorus during winter mixing

introduced signal crayfish (*Pacifastacus leniusculus*) has become the main target species for the fisheries in Lake Vättern and an important complementary species in Lake Vänern. Salmonids are stocked in both lakes, enhancing the predation on pelagic prey fish such as smelt and vendace, while Lake Vänern also has a significant fishery on vendace.

Statistics on commercial fisheries catches have been recorded since 1914 in both lakes. In Lake Vänern, however, no statistics are available for the period 1924–1961. Long-term data from hydroacoustic surveys combined with mid-water trawling have been used to detect trends in the recruitment of the key pelagic fish in both lakes. Survey data on Lake Vättern are available for 1988–2009 and from 1995 to 2009 on Lake Vänern. Details on survey design and apportionment methods are given in Nyberg et al. (2001) and Axenrot (2010a, b). In addition to hydroacoustics, the benthic fish assemblages have also been monitored using multi-mesh gillnets in Lake Vättern. Such monitoring has been carried out in late summer for 21 years during the period 1973–2010 (A. Sandström et al., unpublished data).

Available data on ice coverage in Lake Vättern span from 1881 to 2010 and daily water temperature measurements (at 5 m depth) exist from 1955 to 2010 (source: Lake Vättern Water Society). In Lake Vänern, ice coverage data for the period 1995–2009 were obtained from a sheltered basin (Brandsfjorden) and for the lake as a whole. Unfortunately, daily water temperature measurements were not available other than for a limited number of years. Instead, in this paper we used air temperature measurements from two weather stations situated close to Lake Vänern and water temperature recordings measured at 5 m depth in May, June, August and October.

Density (ind. ha^{-1}) of 0^{+} smelt and vendace obtained from hydroacoustic surveys and relative year class strength of vendace obtained from age determinations of trawl catches were used as response variables. A large set of predictor variables was used: adult fish densities (obtained from hydroacoustic surveys, ind. ha^{-1}), fisheries yield (obtained from Swedish official catch statistics, tonnes), air and water temperatures (annual mean, monthly mean and monthly sum above 10°C) and ice coverage (presence/absence of ice, number of days with ice, Julian day of ice-break in spring), TOC, as well as annual mean TP concentrations and annual mean chl *a* concentrations, both measured at the surface layers (0–10 m).

Lake Søbygaard, Denmark

Lake Søbygård is small, shallow, hypertrophic and polymictic. The lake has suffered from extremely high external nutrient loading which was, however, substantially reduced as from 1982 (Jeppesen et al., 1998).

The lake hosts eight fish species, but the fish assemblage is overwhelmingly dominated by roach and perch with the piscivorous pike–perch and pike also present. Annual gill net surveys were conducted

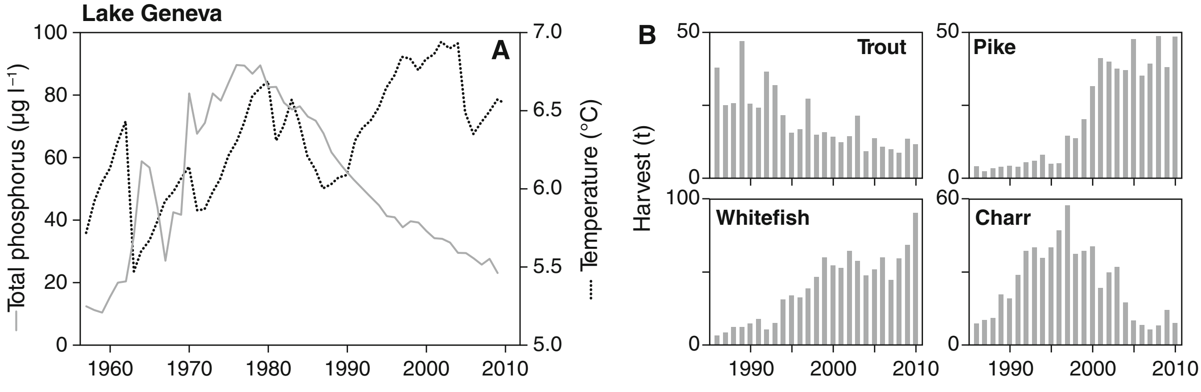


Fig. 11 Lake Geneva. **A** Annual mean water temperature above the bottom at 309 m and annual mean total phosphorus concentration. **B** Annual commercial harvest of key fish species (tonnes)

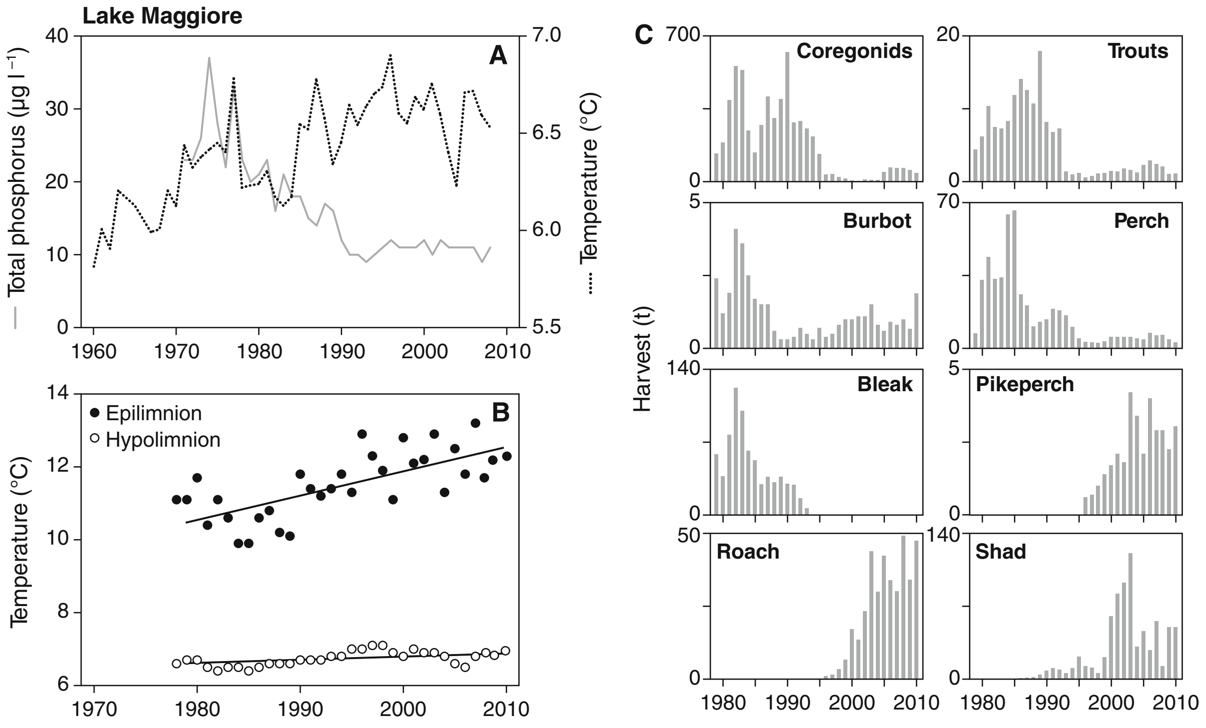


Fig. 12 Lake Maggiore. **A** Mean water temperature and total phosphorus at the spring overturn. **B** Annual mean water temperature of the epilimnion (0–25 m depth) and hypolimnion (25–360 m depth). **C** Annual commercial harvest (in tonnes) of the most important fish species as registered in the fishery statistics by CISPP

from 1989 to 2010 (except 1998) between 15 August and 15 September every year (except for 1988 when it was undertaken in November) to include 0^+ fish in the catches. The lake was divided into six sections and in each section three multi-mesh size gill nets (14 different mesh sizes ranging from 6.25 to 75 mm) were set overnight. One gill net was set perpendicular to the shoreline, another parallel to and about 25 m from the shoreline, and the third about half the distance from the centre of the lake (more details in Jeppesen et al., 1998).

Water samples were collected fortnightly or more often with a Patalas sampler at a mid-lake station at 0.5 and 1.5 m depth and analysed according to standard methods.

Windermere, UK

Windermere is a large, relatively deep and meso-eutrophic lake comprising elongated north and south basins with a combined surface area of 14.8 km^2, which makes it England's largest natural lake. Its catchment is dominated by unimproved pasture, although nutrient loadings from sewage treatment works to the lake have been significant.

The present fish assemblage of the lake consists of 16 species, although only seven are of numerical importance, i.e. Arctic charr, Atlantic salmon, brown trout, European eel, perch, pike and roach. The latter and some other cyprinid species are known to have been introduced, probably by anglers as live bait during angling for pike (Winfield et al., 2010a, 2011). The lake has not been influenced by any significant removal fisheries for many decades (Le Cren, 2001).

The major fish populations of the north and south basins of the lake have been monitored and researched at individual and population levels from the early 1940s, in association with short-lived removal fisheries and other large-scale population manipulations (Le Cren, 2001). Methodologies have included independent gill nets targeted at Arctic charr (Winfield et al., 2008a) and pike (Winfield et al., 2008b; Paxton et al., 2009), together with traps targeted at perch (Paxton et al., 2004) since the early 1940s, the examination of

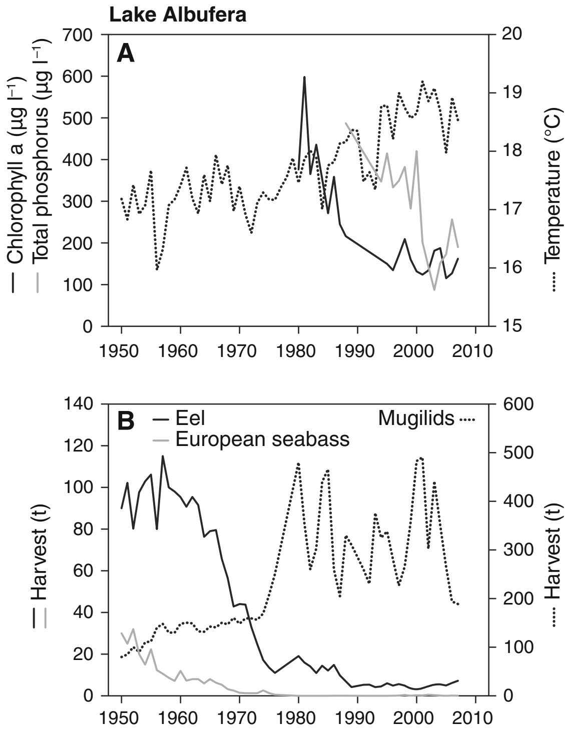


Fig. 13 Lake Albufera. **A** Annual means of temperature, chlorophyll *a* and total phosphorus. **B** Annual commercial harvest of key fish species (in tonnes)

effectively recreational angling for Arctic charr since the mid-1960s (Winfield et al., 2008a), the use of monthly hydroacoustic surveys for the total open-water fish assemblage since the early 1990s (Winfield et al., 2008a), and the use of survey gill nets at 5-year intervals since 1995 targeted at developing the roach component of the fish assemblage (Winfield et al., 2008b). With the exception of the survey gill netting, all of this biological sampling has been undertaken annually over approximately 6-week periods each year.

These fish studies have been accompanied by more frequent, typically weekly or fortnightly, monitoring of the lake's abiotic and biotic features including water temperature and TP (Winfield et al., 2008a).

Lake Stechlin, Germany

Lake Stechlin is dimictic, large, deep and oligo-mesotrophic and is situated ca. 120 km north of Berlin, Germany.

Eleven fish species with reproducing populations have been observed (Anwand et al., 2003); the pelagic habitat below the thermocline is dominated by common vendace and the smaller, lake-endemic Fontane cisco (*Coregonus fontanae*). Peak spawning activity of vendace in the lake occurs around 20 December. Vendace has a cold-water thermal window characterised by a metabolic optimum around 7–9°C (Ohlberger et al., 2008a, b). The spring-spawning Fontane cisco (spawning period between late April and early July) has a lower thermal window with an optimum at about 4–5°C (Ohlberger et al., 2008a, b). Other fish species occur in low densities primarily in the littoral and epipelagic habitats.

Densities (ind. (1,000 m^{-3})) of pelagic fish split into 0^+ and older coregonids were estimated by annual hydroacoustic surveys conducted during night-time in June between 2000 and 2010 (2004 and 2007 missing). Additional stratified pelagic trawl sampling has been conducted annually in June since 2005, thus providing density estimates for juvenile and adult coregonids of both co-existing species. These spatially explicit analyses were required because 0^+ coregonids perform a habitat shift from the littoral to pelagic areas after their first weeks of life, and juvenile and adult coregonids undergo diel vertical migration in the lake. The methodology is described in detail in Mehner et al. (2011).

Monthly temperature means were obtained for each water strata, and the index of North-Atlantic Oscillation (NAO) was recorded during winter (January until March). The fish densities were also correlated with epilimnetic and hypolimnetic zooplankton densities (ind. l^{-1}).

Lake Constance, Austria/Germany/Switzerland

Lake Constance, the second largest peri-alpine lake in Europe, is situated at the northern fringe of the European Alps and consists of two basins: Deep Upper Lake Constance (hereafter ULC) and Lower Lake Constance, which is smaller and more shallow (Table 1). ULC was originally oligotrophic, but has undergone pronounced eutrophication during the twentieth century. TP during winter mixing peaked at >80 µg l^{-1} around 1980 (Güde et al., 1998). As a result of a drastically reduced P input, the lake became oligotrophic by the beginning of the twenty-first century and average chl *a* of the upper 20 m declined from 4.2 μg l^{-1} in the 1980s to 2.3 μg l^{-1} in the 2000s.

Twenty-nine species occur in the lake (Eckmann & Rösch, 1998) of which only a few are of commercial interest and exploited intensively: two forms of lake whitefish, an inshore and a pelagic spawning form (>80% of the commercial harvests); perch, the second-most important species in this lake during eutrophication; European eel (regularly stocked); brown trout; pike; Arctic charr and pike–perch. Bycatch of cyprinid species has little commercial value.

ULC is shared by Austria, Germany and Switzerland, and the fisheries have been managed jointly by a commission of the bordering countries since 1893 (International Commission for the Fisheries Management of ULC). An uninterrupted record of commercial catches from UCL since 1910 is available based on monthly catch anonymous reports from all fishermen (Eckmann & Rösch, 1998). Drifting and bottom-set gill nets are the main fishing gear used. Biological data on coregonids have been collected biweekly or monthly since the early 1960s through regular test catches by research institutes and management agencies. Biological data on perch have been collected monthly since the early 1970s by fishery wardens, while the biology and population dynamics of other species are studied infrequently. Age, growth and virtual year class strength of coregonids and perch are published in yearly reports by the mentioned commission. Juvenile and small-sized fish in the shallow littoral area have been monitored at regular intervals since 1997 (cf. Reyjol et al., 2005).

A regular monthly sampling of basic limnological data has been carried out since the early 1960s on behalf of the International Commission for the Protection of Lake Constance (IGKB, 2004).

Lake Geneva, France/Switzerland

Lake Geneva forms the border between France and Switzerland at the north of the French Alps and is a large, deep and eutrophic lake, though water transparency is high (between 5 and 12 m) depending on season. Temperatures at the surface rarely exceed 22°C in summer and never fall below 4°C in winter. The lake is monomictic and is never covered by ice. The lake went through a eutrophication phase from 1960 to the mid-1970s, where TP increased from 20 to 90 μg l^{-1}, followed by a long recovery period. This oligotrophication changed the structure of algae communities and the depth of maximum of production (Anneville et al., 2002).

The fish assemblage consists of 23 species, mainly composed of salmonids including whitefish and Arctic charr, with some brown trout, together accounting for 50% of the total catch by weight. Pike and perch are also caught (40%). Burbot (*Lota lota*) and some cyprinids, of which roach is the major species, are also present and constitute the remaining 10%. The total fish yield in the lake is >15 kg ha^{-1} $year^{-1}$.

The commercial fishery traditionally uses gill nets to catch the seven most important fishery species: whitefish, Arctic charr, brown trout, perch, burbot, pike and roach. Data on commercial and recreational catches have been available from official catch statistics since 1960. An International Commission for the Protection of Lake Geneva Waters (CIPEL, in French abbreviation, www.cipel.org) has since 1962 managed surveys of the lake and publishes an annual report. As from 1986, fishermen have declared the weight of their catches daily instead of monthly as before (Gerdeaux, 1988). Total catches yield a good estimate of stock abundance (Caranhac & Gerdeaux, 1998). Furthermore, whitefish and Arctic charr are regularly caught by fishermen during winter in order to provide eggs for hatchery use. The ages of these fish are determined and the catch is expressed as CPUE.

A regular fortnightly sampling has been carried out since the early 1960s on behalf of CIPEL. All the classical physical and chemical parameters are measured on a vertical profile: temperature, oxygen, phosphorus and nitrogen concentrations. Daily surface temperatures have been recorded in a littoral location of the lake since 1951.

Lake Maggiore, Italy/Switzerland

Lake Maggiore is a large warm-monomictic, oligo-mesotrophic pre-alpine lake (Table 1), situated in north-western Italy. From being naturally oligotrophic (Marchetto et al., 2004), the lake has undergone eutrophication since the mid-1960s, followed by a recovery period since the mid-1970s (Mosello & Ruggiu, 1985; Salmaso et al., 2007).

At present, 32 fish species, of which only 20 are native, inhabit the lake. As in other large south alpine lakes, commercial fishing was traditionally targeted towards cold water species such as coregonids (*Coregonus lavaretus* and *C. macrophthalmus*) and trout [migratory brown trout and marble trout (*Salmo trutta marmoratus*)]. Alborella (*Alburnus arborella*) and perch were also frequently caught. Commercial fishery data (total annual catch of each species) are registered by commercial fishermen and collected by the Swiss-Italian Commission for the Fishery (CISPP in Italian abbreviation) since 1979.

An International Commission for the Protection of Italian-Swiss Waters (CIPAIS in Italian abbreviation, www.CIPAIS.org) manages the survey of limnological, meteorological and hydrological parameters of the lake and its catchment. Additional data are directly obtained from the CNR-Institute of Ecosystem Study.

Lake Albufera, Spain

Lake Albufera is the largest Spanish coastal lake and is located in the Natural Park of the Albufera. It is shallow, polymictic, hypertrophic and oligohaline (salinity: 1–2‰). The water level is regulated by sluice gates and the hydrological cycle of the lake is related to seasonal rainfall and rice cultivation in the areas surrounding the lake. The annual lake water turnover varies between 5.5 and 9.5 year^{-1}. The lake has been hypertrophic since the 1970 s and cyanobacteria dominate throughout the year, except for sporadic periods (few days or weeks) of clear water in recent years following external nutrient loading reduction (Villena & Romo, 2003; Romo et al., 2005). Since 2002, the abundance of potentially toxic cyanobacteria (*Microcystis aeruginosa* and *Cylindrospermopsis raciborski*) has increased (Romo et al., 2008) with microcystins being detected even in the tissue of the main exploited fish species (Romo et al., 2012a).

The fish assemblage is dominated by omnivorous species (Blanco et al., 2003). The composition of the fish assemblage was determined from annual commercial captures from 1950 to 2007 recorded by local fishermen using similar traditional methods, mainly gill (30 mm mesh size) and fyke nets, and during summer 2000 and spring 2002 using fyke nets and multiple (14) mesh-sized gill nets (6.5–75 mm). About 300 tonnes (150 kg ha^{-1}) of mugilids (mainly golden and thinlip mullet, *Liza* spp. and flathead mullet, *Mugil cephalus*) are harvested annually (Blanco et al., 2003; Blanco & Romo, 2006).

Water was analysed using standard methods (APHA, 1992), determining TP from the upper 50 cm of the water column. Data on air temperature and rain were recorded at a nearby weather station.

Trends in the case studies

Lake Elliðavatn: strong decline in abundance and increase in size of Arctic charr

During 1989–2010, June–September mean water temperature has risen significantly (Fig. 1, linear regression, $R^2 = 0.54$, $F_{1,20} = 23.17$, $P < 0.001$) in line with an increasing air temperature in the catchment area (Malmquist et al., 2009). Lake temperature has increased in all months except October-December, with the most profound warming occurring in late winter/early spring and summer. For April, the average increase in daily mean temperature between 1989 and 2010 was 2.9°C ($R^2 = 0.38$, $F_{1,653} = 108.8$, $P < 0.001$), 2.6°C for July ($R^2 = 0.37$, $F_{1,680} = 108.3$, $P < 0.001$) and 1.5°C for September ($R^2 = 0.19$, $F_{1,680} = 25.4$, $P < 0.001$).

For the past 20 years, the Arctic charr population in the lake has undergone a major reduction coinciding with the warming of the lake (Fig. 1). Catch per unit effort of charr during 1987–2010 has declined significantly ($R^2 = 0.71$, $F_{1,22} = 54.42$, $P < 0.001$) and for the past 10 years it has been only about 25% of the level seen more than 20 years before (Malmquist et al., 2009). In contrast, the population of brown trout, which is more heat-tolerant than charr (Elliott & Elliott 2010), has remained largely unchanged ($P = 0.627$), albeit it shows some interannual fluctuations. The observed decline in density of adult charr, which has also been observed for juvenile fish (Antonsson & Árnason, 2011), is attributed to the increasing water temperatures, with $\geq$14°C extending over 1–2 months and up to 18–21°C for a week or two as observed in, for instance, 2003, 2007 and 2010. This is far above the upper thermal optimum for the growth of adult charr, reported at ~12.0°C, with negative effects at 14.0°C (Jobling, 1983; Lyytikäinen et al., 2002). The thermal optimum is even lower for egg development and growth of charr fry (Jobling, 1983).

The thermal problems that charr is facing may be linked not only directly to reproduction, metabolism and growth, but also indirectly to susceptibility to thermally linked diseases, such as proliferative kidney disease (PKD) (Sterud et al., 2007). In October 2008, PKD was detected for the first time in Iceland in Arctic charr from this lake (Kristmundsson et al., 2010). Since then, PKD has been observed in both charr and brown trout in Lake Elliðavatn, as well as in four other shallow lakes (Kristmundsson et al., 2011). In all cases, Arctic charr, but not brown trout, have shown a high prevalence of PKD (up to 100%) often accompanied by severe pathological signs, especially in 1- to 2-year charr. The fact that PKD infections affect young charr most severely indicates that high mortality of young fish may be an important cause for the population decline in Arctic charr, although further studies are needed to draw firm conclusions.

Along with the changes in abundance, the mean length (fork length) of 3^+-year charr has increased significantly during 1988–2010 ($R^2 = 0.54$, $F_{1,21} = 24.48$, $P < 0.001$). For the 5-year period 1988–1992, the mean length of 3^+-year charr was 22.8 cm (± 0.52) as compared to 28.3 cm (± 0.70) for the period 2006–2010. Brown trout showed no differences in mean length between periods. For both charr and brown trout, the somatic condition (Fulton's condition factor) was in general high (>1.10) and did not vary significantly over the period 1988–2005 (charr, $P > 0.4$; trout, $P > 0.7$). Moreover, stomach analyses did not indicate any food shortage or consistent changes in dietary composition by the fish, and data on potential food resources, though sparse, do not suggest any consistent decline of macroinvertebrates or changes in the resource base for the fish.

Lake Valkea-Kotinen: reduction in the growth of perch following an increase in organic load

During the 20-year monitoring period, epilimnetic temperature (Fig. 2A), TOC (Fig. 2B), water colour, pH and alkalinity have increased significantly, while sulphate and base cations decreased, mainly as a result of lower sulphur deposition (Futter et al., 2009). Chl *a* declined (Fig. 2A), but no significant changes in concentrations of TP and TN were observed in either precipitation or runoff (Vuorenmaa & Horppila, 2011). Climatic drivers have been suggested to contribute remarkably to variation in hydrology and, consequently, in TOC fluxes from catchments to surface waters (Futter et al., 2009; Arvola et al., 2010).

Density of perch with a total length >8 cm varied between 660 and 3,300 fish ha^{-1} along the 20-year period. Irregular fluctuations occurred due to variations in year class strength. No significant relationships between population density and year class strength with temperature or TP or chl *a* were recorded. Thus, the variation in abundance of perch seems to result from the population dynamics typical for this percid in this lake type, where large cannibalistic perch prevent recruitment of 0^+ perch until the density of large individuals is small enough to enable the development of a new strong year class (Persson et al., 2000).

As is typical for small forest lakes of the boreal region, perch grew slowly (Rask, 1983) and reached a mean total length of 15 cm after 4–7 years. The growth of perch during the first year declined during the monitoring period (Fig. 2B). There was no significant relationship between the 0^+ growth and the relative year class strength of the population ($P > 0.1$) as the latter fluctuated irregularly, suggesting that the first summer growth of perch was not density dependent. Multiple regression on log-transformed data showed that the length of 0^+ perch was strongly negatively correlated with TOC (Fig. 2D) and more weakly with TP ($R^2 = 0.71$, $F_{2,18} = 22.44$, $P < 0.001$), while temperature and chl *a* did not contribute significantly ($P > 0.2$) (Fig. 2C).

Deterioration of underwater light conditions due to increased TOC seems the main reason for the declining growth of perch, as it is a visually oriented fish species and active only in daylight. These observations are consistent with recent field and experimental studies on the effects of light conditions on the interactions and feeding efficiency of perch (Estlander, 2011; Estlander et al., 2010). In addition, the growth of perch may also have been affected by a decrease in the overall productivity of the food web, as suggested by the decreasing trend in chl *a* (Fig. 2A). This might be ascribed to an increased organic carbon load resulting in a higher proportion of bacterial production compared to autotrophic algal production (Ask et al., 2009; Karlsson et al., 2009), likely leading to a limited availability of fatty acids essential for zooplankton and fish (Brett et al., 2009). Although the changes in TOC and effects on perch in Lake Valkea-Kotinen may so far largely be attributed to reduced acidification (Vuorenmaa, 2004), the results indicate that a predicted increase in the organic load to lakes from catchments due to climate change (Tranvik et al., 2009; Forsius et al., 2010), and subsequent changes in transparency, may directly affect the fish size structure in small boreal lakes.

Swedish forest lakes: increasing first year growth of perch?

During the study period, sulphate concentrations decreased significantly as in other Swedish lakes (Fölster et al., 2005), reflecting a long-term decrease in airborne acidifying deposition. TP tended to decrease and surface water temperature to increase. TOC generally increased, as recorded for dissolved organic carbon across eastern North America and northern and central Europe since 1990 (Monteith et al., 2007).

During 1993–2009, the water temperature varied in a more or less synchronised fashion among lakes, with relatively warmer growth seasons in 1994, 1997, 1999, 2002 and 2006 (Fig. 3A). Monotonic increases or decreases in fish abundance and/or biomass were previously reported for some of the species in some of the 11 lakes (Holmgren, 2009, and summarised in Table 2). A positive effect of temperature on the first year growth of perch could be observed for the set of lakes included and from the overall relationship based on data from all years (Fig. 3C). The year-to-year variation in length of 0^+ perch followed a similar pattern in the lakes, peaking in the warm years of 1997, 2002 and 2006 (Fig. 3B). 0^+ perch were shortest in the northernmost lakes (mean length = 61 mm), albeit these fish were relatively long considering the lower temperature of their environment. In other lakes at similar latitudes (58–64°N), the mean length of perch is often less than 55 mm after its first year of life (Heibo et al., 2005).

Prolonged day length during summer might to some extent compensate for the lower temperature in these lakes. Residuals in the length-temperature relationship differed significantly between lakes (one-way ANOVA, $P < 0.001$) (Fig. 3D). The largest negative residuals (i.e. a growth lower than expected) were found in two of the smallest, but rather deep lakes with pelagic populations of vendace. The largest positive residuals were found in one of the largest lakes, and also the most shallow one, with no or weak thermal stratification in summer.

In contrast to Lake Valkea-Kotinen, however, this 11-lake study shows no evidence that a negative effect of increasing TOC levels overrules the positive effect of increasing temperature on the growth of 0^+ perch.

Lake Säkylän Pyhäjärvi: major decline in vendace

The maximum summer water temperature increased highly significantly during 1962–2010 (Fig. 4A; 0.9°C per decade; adjusted $R^2 = 0.41$, $F_{1,47} = 34.75$, $P < 0.001$). Spring temperatures have not increased correspondingly, as seen from May temperature records that show no significant change over years (temperature vs. year in 1968–2010: $P > 0.18$).

During the last hundred years, no consistent directional changes at the level of the whole fish assemblage attributable to climate change were observed (Sarvala et al., 1998). Catches of all species fluctuated considerably during 1989–2009. For most species, a linear trend was non-significant ($P = 0.21$–0.71, explained variance: 0.7–7.7%), but whitefish exhibited a significant declining trend with time ($R^2 = 0.48$, $F_{1,20} = 18.59$, $P < 0.001$). For vendace, there was a significant decline in year-class size during the period 1971–2010 (adjusted $R^2 = 0.20$, $F_{1,38} = 10.57$, $P < 0.003$), related to increasing annual maximum temperatures (linear regression of $\log_{10}$-transformed variables: adjusted $R^2 = 0.18$, $F_{1,38} = 9.82$, $P < 0.004$), but not to summer mean temperature ($P > 0.51$). In multiple linear regressions including either TP or chl *a* of May–September, the temperature effect on vendace year-class size remained significant, while none of the trophic state variables was significant (period 1980–2010, $\log_{10}$-transformed variables, temperature and phosphorus ($R^2 = 0.21$, $F_{2,28} = 3.77$, $P < 0.04$) or chl *a* ($R^2 = 0.22$, $F_{2,28} = 3.86$, $P < 0.04$). In all species, the signs of the slopes were consistent with postulated climate warming effects: positive slopes for the warmer-water species perch, roach and ruffe, and negative slopes for the colder-water species vendace, whitefish and smelt, although the whitefish decline may rather be related to food web interactions (e.g. competition with vendace, egg predation by the introduced signal crayfish) (Sarvala et al., 1998). The observed change towards smaller fish in the contemporary fish assemblage is likely mostly attributable to intensified fishery and species introductions (e.g. whitefish, vendace) (Sarvala et al., 1998). In addition, erratic stock fluctuations in individual species influence the size distributions. Strong

Table 2 Summary of the suggested climate-induced changes in fish assemblage composition, abundance and size structure in the case studies based on data presented in this paper or in earlier cited studies

Lake	Latitude	Cold deep water refuge	Length of fish time series (years)	Arctic charr	Other cold-water species	Perch/roach	Warm-water species	Fish body size
Elliðavatn, Iceland	64°1′N	No	23 (1987–2010)	Major decrease in abundance	No change in brown trout abundance	–	–	Size (length) of (3^+) charr increasing, condition factor remains the same. The same applies to brown trout
Valkea-Kotinen, Finland	61°15′N	No	21 (1989–2009)	–	–	No temperature response of perch	–	Size of 0^+ perch decreasing
Eleven forest lakes, Sweden	56–64°N	Yes	17–18 (1993–2010)	–	Decreasing or insignificant trends for burbot, smelt, vendace and whitefish	Variable trends for both perch and roach		Increasing or insignificant trends in first year growth of perch
Säkylän Pyhäjärvi, Finland	60°54′–61°06′N	No	40 (1971–2010)		Increased mortality and reduced recruitment of vendace. Declining whitefish catches	More frequent strong year classes of perch	Not enough data	0^+ and 1^+ vendace size increasing, weaker year classes (lower 0^+ abundance)
Peipsi, Estonia/Russia	57°5′–59°0′N	No	80 (1931–2010)	–	Decreasing trends for smelt, vendace, peipsi whitefish and burbot. Eutrophication amplifies the effect of temperature extremes	Increasing catches of perch; catches of roach stable	Abundance of pike–perch and bream has increased	Size of 0^+ pike–perch in autumn has decreased due to collapse of smelt population (first prey fish)
Vänern; Vättern, Sweden	57–59°N	Yes	16–23 (1988–2010)	Large population in Vättern. Long-time trend of decline (1973–2011). On a short-time scale increasing due to fisheries restrictions (2005–2011)	Smelt recruitment correlated negatively with water temperature in July, but positively with April temperature. Vendace recruitment more successful in years with long winters. Climate signals seem strongest in the more productive of the two lakes	Perch CPUE in fisheries stable in Vättern. In Vänern notable local variation in roach/perch ratios due to heterogeneous archipelago regions and pronounced gradients in productivity and bathymetry	Lack of detailed fisheries independent long-term data. Commercial catch of pike–perch in L. Vänern is increasing	Vättern: commercial fish densities (Arctic charr and trout) have increased due to fisheries restrictions. Decreasing mean size of vendace and whitefish. Vänern: no clear trend. In both lakes the size of YOY smelt and vendace is negatively influenced by adult vendace density

Table 2 continued

Lake	Latitude	Cold deep water refuge	Length of fish time series (years)	Arctic charr	Other cold-water species	Perch/roach	Warm-water species	Fish body size
Søbygård, Denmark	56°15′N	No	22 (1989–2010)	–	–		–	Size of roach and perch decreasing
Windermere, UK	54°22′N	Yes	41 (1970–2010)	Major decline in abundance		Increasing roach abundance. Perch spawn earlier	Shift from a salmonid-percid-pike dominated state to one with many more cyprinids	–
Stechlin, Germany	53°01′N	Yes	11 (2000–2010)	–	Increase in total coregonid density after warm winter and spring, density of ultra-cold stenothermal Fontane cisco increased in warm summers, density of cold-stenothermal vendace decreased in warm summers	Present only in littoral and epilimnetic layers, dynamics not studied	–	–
Constance, Austria/ Germany/ Switzerland	47°39′N	Yes	101 (1910–2010)	Major increase in commercial catches, attributed to oligotrophication and effective management	No clear effect of changes in coregonids related to climate warming, but a reduction in catches following nutrient loading reduction	Perch yields decreasing with increasing oligotrophication	Major increases in commercial catches of common carp	–
Geneva, France/ Switzerland	46°27′N	Yes	25 (1986–2010)	Decline in abundance is negatively correlated with the temperature in the deep water	Major increase in commercial whitefish catches: postponed spawning, but stable hatching time and thereby good match with zooplankton food	Roach spawn earlier, no change for perch. Roach juveniles grow as fast as perch and are no longer prey for perch juveniles that grow more slowly	Return of bleak, but no accurate data	–

Table 2 continued

Lake	Latitude	Cold deep water refuge	Length of fish time series (years)	Arctic charr	Other cold-water species	Perch/roach	Warm-water species	Fish body size
Maggiore, Italy	45°57′N	Yes	32 (1979–2010)	–	Major decline in commercial catches of coregonids, trout and bleak	Major decrease in commercial catches of perch and major increase in roach catches	Major increase in commercial catches of shad and pike–perch	–
Albufera, Spain	39°20′N	No	54 (1950–2007)	–	No	No	Well adapted warm-eurythermic species	–

Lakes are ordered by decreasing latitude. For references, see the case study descriptions

year class variations are typical for many northern fish species (e.g. Townsend, 1989).

In spite of large inter-annual fluctuations, vendace year class strength in the lake declined significantly from 1971 to 2010 (with pronounced lows in 1990–1991, through 1993–1998 and again in 2003 and 2009–2010) (Fig. 4B). During the same period, there was a significant increase in the body size of one-summer- and two-summer-old vendace.

The timing of ice break and the following temperature development are key factors affecting the year class variation in vendace (Helminen & Sarvala, 1994). Ice-out triggers the hatching of vendace larvae highly vulnerable to predation from 8 to about 15 mm total length. A longer early larval period results in higher larval mortality (Helminen et al., 1997). The critical period for their survival is 2–4 weeks after the ice break, when the temperature should be high enough to enable rapid growth of the larvae (Helminen & Sarvala, 1994). For example, in 1989 and 1990, the early ice break in the lake led to an unusually early hatching of vendace larvae. In 1989, temperature increased quickly and larval mortality remained moderate. In 1990, in contrast, a much slower warming of the water after the very early ice break resulted in high mortality of vendace larvae (Helminen et al., 1997). With climate change, ice-out occurs earlier (Ventelä et al., 2011), but spring temperature has not increased correspondingly, creating increasingly unfavourable conditions for vendace larvae survival. Moreover, triggered by the more frequent warmer summers, strong year classes of perch (Böhling et al., 1991; Sarvala & Helminen, 1996) have appeared more often in the 1990s and 2000s than in the 1970s or 1980s (Sarvala & Helminen, 1996 and unpublished), increasing predation on vendace, and we may expect this trend to continue.

The commercial fishery in the lake is mainly based on winter seining through the ice. Usually, 70–90% of each year class of vendace is harvested during its first winter, leading to negligible intra-specific competition among the remaining vendace. High winter temperatures (e.g. 2007–2008) result in short periods of ice cover and a short winter fishing season (Ventelä et al., 2011), augmenting the food competition between the young-of-the-year and adult fish and leading to poor recruitment (as in 2008 and 2009). Because the lake is mostly unstratified in summer, vendace do not have any cold-water refuge in the deeper water layers.

Further increasing summer temperatures may thus lead to rising mortality and reduced recruitment.

Lake Peipsi: major changes from cold-water to warm-water species

The start of the ice-covered period, ice-off dates and the water temperature in the open water period have been highly variable in recent years in Lake Peipsi and the mean temperature (open water period) has increased 0.17°C per decade ($R^2 = 0.22$, $F_{1,86} = 23.97$; $P < 0.001$) since 1924. Furthermore, extraordinarily hot summers with temperatures exceeding 20°C for long periods (up to 110 days in 2002) have apparently become more frequent (Fig. 5A).

Since the 1930s, remarkable changes have occurred in the composition of the fish stock and the total harvest by commercial fishermen. The log-transformed total catch and catch of smelt have decreased substantially since 1930 ($R^2 = 0.37$, $F_{1,69} = 41.38$; $P < 0.0001$ and $R^2 = 0.22$, $F_{1,66} = 19.04$; $P < 0.0001$, respectively) (Fig. 5C). The decline in total catch coincided, though weakly, with an increase in TP ($R^2 = 0.28$, $F_{1,22} = 8.86$; $P < 0.008$), but not with summer mean temperature ($P > 0.1$). At the turn of the 1980/1990 decades, a sharp decline in the vendace population coincided with a major increase in pike–perch abundance (Kangur et al., 2007b). The major decline of the vendace population has been attributed to sequential extreme weather events in summer and winter (Kangur et al., unpublished data). Winters (without permanent ice) influence the reproduction success of autumn spawning fishes (vendace, burbot, peipsi whitefish (*Coregonus lavaretus maraenoides* Poljakow)). During warm summers, vendace face not only high water temperature, but also low oxygen concentrations and predation pressure by the abundant pike–perch. Concurrently with the decline in Lake Peipsi, vendace also declined in some Finnish lakes (e.g. Lake Pyhäjärvi and Lake Puulavesi), suggesting a relationship with climatic factors common to the whole region (Sarvala et al., 1998; Marjomäki & Huolila, 2001; Marjomäki et al., 2004).

The fish assemblage has shifted from cold-adapted species living in an oligotrophic environment towards more warm-adapted and eutrophication-tolerant species: the abundances of smelt, vendace, peipsi whitefish and burbot have declined, while the abundances of pike–perch and common bream have increased (Kangur et al., 2007b).

Eutrophication may have amplified the effect of temperature extremes. In hot summers with calm weather, cyanobacteria blooming and fish kills have co-occurred during the past decades (Kangur et al., 2005). Using regression analysis, Kangur et al. (2007a) found a strong negative effect of high water temperature (≥20°C) on the abundance of the smelt population with a lag of 1 and 2 years. In recent years, smelt abundance has declined to a historically low level and, accordingly, since 2007 smelt have not occurred in the commercial catches (Fig. 5C). Recent data from trawl samples confirm the low abundance (Kangur et al., unpublished data).

Lake Vänern and Lake Vättern: strongest temperature effect in the more nutrient-rich of the two lakes

In Lake Vättern, the water temperature (at 5 m depth) increased significantly during the period 1955–2010 (Fig. 6A, B; $R^2 = 0.50$, $F_{1,55} = 54.7$, $P < 0.001$), most pronouncedly during the last 10-year period. The main change was an increase in autumn and early winter temperatures, while there was no clear trend in ice-on dates during 1881–2010 ($P > 0.9$) or presence/absence of ice-cover ($P > 0.9$). Also in Lake Vänern there was a significant increase ($R^2 = 0.55$, $F_{1,27} = 32.77$, $P < 0.001$) in water temperature (mean temperature May, June, August and September at 5 m). Comparable long-term data on ice cover from Lake Vänern are not available.

There are several marked changes in the commercial catch for the key fish species in both lakes. Analysis of time trends in commercial fish catches is, however, notoriously difficult and trends may not necessarily reflect true stock sizes. Despite the substantial decrease from approximately 1,000 commercial and around 1,800 semi-commercial fishermen in the early 1920s to about 100 commercial fishermen today, there is no trend in total catch over time ($P > 0.6$). The catch is kept around 750 tonnes (mean = 747 ± SD = 186) due to a continuous development of the individual effort and effectiveness of each fisherman. We identified two important trends for the target species of the fishery in these two lakes that are likely related to recent climate change. First, in Lake Vänern the catches of pike–perch, although highly variable, have increased over time ($R^2 = 0.17$, $F_{1,58} = 11.47$, $P < 0.001$). Second, in Lake Vättern the catches of Arctic charr, the traditionally most important species, have declined steadily from the mid-1950s and onwards, negatively correlated with an increase in mean temperature ($R^2 = 0{,}36$, $F_{1,54} = 30.88$; $P = 0.001$). A similar negative trend has also been observed in a multi-mesh gill-net monitoring programme (A. Sandström et al., unpublished data). Even though there has been a recent positive response of this population to a series of new and stricter fisheries regulations, there is a clear long-term decline in Arctic charr that appears to be related to a warming climate.

In both lakes the pelagic fish assemblage is dominated by vendace and smelt (Fig. 6C, D). Recruitment in L. Vättern was characterised by strong oscillations in vendace recruitment at 8- or 4-year intervals. Vendace recruitment is known to fluctuate, often in cycles of 2–5 years (Hamrin & Persson, 1986; Helminen & Sarvala, 1994). The 1992 year class of vendace was extremely strong and dominated the population for 7 years, making up more than 60% of the adult population even as late as 1998 and 1999. In this lake, smelt recruitment followed the same oscillation patterns as vendace ($R^2 = 0.65$, $F_{1,19} = 32.9$, $P < 0.001$) and was negatively correlated with water temperature in July (Fig. 6F; $R^2 = 0.32$, $F_{1,16} = 7.06$, $P < 0.02$) in years without vendace recruitment outbursts.

In meso-oligotrophic Lake Vänern smelt recruitment correlated positively with the temperature in April (Fig. 6E; $R^2 = 0.83$; $F_{1,11} = 56.11$, $P < 0.001$). Long ice winters (in sheltered areas), where the ice lasted until the beginning of March or longer, yielded strong vendace recruitment in Lake Vänern (Fig. 6E; $R^2 = 0.40$, $F_{1,11} = 8.03$, $P < 0.02$). A similar trend has been observed in Lake Mälaren located in Sweden at the same latitude (Nyberg et al., 2001). Variations in productivity (TP) did not contribute significantly in any of these analyses (data not shown).

There was no obvious synchrony in vendace recruitment patterns between the two lakes ($P > 0.4$). In contrast to Lake Vänern, the patterns in Lake Vättern seemed largely regulated by the intrinsic dynamics of the vendace stock, possibly due to the fact that Lake Vättern is less productive, has no fishery on vendace and exhibits a lower predation rate from piscivores due to lower salmonid stocking levels (four times higher per surface area in Lake Vänern). Our results indicate that climate forcing may influence both vendace and smelt recruitment although the effects may differ depending on the conditions in the specific lake.

Lake Søbygaard: major reduction in the size of roach and perch

The April and summer air temperature in the lake region have increased 1.2 and 0.5°C per decade, respectively ($R^2 = 0.39$, $F_{1,20} = 13.25$, $P < 0.002$ and $R^2 = 0.20$, $F_{1,20} = 4.99$, $P = 0.04$, respectively).

Since 1989, total CPUE in terms of biomass has shown a declining trend in Lake Søbygaard, coinciding with a decrease in nutrient concentrations (Fig. 7A, B). A major change has occurred from roach dominance to dominance by a mixed assemblage of roach and perch. This is to be expected when lakes recover from eutrophication (Persson et al., 1991; Jeppesen et al., 2000). The fish assemblages respond surprisingly fast to improved lake water conditions during oligotrophication (Jeppesen et al., 2005).

Although in theory oligotrophication leads to increased body size of cyprinids and perch (Jeppesen et al., 2000), we recorded the opposite pattern. We found a significant (linear regression, $R^2 = 0.48$, $F_{1,19} = 17.9$, $P < 0.001$) reduction in the average size of roach, perch and rudd pooled together (Fig. 7C). This decline coincided with the change in April air temperatures (linear regression, $R^2 = 0.28$, $F_{1,19} = 7.5$, $P < 0.013$) (Fig. 7C), and even more with the average summer air temperature (April–September) ($R^2 = 0.32$, $F_{1,19} = 8.97$, $P < 0.008$) (Fig. 7D). In a multiple regression including also phytoplankton chl *a* and TP, only temperature was retained in the final model, further emphasising the key role of temperature for the body size change. Concurrently, studies of numerous Danish lakes have shown an overall decrease in the body size of some cyprinids and particularly of perch in recent years when the lakes have become warmer, despite a general improvement of trophic state (Jeppesen et al., 2011).

The results from the long-term study of Lake Søbygaard and from the less frequent samplings from numerous other Danish lakes indicate that despite a reduction in loading and a subsequent reduction in the total biomass of fish, fish density is increasing and the average body size is decreasing, with potentially strong cascading effects. This body size change might be a result of improved recruitment of fish due to higher temperatures in spring, but is likely also a result of increasing survival of young fish during winter due to a shorter ice cover period (see "General discussion").

Windermere: decrease in Arctic charr and increase in roach densities

The water temperature has increased significantly in both basins of the lake, for example in the north basin by 0.26°C per decade since 1970 (N-basin: $R^2 = 0.23$, $F_{1,39} = 11.34$, $P < 0.002$, S-basin: $R^2 = 0.413$, $F_{1,39} = 9.81$, $P < 0.004$) (Fig. 8A), which has resulted in an increase in the duration and strength of stratification (Feuchtmayr et al., 2012). The lake has experienced some degree of eutrophication, although this has been much more marked for the south basin as illustrated by its long-term trend in TP which peaked in 1990, prior to the local introduction of tertiary stripping (Fig. 8B) and by the consistently lower dissolved oxygen availability (Jones et al., 2008).

Although the recruitment and thus population dynamics of perch are known to be strongly affected by water temperature (Paxton et al., 2004), no significant relationship between temperature and abundance was recorded for this lake ($P > 0.2$) (Fig. 8C). Development of trophic level asynchrony amongst the plankton and fish of the lake has been recorded in recent years (Thackeray et al., 2010), in part by perch spawning earlier in the spring (Winfield et al., 2004).

While no overall relationship between CPUE of pike and temperature was recorded ($P > 0.1$), local recruitment and population dynamics of pike have also been found to be strongly influenced by water temperature (Paxton et al., 2009). In recent decades, the abundance (Fig. 8D) and individual condition (length/weight relationship) of pike have shown some remarkable changes (Winfield et al., 2008b; Langangen et al., 2011), coinciding with a change in the early winter (the only time of year for which long-term data are available) diet of pike, most notably with a decline in Arctic charr and an increase in roach (Winfield et al., 2012a).

Arctic charr abundance has recently declined in both the north and south basins (Fig. 8E), but particularly so in the more eutrophic south basin. In recent years, dissolved oxygen levels have approached the lower tolerance limits of this species and so have restricted its vertical distribution (Jones et al., 2008). Multiple regression on log-transformed data showed strong negative effect of temperature and positive effect of TP on CPUE of Arctic charr in the south basin ($R^2 = 0.29$, $F_{2,36} = 34.75$, $P < 0.002$), while no relationships were found in the north basin ($P > 0.2$). Arctic charr has also shown a shift in diet in recent years away from zooplanktivory towards benthivory (Corrigan et al., 2011), potentially as a consequence of inter-specific competition after the recent local increase in the abundance of roach (Fig. 8F), which is an efficient open-water zooplanktivore (Winfield et al., 2008a). Arctic charr has recently shown a widespread decline elsewhere in the UK (Winfield et al., 2010b).

Despite having been introduced to Windermere ca. 100 years ago (Watson, 1899), roach populations began to increase in the 1990s after a period of elevated water temperatures (Winfield et al., 2008a). This population increase thus took place against a background of decreasing eutrophication, suggesting that climate warming has been an over-riding factor. The current decrease in roach population (Fig. 8F) may be related to a relatively cool single year (2008). However, concerns remain about the potential competitive impacts of an elevated roach population on the lake's native fish assemblage, most notably on the Arctic charr. Common bream, likely also an introduced species, has also increased in abundance although it presently remains relatively rare (Winfield et al., 2011).

The fish assemblage of Windermere has changed remarkably from its original salmonid–percid-pike domination to one with a much greater component of cyprinids and higher total fish abundance in both basins of the lake (Fig. 8G). The decrease in abundance of Arctic charr appears to have been outweighed by a much greater relative increase in the abundance of roach, and a more detailed analysis of the extensive hydroacoustic data reveals that the overall increase in fish abundance has been driven primarily by an increase of small individuals in the surface waters of both basins. Abundance has significantly increased with temperature and decreased with TP in the more eutrophic south basin ($R^2 = 0.48$, $F_{2,18} = 8.54$, $P < 0.003$), but not in the north basin.

Lake Stechlin: no obvious climate effect on the fish assemblage

Annual average ($P > 0.06$), spring ($P > 0.9$) and summer ($P > 0.9$) water temperatures have not varied systematically between 2000 and 2010 (Fig. 9A). Lake productivity have not changed substantially since 2000 (Fig. 9A).

The overall densities of pelagic coregonids, as estimated by hydroacoustics ($\log_{10}$ individuals (1,000 m^{-3})), fluctuated about sevenfold between the years (Fig. 9B) and had a marginally positive relationship with average spring temperatures in March and April (Fig. 9C, adj. $R^2 = 0.31$, $F_{1,7} = 4.71$, $P = 0.06$). However, the response differed between pre-mature and mature fish and between the sympatric coregonid species (Mehner et al., 2011). Densities of the 0^+ coregonids (dominated by vendace) increased after warm winters, as indicated by positive correlations of fish densities in June with metalimnetic winter temperatures and the NAO index between January and March (Mehner et al., 2011). In contrast, densities of juveniles and adults were correlated with metalimnetic June temperatures, but an opposite response direction of the sympatric species was triggered by their discrete thermal windows. Densities of Fontane cisco increased in years with a warm June, whereas vendace densities declined in these warm years. This opposite response caused the species proportions to fluctuate within a bi-annual cycle.

Besides, zooplankton abundances in hypolimnetic layers (the daytime habitat of coregonids where fish feed) of the previous summer were positively correlated with adult coregonid densities in the subsequent year. The depths occupied by both populations at night shifted towards less suitable water temperatures if densities of the competing species increased, suggesting interactive niche segregation. Temperature-driven inter- and intra-specific competition in the metalimnetic layer may cause a complex response of cold-water fish assemblages in lakes to annual temperature changes (Mehner et al., 2011). A generally higher vulnerability of cold-water fish species to warming could not be deduced from the time series from this lake. However, the time series is relatively short and encompasses only the period since 2000 without pronounced warming trends.

Lake Constance: warm-water fish benefit from a warmer epilimnion

The average water temperature of the upper 20 m increased by 0.22°C per decade (adj. $R^2 = 0.35$, $F_{1,43} = 24.95$, $P < 0.001$) between 1965 and 2009.

The drastic changes in lake productivity during the second half of the twentieth century (Fig. 10A) were the single most important factor influencing fishery yields from ULC. Annual commercial yields peaked during the 1970s at around 30 kg ha^{-1} and declined to almost pre-eutrophication levels (17 kg ha^{-1}) during the 2000s (Fig. 10B). The proportion of whitefish in commercial harvests was around 70% during the first half of the twentieth century, dropped to around 30% at the height of eutrophication and has increased again to around 80% in recent years (corresponding to 13 kg ha^{-1}) (Fig. 10B). Commercial harvests of Arctic charr increased markedly in the 2000s to levels that have never been registered since the beginning of the official statistics in 1910 (Fig. 10C). This increase suggests that lake oligotrophication has improved the conditions for charr, counteracting the effect of increasing temperature. Additionally, every year charr are fished during spawning time and stripped, eggs are incubated in hatcheries, and larvae and juveniles are restocked into the lake.

Multiple regressions on log-transformed data showed no effect of temperature and TP on the yield of coregonids ($P > 0.10$), while the perch yield was significantly related to TP but not to temperature (adj. $R^2 = 0.45$, $F_{2,42} = 18.77$, log temperature: $P < 0.001$, log TP: $P > 0.6$). Hence, an effect of the temperature increase during the last decades on the harvest of the two dominant fish species could not be detected. Under enduring oligotrophic conditions, however, such an effect might materialise in the future.

Year class strength of the pelagic spawning whitefish type did not show any significant trend from 1947 to 1998 (Straile et al., 2007), likely as a result of large year-to-year variations in year class strength (Trippel et al., 1991). However, whitefish year class strength was significantly correlated with the actual winter NAO index and that of the previous winter. Whitefish spawn in late November/early December in the pelagic zone, and the eggs sink to the lake bottom where they develop at the hypolimnetic temperature that was established under full mixing during the previous winter. A higher hypolimnetic temperature accelerates embryogenesis and enhances embryo survival. The larvae, on the other hand, experience the epilimnetic temperature that is influenced by the actual NAO index, whereby higher temperature furthers larval growth and reduces mortality. As the timing of hatching is uncoupled from the actual meteorological conditions (Straile et al., 2007), a mismatch between the larvae and their food might occur, but this has not been observed so far in ULC (Straile et al., 2007). Should climate change promote stronger whitefish year classes in the future, intraspecific competition for food will likely increase with a concomitant reduction of growth rates (cf. Thomas & Eckmann, 2007).

So far, there is no strong evidence that cold-water fish in the lake are severely affected by climate change, not least because this deep lake always provides a cold-water refuge (cf. Thomas et al., 2010). Warm-water species, however, which now live under suboptimal conditions in the lake, will likely benefit from warming. Common carp, for example, which was introduced into Lake Constance in medieval times, clearly benefits from higher temperature. Commercial yields fluctuated around 2 t year^{-1} during the first half of the twentieth century and were as low as 1 t year^{-1} during the lake's eutrophic phase, but increased dramatically to >15 t year^{-1} in the mid-2000s (Fig. 10D). This was a result of successful reproduction in early summer 2003, the warmest summer recorded since 1870, when the surface temperature surpassed 25°C. As the 2003 cohort was fished out, yields returned to the previous level. This example suggests that the population dynamics of fish species characteristic of eutrophic lakes may not primarily be controlled by food availability in oligotrophic peri-alpine lakes, but rather by temperature during the critical embryonic and larval periods.

Lake Geneva: reduction in Arctic charr and increase in whitefish and roach

The mean temperature of Lake Geneva has increased by 0.17°C per decade since 1986 ($R^2 = 0.53$, $F_{1,52} = 58.52$, $P < 0.001$) (Fig. 11A), affecting the development of lake stratification, which now starts 1 month earlier than 30 years ago. The de-stratification thus occurs later due to a very stable epilimnion. Also phenological events of phytoplankton and zooplankton, including the clear water phase, now take place 1 month earlier than 30 years ago (Anneville et al., 2002, 2004).

The most important change in the fish assemblage over the past decades has been a major increase in commercial whitefish catches, positively correlated with mean temperature and negatively with TP (multiple regression on log-transformed data; $R^2 = 0.90$, $F_{2,21} = 95.54$, $P < 0.001$), which during the last 10 years have increased threefold (from <100 to >300 tonnes) (Gerdeaux, 2004), reflecting an increase in the stock. The changes in the whitefish fishery are interpreted as the result of changes in lake trophic state following nutrient loading reduction and fishery management. However, climate change is likely also an important cause of variation (Anneville et al., 2009). Today, spawning of whitefish occurs 2 weeks later than 20 years ago, but the water temperature is warmer and the hatching time has not changed. The change in seasonal dynamics of primary production means that food for whitefish is available earlier in the year for the larvae hatched in February. The warming of the lake is thus favourable for whitefish recruitment (Fig. 11B).

In contrast, the warming of the lake seems to negatively impact the dynamics of Arctic charr, the catches being negatively related to both mean temperature and TP (multiple regression on log-transformed data: $R^2 = 0.66$, $F_{2,21} = 11.47$, $P < 0.001$) (Fig. 11B) (see also Gerdeaux, 2011). The recruitment of Arctic charr was negatively correlated with deep water temperature ($R^2 = 0.55$, $F_{1,10} = 9.58$, $P < 0.02$). Perch, on the other hand, has not changed its spawning time, while roach spawns almost 1 month earlier (Gillet & Quetin, 2006; Gillet & Dubois, 2007). Therefore, the time interval between perch and roach spawning has decreased, and there is a mismatch between perch juveniles and roach larvae as a food resource. Warming thus seems to favour the dynamics of roach, which avoid predation from perch juveniles. We found no significant relationship between temperature and reported catches of pike and trout, while there was a significant positive relationship between P reduction and capture of pike ($R^2 = 0.83$, $F_{1,22} = 109.2$, $P < 0.001$) and a negative relationship for trout catches ($R^2 = 0.69$, $F_{1,22} = 48.58$, $P < 0.001$).

Lake Maggiore: reduction in cold water species and increase in warm-water species

Besides changes in trophic status, the effects of climate warming on Lake Maggiore have become particularly evident during recent decades (Ambrosetti & Barbanti, 1999) (Fig. 12A). From 1978 the water temperature rose significantly both in the hypolimnion ($R^2 = 0.49$, $F_{1,31} = 28.86$, $P < 0.001$) and the epilimnion ($R^2 = 0.33$, $F_{1,31} = 14.76$, $P < 0.001$) (Fig. 12B). Ambrosetti and colleagues (2006) have shown an increase of short and very intense rain events coupled with long drought periods, and increased pollutant loads from the catchment (Galassi et al., 2006; Volta et al., 2009; Guilizzoni et al. 2012), due to changes in hydrology and precipitation regimes, have been also identified. Furthermore, an increase in the duration of the thermal stratification and stability of the water column was observed, probably triggering cyanobacteria blooms (Morabito, 2007).

Since the 1980s, the total fishing yield has decreased significantly ($R^2 = 0.62$, $F_{1.31} = 29.48$, $P < 0.001$) from ca. 45 kg ha^{-1} to the current 8 kg ha^{-1} (Fig. 12B). Fish species contribution to the commercial catches has changed markedly, reflecting the changes in lake fish assemblages probably triggered by multiple stressors, such as the increased water temperature, changes in trophic state and the introduction of invasive non-native species (Volta & Jepsen, 2008; P. Volta unpublished data). Regression on log-transformed data showed that coregonid ($R^2 = 0.49$, $F_{1,31} = 28.22$, $P < 0.001$) and trout ($R^2 = 0.50$, $F_{1,31} = 30.39$, $P < 0.001$) harvests have decreased significantly (Fig. 12C), while bleak ($R^2 = 0.50$, $F_{1,15} = 17.05$, $P < 0.001$) has almost disappeared. In contrast, eurythermal species such as the native shad (*Alosa agone*) ($R^2 = 0.72$, $F_{1,27} = 69.80$, $P < 0.001$) and roach ($R^2 = 0.76$, $F_{1,14} = 40.42$, $P < 0.001$) recently appeared abundantly in the catches. Also, pike–perch has increased ($R^2 = 0.64$, $F_{1,14} = 23.04$, $P < 0.001$) reaching a comparable catch level as that of perch (Fig. 12C), which has itself declined substantially ($R^2 = 0.60$, $F_{1,31} = 45.03$, $P < 0.001$). Besides these primary commercial species, other tolerant and eurythermal non-native species, such as ruffe and wels catfish (*Silurus glanis*), now appear more constantly in the catches (P. Volta, pers. obs.).

Multiple regressions on log-transformed data have shown that the changes registered in the catches of most of the fish species were often significantly correlated with TP at winter mixing, with chl *a* concentration and with water temperature. For instance, the coregonids harvest was positively correlated with chl *a* and negatively with hypolimnetic temperature ($R^2 = 0.70$, $F_{5,26} = 11.99$, $P < 0.001$), while trout was negatively correlated with hypolimnetic temperature ($R^2 = 0.77$, $F_{5,26} = 17.18$, $P < 0.001$). Also the perch catches were markedly negatively correlated with the hypolimnetic temperature ($R^2 = 0.77$, $F_{5,26} = 17.18$, $P < 0.001$), whilst bleak harvest was positively correlated with TP in the epilimnion ($R^2 = 0.76$, $F_{4.12} = 7.78$, $P = 0.002$) but not with temperature. On the contrary, the shad catches were positively correlated with the temperature in the epilimnion but negatively with chl *a* ($R^2 = 0.90$, $F_{4,24} = 49.73$, $P < 0.001$), while the harvests of roach, pikeperch, and char did not show any significant relationship ($P > 0.05$) with any of the variables tested.

Lake Albufera: synergistic effects of eutrophication and climate warming

The temperature in Lake Albufera has increased 0.34°C per decade since 1950 ($R^2 = 0.63$, $F_{1,56} = 97.50$, $P < 0.001$) (Fig. 13A).

Eutrophication (Fig. 13A), disappearance of macrophyte beds, introduction of exotic species and perhaps fish harvesting and climate warming have affected the fish species composition from 1950 to 2007. A remarkable reduction in fish species richness from about 23 to nine species was observed between 1950 and 2007, while there has been a noticeable increase in the presence and development of exotic species such as eastern mosquitofish (*Gambusia holbrooki*), pumpkinseed sunfish (*Lepomis gibbosus*) and common carp.

Similarly to findings in subtropical lakes (Meerhoff et al., 2007a; Teixeira-de Mello et al., 2009), submerged macrophyte beds are important for sustaining a high diversity of small-sized fish species in Mediterranean lakes (Blanco et al., 2003). Some of the exotic species have replaced autochthonous species, especially those using submerged macrophyte beds, such as Spanish cyprinodont (*Aphanius iberus*), *Barbus bocagei*, *Chondrostoma arrigonis* or Valencia cyprinodont (*Valencia hispanica*). Species well distributed in Europe, such as three-spined stickleback, have also disappeared with the loss of submerged vegetation.

Other species introduced in the early 1960s, such as pike, largemouth bass (*Micropterus salmoides*) and pike–perch, have not proliferated in the lake, probably due to rising water turbidity and lack of spawning habitat. Since the 1950s, mugilid captures have increased by 75% (from 80 to 325 t year^{-1}) (unrelated to temperature or chl *a*, $P > 0.2$) to the detriment of species such as eel (from 90 to 7.7 t year^{-1}) (negatively related to temperature, but positively to chl *a*: multiple regression on log-transformed data, $R^2 = 0.84, F_{2,17} = 43.70, P < 0.001$) and European seabass (*Dicentrarchus labrax*) (from 30 to 0.1 t year^{-1}) (negatively related to chl *a* and positively to temperature: multiple regression on log-transformed data, $R^2 = 0.54, F_{2,14} = 8.00, P < 0.005$) (Fig. 13B). Such decrease may also be attributed to over-fishing of these valuable commercial species since the beginning of the twentieth century (Blanco & Romo, 2006).

A main shift in the captured species was recorded in 1974 following an earlier change around 1966 (Fig. 13B). The shift corresponds well with the doubling of the phytoplankton chl *a* concentration observed in 1974 (mean: 53 μg l^{-1}) and a major shift to a turbid state after a rapid loss of submerged macrophytes (Romo et al., 2005). The ratio of piscivorous fish (European seabass and eel) to total mugilids captured was nearly 1 during the macrophyte-dominated state of Lake Albufera, but remained very low thereafter. Dense cover of macrophytes and the presence of some piscivorous species (such as European seabass) probably prevented massive mugilid entry from the sea and development in the lake before the 1970s.

Despite variations depending on the physiological optima of the different species, the direct effects of an increasing temperature may be small as eurythermal fishes dominate completely. However, warming may indirectly affect lake fish communities as longer water retention time leads to more frequent oxygen depletion as well as harmful cyanobacteria blooms (Romo et al., 2012b). The long-term data series from the lake therefore indicates a combined effect of climate change and eutrophication favouring eurythermal, omnivorous and small-sized fish species suffering from variations in water levels, salinity and frequent fish kills during summer-autumn (Blanco et al., 2003), although effects of harvesting and invasion of exotic species have likely contributed to the changes.

General discussion

Leaving interactions aside, theoretical works based on temperature effects on individual metabolism predict an increase in species richness and a reduction in biomass, density, and mean body size with warming, particularly for ectotherms (Allen et al., 2002; Brown et al., 2004). While the fish assemblages in most of the presented case studies have also been strongly influenced by stressors other than changes in climate, particularly changes in nutrient loading, commercial fish harvesting and species invasions, changes attributable to warming have emerged in recent decades in European lakes (summarised in Table 2).

We found a clear trend towards higher importance of eurythermal species with warming in several of the lakes (Lake Peipsi, Windermere, Lake Geneva, Lake Maggiore and Lake Constance), as judged from fish harvests and surveys. Lake Maggiore seems the most striking example of such changes, although the evidence is provided by harvests that may themselves show a more drastic non-linear change than the fish populations. In this lake, a major shift occurred in the harvest: cold-adapted species (trout and whitefish) declined and more eurythermal species (native shad, roach and pike–perch) increased substantially. Also ruffe and catfish appeared more often after a temperature increase. Harvest of pike–perch increased in Lake Peipsi and Lake Vänern, of common bream in Lake Peipsi and of carp in Lake Constance. These shifts to more eurythermal species occurred even though four of the five lakes experienced oligotrophication during the study period, which should have favoured the cold-adapted species in a slightly warmer climate due to improved oxygen conditions in the cold hypolimnion and less severe competition for food with the eurythermal species (Hartmann, 1977; Persson et al., 1991; Jeppesen et al., 2000).

The cold-stenothermic Arctic charr has been particularly affected by warming, showing a clear decline in the majority of the lakes where its presence is recorded (4 out of 5, i.e. Lake Elliðavatn, Windermere, Lake Geneva, and Lake Vättern). Despite warming, a marked increase has occurred in the charr harvest of Lake Constance during the last 15 years, although here nutrient loading reduction and systematic stocking must have played a pivotal role in boosting the local production of this species. A recent study indicated pronounced negative long-term effects on Arctic charr growth in Scandinavian hydroelectric reservoirs (Milbrink et al., 2011). As illustrated by a review of charr population declines in the UK (Winfield et al., 2010b), the thermal problems faced by this species are expectedly more adverse in shallow than in deep lakes due to higher temperatures and lack of a cold hypolimnion refuge. In Iceland, charr appears also to suffer from the thermally linked PKD (Sterud et al., 2007), as is the case in Lake Elliðavatn (Kristmundsson et al., 2011). This highlights the importance of complex and potential synergetic effects of warming on fish, including both direct effects (e.g. on metabolism and growth) and indirect effects, such as diseases.

Other cold-water-adapted species, such as coregonids and smelt, have also responded to increasing temperatures, although with varying patterns. While commercial catches of whitefish have increased in Lake Geneva, perhaps reflecting an earlier increase in spring water temperature favouring recruitment (see also the whitefish in Lake Constance), whitefish harvest has declined substantially in Lake Maggiore, Lake Vättern and Lake Peipsi, and to some extent also in Lake Säkylän Pyhäjärvi. In the UK and Ireland, a decline in the coregonid pollan (*Coregonus autumnalis*) in recent decades has also been attributed to changes in temperature (Harrod et al., 2002). The population of brown trout, which is a more heat-tolerant species than Arctic charr (Elliott & Elliott, 2010), has remained largely unchanged in Lake Elliðavatn, but has decreased substantially in the warmer Lake Maggiore.

We observed variable responses of vendace to warming, likely because temperature effects on vendace depend on the initial situation, as well as on the life stage relative to the seasonal timing of the changes. Except in Lake Vättern, where no correlation between the dynamics of vendace and climate parameters occurred but instead intra-specific competition seemed more important, negative effects of rising temperatures seemed substantial in most lakes. Although rapid warming of water after the hatching of larvae in spring generally enhances vendace survival (Helminen & Sarvala, 1994), late summer temperatures in the southernmost vendace lakes have occasionally risen so high as to increase particularly adult mortality. Adult vendace population has declined in the deep Lake Stechlin in warm summers (Mehner et al., 2011), and more drastic reductions have occurred in shallow Lake Peipsi after summer heat waves. Mild winters leading to early ice-off dates have been detrimental to vendace recruitment in Lake Säkylän Pyhäjärvi, Lake Peipsi, and Lake Vänern. In contrast, warming has apparently favoured vendace recruitment further north in subarctic Lake Inari (Finland) (Puro-Tahvanainen & Salonen, 2010). Vendace recruitment has been indirectly disturbed in Lake Säkylän Pyhäjärvi through climate-induced changes in winter fishing length and intensity (Ventelä et al., 2011). An additional indirect climate effect is that the predation pressure from perch on young vendace has apparently increased with warmer summers in several lakes, particularly in the north. The UK's last surviving native population of vendace in Derwent Water, where the species is not exploited in a fishery, has shown a declining tendency over the last decade (Winfield et al., 2012b) which may be due in part to warming.

The response of smelt also varied among lakes. While the recruitment of this species in deep northern Lake Vättern was negatively related with the water temperature in July, it increased with April temperature in Lake Vänern. This was similar to the opposite effects of winter/spring or summer temperatures on the recruitment and densities of vendace. In contrast, a drastic reduction in smelt occurred in shallow Lake Peipsi as judged from commercial harvest, the decline being particularly remarkable in years with heat waves.

Perch and roach, which typically dominate northern European lakes (Mehner et al., 2007), show an ambiguous pattern of response to warming. No obvious climate-induced changes could be traced for nutrient-poor northern Lake Vänern and Lake Vättern. Observations from 11 Swedish forest lakes indicate, however, increased growth of 0^+ perch in years with higher temperatures, potentially enhancing their winter survival. The harvest of perch has increased in Lake Peipsi and strong year-classes of this species have occurred more frequently in Lake Säkylän Pyhäjärvi and in Lake Søbygaard, although in the latter it may also be attributed to a major reduction in nutrient loading. Other studies have also found strong year classes of perch to be associated with warm summers (Böhling et al., 1991; Lappalainen et al., 1996; Sarvala & Helminen, 1996; Mehner et al., 1998; Paxton et al., 2004), and in Lake Pyhäselkä in north-eastern Finland perch density increased with increasing temperature from 1975 to 2005 (Voutilainen & Huuskonen, 2010). The southern distribution limit of this species corresponds with the 31°C summer isotherm (Thorpe, 1977), the larvae growth optimum of 25–30°C is higher than that for adults (18–27°C), and gonadal development is most favourable at temperatures <6°C for prolonged periods (Graham & Harrod, 2009). The latter two factors, in particular, may explain why we observed stimulation of perch recruitment in the north and a major decline in perch harvest in southern Lake Maggiore.

In our study, long-term data on roach were limited. The harvest of roach increased in Lake Maggiore (Volta & Jepsen, 2008) and roach abundance increased substantially in Windermere since the 1990s, despite varying in time since first introduction and indicating that this species has encountered a ‘window of opportunity’ in recent years. The primary factor behind the increases of this non-native (to these lakes) cyprinid is probably the increase in water temperature, because roach is unlikely to have benefitted from the reduced nutrient loadings occurring during this period in both of the lakes.

Higher winter survival, longer growing seasons and, for some species, higher year-class strengths in warm years can be expected to lead to higher proportions of small fish in the populations. Spawning occurs earlier at lower latitudes, as seen for important European species such as roach (Lappalainen & Tarkan, 2007) and perch (Tolonen et al., 2003). We found a major decline in the body size of roach and perch in Danish Lake Søbygaard. This increase in the proportion of small fish occurred despite an overall major reduction in nutrient levels following an external nutrient loading reduction, which according to monitoring data from numerous Danish lakes should have resulted in a lower proportion of small fish (Jeppesen et al., 2000). Moreover, an analysis of gill-net monitoring data on the age structure of perch and roach from 50 Swedish lakes, covering a latitude gradient from 67° to 55°N, revealed that the proportion of perch <10 cm and of age groups 1^+ to 3^+ of the total catch (by numbers) increased markedly with decreasing latitude (and increasing air temperature) (Jeppesen et al., 2010a). These findings concur with a meta-analysis of the effects of warming on the body size of ectothermic aquatic organisms, showing a significant increase in the proportion of small-sized species and organisms at warmer temperatures (Daufresne et al., 2009).

The fish assemblage is not only affected directly by the heating and changes in the thermal stability of the lakes. Numerous recent studies and reviews indicate that warming will exacerbate existing eutrophication problems (McKee et al., 2003; Feuchtmayr et al., 2009; Jeppesen et al., 2010b; Moss et al., 2011; Romo et al., 2012b), and this will, in a self-amplifying manner, likely further stimulate a shift to small-bodied fish and to dominance of eurythermal species, which typically tolerate low oxygen levels and high ammonia concentrations (see review in Graham & Harrod, 2009). In Northern and Central Europe, increased eutrophication is in part due to a higher external nutrient loading mediated by higher precipitation-induced nutrient runoff, but it is also a consequence of higher internal phosphorus loading and higher dominance of cyanobacteria in warm lakes (Mooij et al., 2007; Jeppesen et al., 2010b; Kosten et al., 2012; Romo et al., 2012b), with detrimental effects mostly on adult fish (Romo et al., 2012a). The effects of eutrophication are further reinforced by the warming-induced shifts in fish assemblages and size structure (Teixeira-de Mello et al., 2009), and in many lakes higher winter survival due to reduced ice cover (Jackson et al., 2007), leading to enhanced fish predation pressure on zooplankton (Meerhoff et al., 2007b; Balayla et al., 2010; Ruuhijärvi et al., 2010) and, as a result of this, lower grazing on phytoplankton (Meerhoff et al., 2012).

It is also to be expected that warming and enhanced precipitation in Central and Northern Europe induced by climate change will enhance the allochthonous carbon inflow to lakes and reduce carbon burial, leading to higher in-lake dissolved organic concentrations and often a higher humic content (Tranvik et al., 2009, Sobek et al., 2007). Succession towards higher bacterial production, together with light limitation, may result in lower overall production available to the higher trophic levels in certain lakes (Ask et al., 2009; Karlsson et al., 2009), as seemingly has occurred to perch in Lake Valkea-Kotinen. In the Mediterranean area, eutrophication may also intensify despite lower external nutrient loading, as nutrient concentrations rise due to higher evaporation and lower precipitation (Jeppesen et al., 2009, 2011; Romo et al., 2012b). As elsewhere, changes in fish size structure here will also exacerbate eutrophication symptoms.

Therefore, we can expect an allied attack by eutrophication and warming in lakes in the future (Moss et al., 2011), and shifts in fish abundance, body size and composition will be reinforced and stimulated by this process. This implies that it will be more difficult to obtain the good ecological status required by the Water Framework Directive in European lakes facing climate warming and suggests that a way to counteract, at least in part, the effect of warming is to reduce the nutrient input to lakes even further than planned under the present-day climate and to regulate fisheries accordingly.

Conclusions

Although local variations occurred, we have revealed profound changes in either fish assemblage composition, biomass, abundance, body size and/or age structure of key species during recent decades in a set of European freshwater lakes. Some patterns coincided with findings by other approaches (e.g. meta-analysis, Daufresne et al., 2009; space-for-time-substitution, Jeppesen et al., 2010a, b; Meerhoff et al., 2012), although responses were species-specific and not universal for our data set. The most obvious alterations encompass a decline in the abundance of cold-stenothermal species, in particular in shallow lakes, and an increase in the abundance of eurythermal species even in deep, stratified lakes. This development has occurred despite a reduction in nutrient loading in most of the case studies, supposedly favouring fish typically living in cold-water low-nutrient lakes and larger-sized individuals. The response of fishes to the warming during recent decades has therefore been surprisingly strong, making fish ideal sentinels for detecting and documenting climate-induced modifications of freshwater ecosystems.

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