

# Hydrobiologia

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

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<b>Abstract:</b>	<p>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: 0.04-5648 km<sup>2</sup>; mean depth: 1-177m; 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 trout has decreased 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.</p>
<b>Response to Reviewers:</b>	<p>Dear Peter</p> <p>We have now revised the paper and our response to the reviewers and your comments is given point-by-point below. As you can see we have followed most of their suggestions. Hopefully it is therefore now ready to be accepted. As we have more statistical analyses in the present version we will let the editors decide whether it</p>

should be called a review or a primary research paper. Not important to us.

As you can see below, one of the referees was rather critical regarding the kind of hybrid paper format and suggested to reorganize it either into a more traditional review paper or run a common analysis on all individual datasets. Try to take the best out of these comments.

-We have now included statistical tests of changes in temperature and of the relationship between the key species studied and temperature and TP/chlorophyll a. We have, however, not made a common meta-analysis of all case studies as they vary very substantially in time period covered, fish species in focus, type of data (harvest, CPUE – even very different gears, mesh-sizes). We collectively do not see how such an analysis would add to the study, rather the contrary.

Reviewer #1: The potential effect of (global) climate change on biological systems has been increasingly dominant in the scientific literature during the past decade. The temperature of the environment is known to be one of the most important variables affecting the life histories of fish. Thus, it has been suggested, that some of the most profound changes due to systematic shift in average temperatures may be witnessed in the structures of fish communities. The authors of the MS have aimed to demonstrate this effect by using long-term data sets from several European lakes. They present that while the temperatures of the environment have increased in the study sites, abundance of arctic charr and some other cool-stenothermal species have decreased in some lakes, while increase in some eurythermal species was observed. In some lakes such an effect was observed in parallel to decrease in nutrient load. Thus, the Authors conclude that although the systematic increase in ambient temperature may have interacting effects with eutrophication, the former is probably the main factor, responsible for witnessed results. This topic is of great interest and would be interesting to scientists from different fields of research. However, in the current form the MS has several shortcomings which diminish the scientific value of it and should be dealt with.

I had two major concerns with this MS. First, the Authors have submitted the MS to be published as a review paper. However, the structure of the MS seems to be an extract from several case studies or a hybrid between case study and review paper. Thus, a great amount of volume is dedicated to Methods and Results (Trends in the case studies), however, these are often quite superficial (although often the citation, where the details are described, is presented though). The review article should be more concentrated for problem-based approach [The increase in temperature is the main problem, it is expected to cause changes in fish communities and life-history traits, the authors present the evidence from literature (and/or data series) to confirm or reject those hypotheses]. Moreover, it seems that different authors have written different parts of the Methods and Results. This has resulted in unevenness in the style of the MS and some confusion in presenting the species names (the latin name of the species should be presented with the first mention of it; e.g. p 20 lines 53-54) and figures (all the figures are cited together in the p 10 line 2, instead relevant figure should be cited in the relevant part of the text). Thus, I suggest that the MS should be rewritten to a classical review article format, where the structure of the MS would be problem-based instead of study-site based as in here (Such approach would also eliminate the reason for far too numerous unpublished data citations present in this MS).

-We have collectively used much effort to revise the MS as requested. We have harmonized the style (with 2 persons in the lead), tightened up the MS and conducted further statistical analyses. We have reduced the length of the case studies, now strictly focusing on the major changes in the fish species/communities. We have added an extra table (Table 1) as requested showing key data from the lakes; this has reduced the length of the Methods section. We have, however, maintained the study-site based format instead of a problem-based one, as suggested, simply because the case studies are different due to a different focus, use of different fishing methods etc. We therefore collectively feel that a problem-based structure would lead to more confusion than clarification and to more speculative judgments and many “ If, then, else statements”.

The second major problem of the MS is that while the title is "Impacts of climate warming on lake fish assemblages: evidence from 24 European long-term data series" then *sensu stricto*, the results should be rather titled "Impacts of climate warming on the long-term dynamics of several fish species in 24 European lakes". In the MS the described trends consider the changes in the abundances of individual fish species (although often several species per lake are considered at once). However, sufficient statistical methods (available in several statistical packages e.g. R or PRIMER-E) have been developed to correctly test if the current data set allows us to reject the null hypotheses that climate change has no effect to the fish assemblages in those lakes. Thus, if the Authors prefer the presentation of their original data to the preparation of more literature based review article, they should apply some correct statistical analysis to their datasets, instead of comparing trends in the abundances of individual species (Such case studies have been done before and cited in this MS. However, such large-scale analysis would still be novel and of great interest to ichthyologists and ecologists).

-We have changed the title as suggested- though we substituted " several fish species" with " key fish species".

-We have now included a statistical test of changes in temperature and the relationship between the key species studied and temperature and TP(chlorophyll a). We have, however, not made a common meta-analysis of all case studies as they vary very substantially in time period covered, fish species in focus, type of data (harvest, CPUE – even very different gears, mesh-sizes). We do not see how such an analysis would add to the study, rather the contrary.

I have also some minor concerns:

1)p 6 lines 22-27. Remove "even", the differences of life-history characters within species on the latitudinal gradient in numerous studies can be considered as strong evidence that some environmental variable on this gradient has strong effect on the life-histories of fish.

-Modified as suggested.

2)p8 lines 24-30. The authors should describe the criteria on what basis these 24 out of all European lakes were included to this study.

-Done. The sentence now reads: "Lakes that had >9 years of paired data of at least one fish metric and one climate metric were included".

3)p12 lines 12-14. "To compare lakes with similar fish assemblages, only circum-neutral lakes (annual mean pH > 6) inhabited by perch, roach and pike are included." What was compared? TP, TOC, sulphate, 0+ perch?

-Sorry, the wording was unclear: Now rephrased: "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".

4)p14 lines 39-49. Please rephrase to "Over the past 80 years, the structure of commercial catch assemblage has not changed. Lake (dwarf) smelt (*Osmerus eperlanus eperlanus m. spirinchus*), vendace and pike-perch (*Sander lucioperca*) have been the main commercial species while the catches have declined to about a half during this period."

-Done.

p 28 lines 7-12. "The fact that PKD infections affect young charr most severely strongly suggests that the main cause for the population decline in Arctic charr is higher mortality of young fish." Such conclusion can not be made on the basis of this data.

-We have now softened the sentence and write: "The fact that PKD infections affect young charr most severely indicates that the main cause of the population decline in Arctic charr is higher mortality of young fish, although further studies are needed to draw firm conclusions".

5)p 30 lines 46-49. "The length was lowest in the two northern-most lakes, albeit it was relatively high considering their lower temperature." Rephrase to: "0+ perch were shortest in the northernmost lakes, albeit these fish were relatively long considering the lower temperature of their environment." Citation is also needed to describe how these fish were relatively long for the temperature of their growth environment.

-Done and citation added. We write: "0+ perch were shortest in northernmost lakes, 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)".

6)p30 lines 53-54. What is "residual length" and how it is calculated? What are the values of the rest of the statistics?

-Sorry, the wording was unclear. We now write: "Residuals in the length-temperature relationship differed significantly between lakes (one-way ANOVA,  $p < 0.001$ ) (Fig. 3D)".

7)p. 31 lines 21-27. "The results therefore indicate that a further increase in water temperature might be beneficial for juvenile perch in these northern lakes." Presented results do not justify such conclusion. The authors only give no evidence that a negative effect of increasing TOC levels overrule the positive effect of increasing temperature.

-Correct. We have removed this sentence.

8)p 36 lines 21-22. "Eutrophication appears to have intensified the blooms." Do the Authors have any data to support this claim? If not such impressions should not be presented.  
year justifies conclusion that the population has no living representatives present in the lake (is extinct)?

Correct – now rephrased: "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. Using regression analysis, Kangur et al. (2007a) found a strong negative effect of high water temperature ( $\geq 20^{\circ}\text{C}$ ) 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)".

9)p 37 lines 21-25. What does this subheading mean? From the figures it seems that those lakes are not the most nutrient rich in the study.

Changed to "strongest temperature effect in the more nutrient-rich of the two lakes" to show that it only reflects a comparison of the two lakes.

10)p 38 lines 17-34. Please explain in more detail how the presented results are allowing such decision. "Our results indicate that climate forcing may influence both vendace and smelt recruitment. The impact of climate variability seemed stronger and easier to detect in the more productive and less resource-limited system where competition between cohorts and species may be less important." Such an generalizing conclusion may be surprising, if we consider that there was no synchrony detected in population dynamics of fish in relatively similar lakes within short distances. Such synchrony could be expected if the climate is the most important factor affecting fish assemblages.

- The sentence has been deleted.

13) p 39 lines 12-13. What does the improvement of trophic state mean here? Cyprinids (e.g. roach) are generally adapted to warm and eutrophic water. Oligotrophication may generally be considered as reduction in habitat quality for roach.

-“Trophic state” is now reworded to “reduced nutrient level” for the purpose of clarification. Yes, oligotrophication can be considered as a reduction of quality for roach, but studies of Danish lakes clearly indicate that mean size of roach increases when the nutrient level decreases (Jeppesen et al., 2000) – so, fewer but larger roach (as well as perch).

11)p 39 lines 17-32. The analysis, supporting the conclusion in this paragraph is lacking. Such correlations, presented here, can not be used for backing up such causative conclusions. I.e. we can also argue that the reduction in the average size of the fish can be the result of oligotrophication and thus growth speed of all individuals is small (slow-growers are not outcompeted by the fast-growers) and thus, the number of individuals is increasing while the total biomass and the individual size are decreasing. Moreover, if such an effect is coinciding with extensive fishery for large predatory fish e.g. pike then such scenario is very likely to prevail with no connection to the changes in ambient temperature at all.

-While this is one possible scenario – the evidence from Danish lakes in general indicates an increase in size with decreasing nutrient level (see above). However, during the last decade size has decreased (Jeppesen et al., 2010) despite lower nutrient levels and decreasing size of zooplankton – all indications of a shift to smaller individuals and higher predation (and it should have been opposite, Jeppesen et al., 2000) unless a temperature increase plays a role. However, to soften the statement we have removed the sentence (line 17-25): “In combination, the results from the long-term study of Lake Søbygaard and the less frequent samplings from numerous other Danish lakes strongly suggest that despite a reduction in loading and a subsequent reduction in the biomass of fish, fish density is increasing and the average body size is decreasing, with potentially strong cascading effects”.

12)p 47-49. Considering the number of invasive species introduced to the Lake Albufera and extensive overfishing of some species, the conclusion that synergistic effects of eutrophication and climate warming are the most important factors affecting local fish community needs a proper statistical analysis to separate these potential factors.

-We agree, but such an analysis is not possible due to limited data on variables in action. We have therefore rephrased and softened the statement. We now write: “The long-term data series from Lake Albufera therefore indicates a combined effect of climate change and eutrophication favouring eurythermal, omnivorous and small-sized fish species suffering from variation in water levels, salinity and frequent fish kills during summer-autumn (Blanco et al., 2003), although effects of harvesting and invasion of exotic species may have contributed to the changes” ... and moved it to the end of the case study.

13) p 54 lines 38-54. This paragraph is considering one of the most important results of the MS, namely that shift towards eurythermal species occurred even in the situation of oligotrophication. However, here five lakes out of 24 are represented. From those only in four oligotrophication occurred in parallel with increase in eurythermal species. Such fish species, which could have benefited from oligotrophication and colder water would have been vendace and arctic charr which are not present in lake Maggiore. To sum up, the most important generalization in this MS is made on the basis of a result, observed in three (four if Lake Maggiore is included) lakes out of 24.

We clearly state that it is based on four lakes and not the 24 lakes, but have now modified the statements slightly. It is correct that charr and vendace are not present in Lake Maggiore, but trout and other coregonid species occur and have declined markedly in the harvest, while the share of eurythermal species has notably increased. Thus, we maintain Lake Maggiore as member of this group.

We now write: “We found a clear trend towards higher importance of eurythermal species in several of the lakes (Lake Peipsi, Windermere, Lake Geneva, Lake Maggiore and Lake Constance) as judged from fish harvests and surveys. This shift occurred even though four out 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).“ By adding the “four of five“ we make it even more clear that the statement is based on the four lakes.

13)p 56 lines 12-23. Lake Peipsi and Vänern have not experienced reduction in nutrient load according to the figures presented.

–We have now changed the text accordingly and write “in most of the case studies”.

14)p 58 lines 28-32 “several case studies show a decrease in the average size of the dominant species roach and perch”. *Sensu stricto*, this was demonstrated only in case of one lake (Danish Lake Søbygård) in this study (if the conclusions are made on the basis of the data set described in the title of the MS. The increase in the number of small individuals in hydroacoustic studies in lake Windermere can not be considered as proof for this statement).

-This has now been corrected saying that the evidence is based on Lake Søbygaard data as well as literature findings. We now write: “We found a major decline in the size of roach and perch in Danish Lake Søbygård. 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 55oN, 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 air temperature) (Jeppesen et al., 2010a)“.

15)The order of citations in the references list is not alphabetic (pp 75-76).

-Corrected.

Reviewer #2: Impacts of climate warming on lake fish assemblages: evidence from 24 European long-term data series by Jeppesen et al.

The MS is an article of the possible impacts of climate warming on fish assemblages in 24 lakes. The lakes range from very small (0.041 km<sup>2</sup>) to large (5648 km<sup>2</sup>) within latitudes of 64 and 39 oN. The MS is interesting and collects the data of changes in fish assemblages in European lakes. It is fluently written, but needs stylistics editing and consistency in the use of terms. There are also new materials and results presented for some of the lakes. Therefore, I suggest that authors add a new Table 1, which could include lake area, coordinates, mean and maximum depth, nutrients levels, the number of fish species, and a note of possible new data analysed and used tests.

-We have revised the MS and harmonized the style and analysis conducted further. We have added an extra table (Table 1) showing key data from the lakes, which has reduced the length of the Method section. However, tests are not described here – we feel that their description is more appropriately placed in the Results section.

\*\* General corrections

Change all fish ages either to “age 3+” or use only “3+”. Now there are terms like one-summer old, X year old, age groups X, YOY (in Table 1) and young-of-the year (0+) (Fig. 6). Use “pikeperch” as a species name. Year is abbreviated both as y and yr.

-Now harmonized.

I review below materials and methods and corresponding results by each lake separately.

\*\*\* Lake Elliðavatn, Iceland

Page 26, line 36: Correct to: The observed decline in the density of “juvenile and” adult charr



-Done.

Page 27, line 27: Correct all "year old"

-Done.

Page 27, lines 20-24: How reliable is the t-test with only five observations per period?  
Delete these t-test results, but show the mean lengths per period

-We agree – the T-test is not included anymore

-We agree. We have now regressed against time instead.

Page 27, line 24: Correct "Brown trout showed the same trend" to "Brown trout showed no differences in mean lengths between periods"

-Done.

Page 27, lines 32-39: This is speculation, delete

Is the PKD occurrence/prevalence connected to salmonid -stockings?

-We have rephrased the sentence to make it less speculative. We now write: "The fact that PKD infections affect young charr most severely indicates that the main cause of the population decline in Arctic charr is higher mortality of young fish, although further studies are needed to draw firm conclusions".

\*\*\* Lake Valkea-Kotinen

Page 28, lines 30-47: Are these new results?

-Yes, they are new and test results are now added.

Fig. 3C: Change x-axis maximum to 13 C

-Done.

\*\*\* Swedish forest lakes

Page 29, line 31: Delete the first sentence, the data is published here (?).

Table 1: Correct "or no", delete "Insignificant trend in catches of bream in one of the lakes"

Fig. 3: Delete "(from K. Holmgren, unpublished data)".

-All done.

\*\*\* Lake Säkylän Pyhäjärvi, Finland

Page 13, line 34: correct "from 1989-2011"

-Modified accordingly. We write: "The winter seine catch of all species was sampled from 1989-2011 and samples for vendace and whitefish have been collected since 1971".

Page 30, line 51: Correct "p >" to "p ="

-Done.

Page 31, lines 44-49: Delete, or show these trends in figure

-Deleted.

\*\*\* Lake Peipsi, Estonia/Russia

Page 33, line 56-58; Page 34, lines 1-12: The cubic polynomial model actually predicts decreasing temperatures for the future. Therefore, delete the line from Fig. 5A and rewrite the corresponding part. If you model this then use some more appropriate method.

-Now removed from the figure.

Page 34, line 22 and line 36: Here the words "collapse" and "disappearance" are used. Is smelt totally disappeared from the lake, or only from catches?

-Text modified to decline.

Table 1: Ruffe is not a coldwater fish species

-Removed from the column.

\*\*\* Lake Vänern (58-59° N) and Lake Vättern (57-58° N), Sweden

Page 36, lines 27-28: Correct the paragraph. The references in figures are in wrong order. Add also reference to Figure 6A

-Corrected.

Page 37, lines 1-6: Are these new results, and if so, then add the corresponding test coefficients and p-values

-Done.

Page 37, line 19: Add seemed "to be" regulated

Page 38, line 7: Add species "."

-All corrected.

Fig. 6F: Check the x-axis! Correct "Julian day" to "Number of days since the 1st of January "

-Corrected.

\*\*\* Lake Søbygaard, Denmark

Page 38, lines 29-32: Move the citation to Fig. 7B to the end of sentence "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)"

-Done.

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\*\*\* Windermere, U.K.

Page 40 and 41: The citation order to figures should be corrected (Fig 8D, then Fig. 8E, 8C, 8F)

-Order modified.

Table 1: What does "Undocumented decline in brown trout abundance" mean? Is it unpublished?

-Sentence on brown trout removed.

Fig. 8: Add: roach (fish 100 m<sup>2</sup> net-1 day-1 "),"

-Done.

\*\*\* Lake Stechlin, Germany

Page 42, line 5: Delete "in Lake Stechlin"

-Done.

Page 42, lines 47- Page 43: Are these trends/correlations significant? This should be added here.

-Tests now added.



Fig. 9: 9B should be deleted, and two digits could be added to 9C to mark different years.

-We prefer to keep the figure to make it consistent with the others/... to ensure consistency.

\*\*\* Lake Constance, Austria/Germany/Switzerland

Page 20, lines 45-47: Is this increase statistically significant? Add this information

-Done.

Page 43, line 56: What is meant with "A beneficial effect of regular stocking with autochthonous material"? Describe this in more details

-Now removed.

Page 44, line 22: Add reference "on the year-to-year variation of year class strength was apparent (Straile et al., 2007)".

-Done.

Table 1: Is there something missing from "Major increase in commercial catches, attributed to oligotrophication and effective management-"?

-No, but a hyphen had been inserted by mistake – now removed.

Table 1: Perch yields decreasing "in?" with increasing oligotrophication.

-Corrected.

\*\*\* Lake Geneva, France/Switzerland

Page 45, line 32: Is the mean increase in temperature statistically significant?

-Yes, test has been added.

Table 1: Correct "Decline in abundance is negatively correlated with the temperature in the deep water" to Declining abundance ?

-Corrected.

Table 1: "Roach spawn earlier , no change for perch and roach juveniles grow as fast as perch." ??

-Now corrected to "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".

\*\*\* Lake Maggiore, Italy/Switzerland

Page 46, line 54: Long sentence: "Impacts of warming have been registered on many physical and chemical parameters of the lake, as well as on the middle and upper food webs: severe short and very intense rain events coupled with long drought periods, an increase in the duration of the thermal stratification and stability of the water column, cyanobacteria blooms, earlier appearance and eutrophication-like densities of herbivorous cladocerans, increased availability of deep refuge for large zooplankters and enhanced availability of pollutants (Bettinetti et al., 2006; Volta et al. 2009; Guilizzoni et al., 2012";)". Rewrite.

-Done. We now write: "Impacts of warming have been registered on many physical and chemical parameters of the lake as well as on the middle and upper levels of the food webs. For instance, Ambrosetti and colleagues (2006) found an increase of several short and very intense rain events coupled with long drought periods. According to this, an increase of the duration of the thermal stratification and stability of the water column was also observed probably favouring cyanobacteria blooms (Morabito 2007). Also,

due to climate warming, earlier appearance and eutrophication-like densities of cladocerans were registered (Visconti et al. 2008) as well an increase of the of deep refuge for large zooplankters (Manca & de Mott 2010). Finally, an increase of pollutant loads from the catchment (Galassi et al. 2006; Volta et al. 2009; Bettinetti et al. 2011; Guilizzoni et al. 2012) due to changes in hydrology and precipitation regimes was found“.

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Page 47, line 22: Initials for Campi?

-As the paper is still in preparation we changed it to P. Volta unpublished data.

\*\*\* Lake Albufera, Spain

Page 24, line 41: Remove citation to "Fig. 13A"

-After the test it is relevant with this citation – as in the other case studies.

Page 25, line 37: Mention here the total number of fish species in the lake

-Done.

Table 1: The text "Well adapted warm-eurythermic species, e.g. cyprinids and mosquitofish." is not suited with the Table caption: "A 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". More appropriate could be "No changes in warmwater species" etc.

-Corrected.

\*\* General discussion

Page 51, lines 24- : Add references to: "Although rapid warming of water after the hatching of larvae in spring generally enhances vendace survival (Reference), late summer temperatures in the southernmost vendace lakes have occasionally risen so high as to harm adults in particular (Reference)."

-Done – changed to: "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“.

What kind of harm?

Concerning the comments on harm:

Adult vendace are more sensitive to high temperatures than young-of-the-year. This difference can be reflected in their different vertical distributions in summer. Excessively high summer temperatures may cause adult vendace severe physiological stress which, combined with simultaneous food competition, may manifest first as ceasing growth, and may ultimately lead to mortality. Text changed to "risen so high as to increase adult mortality in particular“.

"In the deep Lake Stechlin the adult vendace population declined in warm summers (Reference) and more drastic changes have occurred in shallower lakes.

-References have been added.

Page 53 line 14: Add "The southern distribution"

-Done.

Page 53 line 22: Remove the citation (Graham & Harrod, 2009) and cite to original references.

-We now write: "see review by Graham & Harrod, 2009" as there are many

references on this topic.

Page 56 lines 7-12: Delete this sentence. Basically all known effects are negative, damming, reduced water levels at late winter causing egg death in Coregonids (whitefish and vendace) etc-

-Done.

\*\* References

van Doorslaer et al. 2007 is mentioned in text (page 7, line 22), but not found in references

Page 66, line 5: Delete APHA (1992) 2X

Page 66, line 34: Weyhenmeyer & M. Winder, "M." 2009.

Page 66, line 40: Amarasinghe, U.S. and Welcomme, R.L. (2002)

Page 68, line 53: Blanco, S., S. Romo, M. J. Villena & S. Martínez, "S.", 2003.

Page 71, line 1-7: T. Hesthagen., t. Mehner, submitted. Environmental temperature is the dominant predictor of the size structure of European lake fish assemblages

Page 73 line 26: Graham, C. T. & Harrod, C., 2009.

Page 74, line 1-35: Wrong alphabetic order

Page 78, line 12: Scientific name in italics

-All corrected.

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2 **Review or Primary Research Paper**  
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8 **Impacts of climate warming on the long-term dynamics of key**  
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17 **Erik Jeppesen**<sup>1,2,3</sup>, **Thomas Mehner**<sup>4</sup>, **Ian J. Winfield**<sup>5</sup>, **Küllü Kangur**<sup>6</sup>,  
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15  
16 Key words: Climate change, fish assemblages, functional traits, long-term data series, Europe  
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21 “The authors assure that this paper has not been submitted elsewhere in identical or similar  
22 form, nor will it be during the first three months after its submission to *Hydrobiologia*.”  
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32  
33 We dedicate this paper to the late Prof. Jürgen Benndorf, a true pioneer and mentor in lake  
34 and reservoir management oriented research, who inspired a number of us to initiate long-  
35 term comprehensive experimental ecological studies on lakes and reservoirs.  
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## 45 **Abstract**

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50 Fish play a key role in the trophic dynamics of lakes. With climate warming, complex  
51 changes in fish assemblage structure may be expected owing to direct effects of temperature  
52 and indirect effects operating through eutrophication, water level changes, stratification and  
53 salinisation. We reviewed published and new long-term (10-100 years) fish data series from  
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60 24 European lakes (area: 0.04-5648 km<sup>2</sup>; mean depth: 1-177m; a north-south gradient from  
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1 Sweden to Spain). Along with an annual temperature increase of about 0.15-0.3 °C per decade  
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4 profound changes have occurred in either fish assemblage composition, body size and/or age  
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6 structure during recent decades and a shift towards higher dominance of eurythermal species.  
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8 These shifts have occurred despite a reduction in nutrient loading in many of the lakes that  
9  
10 should have benefited the larger-sized individuals and the fish species typically inhabiting  
11  
12 cold-water, low-nutrient lakes. The cold-stenothermic Arctic charr has been particularly  
13  
14 affected and its abundance has decreased in the majority of the lakes where its presence was  
15  
16 recorded. The harvest of cool-stenothermal trout has decreased substantially in two southern  
17  
18 lakes. Vendace, whitefish and smelt show a different response depending on lake depth and  
19  
20 latitude. Perch has apparently been stimulated in the north, with stronger year classes in warm  
21  
22 years, but its abundance has declined in the southern Lake Maggiore, Italy. Where introduced,  
23  
24 roach seems to take advantage of the higher temperature after years of low population  
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26 densities. Eurythermal species such as common bream, pike-perch and/or shad are apparently  
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28 on the increase in several of the lakes. The response of fish to the warming has been  
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30 surprisingly strong and fast in recent decades, making them ideal sentinels for detecting and  
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32 documenting climate-induced modifications of freshwater ecosystems.  
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## 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

1 to cope with the new thermal regimes and so experience no loss and potentially even an  
2 increase in thermal habitat (Lappalainen & Lehtonen, 1997). By contrast, tropical species  
3 typically experience mean temperatures that are close to their physiological optima, and even  
4 a small increase in temperature may thus put them at high risk of extinction (Tewksbury et al.,  
5 2008). Many fish species are also adapted to low oxygen concentrations, specifically at either  
6 low or high temperatures (Holopainen et al., 1997; Soares et al., 2006). When temperature  
7 increases, oxygen may drop to critical levels as warm water holds less oxygen and the  
8 respiration rates increase. Global warming may therefore create novel fish assemblages by  
9 effectively favouring species which have responded to range shifts in addition to those already  
10 locally present within their native range, thereby potentially increasing competition for space  
11 and food. As fish species richness is currently higher in warmer climates (Griffiths, 1997;  
12 Amarasinghe & Welcomme, 2002; Zhao et al., 2006; Meerhoff et al., 2007a; Teixeira-de  
13 Mello et al., 2009), richness may increase in present-day cold lakes in a future warmer  
14 climate, depending on local conditions, original assemblages and physical barriers to  
15 colonisation.

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

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4 The general pattern also seems to be common for fishes in marine habitats (Vila-Gispert et al., 2002).

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9 In a recent review, Jeppesen et al. (2010a) showed that climate warming will probably  
10  
11 generate changes in lake fish assemblage structure, life history traits, feeding modes, habitat  
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13 use and winter survival. Their conclusions were mainly based on space-for-time-substitution  
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15 studies comparing lake fish assemblages and cross-latitude experiments from different climate  
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17 zones and, thus, different mean temperatures. The strength of this approach is that the fish  
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19 assemblages *per se* have had time to evolve and adapt to the climate in which they live, but a  
20  
21 potential weakness is that they may not yet have reached a mature state. This is especially true  
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23 in the cold regions where speciation is currently occurring, for instance among the dominant  
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25 species there: Arctic charr, three-spined stickleback (*Gasterosteus aculeatus*) and whitefish  
26  
27 (*Coregonus* spp.) (Robinson & Schluter, 2000; Snorrason & Skúlason, 2004; Klemetsen,  
28  
29 2010; Hudson et al., 2011). Moreover, regional biogeographical constraints are not taken into  
30  
31 account. Current patterns in species richness and assemblage composition of fish are strongly  
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33 influenced by past glaciations, their present distance from the refuges available during these  
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35 periods, and the dispersal barriers that appeared following deglaciation, such as the mountains  
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37 of Europe (Griffiths, 2006; Abell et al., 2008; Volta et al., 2011). Finally, although the  
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39 differences in life history traits between populations at varying latitudes may reflect long-term  
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41 evolution, they do not indicate how local populations might respond to accelerated climate  
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43 warming at decadal to centurial scales. Rapid microevolution of life history traits, for example  
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45 survival and aspects of individual performance (e.g. age at reproduction and number of  
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47 offspring), was recorded for the freshwater cladoceran *Simocephalus* by Van Doorslaer et al.  
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49 (2007), suggesting that populations may buffer changes in community structure and persist  
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1 locally under the conditions of the predicted climate warming. Such a response, however, has  
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4 not yet been demonstrated for fishes.  
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9 An obvious alternative, or complementary method, to space-for-time comparisons is to  
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11 analyse time series from a given lake or region under the influence of climate variability and  
12  
13 recent climate change. This approach has been successfully used to demonstrate strong  
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15 responses of lake ecosystems to warming over the last 30-50 years (Straile et al., 2003;  
16  
17 Blenckner et al., 2007; Adrian et al., 2009). However, in the great majority of the case studies  
18  
19 summarised so far, the response of lake fish assemblages to changes in temperature and  
20  
21 thermal stratification has been neglected. Analyses of long-term data from fish assemblages  
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23 (as well as other biotic communities) in lakes are frequently hampered by the combined  
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25 effects of increases in nutrient load and (for fish specifically) fisheries intensity which have  
26  
27 occurred over recent decades in different regions of the globe, not least in Europe (Thomas et  
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29 al., 2009; Anneville et al., 2009). With respect to fish in European lakes, eutrophication  
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31 generates a dominance shift from salmonids to percids and then from percids to cyprinids  
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33 (Hartmann, 1977; Persson et al., 1991; Jeppesen et al., 2000), and particularly to low-oxygen-  
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35 tolerant cyprinids in stratified lakes (Mehner et al., 2005).  
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45 In the present review, we focus on the response of fish assemblages to climate change and climate  
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47 variability by discussing trends in long-term data series from 24 European shallow and deep lakes  
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49 (Table 1). Lakes that had >9 years of paired data on at least one fish metric and one climate metric  
50  
51 were included. European lakes constitute an appropriate and tractable sample of the world's lakes  
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53 since many of them have been monitored more intensively and for a longer period of time than have  
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55 most lakes elsewhere. Where possible, we seek to disentangle the effects of climate from those of  
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57 other anthropogenic factors such as local changes in nutrient loading and fisheries. Overall, we argue  
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1 that lake fish assemblages are sensitive to even subtle changes in temperatures, making them ideal  
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4 sentinels for detecting and documenting climate-induced modifications of freshwater ecosystems.  
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## 8 **Materials and Methods**

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12 We aim to extract patterns of change by analysing specific case studies at different locations  
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14 and, thus, different climates within Europe. For the majority of the studies, the methods used  
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16 are described in detail in published papers to which we refer. Accordingly, we give below  
17  
18 only a brief overview of the lake characteristics, methods and add specific information when  
19  
20 unpublished data are used, with lakes ordered by decreasing latitude. Some basic information  
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22 on location, morphometry and physical and chemical variables is given in Table 1, Fig.1 and  
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24 Figs. 2A-13A.  
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### 32 **Lake Elliðavatn, Iceland**

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35 Lake Elliðavatn is a small, clear water oligo-mesotrophic shallow lake within the metropolitan  
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37 area of the capital city Reykjavík. The lake is largely (~ 50%) fed by cold (3-6 °C) subsurface  
38  
39 spring water with a high natural pH ( $\geq 7.5$  all year round and pH 9.0-10.0 for several weeks in  
40  
41 July-August) due to neo-volcanic bedrock in the catchment area (270 km<sup>2</sup>). The lake and its  
42  
43 inlet rivers have been subjected to various impacts following urbanisation in the catchment  
44  
45 area, including damming of the outlet river Elliðaár in 1924-25 and regulation of the water  
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47 levels (ca. ~0.4 m), phytoplankton biomass is low (chlorophyll (chl) *a*: 1.7–2.8 µg l<sup>-1</sup>, annual  
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49 mean in the last decade) and the water clarity and abundance of submerged macrophytes are  
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51 high (Thórðarson, 2003; Malmquist et al., 2009, 2010).  
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1 The fish assemblage consists of a few species, dominated by Arctic charr and brown trout  
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4 (*Salmo trutta*). Charr spawn primarily within the lake and trout mainly in the tributaries.  
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6 Three-spined stickleback are also abundant in the lake, while Atlantic salmon (*Salmo salar*)  
7  
8 and European eel (*Anguilla anguilla*) are less common.  
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12 The lake has one of the best long-term data series in Iceland on the relationship between  
13  
14 climate warming and freshwater fish (Malmquist et al., 2009). The published fish data cover  
15  
16 the period 1974-2006, but in the present paper we use annual data from 1987-2010 based on a  
17  
18 common sampling protocol described by Malmquist et al. (2009). The fish data were  
19  
20 extracted from annual reports published by the Institute of Freshwater Fisheries, Iceland  
21  
22 (Antonsson & Árnason, 2011). In short, sampling was conducted in late September/early  
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24 October with two gill-net series, each comprising 10 nets with different mesh sizes (16.5-60,  
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26 mm, knot to knot). In 1993, a 12.0 mm mesh sized net was added to the net series. Nets were  
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28 set overnight (~12 hrs) in one of two main basins of the lake.  
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38 Data on lake temperature were provided by the Icelandic Meteorological Institute and  
39  
40 temperature has been measured at the lake outlet since August 1988 (1-4 records h<sup>-1</sup>).  
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42 Nutrients, including total phosphorus (TP), were measured in 2001-2002 in a few samples (n  
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44 = 18) taken at ~0.4 m depth in both basins (Thórðarson, 2003).  
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### 50 **Lake Valkea-Kotinen, Finland**

51  
52 Lake Valkea-Kotinen is a small, mesotrophic shallow brown-water lake located in a small headwater  
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54 catchment (0.3 km<sup>2</sup>) in a remote protected forest area in southern Finland, only affected by pollution  
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56 from airborne sources (for details see Ukonmaanaho et al., 1998). Steep thermal and oxygen  
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1 stratification is typical for the lake, resulting in a 2-m thick warm and oxygenated epilimnion and a  
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3 cold and anoxic hypolimnion during the growing season (Forsius et al., 2010).  
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8 Perch (*Perca fluviatilis*) and pike (*Esox lucius*) are the only fish species present in the lake.  
9

10 The size and structure of the perch population have been monitored since 1991 (Rask et al.,  
11 1998). Annual abundance estimates were obtained from 2 weeks of continuous marking and  
12 1998). Annual abundance estimates were obtained from 2 weeks of continuous marking and  
13 1998). Annual abundance estimates were obtained from 2 weeks of continuous marking and  
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19 1998). Annual abundance estimates were obtained from 2 weeks of continuous marking and  
20 1998). Annual abundance estimates were obtained from 2 weeks of continuous marking and  
21  $\geq 2$  years in age. The fish were subsequently measured to record total length, after which they  
22 were fin-clipped and released. Samples for age determination were taken after the mark-  
23 recapturing, with opercular bones being used to determine age and to back-calculate growth  
24 (Raitaniemi et al., 1988).  
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31 Regular monitoring of water quality and hydrobiology has been carried out since 1990  
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33 (Keskitalo et al., 1998; Rask et al., 1998).  
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#### 40 **Eleven forest lakes, Sweden**

41 The 11 lakes are situated at low to mid altitudes (35-268 m a.s.l.) and vary in area and depth.  
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43 The lakes range from oligo- to mesotrophic and total organic carbon (TOC) varies from 4-11  
44 mg l<sup>-1</sup>.  
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51 Total fish species richness per lake was 4-8, and a total of 14 fish species was observed at  
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53 least once in one lake (Holmgren, 2009). The following species were caught each year: perch  
54 and roach (*Rutilus rutilus*) (all lakes), ruffe (*Gymnocephalus cernuus*) (6 lakes), rudd  
55 (*Scardinius erythrophthalmus*) (3 lakes), vendace (*Coregonus albula*) (3 lakes), whitefish (3  
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1 lakes), smelt (*Osmerus eperlanus*) (2 lakes), bleak (*Alburnus alburnus*, 2 lakes) and common  
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4 bream (*Abramis brama*) (1 lake).  
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9 Fish were monitored annually in July or August using multi-mesh gill nets (CEN, 2005;  
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11 Holmgren, 1999). To ensure a set of lakes with similar fish assemblages, only circum-neutral  
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13 lakes (annual mean pH > 6) inhabited by perch, roach and pike were included. Age of perch  
14  
15 was determined using operculum bones and sagittal otoliths, and length was, after the first  
16  
17 year, back-calculated according to Holmgren & Appelberg (2001). Mean length at 0<sup>+</sup> was  
18  
19 used as a measure of first year growth for each of the perch cohorts hatched in 1993-2009.  
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26 Water temperature during the first growth season has been expressed as annual mean values at  
27  
28 1-1.5 m depth during May-September. Concentrations of TP, TOC and sulphate are means of  
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30 7-8 samples per lake and year, sampled at 0.5 m depth at a mid-lake station.  
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### 35 36 **Lake Säkylän Pyhäjärvi, Finland**

37  
38 Säkylän Pyhäjärvi is a large, polymictic, meso-eutrophic shallow lake with a hydraulic  
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40 retention time of about 4-5 years. The catchment area is 615 km<sup>2</sup> (including the lake surface).  
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42  
43 Two incoming rivers with a strong agricultural nutrient load impact account for more than  
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45 70% of the annual TP load. The lake is located in the boreal temperate zone (cold climate  
46  
47 type) and is, on average, ice covered for 141 days.  
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53 The fish assemblage consists of 18 species, dominated by perch, ruffe, roach and vendace.  
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55  
56 The most important commercial catch species is vendace, which is the main planktivore in the  
57  
58 lake (Sarvala et al., 1998). The annual harvest rate approaches the total production of  
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60 vendace. In addition to this self-supporting biomanipulation, a restoration project has  
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1 subsidised the harvest of commercially unwanted fish since 1995. The fishing was especially  
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4 intensive in 2002-2004 and apparently resulted in improved water quality (Ventelä et al.,  
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6 2007).  
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11 Data on fish assemblage composition were obtained from extensive test fishing with gill nets  
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13 in 1984 (non-standard series) and in 2000, 2004, 2006 and 2009 (Nordic gill nets; CEN,  
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15 2005), as well as from catch samples and surveys (Sarvala et al., 1998; Ventelä et al., 2011  
16  
17 and unpublished). The majority of the annual fish catch is taken in winter by seining through  
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19 holes in the ice. In addition, fyke nets are applied by professional fishermen in the open-water  
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21 season. Samples for vendace and whitefish have been collected since 1971 and the winter  
22  
23 seine catch of all species has been sampled from 1989-2011. Subsamples of each species for  
24  
25 individual weight and length and age determination were obtained from the fishermen's  
26  
27 catches; at least thirty 0<sup>+</sup> vendace individuals were measured each time. Daily seine catch  
28  
29 records for vendace (age 0<sup>+</sup> and older fish separately) were obtained for the winters 1980-  
30  
31 2011 from each seine crew and/or the most important wholesale fish agent. For most years,  
32  
33 the 0<sup>+</sup> year class size of vendace in autumn could then be calculated from the decrease in  
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35 catch per unit effort (CPUE) during winter (Helminen et al., 1993). For other years, year class  
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37 size was estimated utilising the strong density dependence of first-summer growth of vendace.  
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48 The water chemistry and hydrology of the lake have been monitored since the 1960s, and in  
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50 1980 monitoring was extended to cover biotic components such as phyto- and zooplankton  
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52 (Ventelä et al., 2007, 2011), chl *a* and nutrients. Ice data for 1958-2010 were recorded by  
53  
54 local observers and the Finnish Environment Institute's Oiva data service  
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56 ([www.ymparisto.fi/oiva](http://www.ymparisto.fi/oiva)); which also provided water temperature and water quality data.  
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## 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).

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), were 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 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 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 1995-2009 on Lake Vänern. Details on survey design and apportionment methods are given in Nyberg et al. (2001) and Axenrot (2010 a,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).

1 Available data on ice coverage in Lake Vättern span from 1881 to 2010 and daily water  
2 temperature measurements (at 5 m depth) exist from 1955 to 2010 (source: Lake Vättern  
3 Water Society). In Lake Vänern, ice coverage data for the period 1995-2009 were obtained  
4 from a sheltered basin (Brandsfjorden) and for the lake as a whole. Unfortunately, daily water  
5 temperature measurements were not available other than for a limited number of years.  
6 Instead, in this paper we used air temperature measurements from two weather stations  
7 situated close to Lake Vänern and water temperature recordings measured at 5 m depth in  
8 May, June, August and October.  
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23 Density (ind. ha<sup>-1</sup>) of 0<sup>+</sup> smelt and vendace obtained from hydroacoustic surveys and relative  
24 year class strength of vendace obtained from age determinations of trawl catches were used as  
25 response variables. A large set of predictor variables was used: adult fish densities (obtained  
26 from hydroacoustic surveys, ind. ha<sup>-1</sup>), fisheries yield (obtained from Swedish official catch  
27 statistics, tonnes), air and water temperatures (annual mean, monthly mean and monthly sum  
28 above 10 °C) and ice coverage (presence/absence of ice, number of days with ice, Julian day  
29 of ice-break in spring), TOC, as well as annual mean TP concentrations and annual mean chl  
30 *a* concentrations, both measured at the surface layers (0-10 m).  
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#### 45 **Lake Søbygaard, Denmark**

46 Lake Søbygård is small, shallow, hypertrophic and polymictic. The lake has suffered from  
47 extremely high external nutrient loading which was, however, substantially reduced since  
48 1982 (Jeppesen et al., 1998).  
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57 The lake hosts 8 fish species, but the fish assemblage is overwhelmingly dominated by roach  
58 and perch with the piscivorous pike-perch and pike also present. Annual gill net surveys were  
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1 conducted from 1989 to 2010 (except 1998) between 15 August and 15 September every year  
2  
3  
4 (except for 1988 when it was undertaken in November) to include 0<sup>+</sup> fish in the catches. The  
5  
6 lake was divided into six sections and in each section three multi-mesh size gill nets (14  
7  
8 different mesh sizes ranging from 6.25 to 75 mm) were set overnight. One gill net was set  
9  
10 perpendicular to the shoreline, another parallel to and about 25 m from the shoreline, and the  
11  
12 third about half the distance from the centre of the lake (more details in Jeppesen et al., 1998).  
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18 Water samples were collected fortnightly or more often with a Patalas sampler at a mid-lake  
19  
20 station at 0.5 m and 1.5 m depth and analysed according to standard methods.  
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### 24 25 **Windermere, U.K.**

26  
27  
28 Windermere is a large, relatively deep and meso-eutrophic lake comprising elongated north  
29  
30 and south basins with a combined surface area of 14.8 km<sup>2</sup>, which makes it England's largest  
31  
32 natural lake. Its catchment is dominated by unimproved pasture, although nutrient loadings  
33  
34 from sewage treatment works to the lake have been significant.  
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39  
40 The present fish assemblage of the lake consists of 16 species, although only seven are of  
41  
42 numerical importance, i.e. Arctic charr, Atlantic salmon, brown trout, European eel, perch,  
43  
44 pike and roach. The latter and some other cyprinid species are known to have been  
45  
46 introduced, probably by anglers as live bait during angling for pike (Winfield et al., 2010a,  
47  
48 2011). The lake has not been influenced by any significant removal fisheries for many  
49  
50 decades (Le Cren, 2001).  
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57 The major fish populations of the north and south basins of the lake have been monitored and  
58  
59 researched at individual and population levels from the early 1940s, in association with short-  
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62

1 lived removal fisheries and other large-scale population manipulations (Le Cren, 2001).  
2  
3  
4 Methodologies have included independent gill nets targeted at Arctic charr (Winfield et al.,  
5  
6 2008a) and pike (Winfield et al., 2008b; Paxton et al., 2009), together with traps targeted at  
7  
8 perch (Paxton et al., 2004) since the early 1940s, the examination of effectively recreational  
9  
10 angling for Arctic charr since the mid-1960s (Winfield et al., 2008a), the use of monthly  
11  
12 hydroacoustic surveys for the total open-water fish assemblage since the early 1990s  
13  
14 (Winfield et al., 2008a), and the use of survey gill nets at 5-year intervals since 1995 targeted  
15  
16 at developing the roach component of the fish assemblage (Winfield et al., 2008b). With the  
17  
18 exception of the survey gill netting, all of this biological sampling has been undertaken  
19  
20 annually over approximately 6-week periods each year.  
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28 These fish studies have been accompanied by more frequent, typically weekly or fortnightly,  
29  
30 monitoring of the lake's abiotic and biotic features including water temperature and TP  
31  
32 (Winfield et al., 2008a).  
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### 38 **Lake Stechlin, Germany**

39  
40 Lake Stechlin is dimictic, large, deep and oligo-mesotrophic and is situated ca. 120 km north  
41  
42 of Berlin, Germany.  
43  
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48 Eleven fish species with reproducing populations have been observed (Anwand et al., 2003);  
49  
50 the pelagic habitat below the thermocline is dominated by common vendace and the smaller,  
51  
52 lake-endemic Fontane cisco (*Coregonus fontanae*). Peak spawning activity of vendace in the  
53  
54 lake occurs around 20 December. Vendace has a cold-water thermal window characterised by  
55  
56 a metabolic optimum around 7-9 °C (Ohlberger et al., 2008a, 2008b). The spring-spawning  
57  
58 Fontane cisco (spawning period between late April and early July) has a lower thermal  
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1 window with an optimum at about 4-5 °C (Ohlberger et al., 2008a, 2008b). Other fish species  
2  
3 occur in low densities primarily in the littoral and epipelagic habitats.  
4  
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6  
7

8  
9 Densities (ind. (1000 m<sup>-3</sup>)) of pelagic fish split into 0<sup>+</sup> and older coregonids were estimated by  
10  
11 annual hydroacoustic surveys conducted during night-time in June between 2000 and 2010  
12  
13 (2004 and 2007 missing). Additional stratified pelagic trawl sampling has been conducted  
14  
15 annually in June since 2005, thus providing density estimates for juvenile and adult  
16  
17 coregonids of both co-existing species. These spatially-explicit analyses were required  
18  
19 because 0<sup>+</sup> coregonids perform a habitat shift from the littoral to pelagic areas after their first  
20  
21 weeks of life, and juvenile and adult coregonids undergo diel vertical migration in the lake.  
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23  
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25  
26 The methodology is described in detail in Mehner et al. (2011).  
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31 Monthly temperature means were obtained for each water strata, and the index of North-  
32  
33 Atlantic Oscillation (NAO) was recorded during winter (January until March). The fish  
34  
35 densities were also correlated with epilimnetic and hypolimnetic zooplankton densities (ind. l<sup>-1</sup>).  
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### 43 **Lake Constance, Austria/Germany/Switzerland**

44  
45 Lake Constance, the second largest peri-alpine lake in Europe, is situated at the northern  
46  
47 fringe of the European Alps and consists of two basins: Deep Upper Lake Constance  
48  
49 (hereafter ULC) and Lower Lake Constance, which is smaller and more shallow (Table 1).  
50  
51 ULC was originally oligotrophic, but has undergone pronounced eutrophication during the  
52  
53 20<sup>th</sup> century. TP during winter mixing peaked at >80 µg l<sup>-1</sup> around 1980 (Güde et al., 1998).  
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56  
57 As a result of a drastically reduced P input, the lake became oligotrophic by the beginning of  
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1 the 21<sup>st</sup> century and average chl *a* of the upper 20 m declined from 4.2 µg l<sup>-1</sup> in the 1980s to  
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3  
4 2.3 µg l<sup>-1</sup> in the 2000s.  
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8  
9 Twenty-nine species occur in the lake (Eckmann & Rösch, 1998) of which only a few are of  
10  
11 commercial interest and exploited intensively: two forms of lake whitefish, an inshore and a  
12  
13 pelagic spawning form (> 80% of the commercial harvests); perch, the second-most important  
14  
15 species in this lake during eutrophication; European eel (regularly stocked); brown trout; pike;  
16  
17 Arctic charr and pike-perch. Bycatch of cyprinid species has little commercial value.  
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23 ULC is shared by Austria, Germany and Switzerland, and the fisheries have been managed  
24  
25 jointly by a commission of the bordering countries since 1893 (International Commission for  
26  
27 the Fisheries Management of ULC). An uninterrupted record of commercial catches from  
28  
29 UCL since 1910 is available based on monthly catch anonymous reports from all fishermen  
30  
31 (Eckmann & Rösch, 1998). Drifting and bottom-set gill nets are the main fishing gear used.  
32  
33 Biological data on coregonids have been collected biweekly or monthly since the early 1960s  
34  
35 through regular test catches by research institutes and management agencies. Biological data  
36  
37 on perch have been collected monthly since the early 1970s by fishery wardens, while the  
38  
39 biology and population dynamics of other species are studied infrequently. Age, growth and  
40  
41 virtual year class strength of coregonids and perch are published in yearly reports by the  
42  
43 mentioned commission. Juvenile and small-sized fish in the shallow littoral area have been  
44  
45 monitored at regular intervals since 1997 (cf. Reyjol et al., 2005).  
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55 A regular monthly sampling of basic limnological data has been carried out since the early  
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57 1960s on behalf of the International Commission for the Protection of Lake Constance  
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59 (IGKB, 2004).  
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## 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 to 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  $\mu\text{g l}^{-1}$ , 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  $>15 \text{ kg ha}^{-1} \text{ yr}^{-1}$ .

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](http://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

1 regularly caught by fishermen during winter in order to provide eggs for hatchery use. The  
2  
3  
4 ages of these fish are determined and the catch is expressed as CPUE.  
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8  
9 A regular fortnightly sampling has been carried out since the early 1960s on behalf of CIPEL.  
10  
11 All the classical physical and chemical parameters are measured on a vertical profile:  
12  
13 temperature, oxygen, phosphorus, and nitrogen concentrations. Daily surface temperatures  
14  
15 have been recorded in a littoral location of the lake since 1951.  
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### 21 **Lake Maggiore, Italy/Switzerland**

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23 Lake Maggiore is a large warm-monomictic, oligo-mesotrophic pre-alpine lake (Table 1),  
24  
25 situated in north-western Italy. From being naturally oligotrophic (Marchetto et al., 2004), the  
26  
27 lake has undergone eutrophication since the mid-1960s, followed by a recovery period since  
28  
29 the mid-1970s (Mosello & Ruggiu, 1985; Salmaso et al., 2007).  
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35 At present, 32 fish species, of which only 20 are native, inhabit the lake. As in other large  
36  
37 south alpine lakes, commercial fishing was traditionally targeted towards cold water species  
38  
39 such as coregonids (*Coregonus lavaretus* and *C. macrophthalmus*) and trout (migratory  
40  
41 brown trout and marble trout (*Salmo trutta marmoratus*)). Alborella (*Alburnus arborella*) and  
42  
43 perch were also frequently caught. Commercial fishery data (total annual catch of each  
44  
45 species) are registered by commercial fishermen and collected by the Swiss-Italian  
46  
47 Commission for the Fishery (CISPP in Italian abbreviation) since 1979.  
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55 An International Commission for the Protection of Italian-Swiss Waters (CIPAIS in Italian  
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57 abbreviation, [www.CIPAIS.org](http://www.CIPAIS.org)) manages the survey of limnological, meteorological and  
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1 hydrological parameters of the lake and its catchment. Additional data are directly obtained  
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4 from the CNR-Institute of Ecosystem Study.  
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### 8 **Lake Albufera, Spain** 9

10 Lake Albufera is the largest Spanish coastal lake and is located in the Natural Park of the  
11 Albufera. It is shallow, polymictic, hypertrophic and oligohaline (salinity: 1-2‰). The water  
12 level is regulated by sluice gates and the hydrological cycle of the lake is related to seasonal  
13 rainfall and rice cultivation in the areas surrounding the lake. The annual lake water turnover  
14 varies between 5.5 and 9.5 y<sup>-1</sup>. The lake has been hypertrophic since the 1970s and  
15  
16 cyanobacteria dominate throughout the year, except for sporadic periods (few days or weeks)  
17 of clear water in recent years following external nutrient loading reduction (Villena & Romo,  
18 2003; Romo et al., 2005). Since 2002, the abundance of potentially toxic cyanobacteria  
19 (*Microcystis aeruginosa* and *Cylindrospermopsis raciborski*) has increased (Romo et al.,  
20 2008) with microcystins being detected even in the tissue of the main exploited fish species  
21 (Romo et al., 2011).  
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40 The fish assemblage is dominated by omnivorous species (Blanco et al., 2003). The  
41 composition of the fish assemblage was determined from annual commercial captures from  
42 1950 to 2007 recorded by local fishermen using similar traditional methods, mainly gill (30  
43 mm mesh size) and fyke nets, and during summer 2000 and spring 2002 using fyke nets and  
44 multiple (14) mesh-sized gill nets (6.5-75 mm). About 300 tonnes (150 kg ha<sup>-1</sup>) of mugilids  
45 (mainly golden and thinlip mullet, *Liza* spp and flathead mullet, *Mugil cephalus*) are  
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55 harvested annually (Blanco et al., 2003; Blanco & Romo, 2006).  
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1 Water was analysed using standard methods (APHA, 1992), determining TP from the upper  
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4 50 cm of the water column. Data on air temperature and rain were recorded at a nearby  
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6 weather station.  
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## 10 11 **Trends in the case studies** 12 13

### 14 15 16 **Lake Elliðavatn: strong decline in abundance and increase in size of Arctic charr** 17

18 During 1989-2010, June-September mean water temperature has risen significantly (Fig. 1,  
19 linear regression,  $R^2 = 0.54$ ,  $F_{1,20} = 23.17$ ,  $p < 0.001$ ) in line with an increasing air  
20  
21 temperature in the catchment area (Malmquist et al., 2009). Lake temperature has increased in  
22  
23 all months except October-December, with the most profound warming occurring in late  
24  
25 winter/early spring and summer. For April, the average increase in daily mean temperature  
26  
27 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 ( $R^2$   
28  
29 = 0.37,  $F_{1,680} = 108.3$ ,  $p < 0.001$ ) and 1.5 °C for September ( $R^2 = 0.19$ ,  $F_{1,680} = 25.4$ ,  $p <$   
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31 0.001).  
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41 For the past 20 years, the Arctic charr population in the lake has undergone a major reduction  
42  
43 coinciding with the warming of the lake (Fig. 1). Catch per unit effort of charr during 1987-  
44  
45 2010 has declined significantly ( $R^2 = 0.71$ ,  $F_{1,22} = 54.42$ ,  $p < 0.001$ ) and for the past 10 years it  
46  
47 has been only about 25% of the level seen more than 20 years before (Malmquist et al., 2009).  
48  
49 In contrast, the population of brown trout, which is more heat-tolerant than charr (Elliott &  
50  
51 Elliott 2010), has remained largely unchanged ( $p = 0.627$ ), albeit it shows some interannual  
52  
53 fluctuations. The observed decline in density of adult charr, which has also been observed for  
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55 juvenile fish (Antonsson & Árnason, 2011), is attributed to the increasing water temperatures,  
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1 with  $\geq 14$  °C extending over 1-2 months and up to 18-21 °C for a week or two as observed in,  
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3  
4 for instance, 2003, 2007 and 2010. This is far above the upper thermal optimum for the  
5  
6 growth of adult charr, reported at  $\sim 12.0$  °C, with negative effects at 14.0 °C (Jobling, 1983;  
7  
8 Lyytikäinen et al., 2002). The thermal optimum is even lower for egg development and  
9  
10 growth of charr fry (Jobling, 1983).  
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16 The thermal problems that charr is facing may be linked not only directly to reproduction,  
17  
18 metabolism and growth, but also indirectly to susceptibility to thermally linked diseases, such  
19  
20 as proliferative kidney disease (PKD) (Sterud et al., 2007). In October 2008, PKD was  
21  
22 detected for the first time in Iceland in Arctic charr from this lake (Kristmundsson et al.,  
23  
24 2010). Since then, PKD has been observed in both charr and brown trout in Lake Elliðavatn,  
25  
26 as well as in four other shallow lakes (Kristmundsson et al., 2011). In all cases, Arctic charr,  
27  
28 but not brown trout, have shown a high prevalence of PKD (up to 100%) often accompanied  
29  
30 by severe pathological signs, especially in 1-2 year charr. The fact that PKD infections affect  
31  
32 young charr most severely indicates that high mortality of young fish may be an important  
33  
34 cause for the population decline in Arctic charr, although further studies are needed to draw  
35  
36 firm conclusions.  
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45 Along with the changes in abundance, the mean length (fork length) of 3<sup>+</sup> year charr has  
46  
47 increased significantly during 1988-2010 ( $R^2 = 0.54$ ,  $F_{1,21} = 24.48$ ,  $p < 0.001$ ). For the 5-year  
48  
49 period 1988-1992, the mean length of 3<sup>+</sup> year charr was 22.8 cm ( $\pm 0.52$ ) as compared to 28.3  
50  
51 cm ( $\pm 0.70$ ) for the period 2006-2010. Brown trout showed no differences in mean length  
52  
53 between periods. For both charr and brown trout, the somatic condition (Fulton's condition  
54  
55 factor) was in general high ( $> 1.10$ ) and did not vary significantly over the period 1988-2005  
56  
57 (charr,  $p > 0.4$ ; trout,  $p > 0.7$ ). Moreover, stomach analyses did not indicate any food shortage  
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1 or consistent changes in dietary composition by the fish, and data on potential food resources,  
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3  
4 though sparse, do not suggest any consistent decline of macroinvertebrates or changes in the  
5  
6 resource base for the fish.  
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### 10 **Lake Valkea-Kotinen: reduction in the growth of perch following an increase in organic** 11 **load** 12 13

14 During the 20-year monitoring period, epilimnetic temperature (Fig. 2A), TOC (Fig. 2B), water  
15  
16 colour, pH and alkalinity have increased significantly, while sulphate and base cations decreased,  
17  
18 mainly as a result of lower sulphur deposition (Futter et al., 2009). Chl *a* declined (Fig. 2A), but  
19  
20 no significant changes in concentrations of TP and TN were observed in either precipitation or  
21  
22 runoff (Vuorenmaa & Horppila, 2011). Climatic drivers have been suggested to contribute  
23  
24 remarkably to variation in hydrology and, consequently, in TOC fluxes from catchments to  
25  
26 surface waters (Futter et al., 2009; Arvola et al., 2010).  
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35 Density of perch with a total length > 8 cm varied between 660 and 3300 fish ha<sup>-1</sup> along the 20-  
36  
37 year period. Irregular fluctuations occurred due to variations in year class strength. No significant  
38  
39 relationships between population density and year class strength with temperature or TP or Chl *a*  
40  
41 were recorded. Thus, the variation in abundance of perch seems to result from the population  
42  
43 dynamics typical for this percid in this lake type, where large cannibalistic perch prevent  
44  
45 recruitment of 0<sup>+</sup> perch until the density of large individuals is small enough to enable the  
46  
47 development of a new strong year class (Persson et al., 2000).  
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55 As is typical for small forest lakes of the boreal region, perch grew slowly (Rask, 1983) and  
56  
57 reached a mean total length of 15 cm after 4-7 years. The growth of perch during the first year  
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59 declined during the monitoring period (Fig. 2B). There was no significant relationship between  
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1 the 0<sup>+</sup> growth and the relative year class strength of the population ( $p>0.1$ ) as the latter fluctuated  
2 irregularly, suggesting that the first summer growth of perch was not density dependent. Multiple  
3 regression on log-transformed data showed that the length of 0<sup>+</sup> perch was strongly negatively  
4 correlated with TOC (Fig. 2D) and more weakly with TP ( $R^2 = 0.71$ ,  $F_{2,18} = 22.44$ ,  $p < 0.001$ ),  
5 while temperature and Chl *a* did not contribute significantly ( $p>0.2$ ) (Fig. 2C).  
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16 Deterioration of underwater light conditions due to increased TOC seems the main reason for the  
17 declining growth of perch, as it is a visually oriented fish species and active only in daylight.  
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20 These observations are consistent with recent field and experimental studies on the effects of  
21 light conditions on the interactions and feeding efficiency of perch (Estlander, 2011; Estlander et  
22 al., 2010). In addition, the growth of perch may also have been affected by a decrease in the  
23 overall productivity of the food web, as suggested by the decreasing trend in chl *a* (Fig. 2A).  
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30 This might be ascribed to an increased organic carbon load resulting in a higher proportion of  
31 bacterial production compared to autotrophic algal production (Ask et al., 2009; Karlsson et  
32 al., 2009), likely leading to a limited availability of fatty acids essential for zooplankton and  
33 fish (Brett et al., 2009). Although the changes in TOC and effects on perch in Lake Valkea-  
34 Kotinen may so far largely be attributed to reduced acidification (Vuorenmaa, 2004), the results  
35 indicate that a predicted increase in the organic load to lakes from catchments due to climate  
36 change (Tranvik et al., 2009; Forsius et al., 2010), and subsequent changes in transparency,  
37 may directly affect the fish size structure in small boreal lakes.  
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### 53 **Swedish forest lakes: increasing first year growth of perch?**

54 During the study period, sulphate concentrations decreased significantly as in other Swedish  
55 lakes (Fölster et al., 2005), reflecting a long-term decrease in airborne acidifying deposition.  
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59 TP tended to decrease and surface water temperature to increase. TOC generally increased, as  
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1 recorded for dissolved organic carbon across eastern North America and northern and central  
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4 Europe since 1990 (Monteith et al., 2007).  
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9 During 1993-2009, the water temperature varied in a more or less synchronised fashion  
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11 among lakes, with relatively warmer growth seasons in 1994, 1997, 1999, 2002 and 2006  
12  
13 (Fig. 3A). Monotonic increases or decreases in fish abundance and/or biomass were  
14  
15 previously reported for some of the species in some of the 11 lakes (Holmgren, 2009, and  
16  
17 summarised in Table 2). A positive effect of temperature on the first year growth of perch  
18  
19 could be observed for the set of lakes included and from the overall relationship based on data  
20  
21 from all years (Fig. 3C). The year-to-year variation in length of 0<sup>+</sup> perch followed a similar  
22  
23 pattern in the lakes, peaking in the warm years of 1997, 2002 and 2006 (Fig. 3B). 0<sup>+</sup> perch  
24  
25 were shortest in the northernmost lakes (mean length = 61mm), albeit these fish were  
26  
27 relatively long considering the lower temperature of their environment. In other lakes at  
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29 similar latitudes (58-64 °N), the mean length of perch is often less than 55 mm after its first  
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31 year of life (Heibo et al., 2005).  
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40 Prolonged day length during summer might to some extent compensate for the lower  
41  
42 temperature in these lakes. Residuals in the length-temperature relationship differed  
43  
44 significantly between lakes (one-way ANOVA,  $p < 0.001$ ) (Fig. 3D). The largest negative  
45  
46 residuals (i.e. a growth lower than expected) were found in two of the smallest, but rather  
47  
48 deep lakes with pelagic populations of vendace. The largest positive residuals were found in  
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50 one of the largest lakes, and also the most shallow one, with no or weak thermal stratification  
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55 in summer.  
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1 In contrast to Lake Valkea-Kotinen, however, this 11-lakes study shows no evidence that a  
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3  
4 negative effect of increasing TOC levels overrules the positive effect of increasing  
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6 temperature on the growth of 0<sup>+</sup> perch.  
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### 10 **Lake Säkylän Pyhäjärvi: major decline in vendace**

11 The maximum summer water temperature increased highly significantly during 1962-2010  
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13 (Fig. 4A; 0.9 °C per decade; adjusted  $R^2 = 0.41$ ,  $F_{1,47} = 34.75$ ,  $p < 0.001$ ). Spring temperatures  
14  
15 have not increased correspondingly, as seen from May temperature records that show no  
16  
17 significant change over years (temperature vs. year in 1968-2010:  $p > 0.18$ ).  
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25 During the last hundred years, no consistent directional changes at the level of the whole fish  
26  
27 assemblage attributable to climate change were observed (Sarvala et al., 1998). Catches of all  
28  
29 species fluctuated considerably during 1989-2009. For most species, a linear trend was non-  
30  
31 significant ( $p = 0.21-0.71$ , explained variance: 0.7-7.7%), but whitefish exhibited a significant  
32  
33 declining trend with time ( $R^2 = 0.48$ ,  $F_{1,20} = 18.59$ ,  $p < 0.001$ ). For vendace, there was a  
34  
35 significant decline in year-class size during the period 1971-2010 (adjusted  $R^2 = 0.20$ ,  $F_{1,38} =$   
36  
37  $10.57$ ,  $p < 0.003$ ), related to increasing annual maximum temperatures (linear regression of  
38  
39  $\log_{10}$ -transformed variables: adjusted  $R^2 = 0.18$ ,  $F_{1,38} = 9.82$ ,  $p < 0.004$ ), but not to summer  
40  
41 mean temperature ( $p > 0.51$ ). In multiple linear regressions including either TP or chl *a* of  
42  
43 May-September, the temperature effect on vendace year-class size remained significant, while  
44  
45 none of the trophic state variables was significant (period 1980-2010,  $\log_{10}$ -transformed  
46  
47 variables, temperature and phosphorus ( $R^2 = 0.21$ ,  $F_{2,28} = 3.77$ ,  $p < 0.04$ ) or chl *a* ( $R^2 = 0.22$ ,  
48  
49  $F_{2,28} = 3.86$ ,  $p < 0.04$ ). In all species, the signs of the slopes were consistent with postulated  
50  
51 climate warming effects: positive slopes for the warmer-water species perch, roach and ruffe,  
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53 and negative slopes for the colder-water species vendace, whitefish and smelt, although the  
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1 whitefish decline may rather be related to food web interactions (e.g. competition with  
2 vendace, egg predation by the introduced signal crayfish) (Sarvala et al., 1998). The observed  
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4 change towards smaller fish in the contemporary fish assemblage is likely mostly attributable  
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9 to intensified fishery and species introductions (e.g. whitefish, vendace) (Sarvala et al., 1998).

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11 In addition, erratic stock fluctuations in individual species influence the size distributions.

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

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18 In spite of large inter-annual fluctuations, vendace year class strength in the lake declined  
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20 significantly from 1971 to 2010 (with pronounced lows in 1990-1991, through 1993-1998 and  
21  
22 again in 2003 and 2009-2010) (Fig. 4B). During the same period, there was a significant  
23  
24 increase in the body size of one-summer- and two-summer-old vendace.  
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31 The timing of ice break and the following temperature development are key factors affecting  
32  
33 the year class variation in vendace (Helminen & Sarvala, 1994). Ice-out triggers the hatching  
34  
35 of vendace larvae highly vulnerable to predation from 8 to about 15 mm total length. A longer  
36  
37 early larval period results in higher larval mortality (Helminen et al., 1997). The critical  
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39 period for their survival is 2-4 weeks after the ice break, when the temperature should be high  
40  
41 enough to enable rapid growth of the larvae (Helminen & Sarvala, 1994). For example, in  
42  
43 1989 and 1990, the early ice break in the lake led to an unusually early hatching of vendace  
44  
45 larvae. In 1989, temperature increased quickly and larval mortality remained moderate. In  
46  
47 1990, in contrast, a much slower warming of the water after the very early ice break resulted  
48  
49 in high mortality of vendace larvae (Helminen et al., 1997). With climate change, ice-out  
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51 occurs earlier (Ventelä et al., 2011), but spring temperature has not increased  
52  
53 correspondingly, creating increasingly unfavourable conditions for vendace larvae survival.  
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59 Moreover, triggered by the more frequent warmer summers, strong year classes of perch  
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1 (Böhling et al., 1991; Sarvala & Helminen, 1996) have appeared more often in the 1990s and  
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4 2000s than in the 1970s or 1980s (Sarvala & Helminen, 1996 and unpublished), increasing  
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6 predation on vendace, and we may expect this trend to continue.  
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11 The commercial fishery in the lake is mainly based on winter seining through the ice. Usually,  
12  
13 70-90% of each year class of vendace is harvested during its first winter, leading to negligible  
14  
15 intra-specific competition among the remaining vendace. High winter temperatures (e.g.  
16  
17 2007-2008), result in short periods of ice cover and a short winter fishing season (Ventelä et  
18  
19 al., 2011), augmenting the food competition between the young-of-the-year and adult fish and  
20  
21 leading to poor recruitment (as in 2008 and 2009). Because the lake is mostly unstratified in  
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23 summer, vendace do not have any cold-water refuge in the deeper water layers. Further  
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25 increasing summer temperatures may thus lead to rising mortality and reduced recruitment.  
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### 32 33 34 35 **Lake Peipsi: major changes from cold-water to warm-water species**

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38 The start of the ice-covered period, ice-off dates and the water temperature in the open water  
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40 period have been highly variable in recent years in Lake Peipsi and the mean temperature  
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42 (open water period) has increased 0.17°C per decade ( $R^2=0.22$ ,  $F_{1,86}=23.97$ ;  $p<0.001$ ) since  
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44 1924. Furthermore, extraordinarily hot summers with temperatures exceeding 20°C for long  
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46 periods (up to 110 days in 2002) have apparently become more frequent (Fig. 5A).  
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52 Since the 1930s, remarkable changes have occurred in the composition of the fish stock and  
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54 the total harvest by commercial fishermen. The log-transformed total catch and catch of smelt  
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56 have decreased substantially since 1930 ( $R^2=0,37$ ,  $F_{1,69}=41,38$ ;  $p<0.0001$  and  $R^2=0,22$ ,  
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58  $F_{1,66}=19,04$ ;  $p<0.0001$ , respectively) (Fig. 5C). The decline in total catch coincided, though  
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1 weakly, with an increase in TP ( $R^2=0,28$ ,  $F_{1,22}=8.86$ ;  $p<0.008$ ), but not with summer mean  
2 temperature ( $p>0.1$ ). At the turn of the 1980/1990 decades, a sharp decline in the vendace  
3 population coincided with a major increase in pike-perch abundance (Kangur et al., 2007b).  
4 The major decline of the vendace population has been attributed to sequential extreme  
5 weather events in summer and winter (Kangur et al., unpublished data). Winters (without  
6 permanent ice) influence the reproduction success of autumn spawning fishes (vendace,  
7 burbot, peipsi whitefish (*Coregonus lavaretus maraenoides* Poljakow)). During warm  
8 summers, vendace face not only high water temperature, but also low oxygen concentrations  
9 and predation pressure by the abundant pike-perch. Concurrently with the decline in Lake  
10 Peipsi, vendace also declined in some Finnish lakes (e.g., Lake Pyhäjärvi and Lake  
11 Puulavesi), suggesting a relationship with climatic factors common to the whole region  
12 (Sarvala et al., 1998; Marjomäki & Huolila, 2001; Marjomäki et al., 2004).

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

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45 Eutrophication may have amplified the effect of temperature extremes. In hot summers with  
46 calm weather, cyanobacteria blooming and fish kills have co-occurred during the past decades  
47 (Kangur et al., 2005).. Using regression analysis, Kangur et al. (2007a) found a strong  
48 negative effect of high water temperature ( $\geq 20^\circ\text{C}$ ) on the abundance of the smelt population  
49 with a lag of 1 and 2 years. In recent years, smelt abundance has declined to a historically  
50 low level and, accordingly, since 2007 smelt have not occurred in the commercial catches  
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1 (Fig. 5C). Recent data from trawl samples confirm the low abundance (Kangur et al.,  
2 unpublished data).  
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### 8 **Lake Vänern and Lake Vättern: strongest temperature effect in the more nutrient-rich** 9 **of the two lakes**

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11 In Lake Vättern, the water temperature (at 5 m depth) increased significantly during the period 1955-  
12 2010 (Fig. 6A, B;  $R^2=0.50$ ,  $F_{1,55}=54.7$ ,  $p<0.001$ ), most pronouncedly during the last 10-year period.  
13  
14 The main change was an increase in autumn and early winter temperatures, while there was no clear  
15 trend in ice-on dates during 1881-2010 ( $p>0.9$ ) or presence/absence of ice-cover ( $p>0.9$ ). Also in  
16 Lake Vänern there was a significant increase ( $R^2=0.55$ ,  $F_{1,27} = 32.77$ ,  $p < 0.001$ ) in water temperature  
17 (mean temperature May, June, August and September at 5 m). Comparable long-term data on ice  
18 cover from Lake Vänern are not available.  
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33 There are several marked changes in the commercial catch for the key fish species in both  
34 lakes. Analysis of time trends in commercial fish catches is, however, notoriously difficult  
35 and trends may not necessarily reflect true stock sizes. Despite the substantial decrease from  
36 approximately 1000 commercial and around 1800 semi-commercial fishermen in the early  
37 1920s to about 100 commercial fishermen today, there is no trend in total catch over time  
38 ( $p>0.6$ ). The catch is kept around 750 tonnes (mean =  $747 \pm SD = 186$ ) due to a continuous  
39 development of the individual effort and effectiveness of each fisherman. We identified two  
40 important trends for the target species of the fishery in these two lakes that are likely related  
41 to recent climate change. First, in Lake Vänern the catches of pike-perch, although highly  
42 variable, have increased over time ( $R^2 = 0.17$ ,  $F_{1,58} = 11.47$ ,  $p < 0.001$ ). Second, in Lake Vättern  
43 the catches of Arctic charr, the traditionally most important species, have declined steadily  
44 from the mid-1950s and onwards, negatively correlated with an increase in mean temperature  
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1 (R<sup>2</sup>=0,36, F<sub>1,54</sub>=30.88; p=0.001). A similar negative trend has also been observed in a multi-  
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4 mesh gill-net monitoring programme (A. Sandström et al., unpublished data). Even though  
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6 there has been a recent positive response of this population to a series of new and stricter  
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8 fisheries regulations, there is a clear long-term decline in Arctic charr that appears to be  
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10 related to a warming climate.  
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16 In both lakes the pelagic fish assemblage is dominated by vendace and smelt (Fig. 6C, D).  
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18 Recruitment in L. Vättern was characterised by strong oscillations in vendace recruitment at  
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20 8- or 4-year intervals. Vendace recruitment is known to fluctuate, often in cycles of 2-5 years  
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22 (Hamrin & Persson, 1986; Helminen & Sarvala, 1994). The 1992 year class of vendace was  
23  
24 extremely strong and dominated the population for seven years, making up more than 60% of  
25  
26 the adult population even as late as 1998 and 1999. In this lake, smelt recruitment followed  
27  
28 the same oscillation patterns as vendace (R<sup>2</sup>=0.65, F<sub>1,19</sub>=32.9, p<0.001) and was negatively  
29  
30 correlated with water temperature in July (Fig. 6F; R<sup>2</sup>=0.32, F<sub>1,16</sub>=7.06, p<0.02) in years  
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32 without vendace recruitment outbursts.  
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40 In meso-oligotrophic Lake Vänern smelt recruitment correlated positively with the  
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42 temperature in April (Fig. 6E; R<sup>2</sup>=0.83; F<sub>1,11</sub>=56.11, p<0.001). Long ice winters (in sheltered  
43  
44 areas), where the ice lasted until the beginning of March or longer, yielded strong vendace  
45  
46 recruitment in Lake Vänern (Fig. 6E; R<sup>2</sup>=0.40, F<sub>1,11</sub>= 8.03, p<0.02). A similar trend has been  
47  
48 observed in Lake Mälaren located in Sweden at the same latitude (Nyberg et al., 2001).  
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50 Variations in productivity (TP) did not contribute significantly in any of these analyses (data  
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52 not shown).  
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1 There was no obvious synchrony in vendace recruitment patterns between the two lakes  
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4 ( $p>0.4$ ). In contrast to Lake Vänern, the patterns in Lake Vättern seemed largely regulated by  
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6 the intrinsic dynamics of the vendace stock, possibly due to the fact that Lake Vättern is less  
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8 productive, has no fishery on vendace and exhibits a lower predation rate from piscivores due  
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10 to lower salmonid stocking levels (4-times higher per surface area in Lake Vänern). Our  
11  
12 results indicate that climate forcing may influence both vendace and smelt recruitment  
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14 although the effects may differ depending on the conditions in the specific lake.  
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### 21 **Lake Søbygaard: major reduction in the size of roach and perch**

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23 The April and summer air temperature in the lake region have increased 1.2 and 0.5 °C per  
24  
25 decade, respectively ( $R^2=0.39$ ,  $F_{1,20}=13.25$ ,  $p<0.002$  and  $R^2=0.20$ ,  $F_{1,20}=4.99$ ,  $p=0.04$ ,  
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27 respectively).  
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33 Since 1989, total CPUE in terms of biomass has shown a declining trend in Lake Søbygaard,  
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35 coinciding with a decrease in nutrient concentrations (Fig. 7A, B). A major change has  
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37 occurred from roach dominance to dominance by a mixed assemblage of roach and perch.  
38  
39 This is to be expected when lakes recover from eutrophication (Persson et al., 1991; Jeppesen  
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41 et al., 2000). The fish assemblages respond surprisingly fast to improved lake water  
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43 conditions during oligotrophication (Jeppesen et al., 2005).  
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50 Although in theory oligotrophication leads to increased body size of cyprinids and perch  
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52 (Jeppesen et al., 2000), we recorded the opposite pattern. We found a significant (linear  
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54 regression,  $R^2=0.48$ ,  $F_{1,19}=17.9$ ,  $p<0.001$ ) reduction in the average size of roach, perch and  
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56 rudd pooled together (Fig. 7C). This decline coincided with the change in April air  
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58 temperatures (linear regression,  $R^2=0.28$ ,  $F_{1,19}=7.5$ ,  $p<0.013$ ) (Fig. 7C), and even more with  
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1 the average summer air temperature (April-September) ( $R^2=0.32$ ,  $F_{1,19}=8.97$ ,  $p<0.008$ ) (Fig.  
2 7D). In a multiple regression including also phytoplankton chl *a* and TP, only temperature  
3 was retained in the final model, further emphasising the key role of temperature for the body  
4 size change. Concurrently, studies of numerous Danish lakes have shown an overall decrease  
5 in the body size of some cyprinids and particularly of perch in recent years when the lakes  
6 have become warmer, despite a general improvement of trophic state (Jeppesen et al., 2011).  
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9 The results from the long-term study of Lake Søbygaard and from the less frequent samplings  
10 from numerous other Danish lakes indicate that despite a reduction in loading and a  
11 subsequent reduction in the total biomass of fish, fish density is increasing and the average  
12 body size is decreasing, with potentially strong cascading effects. This body size change  
13 might be a result of improved recruitment of fish due to higher temperatures in spring, but is  
14 likely also a result of increasing survival of young fish during winter due to a shorter ice cover  
15 period (see general discussion).  
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### 38 **Windermere: decrease in Arctic charr and increase in roach densities**

39 The water temperature has increased significantly in both basins of the lake, for example in  
40 the north basin by 0.26°C per decade since 1970 (N-basin:  $R^2 = 0.23$ ,  $F_{1,39} = 11.34$ ,  $p<0.002$ ,  
41 S-basin:  $R^2 = 0.413$ ,  $F_{1,39} = 9.81$ ,  $p<0.004$ ) (Fig. 8A), which has resulted in an increase in the  
42 duration and strength of stratification (Feuchtmayr et al., 2012). The lake has experienced  
43 some degree of eutrophication, although this has been much more marked for the south basin  
44 as illustrated by its long-term trend in TP which peaked in 1990, prior to the local introduction  
45 of tertiary stripping (Fig. 8B) and by the consistently lower dissolved oxygen availability  
46 (Jones et al., 2008).  
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1 Although the recruitment and thus population dynamics of perch are known to be strongly  
2 affected by water temperature (Paxton et al., 2004), no significant relationship between  
3 temperature and abundance was recorded for this lake ( $p>0.2$ ) (Fig. 8C). Development of  
4 trophic level asynchrony amongst the plankton and fish of the lake has been recorded in  
5 recent years (Thackeray et al., 2010), in part by perch spawning earlier in the spring (Winfield  
6 et al., 2004).

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18 While no overall relationship between CPUE of pike and temperature was recorded ( $p>0.1$ ),  
19 local recruitment and population dynamics of pike have also been found to be strongly  
20 influenced by water temperature (Paxton et al., 2009). In recent decades, the abundance (Fig.  
21 8D) and individual condition (length/weight relationship) of pike have shown some  
22 remarkable changes (Winfield et al., 2008b; Langangen et al., 2011), coinciding with a  
23 change in the early winter (the only time of year for which long-term data are available) diet  
24 of pike, most notably with a decline in Arctic charr and an increase in roach (Winfield et al.,  
25 2012a).

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40 Arctic charr abundance has recently declined in both the north and south basins (Fig. 8E), but  
41 particularly so in the more eutrophic south basin. In recent years, dissolved oxygen levels  
42 have approached the lower tolerance limits of this species and so have restricted its vertical  
43 distribution (Jones et al., 2008). Multiple regression on log-transformed data showed strong  
44 negative effect of temperature and positive effect of TP on CPUE of Arctic charr in the south  
45 basin ( $R^2 = 0.29$ ,  $F_{2,36} = 34.75$ ,  $p<0.002$ ), while no relationships were found in the north basin  
46 ( $p>0.2$ ). Arctic charr has also shown a shift in diet in recent years away from zooplanktivory  
47 towards benthivory (Corrigan et al., 2011), potentially as a consequence of inter-specific  
48 competition after the recent local increase in the abundance of roach (Fig. 8F), which is an  
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1 efficient open-water zooplanktivore (Winfield et al., 2008a). Arctic charr has recently shown  
2 a widespread decline elsewhere in the U.K. (Winfield et al., 2010b).  
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6 Despite having been introduced to Windermere ca. 100 years ago (Watson, 1899), roach  
7 populations began to increase in the 1990s after a period of elevated water temperatures  
8 (Winfield et al., 2008a). This population increase thus took place against a background of  
9 decreasing eutrophication, suggesting that climate warming has been an over-riding factor.  
10

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13 The current decrease in roach population (Fig. 8F) may be related to a relatively cool single  
14 year (2008). However, concerns remain about the potential competitive impacts of an elevated  
15 roach population on the lake's native fish assemblage, most notably on the Arctic charr.  
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19 Common bream, likely also an introduced species, has also increased in abundance although it  
20 presently remains relatively rare (Winfield et al., 2011).  
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31 The fish assemblage of Windermere has changed remarkably from its original salmonid-  
32 percid-pike domination to one with a much greater component of cyprinids and higher total  
33 fish abundance in both basins of the lake (Fig. 8G). The decrease in abundance of Arctic charr  
34 appears to have been outweighed by a much greater relative increase in the abundance of  
35 roach, and a more detailed analysis of the extensive hydroacoustic data reveals that the overall  
36 increase in fish abundance has been driven primarily by an increase of small individuals in the  
37 surface waters of both basins. Abundance has significantly increased with temperature and  
38 decreased with TP in the more eutrophic south basin ( $R^2 = 0.48$ ,  $F_{2,18} = 8.54$ ,  $p < 0.003$ ), but not  
39 in the north basin.  
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55 **Lake Stechlin: no obvious climate effect on the fish assemblage**  
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1 Annual average ( $p>0.06$ ), spring ( $p>0.9$ ) and summer ( $p>0.9$ ) water temperatures have not  
2 varied systematically between 2000 and 2010 (Fig. 9A). Lake productivity did not change  
3 substantially since 2000 (Fig. 9A).  
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7  
8 The overall densities of pelagic coregonids, as estimated by hydroacoustics ( $\log_{10}$  individuals  
9 ( $1000 \text{ m}^{-3}$ )), fluctuated about seven-fold between the years (Fig. 9B) and had a marginally  
10 positive relationship with average spring temperatures in March and April (Fig. 9C, adj.  
11  $R^2=0.31$ ,  $F_{1,7}=4.71$ ,  $p=0.06$ ). However, the response differed between pre-mature and mature  
12 fish and between the sympatric coregonid species (Mehner et al., 2011). Densities of the 0<sup>+</sup>  
13 coregonids (dominated by vendace) increased after warm winters, as indicated by positive  
14 correlations of fish densities in June with metalimnetic winter temperatures and the NAO  
15 index between January and March (Mehner et al., 2011). In contrast, densities of juveniles  
16 and adults were correlated with metalimnetic June temperatures, but an opposite response  
17 direction of the sympatric species was triggered by their discrete thermal windows. Densities  
18 of Fontane cisco increased in years with a warm June, whereas vendace densities declined in  
19 these warm years. This opposite response caused the species proportions to fluctuate within a  
20 bi-annual cycle.  
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43 Besides, zooplankton abundances in hypolimnetic layers (the daytime habitat of coregonids  
44 where fish feed) of the previous summer were positively correlated with adult coregonid  
45 densities in the subsequent year. The depths occupied by both populations at night shifted  
46 towards less suitable water temperatures if densities of the competing species increased,  
47 suggesting interactive niche segregation. Temperature-driven inter- and intra-specific  
48 competition in the metalimnetic layer may cause a complex response of cold-water fish  
49 assemblages in lakes to annual temperature changes (Mehner et al., 2011). A generally higher  
50 vulnerability of cold-water fish species to warming could not be deduced from the time series  
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1 from this lake. However, the time series is relatively short and encompasses only the period  
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3 since 2000 without pronounced warming trends.  
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### 8 **Lake Constance: warm-water fish benefit from a warmer epilimnion**

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10 The average water temperature of the upper 20 m increased by 0.22°C per decade (adj.  
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12  $R^2=0.35$ ,  $F_{1,43}=24.95$ ,  $p<0.001$ ) between 1965 and 2009.  
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17 The drastic changes in lake productivity during the second half of the 20<sup>th</sup> century (Fig. 10A)  
18  
19 were the single most important factor influencing fishery yields from ULC. Annual  
20  
21 commercial yields peaked during the 1970s at around 30 kg ha<sup>-1</sup> and declined to almost pre-  
22  
23 eutrophication levels (17 kg ha<sup>-1</sup>) during the 2000s (Fig. 10B). The proportion of whitefish in  
24  
25 commercial harvests was around 70% during the first half of the 20<sup>th</sup> century, dropped to  
26  
27 around 30% at the height of eutrophication and has increased again to around 80% in recent  
28  
29 years (corresponding to 13 kg ha<sup>-1</sup>) (Fig. 10B). Commercial harvests of Arctic charr increased  
30  
31 markedly in the 2000s to levels that have never been registered since the beginning of the  
32  
33 official statistics in 1910 (Fig. 10C). This increase suggests that lake oligotrophication has  
34  
35 improved the conditions for charr, counteracting the effect of increasing temperature.  
36  
37 Additionally, every year charr are fished during spawning time and stripped, eggs are  
38  
39 incubated in hatcheries, and larvae and juveniles are restocked into the lake.  
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50 Multiple regressions on log-transformed data showed no effect of temperature and TP on the  
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52 yield of coregonids ( $p>0.10$ ), while the perch yield was significantly related to TP but not to  
53  
54 temperature (adj.  $R^2=0.45$ ,  $F_{2,42}=18.77$ , log temperature:  $p<0.001$ , log TP:  $p>0.6$ ). Hence, an  
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56 effect of the temperature increase during the last decades on the harvest of the two dominant  
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1 fish species could not be detected. Under enduring oligotrophic conditions, however, such an  
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4 effect might materialize in the future.  
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9 Year class strength of the pelagic spawning whitefish type did not show any significant trend  
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11 from 1947 to 1998 (Straile et al., 2007), likely as a result of large year-to-year variations in  
12  
13 year class strength (Trippel et al., 1991). However, whitefish year class strength was  
14  
15 significantly correlated with the actual winter NAO index and that of the previous winter.  
16  
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18 Whitefish spawn in late November/early December in the pelagic zone, and the eggs sink to  
19  
20 the lake bottom where they develop at the hypolimnetic temperature that was established  
21  
22 during full mixing during the previous winter. A higher hypolimnetic temperature accelerates  
23  
24 embryogenesis and enhances embryo survival. The larvae, on the other hand, experience the  
25  
26 epilimnetic temperature that is influenced by the actual NAO index, whereby higher  
27  
28 temperature furthers larval growth and reduces mortality. As the timing of hatching is  
29  
30 uncoupled from the actual meteorological conditions (Straile et al., 2007), a mismatch  
31  
32 between the larvae and their food might occur, but this has not been observed so far in ULC  
33  
34 (Straile et al., 2007). Should climate change promote stronger whitefish year classes in the  
35  
36 future, intraspecific competition for food will likely increase with a concomitant reduction of  
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38 growth rates (cf. Thomas & Eckmann, 2007).  
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47 So far, there is no strong evidence that cold-water fish in the lake are severely affected by  
48  
49 climate change, not least because this deep lake always provides a cold-water refuge (cf.  
50  
51 Thomas et al., 2010). Warm-water species, however, which now live under suboptimal  
52  
53 conditions in the lake, will likely benefit from warming. Common carp, for example, which  
54  
55 was introduced into Lake Constance in medieval times, clearly benefits from higher  
56  
57 temperature. Commercial yields fluctuated around  $2 \text{ t y}^{-1}$  during the first half of the 20<sup>th</sup>  
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1 century and were as low as  $1 \text{ t y}^{-1}$  during the lake's eutrophic phase, but increased  
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4 dramatically to  $>15 \text{ t y}^{-1}$  in the mid-2000s (Fig. 10 D). This was a result of successful  
5  
6 reproduction in early summer 2003, the warmest summer recorded since 1870, when the  
7  
8 surface temperature surpassed  $25^{\circ}\text{C}$ . As the 2003 cohort was fished out, yields returned to the  
9  
10 previous level. This example suggests that the population dynamics of fish species  
11  
12 characteristic of eutrophic lakes may not primarily be controlled by food availability in  
13  
14 oligotrophic peri-alpine lakes, but rather by temperature during the critical embryonic and  
15  
16 larval periods.  
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### 23 **Lake Geneva: reduction in Arctic charr and increase in whitefish and roach**

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25 The mean temperature of Lake Geneva has increased by  $0.17^{\circ}\text{C}$  per decade since 1986 ( $R^2=$   
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27  $0.53$ ,  $F_{1,52} = 58.52$ ,  $p < 0.001$ ) (Fig. 11A), affecting the development of lake stratification,  
28  
29 which now starts one month earlier than 30 years ago. The de-stratification thus occurs later  
30  
31 due to a very stable epilimnion. Also phenological events of phytoplankton and zooplankton,  
32  
33 including the clear water phase, now take place one month earlier than 30 years ago  
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36 (Anneville et al., 2002, 2004).  
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43 The most important change in the fish assemblage over the past decades has been a major  
44  
45 increase in commercial whitefish catches, positively correlated with mean temperature and  
46  
47 negatively with TP (multiple regression on log-transformed data;  $R^2 = 0.90$ ,  $F_{2,21} = 95.54$ ,  
48  
49  $p < 0.001$ ), which during the last 10 years have increased 3-fold (from  $<100$  to  $>300$  tonnes)  
50  
51 (Gerdeaux, 2004), reflecting an increase in the stock. The changes in the whitefish fishery are  
52  
53 interpreted as the result of changes in lake trophic state following nutrient loading reduction  
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55 and fishery management. However, climate change is likely also an important cause of  
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57 variation (Anneville et al., 2009). Today, spawning of whitefish occurs two weeks later than  
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1 20 years ago, but the water temperature is warmer and the hatching time has not changed. The  
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4 change in seasonal dynamics of primary production means that food for whitefish is available  
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6 earlier in the year for the larvae hatched in February. The warming of the lake is thus  
7  
8 favourable for whitefish recruitment (Fig 11B).  
9

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13 In contrast, the warming of the lake seems to negatively impact the dynamics of Arctic charr,  
14  
15 the catches being negatively related to both mean temperature and TP (multiple regression on  
16  
17 log-transformed data:  $R^2 = 0.66$ ,  $F_{2,21} = 11.47$ ,  $p < 0.001$ ) (Fig. 11B) (see also Gerdeaux, 2011).  
18  
19 The recruitment of Arctic charr was negatively correlated with deep water temperature ( $R^2 =$   
20  
21  $0.55$ ,  $F_{1,10} = 9.58$ ,  $p < 0.02$ ). Perch, on the other hand, has not changed its spawning time, while  
22  
23 roach spawns almost one month earlier (Gillet & Quetin, 2006; Gillet & Dubois, 2007).  
24  
25 Therefore, the time interval between perch and roach spawning has decreased, and there is a  
26  
27 mismatch between perch juveniles and roach larvae as a food resource. Warming thus seems  
28  
29 to favour the dynamics of roach, which avoid predation from perch juveniles. We found no  
30  
31 significant relationship between temperature and reported catches of pike and trout, while  
32  
33 there was a significant positive relationship between P reduction and capture of pike ( $R^2 =$   
34  
35  $0.83$ ,  $F_{1,22} = 109.2$ ,  $p < 0.001$ ) and a negative relationship for trout catches ( $R^2 = 0.69$ ,  $F_{1,22} =$   
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37  $48.58$ ,  $p < 0.001$ ).  
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#### 48 **Lake Maggiore: reduction in cold water species and increase in warm-water species**

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50 Besides changes in trophic status, the effects of climate warming on Lake Maggiore have  
51  
52 become particularly evident during recent decades (Ambrosetti & Barbanti, 1999) (Fig. 12A).  
53

54  
55 From 1978 the water temperature rose significantly both in the hypolimnion ( $R^2 = 0.49$ ,  
56  
57  $F_{1,31} = 28.86$ ,  $p < 0.001$ ) and the epilimnion ( $R^2 = 0.33$ ,  $F_{1,31} = 14.76$ ,  $p < 0.001$ ) (Fig. 12B).  
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59  
60 Ambrosetti and colleagues (2006) have shown an increase of short and very intense rain  
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1 events coupled with long drought periods, and increased pollutant loads from the catchment  
2 (Galassi et al., 2006; Volta et al., 2009; Guilizzoni et al., 2012), due to changes in hydrology  
3 and precipitation regimes, have been also identified. Furthermore, an increase in the duration  
4 of the thermal stratification and stability of the water column was observed, probably  
5 triggering cyanobacteria blooms (Morabito, 2007).  
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16 Since the 1980s, the total fishing yield has decreased significantly ( $R^2=0.62$ ,  $F_{1,31}=29.48$ ,  
17  $p<0.001$ ) from ca. 45 kg ha<sup>-1</sup> to the current 8 kg ha<sup>-1</sup>. (Fig 12B). Fish species contribution to  
18 the commercial catches has changed markedly, reflecting the changes in lake fish assemblages  
19 probably triggered by multiple stressors, such as the increased water temperature, changes in  
20 trophic state and the introduction of invasive non-native species (Volta & Jepsen, 2008; P.  
21 Volta unpublished data). Regression on log-transformed data showed that coregonid  
22 ( $R^2=0.49$ ,  $F_{1,31}=28.22$ ,  $p<0.001$ ) and trout ( $R^2=0.50$ ,  $F_{1,31}=30.39$ ,  $p<0.001$ ) harvests have  
23 decreased significantly (Fig. 12C), while bleak ( $R^2=0.50$ ,  $F_{1,15}=17.05$ ,  $p<0.001$ ) has almost  
24 disappeared. In contrast, eurythermal species such as the native shad (*Alosa agone*) ( $R^2=0.72$ ,  
25  $F_{1,27}=69.80$ ,  $p<0.001$ ) and roach ( $R^2=0.76$ ,  $F_{1,14}=40.42$ ,  $p<0.001$ ) recently appeared  
26 abundantly in the catches. Also, pike-perch has increased ( $R^2=0.64$ ,  $F_{1,14}=23.04$ ,  $p<0.001$ )  
27 reaching a comparable catch level as that of perch (Fig. 12C), which has itself declined  
28 substantially ( $R^2=0.60$ ,  $F_{1,31}=45.03$ ,  $p<0.001$ ). Besides these primary commercial species,  
29 other tolerant and eurythermal non-native species, such as ruffe and wels catfish (*Silurus*  
30 *glanis*), now appear more constantly in the catches (P. Volta, pers. obs.).  
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55 Multiple regressions on log-transformed data have shown that the changes registered in the  
56 catches of most of the fish species were often significantly correlated with TP at winter  
57 mixing, with Chl *a* concentration and with water temperature. For instance, the coregonids  
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1 harvest was positively correlated with Chl *a* and negatively with hypolimnetic temperature  
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4 ( $R^2=0.70$ ,  $F_{5,26}= 11.99$ ,  $p<0.001$ ), while trout was negatively correlated with hypolimnetic  
5  
6 temperature ( $R^2=0.77$ ,  $F_{5,26}=17.18$ ,  $p<0.001$ ). Also the perch catches were markedly  
7  
8 negatively correlated with the hypolimnetic temperature ( $R^2=0.77$ ,  $F_{5,26}=17.18$ ,  $p<0.001$ ),  
9  
10 whilst bleak harvest was positively correlated with TP in the epilimnion ( $R^2=0.76$ ,  $F_{4,12}=7.78$ ,  
11  
12  $p=0.002$ ) but not with temperature. On the contrary, the shad catches were positively  
13  
14 correlated with the temperature in the epilimnion but negatively with Chl *a* ( $R^2=0.90$ ,  
15  
16  $F_{4,24}=49.73$ ,  $p<0.001$ ), while the harvests of roach, pikeperch, and char did not show any  
17  
18 significant relationship ( $p>0.05$ ) with any of the variables tested.  
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### 26 **Lake Albufera: synergistic effects of eutrophication and climate warming**

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28 The temperature in Lake Albufera has increased 0.34 °C per decade since 1950 ( $R^2 = 0.63$ ,  
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30  $F_{1,56} =97.50$ ,  $p<0.001$ ) (Fig 13A).  
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36 Eutrophication (Fig. 13A), disappearance of macrophyte beds, introduction of exotic species  
37  
38 and perhaps fish harvesting and climate warming have affected the fish species composition  
39  
40 from 1950 to 2007. A remarkable reduction in fish species richness from about 23 to nine  
41  
42 species was observed between 1950 and 2007, while there has been a noticeable increase in  
43  
44 the presence and development of exotic species such as eastern mosquitofish (*Gambusia*  
45  
46 *holbrooki*), pumpkinseed sunfish (*Lepomis gibbosus*) and common carp.  
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52 Similarly to findings in subtropical lakes (Meerhoff et al., 2007a; Teixeira-de Mello et al.,  
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54 2009), submerged macrophyte beds are important for sustaining a high diversity of small-  
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56 sized fish species in Mediterranean lakes (Blanco et al., 2003). Some of the exotic species  
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58 have replaced autochthonous species, especially those using submerged macrophyte beds,  
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1 such as Spanish cyprinodont (*Aphanius iberus*), *Barbus bocagei*, *Chondrostoma arrigonis* or  
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4 Valencia cyprinodont (*Valencia hispanica*). Species well distributed in Europe, such as three-  
5  
6 spined stickleback, have also disappeared with the loss of submerged vegetation.  
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11 Other species introduced in the early 1960s, such as pike, largemouth bass (*Micropterus*  
12  
13 *salmoides*) and pike-perch, have not proliferated in the lake, probably due to rising water  
14  
15 turbidity and lack of spawning habitat. Since the 1950s, mugilid captures have increased by  
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17 75% (from 80 to 325 t y<sup>-1</sup>) (unrelated to temperature or Chl *a*, p>0.2) to the detriment of  
18  
19 species such as eel (from 90 to 7.7 t y<sup>-1</sup>) (negatively related to temperature, but positively to  
20  
21 Chl *a*: multiple regression on log-transformed data, R<sup>2</sup>= 0.84, F<sub>2,17</sub> = 43.70, p<0.001) and  
22  
23 European seabass (*Dicentrarchus labrax*) (from 30 to 0.1 t y<sup>-1</sup>) (negatively related to Chl *a*  
24  
25 and positively to temperature: multiple regression on log-transformed data, R<sup>2</sup>= 0.54, F<sub>2,14</sub> =  
26  
27 8.00, p<0.005) (Fig. 13B). Such decrease may also be attributed to over-fishing of these  
28  
29 valuable commercial species since the beginning of the 20<sup>th</sup> century (Blanco & Romo, 2006).  
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38 A main shift in the captured species was recorded in 1974 following an earlier change around  
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40 1966 (Fig. 13B). The shift corresponds well with the doubling of the phytoplankton Chl *a*  
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42 concentration observed in 1974 (mean: 53 µg l<sup>-1</sup>) and a major shift to a turbid state after a  
43  
44 rapid loss of submerged macrophytes (Romo et al., 2005). The ratio of piscivorous fish  
45  
46 (European seabass and eel) to total mugilids captured was nearly 1 during the macrophyte-  
47  
48 dominated state of Lake Albufera, but remained very low thereafter. Dense cover of  
49  
50 macrophytes and the presence of some piscivorous species (such as European seabass)  
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52 probably prevented massive mugilid entry from the sea and development in the lake before  
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54 the 1970s.  
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2 Despite variations depending on the physiological optima of the different species, the direct  
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4 effects of an increasing temperature may be small as eurythermal fishes dominate completely.  
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6 However, warming may indirectly affect lake fish communities as longer water retention time  
7  
8 leads to more frequent oxygen depletion as well as harmful cyanobacteria blooms (Romo et  
9  
10 al., 2012). The long-term data series from the lake therefore indicates a combined effect of  
11  
12 climate change and eutrophication favouring eurythermal, omnivorous and small-sized fish  
13  
14 species suffering from variations in water levels, salinity and frequent fish kills during  
15  
16 summer-autumn (Blanco et al., 2003), although effects of harvesting and invasion of exotic  
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18 species have likely contributed to the changes.  
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## 26 **General discussion**

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28 Leaving interactions aside, theoretical works based on temperature effects on individual  
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30 metabolism predict an increase in species richness and a reduction in biomass, density, and  
31  
32 mean body size with warming, particularly for ectotherms (Allen et al., 2002; Brown et al.,  
33  
34 2004). While the fish assemblages in most of the presented case studies have also been  
35  
36 strongly influenced by stressors other than changes in climate, particularly changes in nutrient  
37  
38 loading, commercial fish harvesting and species invasions, changes attributable to warming  
39  
40 have emerged in recent decades in European lakes (summarised in Table 2).  
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48 We found a clear trend towards higher importance of eurythermal species with warming in  
49  
50 several of the lakes (Lake Peipsi, Windermere, Lake Geneva, Lake Maggiore and Lake  
51  
52 Constance), as judged from fish harvests and surveys. Lake Maggiore seems the most striking  
53  
54 example of such changes, although the evidence is provided by harvests that may themselves  
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56 show a more drastic non-linear change than the fish populations. In this lake, a major shift  
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1 occurred in the harvest: cold-adapted species (trout and whitefish) declined and more  
2  
3 eurythermal species (native shad, roach and pike-perch) increased substantially. Also ruffe  
4  
5 and catfish appeared more often after a temperature increase. Harvest of pike-perch increased  
6  
7 in Lake Peipsi and Lake Vänern, of common bream in Lake Peipsi and of carp in Lake  
8  
9 Constance. These shifts to more eurythermal species occurred even though four of the five  
10  
11 lakes experienced oligotrophication during the study period, which should have favoured the  
12  
13 cold-adapted species in a slightly warmer climate due to improved oxygen conditions in the  
14  
15 cold hypolimnion and less severe competition for food with the eurythermal species  
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21 (Hartmann, 1977; Persson et al., 1991; Jeppesen et al., 2000).  
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26 The cold-stenothermic Arctic charr has been particularly affected by warming, showing a  
27  
28 clear decline in the majority of the lakes where its presence is recorded (4 out of 5, i.e. Lake  
29  
30 Elliðavatn, Windermere, Lake Geneva, and Lake Vättern). Despite warming, a marked  
31  
32 increase has occurred in the charr harvest of Lake Constance during the last 15 years,  
33  
34 although here nutrient loading reduction and systematic stocking must have played a pivotal  
35  
36 role in boosting the local production of this species. A recent study indicated pronounced  
37  
38 negative long-term effects on Arctic charr growth in Scandinavian hydroelectric reservoirs  
39  
40 (Milbrink et al., 2011). As illustrated by a review of charr population declines in the U.K.  
41  
42 (Winfield et al., 2010b), the thermal problems faced by this species are expectedly more  
43  
44 adverse in shallow than in deep lakes due to higher temperatures and lack of a cold  
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46 hypolimnion refuge. In Iceland, charr appears also to suffer from the thermally-linked  
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48 proliferative kidney disease (PKD) (Sterud et al., 2007), as is the case in Lake Elliðavatn  
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50 (Kristmundsson et al., 2011). This highlights the importance of complex and potential  
51  
52 synergetic effects of warming on fish, including both direct effects (e.g. on metabolism and  
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54 growth) and indirect effects, such as diseases.  
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4 Other cold-water-adapted species, such as coregonids and smelt, have also responded to  
5 increasing temperatures, although with varying patterns. While commercial catches of  
6  
7 whitefish have increased in Lake Geneva, perhaps reflecting an earlier increase in spring  
8  
9 water temperature favouring recruitment (see also the whitefish in Lake Constance), whitefish  
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11 harvest has declined substantially in Lake Maggiore, Lake Vättern and Lake Peipsi, and to  
12  
13 some extent also in Lake Säkylän Pyhäjärvi. In the U.K. and Ireland, a decline in the  
14  
15 coregonid pollan (*Coregonus autumnalis*) in recent decades has also been attributed to  
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17 changes in temperature (Harrod et al., 2002). The population of brown trout, which is a more  
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19 heat-tolerant species than Arctic charr (Elliott & Elliott, 2010), has remained largely  
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21 unchanged in Lake Elliðavatn, but has decreased substantially in the warmer Lake Maggiore.  
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32 We observed variable responses of vendace to warming, likely because temperature effects on  
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34 vendace depend on the initial situation, as well as on the life stage relative to the seasonal timing of  
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36 the changes. Except in Lake Vättern, where no correlation between the dynamics of vendace and  
37  
38 climate parameters occurred but instead intra-specific competition seemed more important, negative  
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40 effects of rising temperatures seemed substantial in most lakes. Although rapid warming of water after  
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42 the hatching of larvae in spring generally enhances vendace survival (Helminen & Sarvala, 1994), late  
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44 summer temperatures in the southernmost vendace lakes have occasionally risen so high as to increase  
45  
46 particularly adult mortality. Adult vendace population has declined in the deep Lake Stechlin in warm  
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48 summers (Mehner et al., 2011), and more drastic reductions have occurred in shallow Lake Peipsi  
49  
50 after summer heat waves. Mild winters leading to early ice-off dates have been detrimental to vendace  
51  
52 recruitment in Lake Säkylän Pyhäjärvi, Lake Peipsi, and Lake Vänern. In contrast, warming has  
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54 apparently favoured vendace recruitment further north in subarctic Lake Inari (Finland) (Puro-  
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1 Tahvanainen & Salonen, 2010). Vendace recruitment has been indirectly disturbed in Lake Säkylän  
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4 Pyhäjärvi through climate-induced changes in winter fishing length and intensity (Ventelä et al.,  
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6 2011). An additional indirect climate effect is that the predation pressure from perch on young vendace  
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8 has apparently increased with warmer summers in several lakes, particularly in the north. The U.K.'s  
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10 last surviving native population of vendace in Derwent Water, where the species is not exploited in a  
11  
12 fishery, has shown a declining tendency over the last decade (Winfield et al., 2012b) which may be  
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14 due in part to warming.  
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21 The response of smelt also varied among lakes. While the recruitment of this species in deep  
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23 northern Lake Vättern was negatively related with the water temperature in July, it increased  
24  
25 with April temperature in Lake Vänern. This was similar to the opposite effects of  
26  
27 winter/spring or summer temperatures on the recruitment and densities of vendace. In  
28  
29 contrast, a drastic reduction in smelt occurred in shallow Lake Peipsi as judged from  
30  
31 commercial harvest, the decline being particularly remarkable in years with heat waves.  
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38 Perch and roach, which typically dominate northern European lakes (Mehner et al., 2007),  
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40 show an ambiguous pattern of response to warming. No obvious climate-induced changes  
41  
42 could be traced for nutrient-poor northern Lake Vänern and Lake Vättern. Observations from  
43  
44 11 Swedish forest lakes indicate, however, increased growth of 0<sup>+</sup> perch in years with higher  
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46 temperatures, potentially enhancing their winter survival. The harvest of perch has increased  
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48 in Lake Peipsi and strong year-classes of this species have occurred more frequently in Lake  
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50 Säkylän Pyhäjärvi and in Lake Søbygaard, although in the latter it may also be attributed to a  
51  
52 major reduction in nutrient loading. Other studies have also found strong year classes of perch  
53  
54 to be associated with warm summers (Böhling et al., 1991; Lappalainen et al., 1996; Sarvala  
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56 & Helminen, 1996; Mehner et al., 1998; Paxton et al., 2004), and in Lake Pyhäselkä in north-  
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1 eastern Finland perch density increased with increasing temperature from 1975 to 2005  
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4 (Voutilainen & Huuskonen, 2010). The southern distribution limit of this species corresponds  
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6 with the 31°C summer isotherm (Thorpe, 1977), the larvae growth optimum of 25-30 °C is  
7  
8 higher than that for adults (18-27 °C), and gonadal development is most favourable at  
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10 temperatures < 6 °C for prolonged periods (Graham & Harrod, 2009). The latter two factors,  
11  
12 in particular, may explain why we observed stimulation of perch recruitment in the north and  
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14 a major decline in perch harvest in southern Lake Maggiore.  
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21 In our study, long-term data on roach were limited. The harvest of roach increased in Lake  
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23 Maggiore (Volta & Jepsen, 2008) and roach abundance increased substantially in Windermere  
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25 since the 1990s, despite varying in time since first introduction and indicating that this species  
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27 has encountered a ‘window of opportunity’ in recent years. The primary factor behind the  
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29 increases of this non-native (to these lakes) cyprinid is probably the increase in water  
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31 temperature, because roach is unlikely to have benefitted from the reduced nutrient loadings  
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33 occurring during this period in both of the lakes.  
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40 Higher winter survival, longer growing seasons and, for some species, higher year-class  
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42 strengths in warm years can be expected to lead to higher proportions of small fish in the  
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44 populations. Spawning occurs earlier at lower latitudes, as seen for important European  
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46 species such as roach (Lappalainen & Tarkan, 2007) and perch (Tolonen et al., 2003). We  
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48 found a major decline in the body size of roach and perch in Danish Lake Søbygaard. This  
49  
50 increase in the proportion of small fish occurred despite an overall major reduction in nutrient  
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52 levels following an external nutrient loading reduction, which according to monitoring data  
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54 from numerous Danish lakes should have resulted in a lower proportion of small fish  
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60 (Jeppesen et al., 2000). Moreover, an analysis of gill-net monitoring data on the age structure  
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1 of perch and roach from 50 Swedish lakes, covering a latitude gradient from 67 to 55°N,  
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3 revealed that the proportion of perch < 10 cm and of age groups 1<sup>+</sup> to 3<sup>+</sup> of the total catch (by  
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5 numbers) increased markedly with decreasing latitude (and increasing air temperature)  
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8 (Jeppesen et al., 2010a). These findings concur with a meta-analysis of the effects of warming  
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10 on the body size of ectothermic aquatic organisms, showing a significant increase in the  
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12 proportion of small-sized species and organisms at warmer temperatures (Daufresne et al.,  
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14 2009).  
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21 The fish assemblage is not only affected directly by the heating and changes in the thermal  
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23 stability of the lakes. Numerous recent studies and reviews indicate that warming will  
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25 exacerbate existing eutrophication problems (McKee et al., 2003; Feuchtmayr et al., 2009;  
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27 Jeppesen et al., 2010b; Moss et al., 2011; Romo et al., 2012), and this will, in a self-  
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29 amplifying manner, likely further stimulate a shift to small-bodied fish and to dominance of  
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31 eurythermal species, which typically tolerate low oxygen levels and high ammonia  
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33 concentrations (see review in Graham & Harrod, 2009). In Northern and Central Europe,  
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35 increased eutrophication is in part due to a higher external nutrient loading mediated by  
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37 higher precipitation-induced nutrient runoff, but it is also a consequence of higher internal  
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39 phosphorus loading and higher dominance of cyanobacteria in warm lakes (Mooij et al., 2007;  
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41 Jeppesen et al., 2010b; Kosten et al., 2012; Romo et al., 2012), with detrimental effects  
42  
43 mostly on adult fish (Romo et al., 2011). The effects of eutrophication are further reinforced  
44  
45 by the warming-induced shifts in fish assemblages and size structure (Teixeira-de Mello et al.,  
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47 2009), and in many lakes higher winter survival due to reduced ice cover (Jackson et al.,  
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49 2007), leading to enhanced fish predation pressure on zooplankton (Meerhoff et al., 2007b;  
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51 Balayla et al., 2010; Ruuhijärvi et al., 2010) and, as a result of this, lower grazing on  
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53 phytoplankton (Meerhoff et al., 2012).  
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4 It is also to be expected that warming and enhanced precipitation in Central and Northern  
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6 Europe induced by climate change will enhance the allochthonous carbon inflow to lakes and  
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8 reduce carbon burial, leading to higher in-lake dissolved organic concentrations and often a  
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10 higher humic content (Tranvik et al., 2009, Sobek et al., 2007). Succession towards higher  
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12 bacterial production, together with light limitation, may result in lower overall production  
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14 available to the higher trophic levels in certain lakes (Ask et al., 2009; Karlsson et al., 2009),  
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16 as seemingly has occurred to perch in Lake Valkea-Kotinen. In the Mediterranean area,  
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18 eutrophication may also intensify despite lower external nutrient loading, as nutrient  
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20 concentrations rise due to higher evaporation and lower precipitation (Jeppesen et al., 2009,  
21  
22 2011; Romo et al., 2012). As elsewhere, changes in fish size structure here will also  
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24 exacerbate eutrophication symptoms.  
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33 Therefore, we can expect an allied attack by eutrophication and warming in lakes in the future  
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35 (Moss et al., 2011), and shifts in fish abundance, body size and composition will be reinforced  
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37 and stimulated by this process. This implies that it will be more difficult to obtain the good  
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39 ecological status required by the Water Framework Directive in European lakes facing  
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41 climate warming and suggests that a way to counteract, at least in part, the effect of warming  
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43 is to reduce the nutrient input to lakes even further than planned under the present-day climate  
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45 and to regulate fisheries accordingly.  
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## 51 52 53 **Conclusions**

54  
55 Although local variations occurred, we have revealed profound changes in either fish  
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57 assemblage composition, biomass, abundance, body size and/or age structure of key species  
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1 during recent decades in a set of European freshwater lakes. Some patterns coincided with  
2 findings by other approaches (e.g. meta-analysis, Daufresne et al., 2009; space-for-time-  
3 substitution, Jeppesen et al., 2010a,b; Meerhoff et al., 2012), although responses were species-  
4 specific and not universal for our data set. The most obvious alterations encompass a decline  
5 in the abundance of cold-stenothermal species, in particular in shallow lakes, and an increase  
6 in the abundance of eurythermal species even in deep, stratified lakes. This development has  
7 occurred despite a reduction in nutrient loading in most of the case studies, supposedly  
8 favouring fish typically living in cold-water low-nutrient lakes and larger-sized individuals.  
9 The response of fishes to the warming during recent decades has therefore been surprisingly  
10 strong, making fish ideal sentinels for detecting and documenting climate-induced  
11 modifications of freshwater ecosystems.  
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39 Recovery, Contract No.: 226273) and REFRESH (Adaptive strategies to Mitigate the Impacts  
40 of Climate Change on European Freshwater Ecosystems, Contract No.: 244121), 'CLEAR' (a  
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3  
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6 providing, respectively, fish capture data and chemical and meteorological data from Lake  
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9 Albufera.

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2 **Legends of figures**  
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7 Fig. 1. Lake Elliðavatn. Catch per unit effort (CPUE, average number of fish caught per net)  
8 of Arctic charr and brown trout together with June-September mean temperatures (modified  
9 from Malmquist et al., 2009; Antonsson & Árnason, 2011; IMO, 2011).  
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16 Fig. 2. Lake Valkea-Kotinen. A: Annual mean total phosphorus concentration, chlorophyll *a*  
17 and water temperature (1 m depth). B: mean length of 0<sup>+</sup> perch and annual mean  
18 concentration of total organic carbon (TOC, 1 m depth). C, D: Relationship between mean  
19 length of 0<sup>+</sup> perch, water temperature and TOC.  
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28 Fig. 3. Eleven Swedish forest lakes. A: Mean surface water temperature in May to September.  
29 B: Mean length of perch after the first year. C: Linear relationship between summer  
30 temperature and 0<sup>+</sup> perch length, D: Lake-specific residual variation in the linear relationship  
31 between temperature and 0<sup>+</sup> perch length. Lakes in D are ordered from south to north, and the  
32 same colour codes are used in all panels.  
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43 Fig. 4. Lake Säkylän Pyhäjärvi. A: Mean total phosphorus, chlorophyll *a* (0-5 m; May-  
44 September) and annual maximum water temperature. B: Year class size of vendace (in  
45 millions).  
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53 Fig. 5. Lake Peipsi. A: Mean water temperature (WT) for days with temperature > 20°C from 1925 to  
54 2010. The occurrences of fish kills during the hottest summers are marked with asterisks. B: Mean  
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1 water temperature, total phosphorus and chlorophyll *a* for the ice-off period. C: Annual catches of  
2 smelt and total fish.  
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8 A: Mean water temperature (WT) for days with temperature > 20°C from 1925 to 2010. The  
9 occurrences of fish kills during the hottest summers are marked with asterisks. B: Mean water  
10 temperature, total phosphorus and chlorophyll *a* for the ice-off period. C: Annual catches of  
11 smelt and total fish.  
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21 Fig. 6. Lake Vänern and Lake Vättern. A, B: Annual mean water temperature, chlorophyll *a*  
22 and total phosphorus (0-10 m). C, D: Annual variation in abundance (ind. ha<sup>-1</sup>) of young-of-  
23 the-year smelt and vendace. E: relationship between abundance of young-of-the-year smelt  
24 and temperature in April and between abundance of young-of-the-year vendace and the date  
25 of ice break in the sheltered basin of Brandsfjorden in the south-eastern part of the lake. F:  
26 Relationship between abundance of young-of-the-year smelt and July water temperature (only  
27 years without strong pulses of vendace recruitment). Note that the year 2009 is an extreme  
28 outlier and was not included in the regression line. In 2009 smelt recruitment in Lake Vänern  
29 collapsed despite optimal temperature conditions. The reason for this collapse is under  
30 investigation.  
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48 Fig. 7. Lake Sjøbygård. A: Summer mean total phosphorus and chlorophyll *a*. B: CPUE by  
49 weight of various key fish species. C, D: Mean per capita biomass of roach, rudd and perch  
50 (pooled together) and average air temperature in April and summer (Apr. 1 to Sept. 1).  
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57 Fig. 8. Windermere. A: Annual mean surface water temperature in the north and south basins.  
58 B: Annual mean total phosphorus in the north and south basins. C-F: Annual abundance of  
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1 perch (fish trap<sup>-1</sup> week<sup>-1</sup>), pike (fish net<sup>-1</sup> day<sup>-1</sup>), Arctic charr (fish angler<sup>-1</sup> hour<sup>-1</sup>), and roach  
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3 (fish 100 m<sup>2</sup> net<sup>-1</sup> day<sup>-1</sup>), data are only available from 1995, 2000, 2005 and 2010). G: Annual  
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5 abundance (fish ha<sup>-1</sup>) of all fish species as recorded by hydroacoustics.  
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11 Fig. 9. Lake Stechlin. A: Annual mean concentrations of total phosphorus ( $\mu\text{g l}^{-1}$ ) and  
12 chlorophyll *a* ( $\mu\text{g l}^{-1}$ ), and annual mean and spring (March-April) temperatures ( $^{\circ}\text{C}$ ) measured  
13 at 2 m depth intervals from the surface to 20 m depth. B: Time series of spring (March-April)  
14 water temperatures and total density of pelagic coregonids ( $\log_{10}$  ind. (1000 m<sup>-3</sup>)) as obtained  
15 by hydroacoustics in June. C: Scatter plot and linear regression line of spring temperature and  
16 hydroacoustic fish densities in June.  
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28 Fig. 10. Lake Constance. A: Total phosphorus concentration during winter mixing, yearly  
29 average temperature from 0-20 m depth, and yearly average chlorophyll *a* concentration from  
30 0-20 m. B, C, D: Commercial fish, Arctic charr and carp harvests (in tonnes), respectively,  
31 from Upper Lake Constance and total phosphorus during winter mixing.  
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40 Fig. 11. Lake Geneva. A: Annual mean water temperature above the bottom at 309 m and  
41 annual mean total phosphorus concentration. B: Annual commercial harvest of key fish  
42 species (tonnes).  
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50 Fig. 12. Lake Maggiore. A: Mean water temperature and total phosphorus at the spring  
51 overturn. B: Annual mean water temperature of the epilimnion (0-25 m depth) and  
52 hypolimnion (25-360 m depth). C: Annual commercial harvest (in tonnes) of the most  
53 important fish species as registered in the fishery statistics by CISPP.  
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1 Fig. 13. Lake Albufera. A: Annual means of temperature, chlorophyll a and total phosphorus. B:  
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4 Annual commercial harvest of key fish species (in tonnes). Mullet (dash), Eel (full thick line) and  
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6 European seabass (fill thin line). Mullet (dash), Eel (dark line) and European seabass (clear line).  
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9 (Error in the graph to be changed in the final version).  
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**Table 1.**

Information about lake locations, morphometry and fish data series

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

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Table 1

Lake	Country	Position	Altitude (m.a.s.l. )	Lake area (km <sup>2</sup> )	Mean depth (m)	Maximum depth (m)	Mean total phosphorus in surface waters ( $\mu\text{g P l}^{-1}$ )
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	21	3555	7.1	15.5	Mean 42 (May-Sep, 1985-2010) Maximum: 78 (1992)
Lake Vänern	Sweden	58.5	44♣	5648	27	106	Mean 6 (May-Sep, 1995-2010) Maximum 8 (in 1995)
Lake Vättern	Sweden	57.5	89	1939	40	126	Mean 5 (May-Sep, 1995-2010) Max 7 (in 1989)
Lake Søbygaard	Denmark	56°15' N,	49	0.4	1	1.2	Mean 507 (May-Sep, 1989-2010)

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Table 1

Lake	Country	Position	Altitude (m.a.s.l.)	Lake area (km <sup>2</sup> )	Mean depth (m)	Maximum depth (m)	Mean total phosphorus in surface waters ( $\mu\text{g P l}^{-1}$ )
		9°48' E					Maximum: 997 (1996)
Windermere	U.K.	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/Ge rmany/Swit zerland	47°39' N, 9°18' E	395	473	101	254	Mean 36 (Winter mixing, 1951- 2010) Maximum: 87 (1979)
Lake Geneva	France/Sw itzerland	46°27' N, 6°32' E	372	582	153	309	Mean 42 (Jan –Dec,1986-2010) Maximum: 71 (1986)
Lake Maggiore	Italy/Switz erland	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)

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**Table 2**

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 <sup>+</sup> ) 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 <sup>+</sup> perch decreasing.
Eleven forest lakes, Sweden	56-64° N		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 <sup>+</sup> and 1 <sup>+</sup> vendace size increasing, weaker year classes (lower 0 <sup>+</sup> abundance).
Peipsi, Estonia/Russia	57°5'- 59°0'N	No	80 (1931-2010)	-	Decreasing trends for smelt, vendace, peipsi	Increasing catches of perch; catches of roach	Abundance of pike-perch and bream has increased.	Size of 0 <sup>+</sup> pike-perch in autumn has decreased due to collapse of

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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
					whitefish and burbot. Eutrophication amplifies the effect of temperature extremes.	stable.		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.
Søbygård, Denmark	56°15' N	No	22	-	-	-	-	Size of roach and perch

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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
Windermere, U.K.	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.	decreasing. -
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	No clear effect of changes in coregonids related to climate warming, but a reduction in catches	Perch yields decreasing with increasing oligotrophication.	Major increases in commercial catches of common carp.	-



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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
				and effective management.	following nutrient loading reduction.			
Geneva, France/ Switzerland	46°27' N	Yes	25 (1986-2010)	Decline in abundance negatively correlated with the temperature in the deep water.	Major increase in commercial catches: 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.	-
Maggiore, Italy	45°57'N	Yes	32 (1979-2010)	-	Major decline in commercial catches of coregonids, trout and bleak.	Major decrease in perch and major increase in roach catches.	Major increase in commercial catches of shad and pike-perch.	-

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<b>Lake</b>	<b>Latitude</b>	<b>Cold deep water refuge</b>	<b>Length of fish time series (years)</b>	<b>Arctic charr</b>	<b>Other cold-water species</b>	<b>Perch/roach</b>	<b>Warm-water species</b>	<b>Fish body size</b>
Albufera, Spain	39°20'N	No	54 (1950-2007)	-	No	No	Well adapted warm-eurythermic species	-

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Fig1

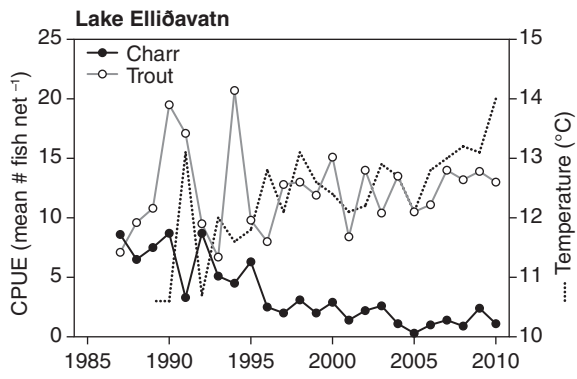


Fig2

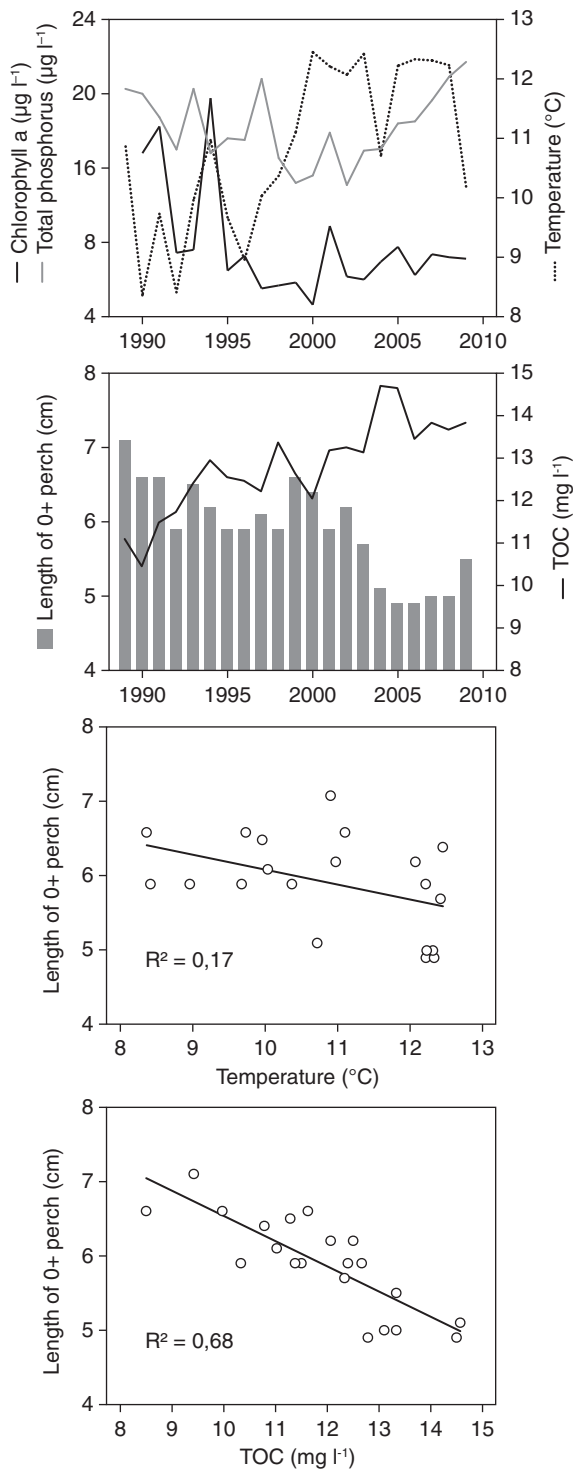


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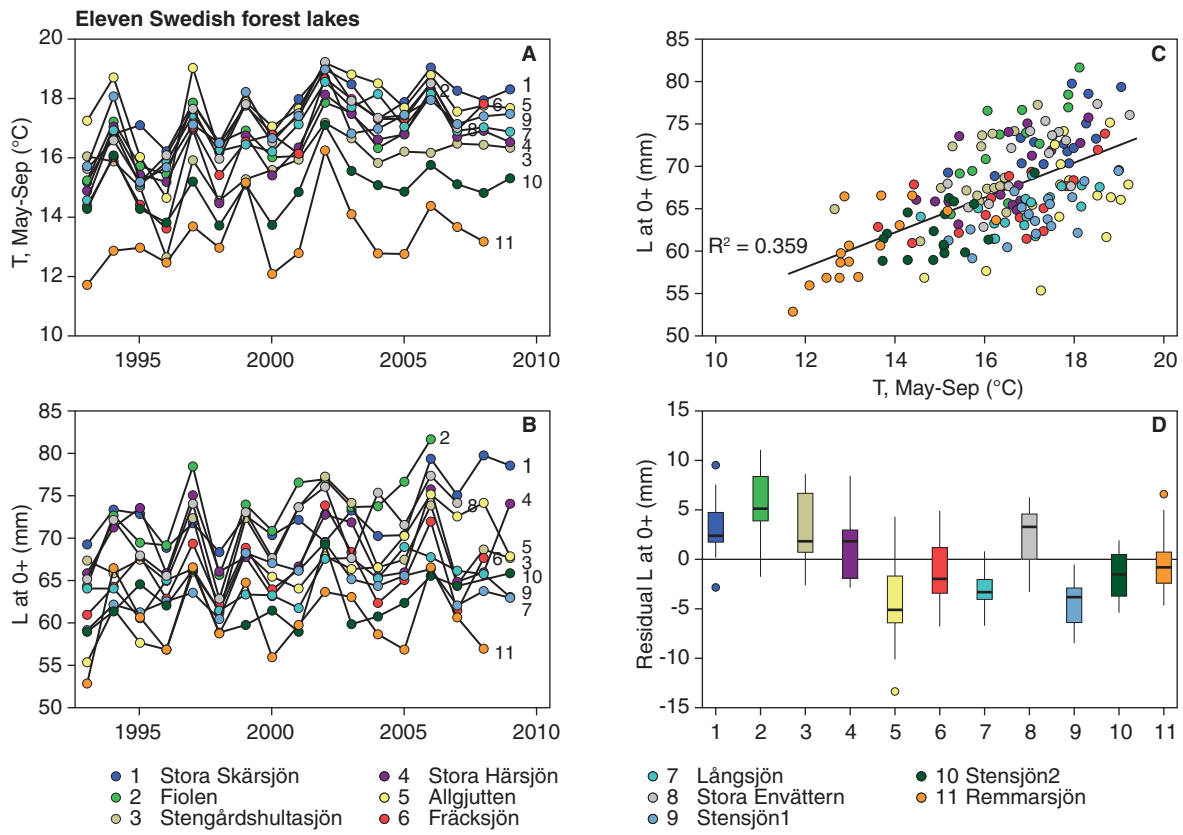


Fig4

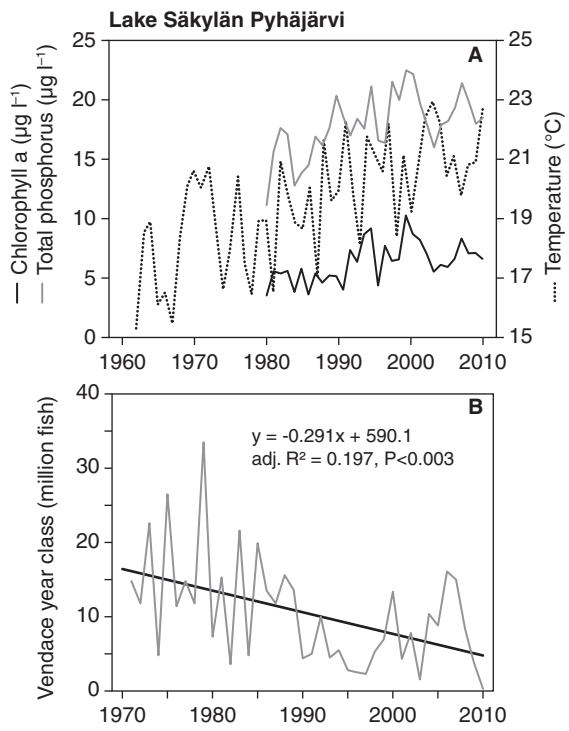


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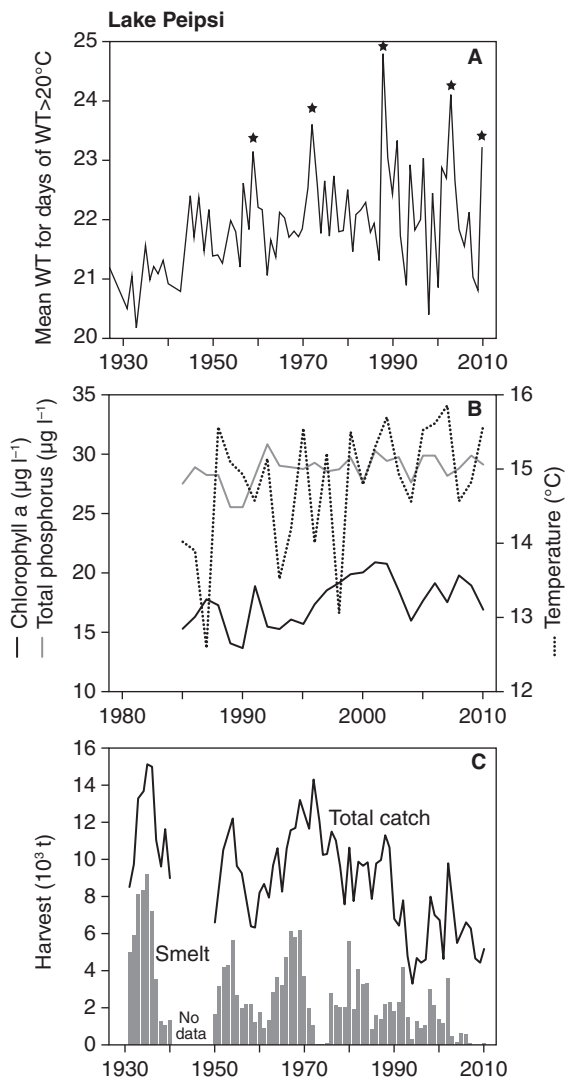




Fig6

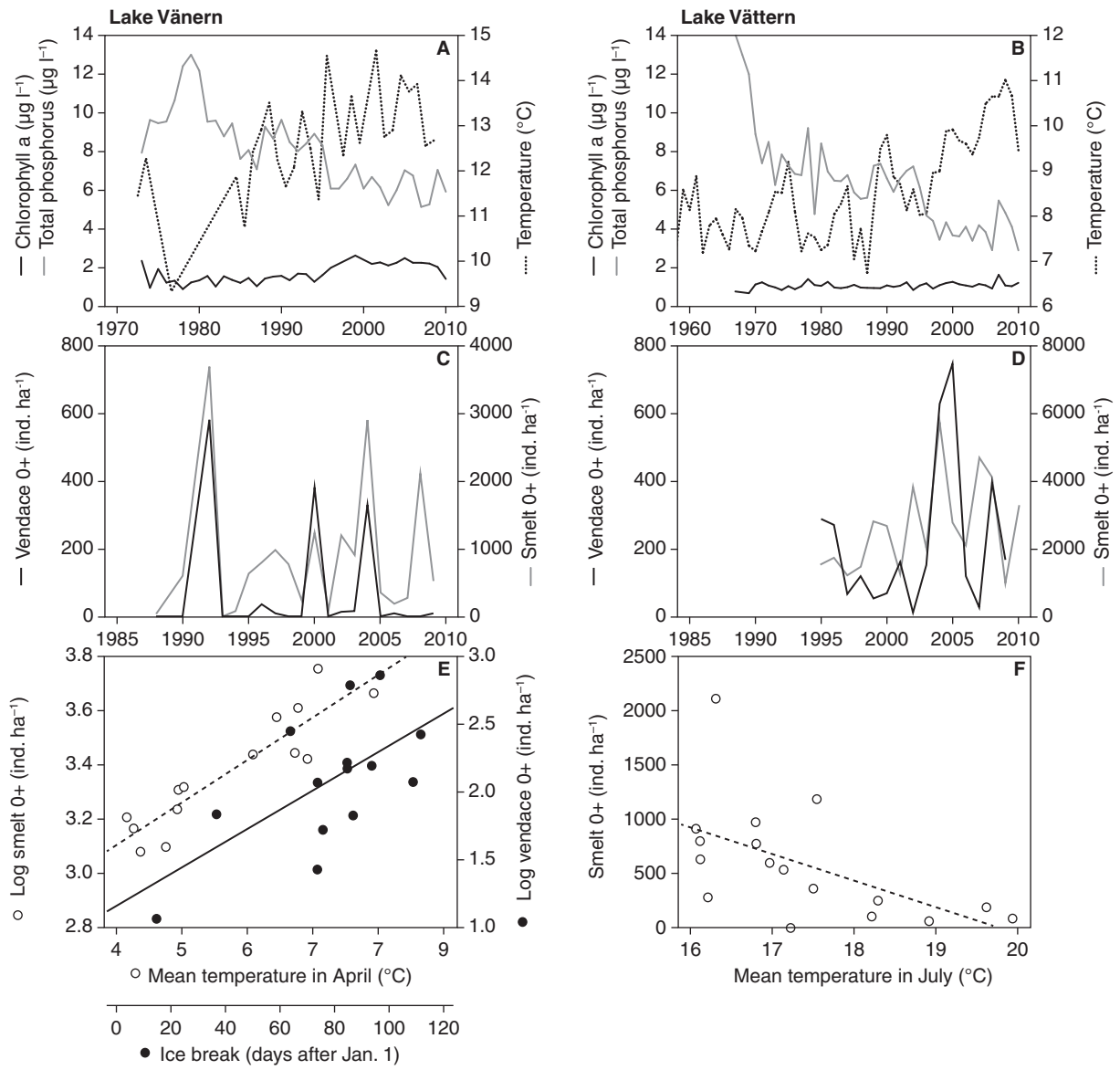


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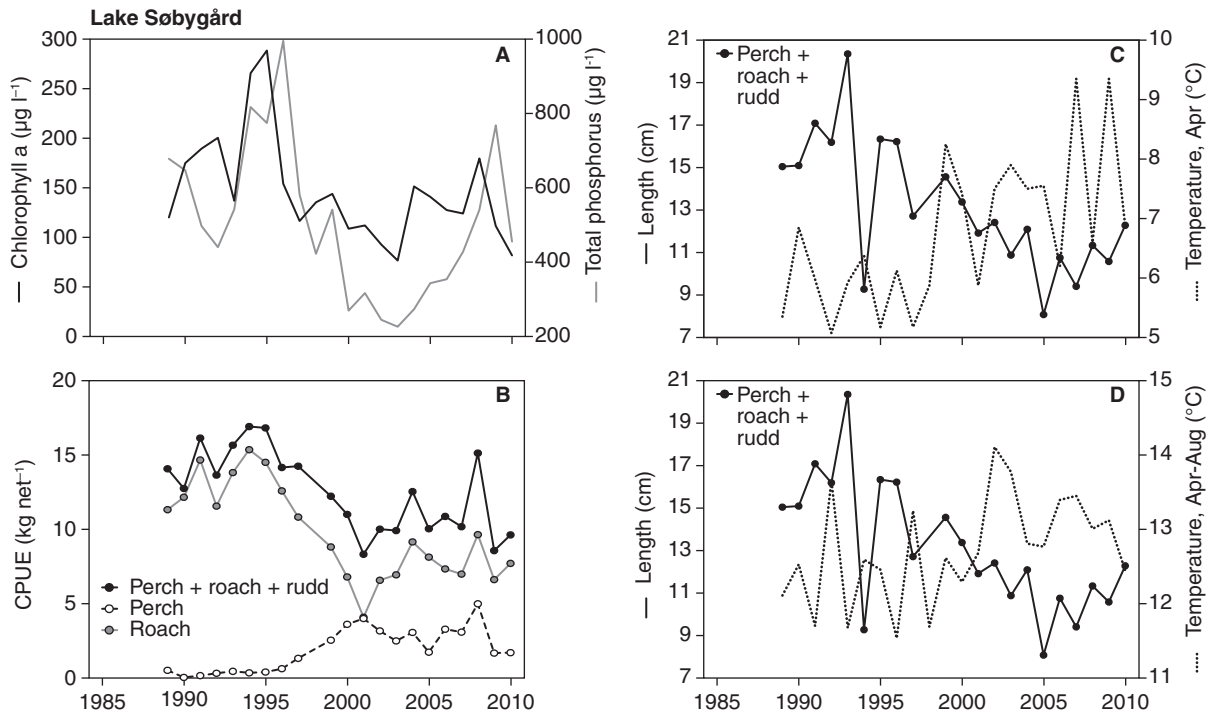


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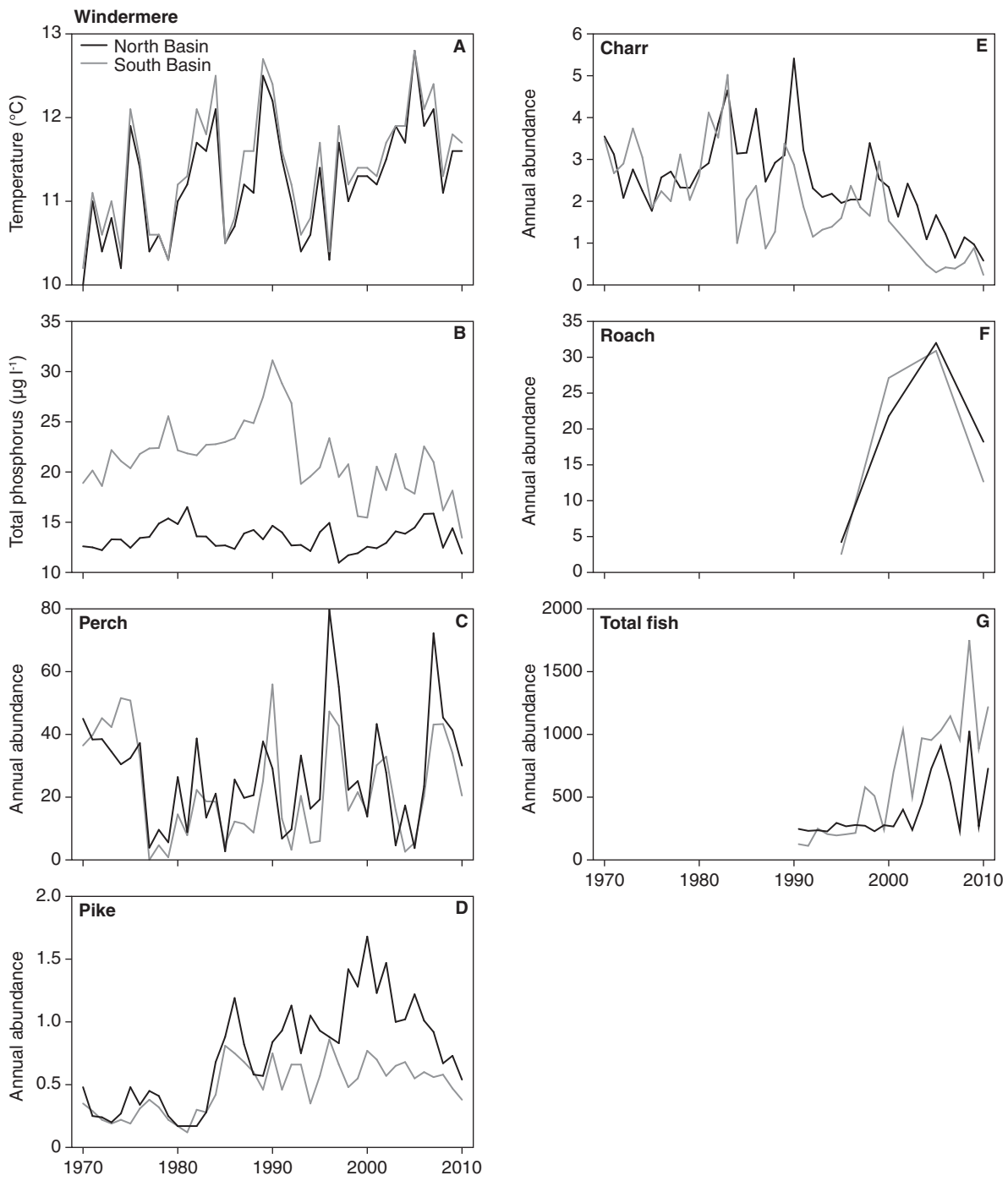


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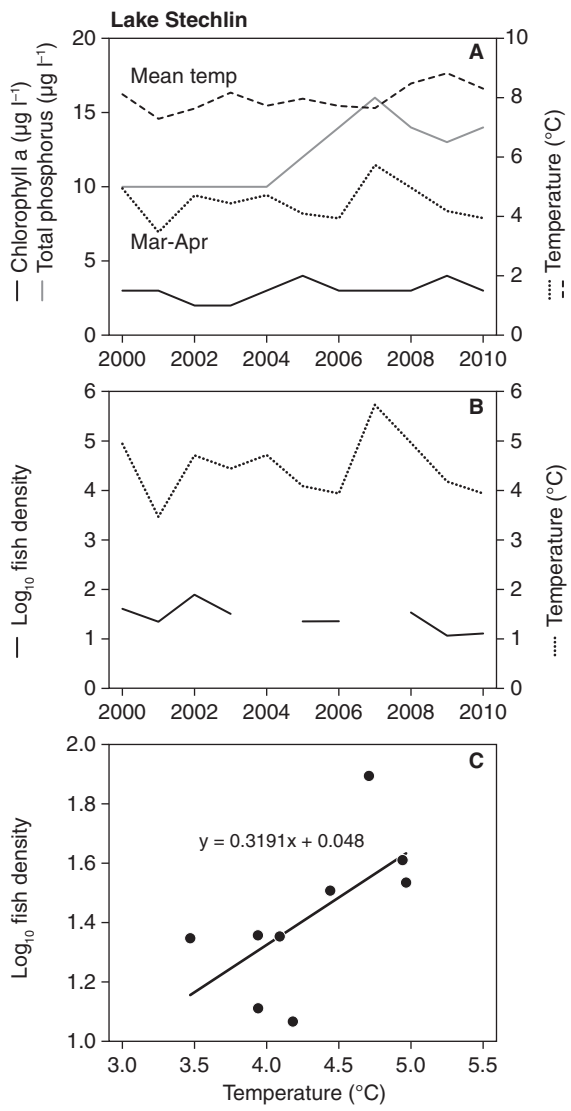


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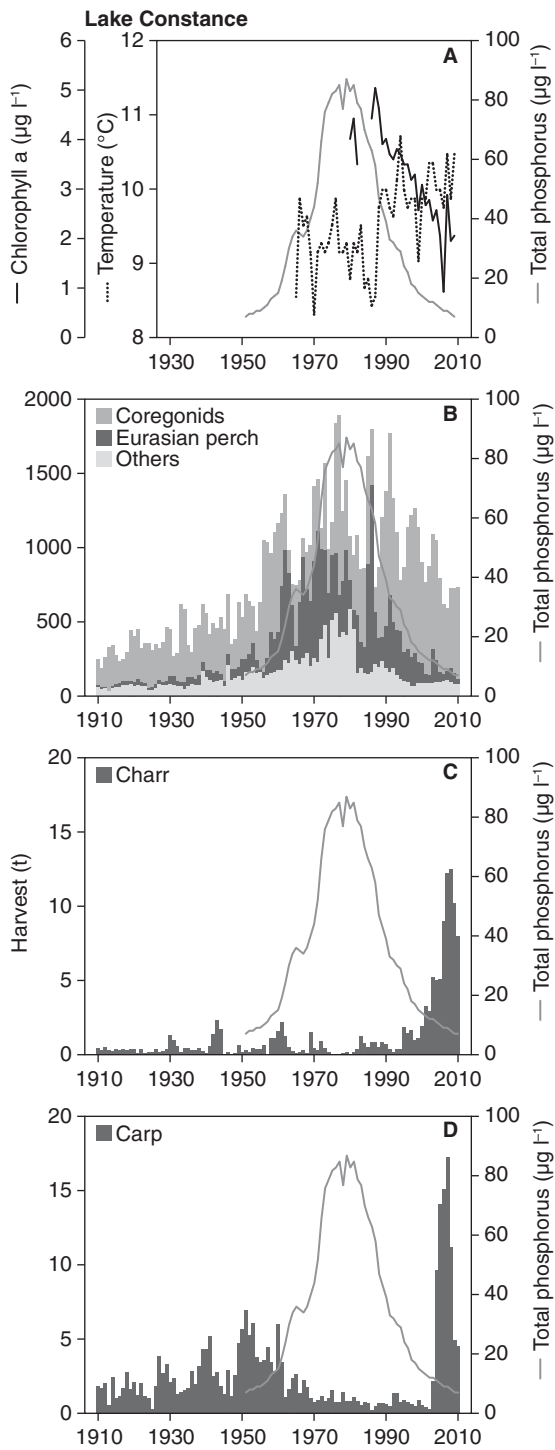


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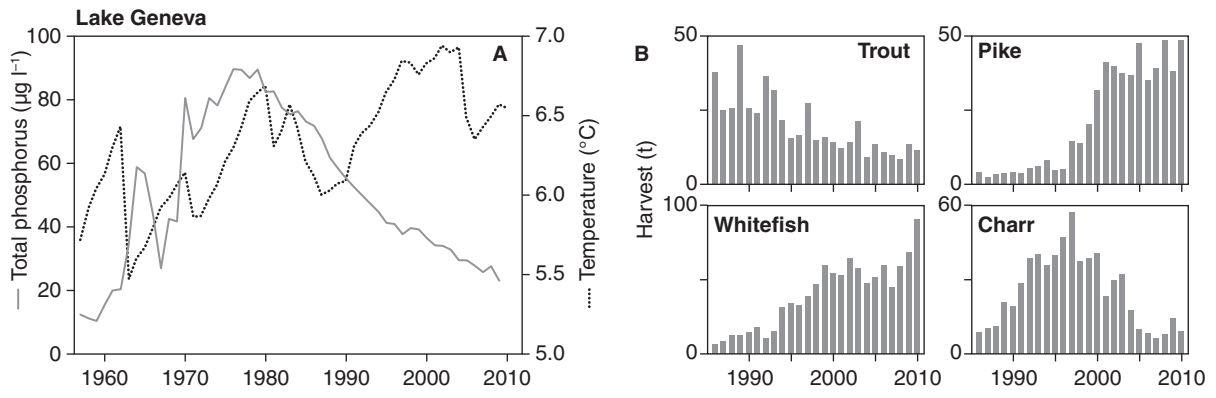


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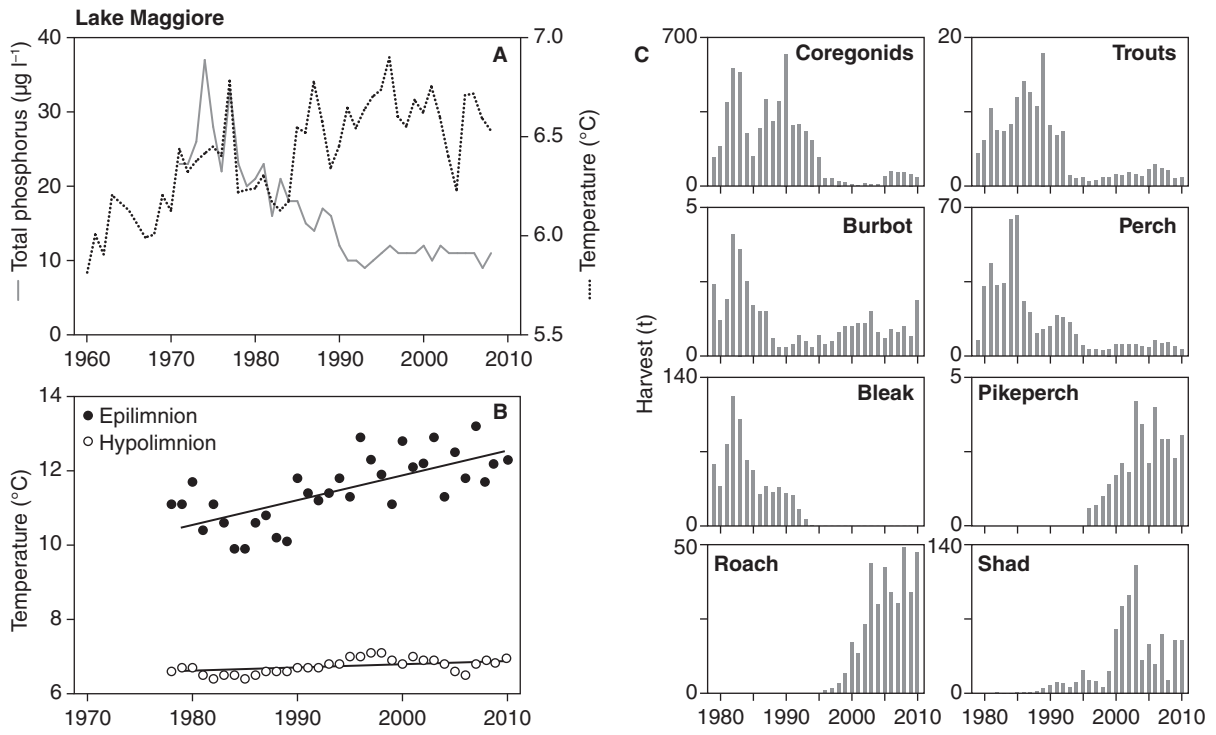


Fig13

