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Are we heading towards a global decrease in coregonine catches?

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Abstract – Coregonines have specific ecological needs, making them potentially very vulnerable to changes in lake conditions. A contemporary concern is that many lakes worldwide are experiencing environmental changes due to anthropogenic pressure and climate warming. Here, we compiled long-term data of coregonine catches from 27 lakes from three continents in the northern hemisphere. Declines in catch were observed in 67% of the lakes during the first two decades of the 21st century, with a significant trend (p-value<0.05) in 44% of the cases. An analysis to determine whether trends are globally linked to environmental conditions and specific lake attributes was carried out on 26 lakes for the period 2000–2019. Several local declines in catches had already been documented in the literature and are likely to be due to local forcing such as nutrients, species invasions and changes in fishing practices. Nevertheless, on a global scale, our results indicate that lakes, which exhibited a significant decrease in catch were larger and more nutrient-poor than other lakes. The rate of change in catches appeared to be related to the trophic state of the lake. The specific effect of warming is difficult to determine during the studied period. When warming occurred outside the period of egg incubation, decreasing trends were more frequently observed in nutrient-poor than in mesotrophic lakes. In conclusion, our findings suggest that achieving oligo- or ultraoligotrophic conditions, as required in developed countries to control phytoplankton blooms and enhance water quality, could pose significant challenges for future management of coregonine fisheries.

Keywords: long-term catch data / fisheries / global warming / re-oligotrophication / water quality

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1 Introduction

Lakes are invaluable freshwater systems that provide numerous benefits to humankind, including drinking water, irrigation, transport, recreation and food supply (Jenny *et al.*, 2020; Weyhenmeyer *et al.*, 2024). In the northern hemisphere, coregonines (*Salmonidae*) are highly prized by commercial and recreational fishers. They have constituted an important protein source for local communities and contributed to substantial revenue incomes to millions of people for centuries (Baer *et al.*, 2017; Tammiksaar and Kangur, 2020; FAO, 2022). Most coregonines are either planktivores or benthivores and their foraging on zooplankton can induce trophic cascades (Vanni *et al.*, 1990). Coregonines also have specific ecological needs. They are cold-water-adapted species with embryos requiring a sufficient oxygenated water-sediment interface for successful development and hatching (Müller, 1992; Eckmann, 2013). Adults require a specific range of oxythermal habitat (Fang *et al.*, 2012; Kumar et al., 2013, Jacobson *et al.*, 2013), although they are more tolerant to hypoxia (dissolved oxygen <2 mg/l) in winter (Rodrigues *et al.*, 2022). These ecological needs make them sensitive to changes in habitat conditions and a useful sentinel of lake water quality and ecological state (Jeppesen *et al.*, 2012).

During the last few decades, scientists have warned that human activities are threatening lakes, and leading to rapid degradation as a result of cumulative impacts combined with other emerging stressors (Jenny *et al.*, 2020). For example, eutrophication, oxythermal habitat loss and inappropriate fisheries management have contributed to the decline of coregonine populations in many lakes (Svärdson, 1976; Vonlanthen *et al.*, 2012; Sandlund *et al.*, 2013; Anneville *et al.*, 2015) and have resulted in major challenges for restoration and management (Bunnell *et al.*, 2024). Furthermore, while local disturbances such as eutrophication and dam construction can be overcome through management actions, climate change is a broader challenge with relatively limited local solutions for natural-resource managers. Climate change is expected to exacerbate the negative impacts of invasive species and anthropogenic stressors, especially eutrophication, with detrimental effects on coregonine populations (Collingsworth *et al.*, 2017). In particular, climate change is expected to induce eutrophication-like problems (Bosch *et al.*, 2014), lower levels of dissolved oxygen (Jane *et al.*, 2021), and reduce ice cover (Jensen *et al.*, 2007; Woolway *et al.*, 2020), each of which could indirectly impair coregonid survival and reproduction success (Brown *et al.*, 1993; Müller and Stadelmann, 2004). In fact, a negative future for coregonines due to climate change is already predicted by *in-situ* observations (Jacobson *et al.*, 2012; Jeppesen *et al.*, 2012; Kangur *et al.*, 2022), experiments and models (e.g. Lynch *et al.*, 2015; Kao *et al.*, 2015, DeWeber *et al.*, 2022; Stewart *et al.*, 2024a). Warmer summers are likely to impact abundances (Jacobson *et al.*, 2012), with heatwaves reducing oxythermal habitats and inducing strong coregonine mortalities. Temperature affects the fish endocrine system, and high temperatures can inhibit the production of ovarian oestrogen and thus delay the reproduction process (Numann, 1970; Gillet 1991; Pankhurst and Munday, 2011; Servili *et al.*, 2020). Furthermore, warmer temperatures or reduced ice cover during incubation enhance egg mortality and larval malformations (Brooke, 1975; Cingi *et al.*, 2010; Stewart *et al.*, 2021). Those changes also alter the dynamics of egg development (Stewart *et al.*, 2021; Roberts *et al.*, 2024; Stewart *et al.*, 2024b), affecting the hatching time, size-at-hatching and may result in spatiotemporal mismatch between larvae and the emergence of the required prey. Taken together, climate-induced changes to water temperature and quality are predicted to reduce reproductive and recruitment success and induce a global decrease in coregonine populations.

The fate of coregonine catches in response to a changing climate is also highly uncertain due to complex ecosystem processes. Total coregonine catch has decreased at the continental scale (Baer *et al.*, 2021), but aggregated national statistics may not reflect the temporal trends in reported catches of individual lakes. Coregonines exhibit intra- and inter-specific differences in temperature tolerances (Stewart *et al.*, 2021), lake warming is non-uniform across the globe (Wahl and Peeters, 2014; O'Reilly *et al.*, 2015; Öğlü *et al.*, 2020), and lake characteristics such as morphology and stratification patterns are highly variable. Therefore, coregonine populations in nearby lakes might not be equally affected by climate change (Sandström *et al.*, 2014), especially if the populations have access to thermal refuges (Kao *et al.*, 2015) and/or if their egg development has remained unaffected by rising temperatures. Furthermore, warming may benefit coregonines in some cases. For example, a warm spring temperature increased coregonid larvae growth in several lakes (Eckmann and Rösch, 1998; Perrier *et al.*, 2012; Göbel *et al.*, 2017). Faster spring warming rates may enhance larvae growth rates and thus reduce size-dependent mortality and improve recruitment success (Zhu *et al.*, 2015). Also, the number of eggs per spawner and egg size has increased in several whitefish species with increasing growth (Rösch, 1987). Those positive effects of temperature suggest possible increased coregonine production if food resources are available for larvae (Trippel *et al.*, 1991). Finally, some stocks have been maintained or increased because of effective water-quality management strategies, stocking, fishing regulation rules and conservation practices (Bunnell *et al.*, 2023; Bunnell *et al.*, 2024; Rogissart *et al.*, 2024). For example, lake recovery from eutrophication can improve coregonine reproduction success and result in significant increases in coregonine yield (Ludsin *et al.*, 2001; Anneville *et al.*, 2017). Coregonine re-introduction has also been achieved in some ecosystems where the taxon was extirpated (Borcherding *et al.*, 2010; Conley *et al.*, 2021). Accordingly, when implementing appropriate management programs, we might expect stability or recovery of coregonine stocks. Nevertheless, the impacts of ongoing global changes on regulatory mechanisms within populations and communities are likely to result in various outcomes for management efforts across lakes and through time (Baer *et al.*, 2023). Much remains to be learned about the overall trends in coregonine fisheries in this context of multiple anthropogenic pressures and a strong desire to protect aquatic ecosystems.

We collected commercial catch statistics data for coregonines from 27 northern hemisphere lakes (Fig. 1). Long-term changes in harvest are already documented in the literature for some of these lakes, but over different time-periods and using different statistical methods between lakes, making it challenging to extract a global pattern. Consequently, in this study,
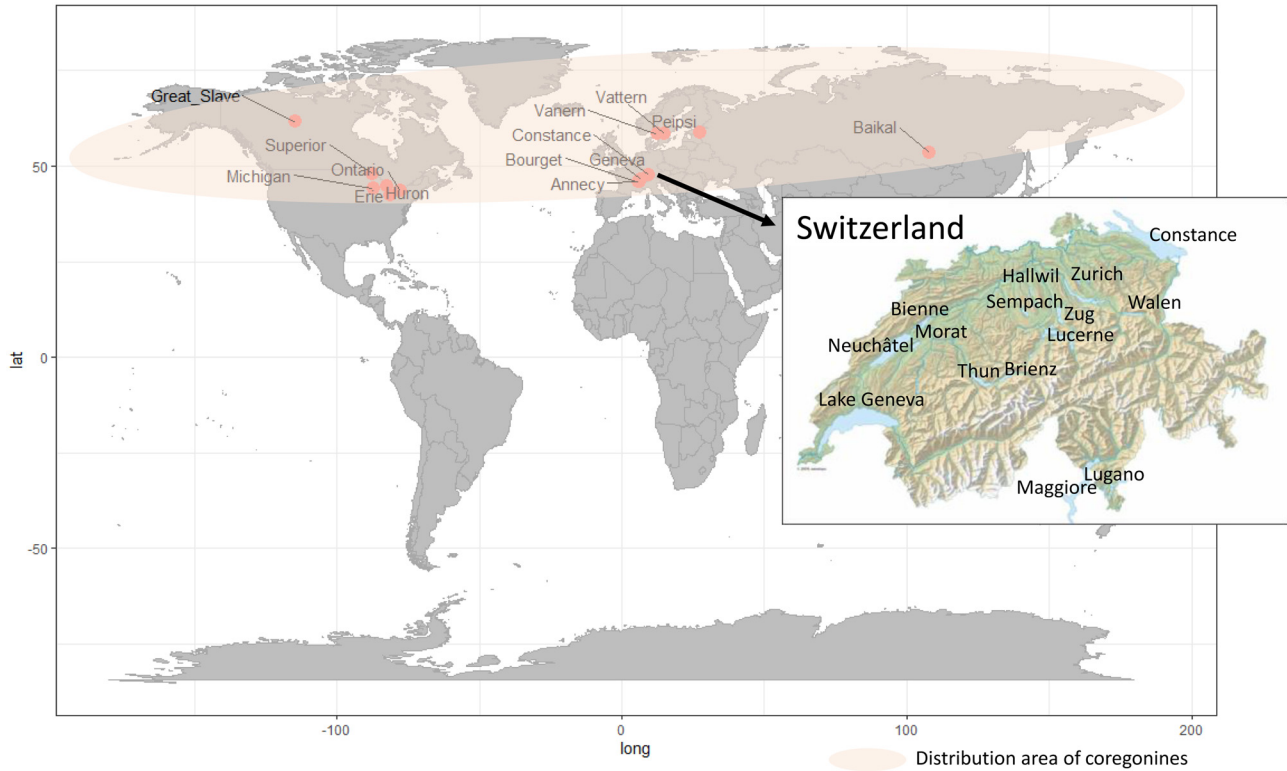
Fig. 1. Map indicating the geographical location of the 27 lakes included in the analysis.

we applied a consistent methodology for global analysis with the objective of determining whether coregonine catches have a globally consistent downward trends during the first two decades of the 21st century as the negative effects of climate change on lake ecosystems became more prevalent worldwide (Woolway *et al.*, 2020). Furthermore, the integrated dataset was also used to ascertain whether trends are globally associated with environmental conditions or lake characteristics (e.g., geographical location, size, water quality). Finally, we discuss implications of our findings for water quality improvement and coregonine fisheries management.

2 Material and methods

2.1 Study sites and data sources

We compiled and harmonized a suite of environmental, and long-term data on climate and coregonine catches from lakes in Asia (n=1), North America (n=6) and Europe (n=20). We used time series of coregonine annual catches in biomass between 2000 and 2019. Any co-occurring coregonine species or morphs were summed due to limited taxonomic resolution in some time series (Supplementary Tab. 1). The data used are therefore total coregonine catches. Catch data came from commercial fisheries statistics (Supplementary Tab. 2), except for Great Slave Lake where all commercial gillnet harvests for coregonines were co-managed by Freshwater Fish Marketing Corporations and Fisheries and Oceans Canada (DFO). Commercial fisheries catches were generally from gillnets and trapnets. Long-term changes in fishing effort or CPUE (Catch Per Unit Effort) were available for only 4 lakes

(Supplementary Tab. 1) and good correlations between CPUE and catches were observed for these lakes (Tab. 1). Therefore, although catches do not perfectly reflect population abundance and should be interpreted with caution, we assume, in accordance with previous work, that catch data are an interesting proxy for changes in stock abundance and remain an important data source to be used (Pauly *et al.*, 2013). However, in 3 lakes (Peipsi, Vänern and Vättern) there have been severe restrictions of fisheries, and special attention has been paid to how this might affect our results (see Statistical analysis section and discussion).

Descriptor data for lake morphology, geography, trophic state, and warming rate were compiled (Tab. 2). Fifty-six percent of the lakes had a surface area larger than 100 km². Lake Baikal was the deepest lake (max depth: 1637 m) and Lake Peipsi was the shallowest (max depth: 15 m). All the lakes, except Great Slave Lake, experienced eutrophication but only four lakes (15%) remain eutrophic. Sixteen lakes (59%) have been restored to an oligotrophic or ultraoligotrophic state (Tab. 2A). The recent lake trophic state communicated by data providers or literature sources were used as an explanatory variable (Steinsberger *et al.*, 2020; Dove and Chapra, 2015; Rimet *et al.*, 2020; MacKenzie *et al.*, 2022). For the analysis, this qualitative variable was converted into a quantitative categorical variable that refers to a phosphorus concentration. Specifically, each lake was given the median value of the theoretical range of total phosphorus (TP) corresponding to its trophic state (Vollenweider and Kerekes, 1982). Eutrophic, mesotrophic, oligotrophic, and ultra-oligotrophic conditions were assigned TP values of 68 µg/L, 23 µg/L, 7 µg/L and 2 µg/L, respectively.

Table 1. Average annual catches and standard deviation (2000–2019) in each of the studied lakes. Changes in fishing effort were documented in some lakes (SupTable 1) and, when data were available, correlations were made between catches and catch per unit effort (CPUE).

Lake	Mean annual catches (Tonnes)	Standard deviation	Substantial change in fishing effort that may have affected trends over the studied period	Correlation between CPUE and catches
Annecy	11.43	3.59	No	Pearson:0.56, p-val<0.05
Baikal	813.46	441.83	Unknown	–
Bienne	88.64	29.01	Unknown	–
Bourget	31.71	28.41	No	Pearson:0.90, p-val<0.01
Brienz	3.89	2.49	Unknown	–
Constance	530.63	227.98	Unknown, actual under analyses	–
Erie	248.15	197.88	No	–
Geneva	385.66	200.34	No	Pearson:0.83, p-val<0.01
Great Slave	493.48	244.52	No	–
Hallwil	9.27	4.72	Unknown	–
Huron	2852.01	1064.74	No	–
Lucerne	91.93	15.77	Unknown	–
Lugano	1.31	01.04	Unknown	–
Maggiore	10.10	4.58	Unknown	–
Michigan	2208.23	593.66	No	–
Morat	1.44	1.10	Unknown	–
Neuchâtel	209.47	63.02	No	Pearson:0.89, p-val<0.01
Ontario	48.77	29.2	No	–
Peipsi	75.72	182.8	Closure from 2001 to 2006 of vendace fishery	–
Sempach	73.93	22.38	Unknown	–
Superior	2246.19	369.85	No	–
Thun	36.13	10.06	Unknown	–
Vänern	291.18	67.79	Reduce whitefish fishery and shift on crayfish − increase vendace fishery	–
Vättern	10.16	6.95	Reduce whitefish fishery and shift on crayfish	–
Walen	5.42	2.11	Unknown	–
Zug	10.95	11.29	Unknown	–
Zurich	123.49	50.2	Unknown	–

The rate of change in summer lake surface water temperature were integrated from O'Reilly *et al.* (2015) and were recorded for fourteen lakes (Tab. 2B). In addition, seasonal air temperature anomalies were downloaded from Climate Reanalyzer (Climate Change Institute, University of Maine (US), https://climatereanalyzer.org/research_tools/monthly_tseries/). Data were simulated for six geographical regions corresponding to the location of the lakes (Tab. 2B). The rate of change and direction of trends were computed using the Sen's slope method which estimates the median rate of linear change over a time-period (Sen, 1968; Hirsch *et al.*, 1982). Sen's slope values were used as proxies to quantify the strength of the pressure related to the changes in weather conditions resulting from climate change. While catch data were only from 2000 to 2019, Sen's slopes of temperature anomalies were computed over the last three decades. A 30-year timeframe is usually required to properly capture the global climate-induced changes and better account for cyclic climate variabilities in response to the large-scale variability of the natural tele-connection modes (Hurrell, 1995; Dahlin and Ault, 2018).

2.2 Statistical analysis

The analysis focused on the period from 2000 to 2019, which was common to all lakes except Baikal (started in 2007).

Because of strong inter-lake differences in the size-related-carrying capacity of the lake (larger lakes are potentially expected to host more fish) and the fishing effort (e.g. number of fishermen, fishing regulations), the range of catch variability differs between lakes (Tab. 1). For this reason, and because of our focus on temporal trends instead of absolute catches, each time series was standardized to zero mean and unit standard deviation prior to the analyses. Analyses were carried out in R version 4.1.0 (R Core Team, 2021) and results were visualized using "ggplot2" (Wickham, 2016).

Our approach combined different methods that provide complementary elements for the analysis of temporal trends in order to obtain a complete overview; accordingly, our study is divided into 3 steps.

In the first step, we compared long-term changes and identified temporal patterns to provide a global picture of inter-annual variabilities and commonalities among lake catches. To determine whether catch rates were synchronous among lakes, we estimated the Pearson's correlation coefficient between catch time series of all possible pairs of lakes. We used a heatmap coupled to hierarchical cluster analysis (R package *pheatmap*) to quantitatively group lakes into clusters based on levels of similarity (or correlation) between their temporal catch trajectories. Individual lake trends in catches were extracted using a non-parametric regression method, the local

Table 2. A. Country, (FR: France; RU: Russian Federation ; CH: Switzerland ; DE: Germany ; AT: Austria ; CA: Canada; US: United States of America; IT: Italy ; EE: Estonia ; SE: Sweden), latitude, morphologic characteristics and current trophic status with total phosphorus estimates (TP) of the 27 studied lakes. The lake volumes were estimated as the product of the average depth and the lake area. B: Trends, expressed as Sen's slope values, in lake summer surface water temperature (LSSWT) from O'Reilly *et al.* (2015), and trend in seasonal air temperatures (Winter: from December of the previous year to February, Spring: March to May; Summer: June to August; Autumn: September to November). Significant trends (p-value<0.05) are indicated with an asterisk.

Table 2A.

Lake	Country	Latitude (dec.deg)	Elevation (m)	Average depth (m)	Maximum depth (m)	Lake area (km²)	Estimated volume (km³)	Trophic status - TP (µg.L⁻¹)
Annecy	FR	45.85	447	41	65	27	1.11	Ultra-oligotrophic - 2
Baikal	RU	53.50	457	749	1637	31500	23 593.50	Oligotrophic - 7
Bienne	CH	47.08	429	30	74	39.3	1.18	Mesotrophic - 23
Bourget	FR	45.76	231	80	147	44	3.52	Mesotrophic - 23
Brienz	CH	46.72	564	173	260	30	5.19	Ultra-oligotrophic - 2
Constance	DE/CH/AU	47.59	395	90	251	536	48.24	Oligotrophic - 7
Erie	US/CA	42.22	173	19	64	25700	488.30	Mesotrophic - 23
Geneva	FR/CH	46.45	372	153	309.7	580.1	88.58	Mesotrophic - 23
Great Slave	CA	61.54	156	41	614	28 568	1171.29	Oligotrophic - 7
Hallwil	CH	47.28	449	28	48	10.3	0.29	Mesotrophic - 23
Huron	US/CA	44.80	176	59	229	59600	3516.40	Ultra-oligotrophic - 2
Lucerne	CH	46.91	434	104	214	113.6	11.81	Oligotrophic - 7
Lugano	CH/IT	46.01	271	134	288	49	6.57	Mesotrophic - 23
Maggiore	CH/IT	45.95	193	177	372	213	37.70	Oligotrophic - 7
Michigan	US	44.05	176	85	282	57800	4913.00	Ultra-oligotrophic - 2
Morat	CH	46.93	429	24	45	21.6	0.52	Eutrophic - 68
Neuchâtel	CH	46.91	429	64	152	218.3	13.97	Oligotrophic - 7
Ontario	US/CA	43.64	74	86	244	18960	1630.56	Oligotrophic - 7
Peipsi	EE/RU	58.68	30	7	15.3	3555	25.24	Eutrophic - 68
Sempach	CH	47.14	504	44	87	14.5	0.64	Eutrophic - 68
Superior	US/CA	47.94	183	147	406	82100	12068.70	Ultra-oligotrophic - 2
Thun	CH	46.68	558	136	217	48.3	6.57	Ultra-oligotrophic - 2
Vänern	SE	58.37	44	27	106	5450	147.15	Oligotrophic - 7
Vättern	SE	58.53	89	40	120	1939	77.37	Ultra-oligotrophic - 2
Walen	CH	47.12	419	105	150	23.2	2.44	Ultra-oligotrophic - 2
Zug	CH	47.13	417	83	198	38.3	3.18	Eutrophic - 68
Zurich	CH	47.30	406	49	133	88.2	4.32	Mesotrophic - 23

Table 2B.

Lake	Lake SSWT trend (°C.decade⁻¹)	Winter air temperature trend (°C.year⁻¹)	Spring air temperature trend (°C.year-1)	Summer air temperature trend (°C.year⁻¹)	Autumn air temperature trend (°C.year⁻¹)
Annecy	-0.14	0.02	0.04	0.05*	0.06*
Baikal	NA	-0.01	0.05*	0.04	0.02
Bienne	NA	0.02	0.04	0.05*	0.06*
Bourget	0.42	0.02	0.04	0.05*	0.06*
Brienz	NA	0.02	0.04	0.05*	0.06*
Constance	0.53	0.02	0.04	0.05*	0.06*
Erie	0.08	0.01	0.01	0.00	0.04
Geneva	0.11	0.02	0.04	0.05*	0.06*
Great Slave	0.15	0.06	-0.02	0.04	0.05
Hallwil	NA	0.02	0.04	0.05*	0.06*
Huron	0.85	0.01	0.01	0.00	0.04
Lucerne	NA	0.02	0.04	0.05*	0.06*
Lugano	NA	0.02	0.04	0.05*	0.06*
Maggiore	0.31	0.02	0.04	0.05*	0.06*
Michigan	0.42	0.01	0.01	0.00	0.04
Morat	NA	0.02	0.04	0.05*	0.06*
Neuchâtel	NA	0.02	0.04	0.05*	0.06*
Ontario	0.33	0.01	0.01	0.00	0.04

Table 2. (continued).

Table 2B.

Lake	Lake SSWT trend (°C.decade^{-1})	Winter air temperature trend (°C.year^{-1})	Spring air temperature trend (°C.year-^{1})	Summer air temperature trend (°C.year^{-1})	Autumn air temperature trend (°C.year^{-1})
Peipsi	NA	-0.01	0.03	0.04	0.06*
Sempach	NA	0.02	0.04	0.05*	0.06*
Superior	1.16	0.01	0.01	0.00	0.04
Thun	NA	0.02	0.04	0.05*	0.06*
Vänern	0.62	0.00	0.03	0.03	0.06*
Vättern	0.63	0.00	0.03	0.03	0.06*
Walen	-0.33	0.02	0.04	0.05*	0.06*
Zug	NA	0.02	0.04	0.05*	0.06*
Zurich	NA	0.02	0.04	0.05*	0.06*

polynomial regression fitting, using the LOESS function (smoothing parameter equal to 0.8) in the R package *stats* (R Core Team, 2021). We used a Dynamic Factor Analysis (DFA), from the R package *MARSS* (Holmes *et al.*, 2012), to further evaluate the coherence of the temporal trends in catches between lakes and detect common patterns in time series. Dynamic Factor Analysis is a dimension-reduction technique designed for time-series data to estimate underlying common patterns in a set of time series by modelling multiple, nonstationary time series of observed data as a linear combination of shared hidden trends, potential explanatory variables, and observed errors. A matrix of factor loadings on the hidden trends determines the exact form of the linear combinations of the common trends. Comparing factor loadings among lakes can help identify which common trends are important to a particular lake and which lakes are related to the specific common trend.

In the second step, we described the temporal trends of catches in individual lakes based on their direction, their rate of change, and their significance. The direction and rate of change were assessed with the aforementioned Sen's slope method (Sen, 1968; Hirsch *et al.*, 1982) and ran on the standardized catches. We then used the Mann-Kendall trend test to determine whether a time series had a significant monotonic upward or downward trend. The package *trend* was used for Sen's slope and Mann-Kendall computations.

In the third and final step, we determined lake characteristics and environmental variables that were most important in explaining the rate of change and decrease in coregonine catches. Spearman rank correlations were first used to identify significant relationships between the rate of changes in catches, expressed as Sen's slopes of individual lakes, versus the explanatory variables listed in Table 2 (latitude, elevation, average depth, maximum depth, lake area, trophic state, water and air temperature warming rates). The correlations were computed considering all lakes (except Baikal) and they were validated on the set of lakes excluding the 3 lakes (L. Peipsi, Vänern and Vättern) where important change in fishing effort were documented during our studied period (Tab. 1). The correlations were also tested on the set of lakes presenting significant (p-value<.0.05) trends in the catches (results shown in supplementary Tab. 3). The explanatory variables that were correlated with the rates of change in catches

(expressed as Sen's slopes) were then used in an ordination approach to identify whether changes in coregonine catches could be explained by the combination of those environmental variables. We used a Hill and Smith Analysis because the data included a mix of quantitative and qualitative variables (Hill and Smith, 1976). We then used a discriminant analysis to test whether the selected environmental conditions could predict lake memberships to categories based on the magnitude and significance of their temporal trends (according to Sen's slopes and p-value from the Mann-Kendall trend). We used the R package "ade4" to run the Hill & Smith and discriminant analysis.

3 Results

3.1 Long-term trends in coregonine catches

Catch time series exhibited some common trends and patterns. Heat maps revealed negative and positive correlations between lakes (Fig. 2A), some of which were significant. The largest coherent group included 13 lakes that were widespread over North America and Europe, and most were characterized by a continuous decline in catch over the entire studied period according to the Dynamic Factor Analysis (Trend 2; Figs. 2B, C and 3). The Dynamic Factor Analysis highlighted two additional patterns (Fig. 2B). Trend 1 exhibited a decline but then a recovery at the end of the time series and Trend 3 exhibited a positive trend from 2000–2007 followed by a decline. Six lakes were associated with Trend 1 (decreasing, then increasing). When exploring for direction and significance of monotonic trends among Trend 1 lakes, Lake Peipsi presented a strong increased in catches although statistically significant at the 10% level (Fig. 3). In contrast, lakes Brienz and Wallen exhibited decreases in catches (respectively, p-value<0.05 and 0.1) over their time series despite having an increase in catches in the last five or so years. When looking for monotonic trends in the eight lakes associated with Trend 3 (increasing, then decreasing), three of these lakes had overall positive Sen's slopes and significant trends (lakes Morat, Bourget and Lugano), even with steep declines in recent years. Lake Baikal, conversely, had an overall significantly decreasing trend over its shorter time series (Fig. 3).
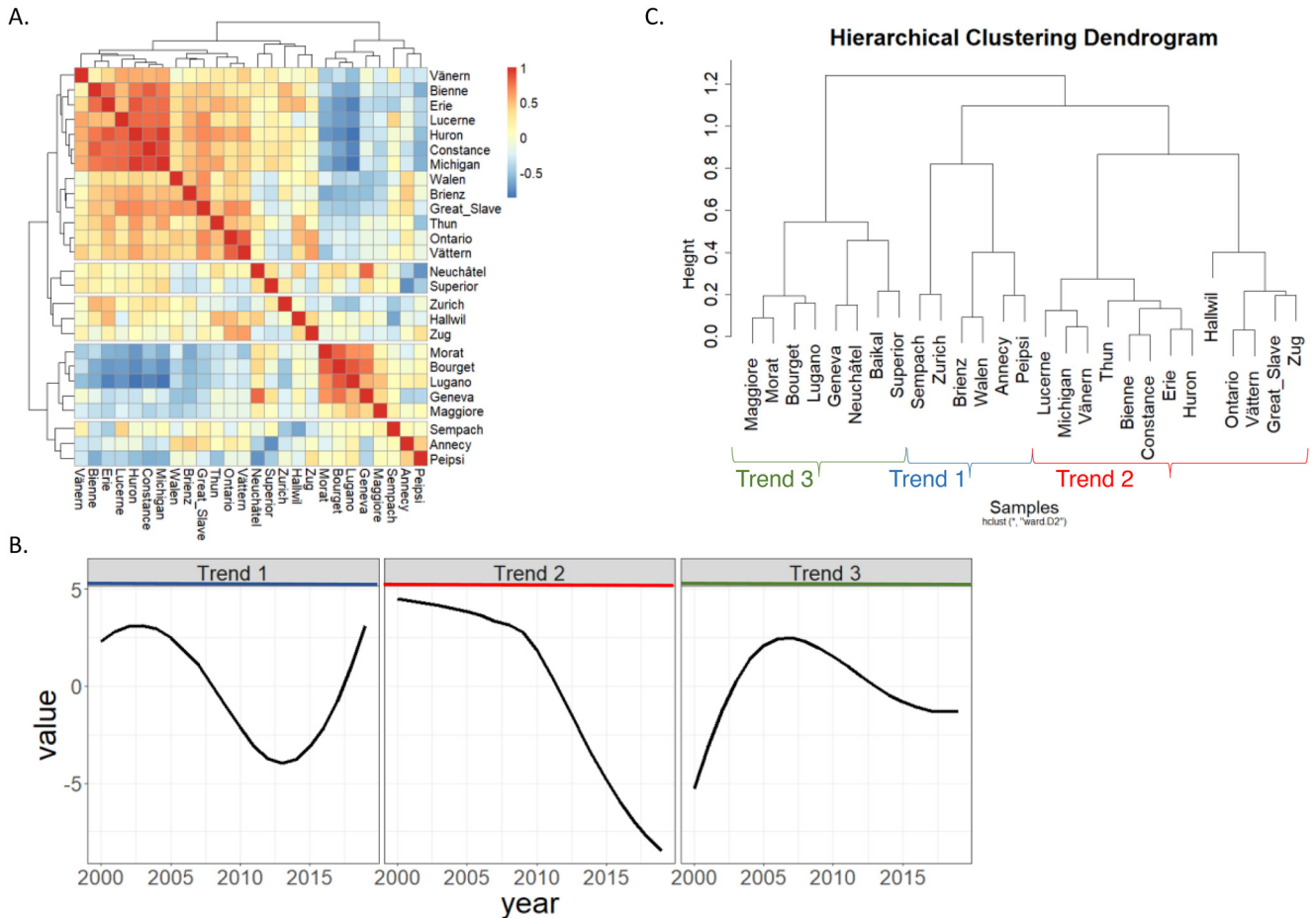
Fig. 2. (A) Heatmap to visualize correlations in coregonine catches among lakes over the period 2000 to 2019 (Baikal not included). (B) Three average temporal patterns identified by Dynamic Factor Analysis. (C) Dendrogram showing the gathering of lakes according to their contributions to the construction of the 3 temporal patterns.

Overall, almost half of the lakes had significant (p-value<0.05) decline in catches over the period from 2000 to 2019. Four lakes were in North America (Lakes Erie, Huron, Michigan, and Great Slave Lake), five in Western Europe (Bienne, Lucerne, Constance, Brienz, and Thun) and two in Sweden (Vänern and Vättern). Lake Baikal had a shorter time-series (2007–2019) but the observed decline of catches was highly significant (p-value<0.01).

3.2 Associating catch trends over 2000–2019 with lake characteristics and environmental variables

Correlations between the rate of changes in catches and lakes characteristics were significant for only three environmental variables (Fig. 4 and Tab. 3). These correlations remain significant (p-value<0.05) in the subset of lakes excluding the 3 lakes (L. Peipsi, Vättern and Vänern) with substantial changes in fishing effort (Tab. 3). Correlations were modest (R=0.48) to strong (R=-0.62) when focusing on lakes where trends were significant (Supplementary Tab. 3). The rates of change in catches were consistently negatively correlated with the lake area and the average lake volume, whereas positively correlated with TP. They differed between small-medium vs.

large lakes (p-value<0.1) and between rich vs poor-nutrient lakes (p-value<0.05). Our results indicated that lakes with lower phosphorus concentrations tended to have more negative Sen's slopes in their catch rates. In contrast, the highest positive rates of changes were recorded in small and eu- or mesotrophic lakes (Fig. 4). Spearman correlations revealed no pattern between declining catch rates and geographical area (e.g., latitude).

Significant (p-value<0.05) declines in coregonid catches were observed in specific lakes where the environmental characteristics differed significantly from the other lakes in terms of trophic state and size (Fig. 5). Accordingly, lakes where coregonine catches declined significantly were poorer in nutrients (Wilcoxon rank sum test, p-value<0.05) and larger (Wilcoxon rank sum test, p-value<0.1). Such a difference was significant at only 10% on the subset of lakes excluding the 3 lakes (Tab. 3). The large and oligotrophic Lake Baikal that was not considered for the comparison, also matched well with this pattern.

All the studied lakes were located in geographical areas with positive trends in air temperature over the last 30 years in at least three seasons (Tab. 2B). The magnitude of the air warming differed among geographical areas, but remained relatively low (between 0.005°C/year and 0.04°C/year) over
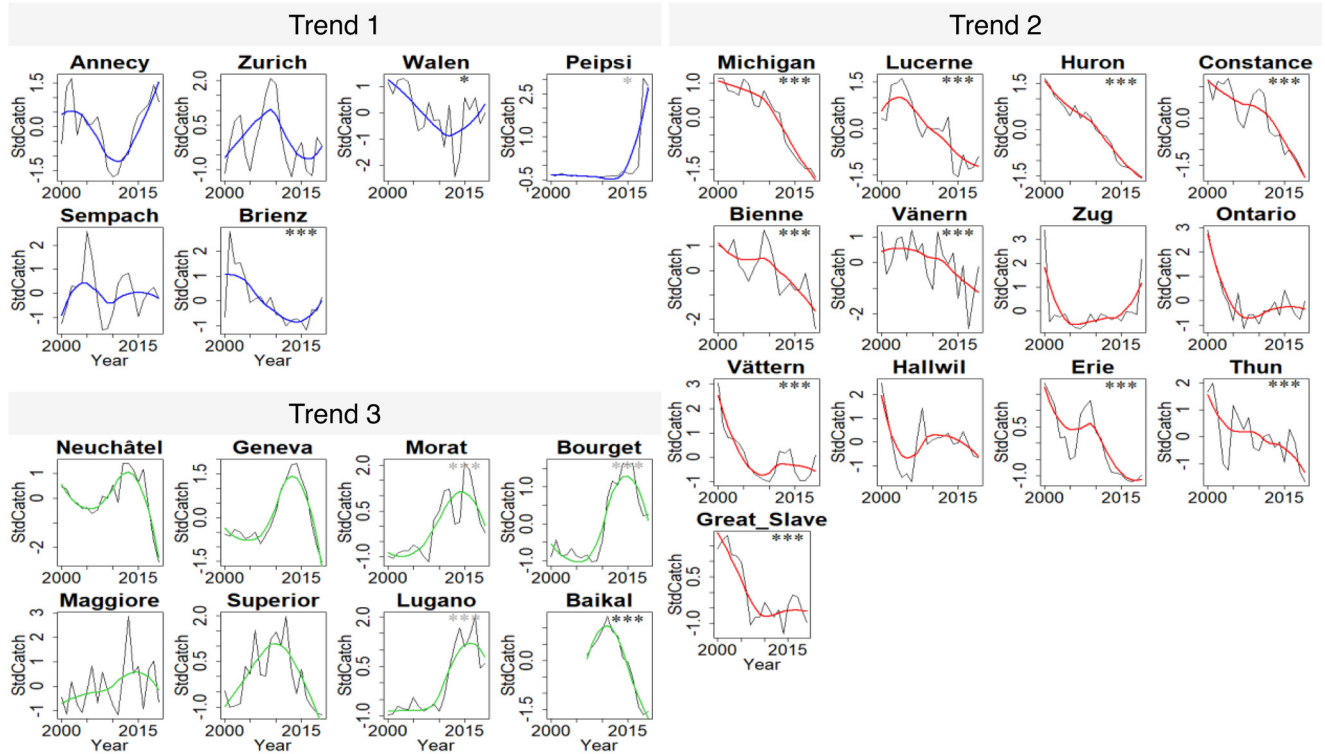
Fig. 3. Standardized catches and loess (80% smoothing pan). Trend 1, 2 and 3 represent the three patterns identified by the Dynamic Factor Analysis. Significant trends are indicated by *** (p-value<0.05), * (p-value<0.1). Blacks and grey asterisks indicate negative and positive Sen's slope respectively.
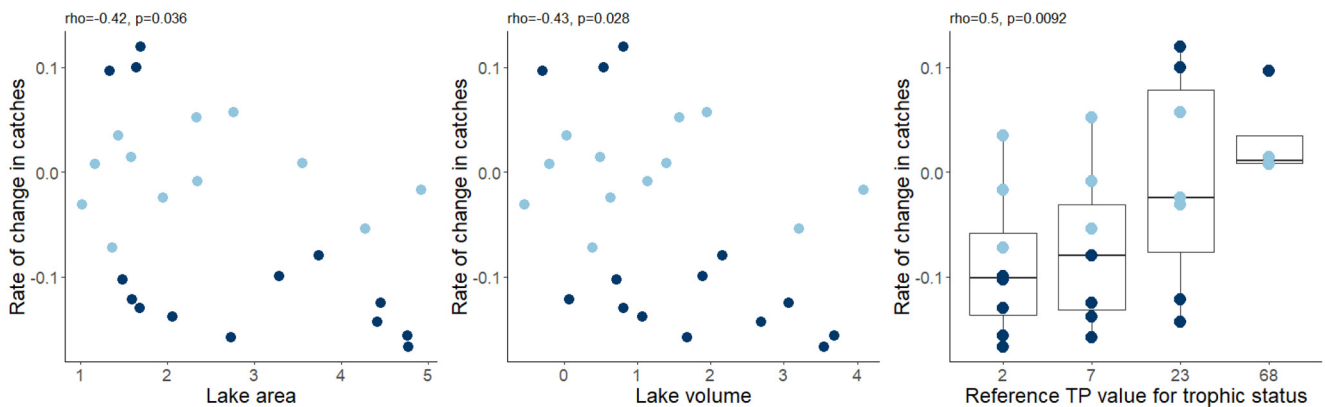

Fig. 4. Environmental characteristics of lakes showing significant relationships (Spearman p-value< 0.05) with the rate of change in catches computed over the period 2000-2019 (Baikal not included). The color of the circles indicates the level of significance of the long-term trend in catches (p-value<0.05: dark blue; not significant: light blue). Environmental characteristics include logarithm of the lake area (Lake area) and logarithm average volume (Lake volume), total phosphorus concentration according to lake trophic state at the end of the studied period (Reference TP value for trophic status).

the area of the Laurentian Great Lakes in North America and reached a maximum of 0.06°C/year in Western Europe and the Alpine area (Tab. 2B). The long-term trends in warming air temperature during winter were not correlated with trends in catches (Fig. 6). Correlations were positive between the rates of change in catches and the rates of air warming in spring, summer, and autumn. Results were consistent when correlations were performed on the subset of lakes excluding L.

Peipsi, Vättern and Vänern (Tab. 3). Lakes located in geographical areas that suffered more severe air warming in spring, summer, and autumn, presented a wide range of variability in catch trends including increasing catches (Fig. 6). In contrast, catches have been decreasing in all the geographical areas that presented a light warming. Finally, no correlation appeared between the rates of changes in catches and warming rates in lake surface temperature.

Table 3. Correlations analysis between rate of changes in catches and the explanatory variables listed in Table 2. Two-groups Wilcoxon comparisons of rate of changes and selected explanatory variables for A: all lakes except L. Baikal, and B: all lakes except L. Peipsi, Vänern, Vättern and Baikal. Small-medium lakes correspond to lakes whose surface area and volume are smaller than $100 km^2$ and $10 km^3$. High nutrient lakes encompass eu- and mesotrophic lakes while poor-nutrient lakes refer to oligo- and ultraoligotrophic lakes. Rapid warming area corresponds to geographic area where air warming was the fastest ($0.06°C.year^{-1}$).

A.

Relationship between the rates of change in catches and variables (Table 2)	All lakes without L. Baïkal	
	Spearman p-value	*Spearman R*
lake_lat_decdeg	0.95	-0.02
elevation_m	0.68	0.09
avg_depth_m	0.76	0.06
max_depth_m	0.56	-0.12
Logarea km2	**0.036**	**-0.42**
Logavg_vol_km3.	**0.028**	**-0.43**
TP	**0.0092**	**0.50**
LakeSSWTtrend	0.31	-0.29
SenSlopeT_Winter	0.27	0.22
SenSlopeT_Spring	**0.022**	**0.45**
SenSlopeT_Summer	**0.025**	**0.44**
SenSlopeT_Autumn	**0.011**	**0.49**
Comparison of rates of change in catches between lake categories	*Wilcoxon p-value*	
Size (Small-medium vs. Large)	0.067	
Productivity (Eutro-mesotrophic vs. oligo-ultraoligotrophic)	**0.013**	
Comparison of variables between lakes showing significant decrease in catches and others	*Wilcoxon p-value*	
Logarea_km2	0.061	
Logavg_vol_km3	0.052	
TP	**0.033**	
Comparison of rates of change in catches between high and poor-nutrient lakes	*Kruskal-Wallis p-value*	
Sen's slope	**<0.01**	
Comparison of rates of change in catches between high and poor-nutrient lakes in rapid warming area	*Wilcoxon p-value*	
Sen's slope	**0.019**	

B.

| Relationship between the rates of change in catches and variables (Table 2)	All lakes without L. Peipsi, Vänern, Vättern Baïkal	
	Spearman p-value	*Spearman R*
lake_lat_decdeg	1	0.00
elevation_m	0.55	0.13
avg_depth_m	0.67	0.10
max_depth_m	0.68	-0.09
Logarea_km2	**0.049**	**-0.42**
Logavg_vol_km3	**0.04**	**-0.43**
TP	**0.019**	**0.49**
LakeSSWTtrend	0.4	-0.27
SenSlopeT_Winter	0.13	0.38
SenSlopeT_Spring	**0.023**	**0.47**
SenSlopeT_Summer	**0.022**	**0.48**
SenSlopeT_Autumn	**0.022**	**0.48**
Comparison of rates of change in catches between lake categories	*Wilcoxon p-value*	
Size (Small-medium vs. Large)	0.059	
Productivity (Eutro-mesotrophic vs. oligo-ultraoligotrophic)	**0.026**	
Comparison of variables between lakes showing significant decrease in catches and others	*Wilcoxon p-value*	
Logarea_km2	0.096	
Logavg_vol_km3	0.089	
TP	0.089	
Comparison of rates of change in catches between high and poor-nutrient lakes	*Kruskal-Wallis p-value*	
Sen's slope	**0.03**	
Comparison of rates of change in catches between high and poor-nutrient lakes in rapid warming area	*Wilcoxon p-value*	
Sen's slope	**0.046**	
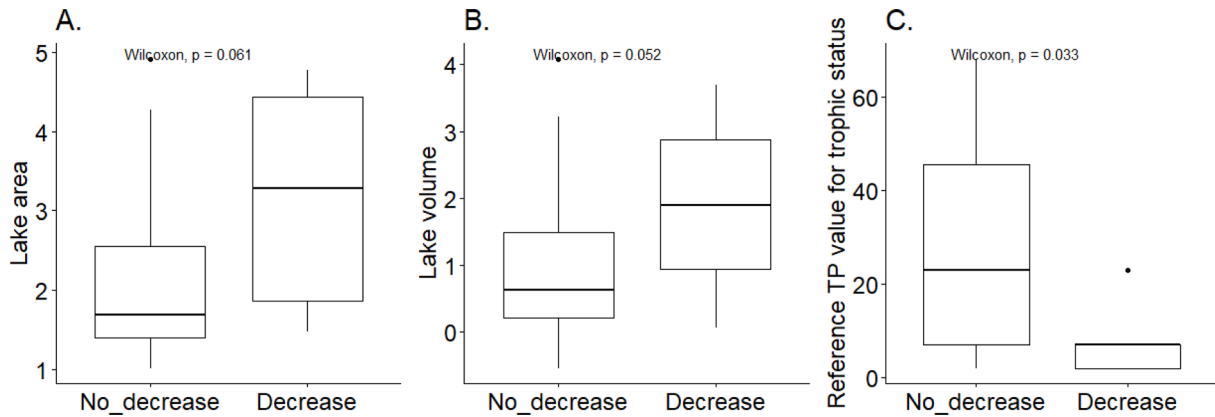
Fig. 5. Comparison of lake characteristics (displayed as box-whisker plots) between the lakes that displayed a significant decrease in coregonine catches and lakes where the trends were not significant or positive over the period 2000–2019 (Lake Baikal not included). (A) logarithm of lake area (km^2), (B) logarithm of average volume (km^3) and (C) Reference TP value for trophic status (μg.L^{-1}).
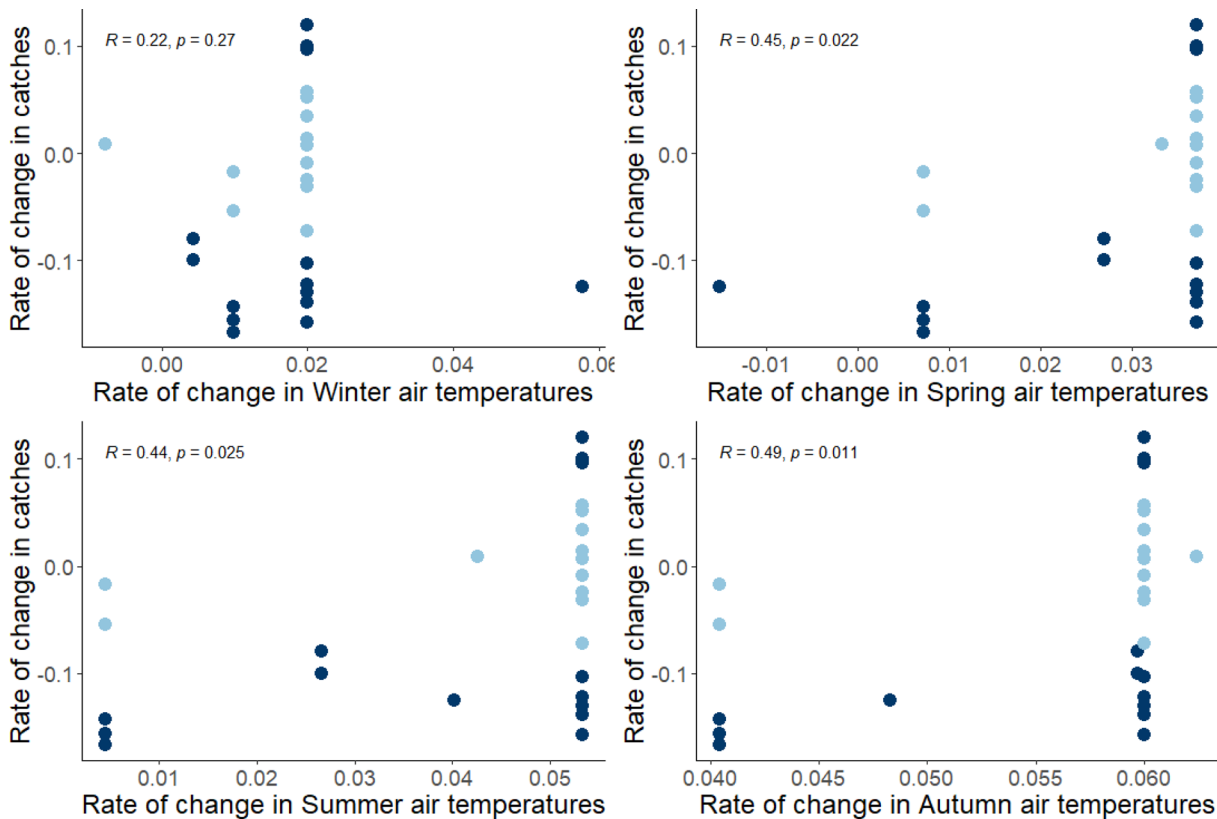

Fig. 6. Relationships (Spearman correlation) between the rate of changes in catches and air temperature measured over geographical area of the lakes for different seasons (Winter: December of the previous year to February; Spring: March to May; Summer: June to August; Autumn: September to November). The color of the circles indicates the level of significance of long-term trends in catches computed over the period 2000–2019 (p-value<0.05: dark blue; no significant: light blue).

Catch trends and trophic state contributed to the formation of the axis 2 while the five other variables (area, average volume, warming rate of air temperature in spring, summer and autumn) contributed to the formation of axis 1 in the Hill & Smith Analysis (Fig. 7A). Axes 1 and 2 represented 85% of the variance in the dataset. The positions of the lakes in the 2-dimensional space enabled the lakes to be visualized and clustered based on their environmental variables (Fig. 7B and C). Discriminant analysis indicated that lakes distributed along axes 1 and 2 according to their membership to groups defined by the rates of changes in catches. This is also the case when the analysis excluded the lakes where significant changes in fishing effort may have influenced the observed trends in catches (Supplementary Fig. 1). The group of lakes with
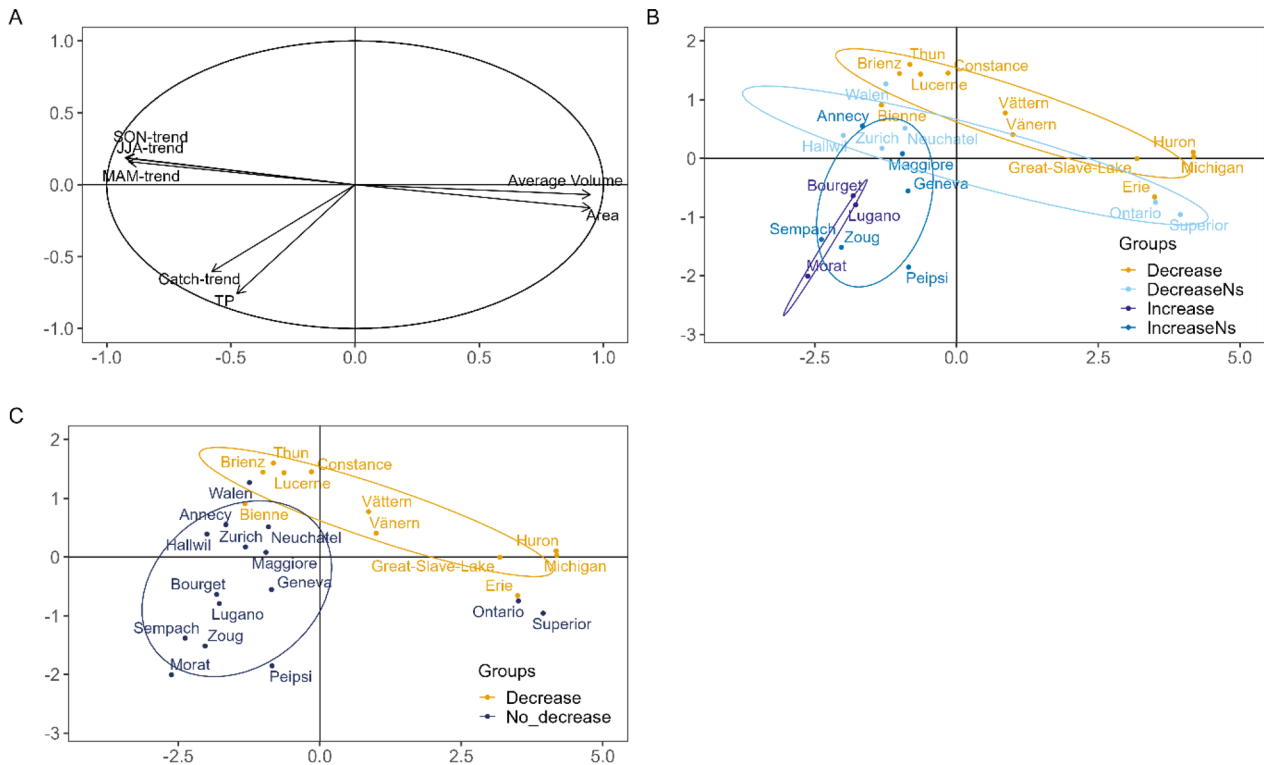
Fig. 7. Hill & Smith analysis of rate of change in catches and environmental variables. (A) projection of the seven variables onto the first factorial plane of the Hill & Smith analysis (axis1 horizontal and axis 2 vertical) with SON-trend, JJA-trend and MAM-trend being for autumn (September-November), summer (July-August) and spring (March-April) air temperature trends respectively. (B–C) projection of the lakes onto the first factorial plane of the Hill & Smith analysis and barycenter of the group of lakes showing significant and non-significant increase or decrease (Increase, IncreaseNs, Decrease, DecreaseNs respectively) in their catches.

significant catch declines segregated significantly (p-value<0.05) from the other lakes, indicating that the selected variables were strong predictors of decline in coregonine catches. Overall, the rate of change in catch trends was significantly different depending on the trophic state and atmospheric warming (Supplementary Fig. 2A), and in the area with the fastest warming significant differences in the rate of change in catch were observed between eu- or mesotrophic and nutrient-poor lakes (Supplementary Fig. 2B), with decreasing trends more often observed in nutrient-poor lakes. This result remains when the tests were carried out on a set of lakes that excludes Lakes Peipsi, Vänern and Vättern.

4 Discussion

Our long-term datasets from 27 lakes over the Northern Hemisphere offer a unique opportunity to address numerous critical issues related to the coregonine ecology and fisheries management. We examined global trends in catches, with a specific emphasis on the countries with more developed economies where coregonine fisheries are primarily located. Although these lakes are now subject to various monitoring, regulations or protective fisheries management measures, overfishing has sometimes led to stock collapses in the past and, for some lakes, fishing continues to weaken populations and/or influence long-term dynamics by combining with

environmental parameters (Allan et al., 2005; Anneville et al., 2015). It is therefore important to know whether certain lakes, because of their morphological or environmental characteristics, are more sensitive and to assess how environmental properties can influence the rate of change in catches. In this study we therefore sought to explore the link between lake characteristics and changes in catches.

4.1 Global changes in catches and suggested reasons for lake-specific trends

Despite management and restoration programs, our results indicated decreases in coregonine catches in 52% of the lakes examined, with significantly declining trends in 44% of them including lakes Baikal, Michigan, Erie, Huron, Great Slave, Vänern, Vättern, Bienne, Lucerne, Brienz, Thun and Constance. We acknowledge that these observed declines could be due to decreases in fishing efforts and other changes associated with the conditions of the fisheries, as our data are total catches and not catch per unit effort. For example, in Lakes Vänern and Vättern, the fishing effort for European whitefish has decreased significantly since the year 2000. One reason for this reduction was due to high levels of dioxins and dioxin-like PCBs (Hållén *et al.*, 2020). Another reason for the decline in coregonine catch in Lake Vättern was that the fishery shifted to the introduced crayfish (*Pacifastacus leniusculus*)

because of markedly better profit margins than coregonines (Blomqvist and Swahnberg, 2020). Thus, the observed declines in coregonine catches might be partially due to a lower fishing effort or changing market conditions.

Catch data are essential for fisheries management and for determining sustainable harvest levels, but catch statistics alone do not provide a correct indication of fish abundance and do not inform on the size of the population (Pauly *et al.*, 2013; Ovando et al., 2022). In our studied lakes, even if some of the observed trends might be influenced by changes in fishing effort, we believe they are representative of changes in stock size. Using reported catch as an index of fish abundance is justified by its practicality, particularly in multi-species fisheries where alternative methods such as detailed stock assessments are not feasible, and indices such as catch per unit effort are difficult to estimate. Pauly *et al.* (2013) highlighted that while catch data should be interpreted with caution, they still provide valuable insights into fish abundance, especially for data-limited fisheries. Additionally, it is reasonable to assume that fishers adjust their efforts in response to changes in fish abundance. The fishing effort and total catch data across global lakes in Kao *et al.* (2020) reinforced this idea. While those data showed a positive correlation between fishing effort and total catch, their year-to-year fluctuations suggested that fish abundance likely influenced both of them. This observation further supports the use of catch data as a practical, albeit imperfect, proxy for fish abundance. Furthermore our results are consistent with the literature as many of the observed local trends in the present paper are documented in the literature and induced by changes in environmental conditions. For example, in the 1960–1970s, the catches in Lake Vättern were approximately 50 times higher than they are now. Beside the reduction of fishing effort, other factors, such as a reduction in phosphorus concentrations (Renberg et al., 2003; Norborg Carlsson, 2023), may have contributed to this downward trends (A. Sandström, Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Freshwater Research, written personal communication, 2023). In Lake Vänern, the fishery targets vendace (*C. albula*) to refine the roe. The catch of vendace also decreased over the study period with a parallel decreasing trend for adult vendace stock biomass assessed by a fisheries independent monitoring program (Rogell and Axenrot, 2023). The cause of this decline is unknown, although recruitment of vendace in Lake Vänern depends on the date of ice-off, with long ice-winters being more favourable for good recruitment (Sandström *et al.,* 2014). Thus, the negative effect of the ongoing reduction in ice duration in combination with lake oligotrophication may explain the observed decline. The main reasons accounting for the collapse of the coregonine populations in Lake Constance are the decrease in food availability due to extreme re-oligotrophication together with competition with other zooplanktivorous species including the introduced three-spined stickleback (*Gasterosteus aculeatus*, Rösch *et al.*, 2018). In addition, the sticklebacks exert a strong predation pressure on eggs and young whitefish since their population outbreak since 2012 (Gugele *et al.*, 2023). Lake Baikal has been described as a stable and healthy ecosystem (Dobiesz *et al.*, 2010) but in recent years, catches have declined. In Great Slave Lake, the taxonomic changes in algal community, resulting from an increase in air and lake surface temperature,

and a decline in ice cover, have implications on the entire food web, providing fewer nutrients for the primary consumers, ultimately affecting the food supply for coregonine fish with consequences for the fisheries (Rühland *et al.*, 2023). In the Laurentian Great Lakes, declines in coregonine catches are likely due to a myriad of potential stressors that are difficult to disentangle but include reduced lake productivity (coincident with invasive mussel proliferation) and potentially lower larval growth and survival (Ebener *et al.*, 2021; Cunningham and Dunlop, 2023), and negative effects from fisheries exploitation in some areas (Rook *et al.*, 2022).

Increases in coregonine catches over the studied period were observed in Lakes Bourget, Lugano, Morat and Peipsi. In Lake Peipsi, an increase in catches might reflect a short-term increase in the vendace stock due to favorable environmental conditions for recruitment success during a few years after a strong vendace fishery regulation that consisted of the closure of the fishery during 6 years in order to help the stock to recover. Nevertheless, the population is still low compared to pre-collapse during the late 1980's (Kangur *et al.*, 2020) and new fishing restrictions are expected soon to sustain the population (Bunnell *et al.*, 2024). In Lake Bourget, the increase in catches was due to a high abundance of *Daphnia sp.* in spring (Bourinet *et al.*, 2023) and likely the improvement towards a lower trophic state that induced the disappearance of the toxic cyanobacteria *Plankthotrix rubescens* that used to bloom in that lake (Kerimoglu *et al.*, 2017).

4.2 Drivers of global changes in coregonine catches and implication for lake managements

Our study also indicated that global patterns can be detected among these widely distributed lakes with variation in trophic state and size. We observed strong inter-lake differences in the rates of change in catches and we highlighted a significant correlation between the rate of changes in catches and the trophic state with most of the trends being negative in low nutrient lakes. The rate of changes and direction of the trends were significantly different between high (eutrophic and mesotrophic) and low (oligotrophic and ultra-oligotrophic) productive systems. Lakes with the strongest decrease in catches were nutrient poor lakes while more productive lakes presented no trend or increase in catches. Our results were tested on a smaller subset of lakes (Tab. 3 and supplementary Tab. 3). They remained consistent although increasing risk of type II error due to a smaller number of observations, which in our case means that the role of trophic state is disregarded while it affects the rate of change in catches. Thus, our results highlight the sensitivity of coregonine populations to extreme re-oligotrophication at a global scale. The case of Lake Baikal, which is ultra-oligotrophic and was only considered in the descriptive analysis, corroborates this finding. The highlighted link between the direction of the trends and the trophic state could be explained by resource limitation (e.g., strong bottom-up control) in oligotrophic lakes where primary production has strongly decreased as a result of reduced nutrient loading (Finger *et al.*, 2013). Coregonine communities in very low nutrient lakes are dominated by smaller, slow-growing individuals (Alexander and Seehausen, 2021), however, some exceptions exist (Lake Walchen, e.g. Mayr, 2001). Those slow-growing species are sometimes sparsely rakered indicating

benthivory that provides better fitness under low availability of pelagic food (Shimoda *et al.*, 2023). Coregonine size differences between lakes with different trophic state may thus reflects a reduced growth potential because of limited pelagic resources and/or an adaptation to oligotrophic conditions. Re-oligotrophication may act to favor specialized benthic feeding coregonine phenotypes if they are still present in the population (Hirsch *et al.*, 2013). Phenotypic and genetic diversity, such as that documented in Lake Constance, offer the possibility to develop a morphology adapted to benthic feeding (Hirsch *et al.*, 2013) and potentially enhance resilience. However, the declining population has been accompanied by a parallel reduction in coregonine size supporting the hypothesis of resource limitation. Resource limitation has also been emphasized in Lake Brienz, with strong impact on fishing yields, because the smaller sized fish could not be caught by legal gillnets (Müller *et al.*, 2007). A transition from eutrophic to mesotrophic conditions generally benefits coregonine populations (Anneville *et al.*, 2009), yet an even higher reduction in phosphorus could have adverse effects on fisheries. In the four Swiss lakes (Bienne, Lucerne, Brienz, Thun), the threshold below which a positive relationship between phosphorus and coregonine yield is obvious at around 10 µg/L of soluble reactive phosphorus during the spring circulation (Müller *et al.*, 2007). An analysis of catches in 11 peri-alpine lakes suggests the ideal trophic state for European whitefish yield is mesotrophic with high yields recorded for total phosphorus concentrations ranging between 20 and 40 µg/L (Gerdeaux *et al.*, 2006). Accordingly, further phosphorus decrease in oligotrophic lakes is likely to result in a decrease in coregonine populations, especially in lakes suffering parallel outbreaks of invasive species that exert strong exploitative competition or indirect bottom-up trophic cascades (David *et al.*, 2017). For example, invading dreissenid mussels exacerbate the impact that food scarcity already has on larval growth rate and recruitment of coregonines (Cunningham and Dunlop, 2023). Extreme oligotrophy can thus impact abundance and life-traits, highlighting the need to (i) monitor fish populations to provide accurate estimates for fisheries policies that can adapt to changes in the environment, (ii) maintain and protect the possibility of evolutionary divergence by implementing fisheries practices that do not reduce genetic diversity, and (iii) better consider the impacts of bottom-up control on fish populations when managing lake water quality and fisheries.

The link between lake size and the rates of changes requires further investigation. Rate of changes in catches differed slightly between large and small-medium size lakes. Trends are more often declining in large lakes. This pattern could be explained by several hypotheses. First, in economically developed countries, large lakes have usually reached low TP levels (Woelmer *et al.*, 2016), making re-oligotrophication more impactful on fish populations. Furthermore, because larger lakes tend to be deeper and thus typically exhibit a higher ratio of pelagic production relative to benthic production, the more frequent decline observed in large lakes might suggest that pelagic coregonines are more sensitive to the common stressors (climate and re-oligotrophication). Eventually, effective management strategies can be efficiently implemented and show results within a few years in small lakes as was the case in Lake Annecy (Bourinet *et al.*, 2023).

Conversely, large lakes have a history of supporting more intense and sometimes industrial fisheries that might have had strong impacts on populations (Rook *et al.*, 2022). Furthermore, large lakes are more likely to provide a higher diversity of ecological niches, allowing co-existence of larger numbers of morphs and several fish stocks that can differ in their response to environmental changes. Such a "response diversity" (Elmqvist *et al.*, 2003) can complicate the assessment of the population if, at the subpopulation scale, the reduction of one or a few populations is balanced by the production of others. These changes in the population composition can pass unnoticed and can delay protection measures that, if established too late, may not prevent the stock to fluctuate at a lower level (Cury and Anneville 1998; Eshenroder *et al.*, 2016). Large lakes are often transboundary, which may also make governance more complex. Nevertheless, given that the majority of lakes are small to medium-sized, prioritizing fisheries management is crucial for safeguarding populations and ensuring stocks sustainability.

The inter-lake differences in the rates of change in catches were not explained by the difference in warming rates of air temperature and lake summer surface temperatures. The number of significantly warming areas were relatively modest, potentially due to the fact that the study period occurred during the "global warming hiatus," which is characterised by a deceleration in global warming (Fyfe et al., 2016). The period considered by O'Reilly *et al.* (2015) was longer but does not perfectly overlap with the studied period. The characteristics of lakes can act as a mediating factor in climatic effects (O'Reilly *et al.*, 2015). Certain lakes may thus be more vulnerable to warming than others. Consequently, lakes with a high rate of surface temperature change may appear more likely to experience significant alterations in their ecosystems. However, our findings do not support this hypothesis. They were unexpected given the restricted thermal niche of coregonines, but they are in coherence with few studies highlighting non-significant or positive effects of rising lake temperatures (Massol *et al.*, 2007; Anneville *et al.*, 2017). The absence of negative effects of rising temperatures might be due to the statistical approach that focusses on trends instead of the impact of isolated cases or extreme meteorological events, like heatwaves that may have detrimental effects in the large shallow northern lakes like Peipsi. Those shallow lakes are particularly sensitive to short-term extreme weather conditions, to which fish respond surprisingly quickly (Jeppesen *et al.*, 2012; Kangur *et al.*, 2020). Heat waves in summer and changing ice conditions during the winter may have profound detrimental effects on cool-water, autumn-spawning, short-lived fish such as vendace in shallow and polymictic lakes. In such shallow lakes, cool-water and oxygen-rich refuges do not exist in summer and wave action can mechanically damage and displace fish eggs, potentially disrupting their survival and development in spawning grounds during mild winters without permanent ice cover (Kangur *et al.*, 2020). The absence of negative effects of global warming could also be explained by the range of variation in environmental data. Indeed, our results indicate that temperatures have remained within the range of coregonine thermal tolerances and, at least over our study period (2000–2019), temperatures have not yet reached the values that could significantly limit coregonine reproductive success. For example, temperatures for egg incubations

should remain below 7–8°C depending on the species (Stewart *et al.*, 2021; Stewart *et al.*, submitted2). Unfortunately, such temperatures are expected to be reached soon even in the most optimistic climatic scenario, with detrimental consequences for reproduction success (Stewart *et al.*, 2024). In lakes where the thermal niche remains within proper conditions for the development and reproduction of the species, warmer conditions might actually favor recruitment. From 2000 to 2019, warming in eu- and mesotrophic lakes Morat, Bourget, Lugano and Peipsi could well have provided a more productive habitat (i.e., warmer and sufficient food). Several papers have reported a positive effect of temperature on larval growth or recruitment (Perrier *et al.*, 2012; Sandström *et al.*, 2014). Accordingly, based on stimulations of larval and juveniles growth, we expect warmer temperatures during spring, summer and autumn to increase growth as long as prey resources are not limiting, potentially resulting in a positive effect on recruitment and on the fishery. Finally, the absence of adverse effects from climate change might also be due to behavioral adaptations of the fish when lake morphology allows fish to seek thermal refuges, especially when lakes are deep and oxygen would not be limiting in deeper waters. Obviously, interplay among lake size, trophic state and climate warming can explain our results and should be considered to properly explain inter-lake differences and to assess the sensitivity of their coregonine populations to global warming.

4.3 Interplay among trophic-state, lake size and air warming jeopardizes future predictions and appeal for a change in management paradigms

Interestingly our results embrace the complexity of confounding and interacting factors that may have strong implications for assessing lake sensitivity to global forcing. For the studied period lake trophic state, lake size and climate pressure explained inter-lake differences in the rate of change in coregonine catches. As previously discussed, decreased catches are not restricted to warming regions. Instead, warming regions are associated with positive trends, especially in nutrient rich lakes. The association between coregonine trends and trophic state is probably strengthened by climate pressure with stronger positive effects of warming in smaller lakes when food is available. These two important lake-characteristics (trophic state and size) are expected to remain relevant and shape coregonine responses to future climatic conditions. Under warmer climate scenarios the stratification behavior of large and deep lakes can change dramatically (Wahl and Peeters, 2014), resulting in changes in plankton phenologies and different food availability for spring-hatching coregonines, which could lead to a decoupling of hatching time and the occurrence of high prey densities of preferred size ranges for newly hatched larvae (Straile *et al.*, 2007). Furthermore, due to climate change, the upper layer of lakes may eventually become too warm for whitefish (DeWeber *et al.*, 2022). In deep lakes the upper water layer is the area with the highest prey density and if whitefish migrate to stay in deeper, cooler regions, where much less food is available, they begin to starve (DeWeber *et al.*, 2022), unless the population has the potential to adapt their feeding behavior and switch to benthic prey. Nevertheless, many oligo- and mesotrophic lakes

with higher water clarity also have phytoplankton production at deep water layers (Scofield *et al.*, 2020; Bonnier *et al.*, 2024) and have zooplankton undergoing diel vertical migration up to 125 m (Nowicki *et al.*, 2017; Piton *et al.*, 2024). Further work on the phenology and vertical distribution of plankton communities is necessary to enhance our understanding of how these changes will interact with and impact coregonine communities in a warming world and under diverse trophic conditions. Given the strong link between the direction of the trends and the trophic state (e.g., Freeberg *et al.*, 1990; Müller *et al.*, 2007; Bunnell *et al.*, 2014), we can expect that the limiting effect of food availability might be exacerbated in a warmer climate if metabolism is increased but prey resources are insufficient to approach maximum consumption rates (Kao *et al.*, 2015). Hence, without comprehensive understanding of these complex and potentially interacting dynamics, the certainty of our predictions on the effects of changing trophic state and climate change on coregonine communities will be relatively low.

When temperatures move outside of the ideal range in which gonadal and embryogenic development have been adapted, reduced fertility and reproduction success is likely (Cingi *et al.*, 2010; Eme *et al.*, 2015; Mueller *et al.*, 2015; Servili *et al.,* 2020). Accordingly, depending on whether the fish can adapt its behavior and find thermal refugia, the temperature increase in air temperature will probably not have the same impact in shallow compared to deep lakes. Our study suggests that trophic state together with lake morphology (area and volume) and thus probably the mixing regime of the lake, will be important variables to consider to evaluate the impact of global warming on coregonines. Specific tools such as end-to-end 3D modelling may reproduce biological processes from phytoplankton to fish by taking into account hydrodynamic processes (Bănaru *et al.*, 2019). Such tools may offer interesting possibilities to predict and test the impacts of management solutions and required nutrient thresholds to mitigate the effect of climate changes.

In conclusion, our findings highlight a link between trophic state and trends in coregonine productivity. This link is "shaped" by changing climate and lake size. Our findings also corroborate that coregonines thrive at intermediate levels of productivity (e.g., mesotrophic, Gerdeaux *et al.*, 2006; Anneville *et al.*, 2009), given that the highest declines of catch rates occurred in oligotrophic and ultra-oligotrophic lakes, when resources are likely to become more limited. In developed countries, many efforts have been made to reduce phosphorus loading, control phytoplankton growth, stop algal blooms and recover pristine water quality conditions as required by many legislations. Those efforts were encouraged by lake managers as eutrophication also compromises coregonine reproduction, thus threatening the survival of the populations. Consequently, a transition from eutrophic to mesotrophic conditions resulted in the recovery of coregonine stocks in many lakes. However, lake managers must be aware that aiming for pristine conditions might reduce the productivity of the fisheries (see meta-analysis by Deines *et al.*, 2015). In a world where local food provisioning can be a sustainability goal (see United Nations General Assembly, 2015; opinion of the European Committee of Regions, 2021; European Green Deal; Blue Transformation), lake sources of protein are important to consider and require managers to find

the balance in nutrient concentrations that provide acceptably clean water while still providing sufficient fish production. Such an effort requires water and fisheries managers to collaborate effectively to clarify each other's expectations and find common lake-specific management objectives that will meet the sometimes divergent needs of all lake users. This cooperation is even more important and urgent with the intensification of climate change impacts and the introduction of invasive species that can have significant and uncontrolled effects on food availability for coregonines.

Acknowledgments

Supplementary material

Supplementary Figure 1. Hill & Smith analysis of rate of change in catches and environmental variables. The 3 lakes (L. Peipsi, Vänern and Vättern) where trends in catches could be influenced by strong changes in fishing effort were not included in the analysis. A: projection of the seven variables onto the first factorial plane of the Hill & Smith analysis (axis 1 horizontal and axis 2 vertical) with SON-trend, JJA-trend and MAM-trend being for autumn (September-November), summer (July-August) and spring (March-May) air temperature trends respectively. B-C: projection of the lakes onto the first factorial plane of the Hill & Smith analysis and barycenter of the group of lakes showing significant and non-significant increase or decrease (Increase, IncreaseNs, Decrease, DecreaseNs respectively) in their catches. The group of lakes with significant catch declines segregated significantly (Discriminant analysis, p-value<0.05) from the other lakes, indicating that the selected variables were strong predictors of decline in coregonine catches.

Supplementary Figure 2. A. Comparison of rate of changes in catches among four lakes categories (A: nutrient-rich in a fast warming area, B: nutrient-rich in a slow warming area, C: nutrient-poor in a fast warming area, D: nutrient-poor in a slow warming area). B. Comparison of rate of changes between nutrient-rich and nutrient-poor lakes located in fast warming area. The color of the circles indicates the level of significance of the long-term trend in catches (p-value<0.05: dark blue; not significant: light blue).

Supplementary Table 1. Information on the taxonomic composition of coregonines catches ("No": only one form was recorded; "Yes": multiple species or forms were recorded; "Not indicated": no information available), fishing practices and stressors that have been identified as main drivers of coregonine stocks over the last decades.

Supplementary Table 2. Metadata of the datasets used in the analysis and details on data availability.

Supplementary Table 3. A) Mann-Kendal p-values of the long-term trend in catches and Sen's slopes values for each lake. B) Results of correlation analysis that were performed on the set of lakes showing significant (p-value <0.05) long-term trends in catches.

The Supplementary Material is available at https://www.limnology-journal.org/10.1051/limn/2025003/olm.

References

Alexander T, Seehausen O. 2021. Diversity, distribution and community composition of fish in perialpine lakes. "Projet Lac" synthesis report. *Eawag: Das Wasserforschungsinstitut des ETH-Bereichs*.

Allan JD, Abell R, Hogan Z, Revenga C, Taylor BW, Welcomme RL, Winemiller K. 2005. Overfishing of Inland Waters. *BioScience* 55: 1041–1051.

Anneville O, Lasne E, Guillard J, Eckmann R, Stockwell J, Gillet, C, Yule, D. 2015. Impact of Fishing and Stocking Practices on Coregonid Diversity. *Food Nutr. Sci.* 06: 1045.

Anneville O, Souissi S, Molinero JC, Gerdeaux D. 2009. Influences of human activity and climate on the stock-recruitment dynamics of whitefish, Coregonus lavaretus, in Lake Geneva. *Fish. Manage. Ecol.* 16: 492–500.

Anneville O, Vogel C, Lobry J, Guillard J. 2017. Fish communities in the Anthropocene: Detecting drivers of changes in the deep peri-alpine Lake Geneva. *Inland Waters* 7: 65–76.

Baer J, Deweber J, Rösch R, Brinker A. 2021. Aquaculture of Coregonid Species—Quo vadis? *Ann. Zool. Fenn.* 58: 307–318.

Baer J, Eckmann R, Rösch R, Arlinghaus R, and Brinker A, 2017. Managing Upper Lake Constance Fishery in a Multi-Sector Policy Landscape: Beneficiary and Victim of a Century of Anthropogenic Trophic Change. in Song A.M., Bower S.D., Onyango P., Cooke S.J., & Chuenpagdee R. (eds.), Inter-sectoral governance of inland fisheries, St John's, NL, Canada: TBTI Publication Series 32–47.

Baer J, Kugler M, Schubert M, Schotzko N, Rösch R, Vonlanthen P, DeWeber, JT. 2023. A matter of time—Efficacy of whitefish stocking in a large pre-alpine lake. *Fish. Manage. Ecol.* 30: 615–626.

Bănaru D, Diaz F, Verley P, Campbell R, Navarro J, Yohia C, Oliveros-Ramos R, Mellon-Duval C, Shin Y-J. 2019. Implementation of an end-to-end model of the Gulf of Lions ecosystem (NW Mediterranean Sea). I. Parameterization, calibration and evaluation. *Ecol. Model.* 401: 1–19.

Blomqvist GE, Swahnberg H. 2020. Ekonomisk och strukturell data rörande svenskt insjöfiske. *Jordbruksverket rapport*, 19: 52 p.

Bonnier M, Anneville O, Woolway RI, Thackeray SJ, Morin GP, Reynaud N, Soulignac F, Tormos T, Harmel T. 2024. Assessing ESA Climate Change Initiative data for the monitoring of phytoplankton abundance and phenology in deep lakes: Investigation on Lake Geneva. *J. Great Lakes Res.* 50: 1–14.

Borcherding J, Heynen M, Jäger-Kleinicke T, Winter HV, Eckmann R. 2010. Re-establishment of the North Sea houting in the River Rhine. *Fish. Manage. Ecol.* 17: 291–293.

Bosch NS, Evans MA, Scavia D, Allan JD. 2014. Interacting effects of climate change and agricultural BMPs on nutrient runoff entering Lake Erie. *J. Great Lakes Res.* 40: 581–589.

Bourinet F, Anneville O, Drouineau H, Goulon C, Guillard J, Richard A. 2023. Synchrony in whitefish stock dynamics: Disentangling the effects of local drivers and climate. *J. Limnol.82.*

Brooke LT. 1975. Effect of Different Constant Incubation Temperatures on Egg Survival and Embryonic Development in Lake Whitefish (*Coregonus clupeaformis*). *Trans. Am. Fish. Soc.* 104: 555–559.

Brown RW, Taylor WW, Assel RA. 1993. Factors affecting therecruitment of lake whitefish in 2 areas of northern Lake Michigan. *J. Great Lakes Res* 19: 418–428.

Bunnell DB, Ackiss AS, Alofs KM, Brant CO, Bronte CR, Claramunt RM, Dettmers JM, Honsey AE, Mandrak NE, Muir AM, Santucci Jr VJ, Smith DR, Strach RM., Sweka JA, Weidel BC, Mattes WP, and Newman KR. 2023. A science and management partnership to restore coregonine diversity to the Laurentian Great Lakes. *Environ. Rev.* 31: 716–738.

Bunnell DB, Anneville O, Baer J, Bean CW, Kahilainen KK, Sandström A, Selz OM, Vonlanthen P, Wanzenböck J, Weidel B.C. 2024. How diverse is the toolbox? A review of management actions to conserve or restore coregonines. *Int. J. Limnol.* 60, 5.

Bunnell DB, Barbiero RP, Ludsin SA, Madenjian CP, Warren GJ, Dolan DM, Brenden TO, Briland R, Gorman OT, He JX, Johengen TH, Lantry BF, Lesht BM, Nalepa TF, Riley SC, Riseng CM, Treska TJ, Tsehaye I, *et al.* 2014. Changing Ecosystem Dynamics in the Laurentian Great Lakes: Bottom-Up and Top-Down Regulation. *BioScience* 64: 26–39.

Cingi S, Keinänen M, and Vuorinen PJ. 2010. Elevated water temperature impairs fertilization and embryonic development of whitefish *Coregonus lavaretus*. *J. Fish Biol.* 76: 502–521.

Collingsworth PD., Bunnell DB, Murray MW, Kao Y-C., Feiner ZS, Claramunt RM, Lofgren BM, Höök TO, and Ludsin SA. 2017. Climate change as a long-term stressor for the fisheries of the Laurentian Great Lakes of North America | U.S. Geological Survey. *Rev. Fish Biol. Fish.* 27: 363–391.

Conley AK, Schlesinger MD, Daley JG, Holst LK, Howard TG. 2021. Modeling habitat suitability and management options for maintaining round whitefish (*Prosopium cylindraceum*) in Adirondack ponds. *Can. J. Fish. Aquat. Sci.* 78: 1371–1382.

Cunningham KE, Dunlop ES. 2023. Declines in lake whitefish larval densities after dreissenid mussel establishment in Lake Huron. *J. Great Lakes Res.* 49: 491–505.

Cury P, Anneville O. 1998. Fisheries resources as diminishing assets: Marine diversity threatened by anecdotes. in Global versus Local Changes in Upwelling Systems, ORSTOM (ed.), Paris 537–548.

Dahlin KM, Ault TR. 2018. Global linkages between teleconnection patterns and the terrestrial biosphere. *Int. J. Appl. Earth Obs. Geoinf.* 69: 56–63.

David P, Thébault E, Anneville O, Duyck P-F., Chapuis E, Loeuille N. 2017. Impacts of Invasive Species on Food Webs: A Review of Empirical Data. *Adv. Ecol. Res.* 56: 1–60.

Deines AM, Bunnell DB, Rogers MW, Beard TD, Taylor WW. 2015. A review of the global relationship among freshwater fish, autotrophic activity, and regional climate. *Rev. Fish Biol. Fish.* 25: 323–336.

FAO. 2022. The state of world fisheries and aquaculture, towards blue transformation. *Food and Agriculture Organization of the United Nations*, Rome: FAO.

DeWeber JT, Baer J, Rösch R, Brinker A. 2022. Turning summer into winter: Nutrient dynamics, temperature, density dependence and invasive species drive bioenergetic processes and growth of a keystone coldwater fish. *Oikos* 2022: e09316.

Dobiesz NE, Hecky RE, Johnson TB, Sarvala J, Dettmers JM, Lehtiniemi M, Rudstam LG, Madenjian CP, Witte F. 2010. Metrics of ecosystem status for large aquatic systems − A global comparison. *J. Great Lakes Res.* 36: 123–138.

Dove A, Chapra SC. 2015. Long-term trends of nutrients and trophic response variables for the Great Lakes. *Limnol. Oceanogr.* 60: 696–721.

Ebener MP, Dunlop ES, Muir AM. 2021. Declining Recruitment of Lake Whitefish to Fisheries in the Laurentian Great Lakes: Management Considerations and Research Priorities. Available from www.glfc.org/pubs/misc/2021-01.pdf

Eckmann R. 2013. A review of the population dynamics of coregonids in European alpine lakes. *Adv. Limnol.* 64: 3–24.

Eckmann R, Rösch R. 1998. Lake Constance fisheries and fish ecology. *Adv. Limnol.* 53: 285–301.

Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J. 2003. Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* 1: 488–494.

Eme J, Mueller CA, Manzon RG, Somers CM, Boreham DR, Wilson JY. 2015. Critical windows in embryonic development: Shifting incubation temperatures alter heart rate and oxygen consumption of Lake Whitefish (*Coregonus clupeaformis*) embryos and hatchlings. *Comp. Biochem. Physiol. Part A: Molecular and Integrative Physiology* 179: 71–80.

Eshenroder RL, Vecsei P, Gorman OT, Yule D, Pratt TC, Mandrak NE, Bunnell DB, Muir AM. 2016. Ciscoes (Coregonus, subgenus Leucichthys) of the Laurentian Great Lakes and Lake Nipigon | U. S. Geological Survey (USGS Publications Warehouse). *Great Lakes Science Center.*

European Committee of Regions, 2021. *From farm to fork − the local and regional dimension (2021/C 37/04; Opinion).*

Fang X, Jiang L, Jacobson PC, Stefan HG, Alam SR, Pereira DL. 2012. Identifying Cisco Refuge Lakes in Minnesota under Future Climate Scenarios. *Trans. Am. Fish. Soc.* 141: 1608–1621.

Finger D, Wüest A, Bossard P. 2013. Effects of oligotrophication on primary production in peri-alpine lakes. *Water Resour. Res.* 49: 4700–4710.

Freeberg MH, Taylor WW, Brown RW. 1990. Effect of Egg and Larval Survival on Year-Class Strength of Lake Whitefish in Grand Traverse Bay, Lake Michigan. *Trans. Am. Fish. Soc.,* 119: 92–100.

Fyfe JC, Meehl GA, England MH, Mann ME, Santer BD, Flato GM. 2016. Making sense of the early-2000s warming slowdown. *Nature Clim Change* 6: 224–228.

Gerdeaux D, Anneville O, Hefti D. 2006. Fishery changes during re-oligotrophication in 11 peri-alpine Swiss and French lakes over the past 30 years. *Acta Oecol.* 30: 161–167.

Gillet C. 1991. Egg production in an Arctic charr (*Salvelinus alpinus* L.) brood stock: Effects of temperature on the timing of spawning and the quality of eggs. *Aquat. Living Resour.* 4: 2.

Göbel S, Baer J, Geist J. 2017. Effects of temperature and rearing density on growth of juvenile European whitefish (*Coregonus macrophthalmus*) in aquaculture. *Fund. Appl. Limnol. / Arch. Hydrobiol.* 189/3: 257–266.

Gugele S, Baer J, Spiessl C, Yohannes E, Blumenshine S, Roberts B, Ferreira M, Brinker A. 2023. Stable isotope values and trophic analysis of invasive three-spined stickleback in Upper Lake Constance points to significant piscivory. *NeoBiota* 87: 73–102.

Hållén J, Waldetoft H, Viktor T, Karlsson M. 2020. Dioxiner i fet fisk från Östersjön, *Vänern och Vättern. IVL Rapport B* 2402. 118 p.

Hill MO, Smith AJE. 1976. Principal Component Analysis of Taxonomic Data with Multi-State Discrete Characters. *TAXON* 25: 249–255.

Hirsch PE, Eckmann R, Oppelt C, Behrmann-Godel J. 2013. Phenotypic and genetic divergence within a single whitefish form − detecting the potential for future divergence. *Evol. Appl.* 6: 1119–1132.

Hirsch RM, Slack JR, Smith RA. 1982. Techniques of trend analysis for monthly water quality data. *Water Resour. Res.* 18: 107–121.

Holmes EE, Ward EJ, Scheuerell MD. 2012. Analysis of multivariate time-series using the MARSS package. *NOAA Fisheries, 2725 Montlake Blvd E., Seattle, WA 98112: Northwest Fisheries Science Center.*

Hurrell JW, 1995. Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. *Science* 269: 676–679.

Jacobson PC, Cross TK, Zandlo J, Carlson BN, Pereira DP. 2012. The effects of climate change and eutrophication on cisco *Coregonus artedi* abundance in Minnesota lakes. *Adv. Limnol.* 63, 417–427.

Jacobson PC, Fang X, Stefan HG, Pereira DL. 2013. Protecting cisco (*Coregonus artedi Leseur*) oxythermal habitat from climate change: Building resilience in deep lakes using a landscape approach. *Adv. Limnol.* 64, 323–332.

Jane SF, Hansen GJA, Kraemer BM, Leavitt PR, Mincer JL, North RL, Pilla RM, Stetler JT, Williamson CE, Woolway RI, Arvola L, Chandra S, DeGasperi CL, Diemer L, Dunalska J, Erina O, Flaim G, Grossart H-P., Hambright KD. *et al.* 2021. Widespread deoxygenation of temperate lakes. *Nature* 594: 66–70.

Jenny J-P., Anneville O, Arnaud F, Baulaz Y, Bouffard D, Domaizon I, Bocaniov SA, Chèvre N, Dittrich M, Dorioz J-M., Dunlop ES, Dur G, Guillard J, Guinaldo T, Jacquet S, Jamoneau A, Jawed Z, Jeppesen E, Krantzberg G, *et al.* 2020. Scientists' Warning to Humanity: Rapid degradation of the world's large lakes. *J. Great Lakes Res.* 46: 686–702.

Jensen OP, Benson BJ, Magnuson JJ, Card VM, Futter MN, Soranno PA, Stewart KM. 2007. Spatial analysis of ice phenology trends across the Laurentian Great Lakes region during a recent warming period. *Limnol. Oceanogr.* 52: 2013–2026.

Jeppesen E, Mehner T, Winfield I, Kangur A, Sarvala J, Gerdeaux D, Rask M, Malmquist H, Holmgren K, Volta P, Romo S, Eckmann R, Sandström A, Blanco S, Kangur A, Ragnarsson Stabo H, Tarvainen M, Ventelä A-M., Søndergaard M, Meerhoff M. 2012. Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. *Hydrobiologia* 694: 1–39.

Kangur K, Ginter K, Kangur A, Möls T. 2020. How Did the Late 1980s Climate Regime Shift Affect Temperature-Sensitive Fish Population Dynamics: Case Study of Vendace (*Coregonus albula*) in a Large North-Temperate Lake. *Water* 12: 2694.

Kangur K, Tammiksaar E, Pauly D. 2022. Using the "mean temperature of the catch" to assess fish community responses to warming in a temperate lake. *Environ. Biol. Fishes* 105: 1405–1413.

Kao Y-C., Madenjian CP, Bunnell DB, Lofgren BM, Perroud M. 2015. Potential effects of climate change on the growth of fishes from different thermal guilds in Lakes Michigan and Huron. *J. Great Lakes Res.* 41: 423–435.

Kao Y-C., Rogers MW, Bunnell DB, Cowx IG, Qian SS, Anneville O, Beard TD, Brinker A, Britton JR, Chura-Cruz R, Gownaris NJ, Jackson JR, Kangur K, Kolding J, Lukin AA, Lynch AJ, Mercado-Silva N, Moncayo-Estrada R, Njaya FJ, *et al.* 2020. Effects of climate and land-use changes on fish catches across lakes at a global scale. *Nat. Commun.* 11 : 2526.

Kerimoglu O, Jacquet S, Vinçon-Leite B, Lemaire BJ, Rimet F, Soulignac F, Trévisan D, and Anneville O. 2017. Modelling the plankton groups of the deep, peri-alpine Lake Bourget. *Ecol. Model.* 359: 415–433.

Kumar, R, Martell, SJ, Pitcher, TJ, Varkey, DA. 2013. Temperature-Driven Decline of a Cisco Population in Mille Lacs Lake, Minnesota. *N. Am. J. Fish. Manage.* 33: 669–681.

Ludsin SA, Kershner MW, Blocksom KA, Knight RL, and Stein RA. 2001. Life After Death in Lake Erie: Nutrient Controls Drive Fish Species Richness, Rehabilitation. *Ecol. Appl.* 11: 731–746.

Lynch AJ, Taylor WW, Beard TD, Lofgren BM. 2015. Climate change projections for lake whitefish (*Coregonus clupeaformis*) recruitment in the 1836 Treaty Waters of the Upper Great Lakes. *J. Great Lakes Res.* 41: 415–422.

MacKenzie CJA, Fortin BL, Stevens CE. 2022. Summary of ecological information relevant to Great Slave Lake fisheries. *Can Manuscr. Rep. Fish. Aquat. Sci.* 3214: vii+63p.

Massol F, David P, Gerdeaux D, Jarne P. 2007. The influence of trophic status and large-scale climatic change on the structure of fish communities in Perialpine lakes. *J. Anim. Ecol.* 76: 538–551.

Mayr C. 2001. The influence of population density on growth of whitefish (*Coregonus lavaretus* L.) in four prealpine lakes. *Limnologica* 31: 53–60.

Mueller C, Eme J, Manzon R, Somers C, Boreham D, Wilson J. 2015. Embryonic critical windows: Changes in incubation temperature alter survival, hatchling phenotype, and cost of development in lake whitefish (*Coregonus clupeaformis*). *J. Comp. Physiol. B* 185: 315-–331.

Müller R. 1992. Trophic state and its implications for natural reproduction of salmonid fish. *Hydrobiologia* 243/244: 261–268.

Müller R. Stadelmann P. 2004. Fish habitat requirements as the basis for rehabilitation of eutrophic lakes by oxygenation. *Fisheries Manage. Ecol.* 11: 251–260.

Müller R, Breitenstein M, Bia MM, Rellstab C, Kirchhofer A. 2007. Bottom-up control of whitefish populations in ultra-oligotrophic Lake Brienz. *Aquat. Sci.* 69: 271–288.

Norborg Carlsson A-C. 2023. Vattenkvalitet i Vättern. *Vätternvårds-förbundet. Rapport* 159: 12–22. ISSN 1102-3791

Nowicki CJ, Bunnell DB, Armenio PM, Warner DM, Vanderploeg HA, Cavaletto JF, Mayer CM, Adams JV. 2017. Biotic and abiotic factors influencing zooplankton vertical distribution in Lake Huron. *J. Great Lakes Res.*, 43: 1044–1054.

Numann W. 1970. The Blaufelchen of Lake Constance, Coregonus wartmani under negative and positive influence of man. *In:* Lindsey C.C. and Wood C.S. (eds.), Biology of Coregonid fishes, University of Manitoba, 531–552.

Öğlü B, Möls T, Kaart T, Cremona F, Kangur K. 2020. Parameterization of surface water temperature and long-term trends in Europe's fourth largest lake shows recent and rapid warming in winter. *Limnologica* 82: 125777.

O'Reilly C, Sharma S, Gray D, Hampton S, Read J, Rowley R, Schneider P, Lenters J, McIntyre P, Kraemer B, Weyhenmeyer G, Straile D, Dong B, Adrian R, Allan M, Anneville O, Arvola L, Austin J, Bailey J, Zhang G. 2015. Rapid and highly variable warming of lake surface waters around the globe. *Geophys. Res. Lett.* 42: 10773–10781.

Ovando D, Free CM, Jensen OP Hilborn R. 2022. A history and evaluation of catch-only stock assessment models. *Fish and Fisheries* 23: 616–630.

Pankhurst N, Munday P. 2011. Effect of climate change on fish reproduction and early life history stages. *Mar. Freshwater Res.* 62: 1015–1026.

Pauly D, Hilborn R, Branch T. 2013. Fisheries: Does catch reflect abundance? *Nature,;1;* 494, 303–306.

Perrier C, Molinero J-C., Gerdeaux D, Anneville O. 2012. Effects of temperature and food supply on the growth of whitefish Coregonus lavaretus larvae in an oligotrophic peri-alpine lake. *J. Fish Biol.* 81: 1501–1513.

Piton V, Reiss R, Lemmin U, Anneville O, Many G, Keller J, Kindschi V, Kyi Wynn HK, Rasconi S, Laine L, Barry DA. 2024. Identifying and quantifying unexpected deep zooplankton diel vertical migration in a large deep lake. *Limnol. Oceanogr.* 9999: 1–16.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria*, https://www.r-project.org/.

Renberg I, Bindler R, Bradshaw E, Emteryd O, Englund J, Leavitt P. 2003. Paleolimnologiska undersökningar i Vättern och Vänern. Vätternvårdsförbundet. *Rapport nr 75*. 30 pages.

Rimet F, Anneville O, Barbet D, Chardon C, Crépin L, Domaizon I, Dorioz J-M., Espinat L, Frossard V, Guillard J, Goulon C, Hamelet V, Hustache J-C., Jacquet S, Lainé L, Montuelle B, Perney P, Quetin P, Rasconi S, *et al.* 2020. The Observatory on LAkes (OLA) database: Sixty years of environmental data accessible to the public: The Observatory on LAkes (OLA) database. *J. Limnol.* 79: 2.

Roberts BJ, Chucholl C, Brinker A. 2024. Coldwater, stenothermic fish seem bound to suffer under the spectre of future warming. *J. Great Lakes Res.* 50: 102351.

Rodrigues T, Chapelsky A, Hrenchuk L, Mushet G, Chapman L, Blanchfield P. 2022. Behavioural responses of a cold-water benthivore to loss of oxythermal habitat. *Environ. Biol. Fishes* 105: 1489–1507.

Rogell B, Axenrot T. 2023. Pelagisk fisk i Vänern 2022. *Aqua notes 2023:13. Uppsala: Institutionen för akvatiska resurser.*

Rogissart H, Goulon C, Guillard J. 2024. Historical rehabilitation of whitefish fisheries in Lake Geneva and Lake Bourget during the eutrophication period: assessing socio-economic impacts through large collaborative research. *Int. J. Limnol.* 60: 13.

Rook BJ, Lenart SJ, Caroffino DC, Muir AM, Bronte CR. 2022. A 90-year record of lake whitefish *Coregonus clupeaformis* abundances in Michigan waters of the upper Laurentian Great Lakes. *J. Great Lakes Res.* 48: 1618–1635.

Rösch R. 1987. Egg—Size of pelagic and nearshore spawning Coregonids (Coregonus lavaretus L.) from Lake Constance correlated with the fish weight. *Arch. Hydrobiol.* 109: 519–523.

Rösch R, Baer J, Brinker A., 2018. Impact of the invasive three-spined stickleback (*Gasterosteus aculeatus*) on relative abundance and growth of native pelagic whitefish (*Coregonus wartmanni*) in Upper Lake Constance. *Hydrobiologia* 824: 243–254.

Rühland K, Evans M, Smol J. 2023. Arctic warming drives striking twenty-first century ecosystem shifts in Great Slave Lake (Subarctic Canada), North America's deepest lake. *Proc. Roy. Soc. London, Ser. B*, 290: 2007.

Sandlund O, Hesthagen T, Brabrand Å. 2013. Coregonid introductions in Norway: Well-intended and successful, but destructive. *Adv. Limnol.* 64: 341–358.

Sandström A, Ragnarsson Stabo H, Axenrot T, Bergstrand E. 2014. Has climate variability driven the trends and dynamics in recruitment of pelagic fish species in Swedish Lakes Vänern and Vättern in recent decades? *Aquat. Ecosyst. Health Manage.* 17: 349–356.

Scofield AE, Watkins JM, Osantowski E, Rudstam LG. 2020. Deep chlorophyll maxima across a trophic state gradient: A case study in the Laurentian Great Lakes. *Limnol. Oceanogr.* 65: 2460–2484.

Sen PK. 1968. Estimates of the Regression Coefficient Based on Kendall's Tau. *J. Am. Stat. Assoc.*, 63: 1379–1389.

Servili A, Canario AVM, Mouchel O, Muñoz-Cueto JA. 2020. Climate change impacts on fish reproduction are mediated at multiple levels of the brain-pituitary-gonad axis. *Gen. Comp. Endocrinol.* 291: 113439.

Shimoda Y, Cai H, Fernando Y, Okoli A, Xu Z, Koops M, Johnson TB, Arhonditsis GB. 2023. How influential is the role of oligotrophication on the integrity of fish assemblages in the littoral zone? *J. Great Lakes Res.* 49: 847–861.

Steinsberger T, Schwefel R, Wüest A, Müller B. 2020. Hypolimnetic oxygen depletion rates in deep lakes: Effects of trophic state and organic matter accumulation. *Limnol. Oceanogr.* 65: 3128–3138.

Stewart TR, Karjalainen J, Zucchetta M, Goulon C, Anneville O, Vinson MR, Wanzenböck J, Stockwell JD. 2024a. Winter is not coming: evaluating impacts of changing winter conditions on coregonine reproductive phenology. *Int. J. Limnol.* 60: 17.

Stewart T, Mäkinen M, Goulon C, Guillard J, Marjomäki T, Lasne E, Karjalainen J, Stockwell JD. 2021. Influence of warming temperatures on coregonine embryogenesis within and among species. *Hydrobiologia* 848: 4363–4385.

Stewart TR, Brun C, Goulon C, Baer J, Karjalainen JS, Guillard J, Lasne E. 2024b. Response of European whitefish embryos to thermal conditions diverges between peri-alpine populations. *Int. J. Limnol*. 60: 19.

Straile D, Eckmann R, Jüngling T, Thomas G, Löffler H. 2007. Influence of climate variability on whitefish (Coregonus lavaretus) year class strength in a warm monomictic lake. *Oecologia* 151: 521–529.

Svärdson G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. *Rep. Inst. Freshw. Res.* 55: 144–171.

Tammiksaar E, Kangur K. 2020. Fish and fishing in Lake Peipsi (Estonia/Russia) since 1851: Similarities and differences between historical and modern times. *J. Great Lakes Res.* 46: 862–869.

Trippel EA, Eckmann R, Hartmann J. 1991. Potential Effects of Global Warming on Whitefish in Lake Constance, Germany. *Ambio* 20: 226–231.

United Nations General Assembly, 2015. Appendix: Transforming Our World: The 2030 Agenda for Sustainable Development (No. A/RES/70/1). *From A New Era in Global Health*. DOI: 10.1891/9780826190123.ap02

Vanni MJ, Luecke C, Kitchell JF, Magnuson JJ. 1990. Effects of planktivorous fish mass mortality on the plankton community of Lake Mendota, Wisconsin: Implications for biomanipulation. *Hydrobiologia* 200: 329–336.

Vollenweider, RA, Kerekes, J. 1982. Eutrophication of Waters: Monitoring, Assessment and Control. OECD Cooperative Program on monitoring inland waters (Eutrophication control). *Environment Directorate, OECD, Paris*.

Vonlanthen P, Bittner D, Hudson AG, Young KA, Müller R, Lundsgaard-Hansen B, Roy D, Di Piazza S, Largiader CR, and Seehausen O. 2012. Eutrophication causes speciation reversal in whitefish adaptive radiations. *Nature* 482: 357–362.

Wahl B, Peeters F. 2014. Effect of climatic changes on stratification and deep-water renewal in Lake Constance assessed by sensitivity studies with a 3D hydrodynamic model. *Limnol. Oceanogr.* 59: 1035–1052.

Weyhenmeyer GA, Chukwuka AV, Anneville O, Brookes J, Carvalho CR, Cotner JB, *et al.* 2024. Global lake health in the Anthropocene: Societal implications and treatment strategies. *Earth's Future* 12, e2023EF004387.

Wickham H. 2016. Ggplot2: Elegant graphics for data analysis (2nd edition). New York: Springer-Verlag.

Woelmer WM, Kao Y-C., Bunnell DB, Deines AM, Bennion DH, Rogers MW, Brooks CN, Sayers MJ, Banach DM, Grimm AG, Shuchman RA. 2016. Assessing the influence of watershed characteristics on chlorophyll a in waterbodies at global and regional scales. *Inland Waters* 6: 379–392.

Woolway RI, Kraemer B, Lenters J, Merchant C, O'Reilly C, Sharma S. 2020. Global lake responses to climate change. *Nat. Rev. Earth Environ.*, 1: 388–403.

Zhu X, Day C, Taptuna F, Carmichael T, Tallman R. 2015. Hierarchical modeling of spatiotemporal dynamics of biological characteristics of Lake Whitefish, *Coregonus clupeaformis* (Mitchill), in Great Slave Lake, Northwest Territories, 1972–2004. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2015/038: 1–56.