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# Are perch (*Perca fluviatilis* L.) getting larger or smaller in Swedish lakes?

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## Abstract

Space-for-time approaches are often used to indicate current or future changes over time. A European gillnet standard facilitates spatial-scale comparisons of fish communities in European lakes. Fish size was generally lower and densities higher in warmer lakes, but less is known about trends over decadal time scales. We analysed the size of European perch (*Perca fluviatilis* L.) in 2121 Swedish lakes sampled during 1996–2021. The aim was to test whether size changed over time, and whether trends were similar in southern and northern regions. We analysed mean length and occurrence or relative abundance of size classes from the smallest (<100 mm) to the largest individuals (≥350 mm), and length at 1 and 5 years. The large data set was used to find general trends over time within regions, and within-lake trends were tested for 40 time-series lakes. The mean length of perch decreased in the southern and increased in the northern region. The proportion of the smallest perch increased in the southern, but not in the northern region. The most general trend was an increasing occurrence and proportion of the largest-sized perch in both regions in the large dataset. The average trends in the southern region of the large dataset also appeared as predominant trends within time-series lakes, although opposite trends occurred within some lakes in each region. This study also revealed that perch size at age 1 often increased within lakes over time, while more variable trends were found for size at age 5. The duration of the growth season has generally increased during the time frame of the present study, while other changes may differ between lakes in the same region. We recommend more studies based on time series of fish monitoring, including studies on possible reasons for the increased occurrence of very large perch in Swedish lakes.

KEYWORDS
European perch, large dataset, multimesh gillnets, size structure, temporal trends, time-series lakes

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## 1 | INTRODUCTION

The size structure of fish communities and their populations varies between lakes, depending on species composition as well as local and regional environmental factors (Arranz et al., 2016; Emmrich et al., 2014; Holmgren & Appelberg, 2000). The size distribution at a certain time is a result of dynamic processes, including recruitment, survival, individual growth and maturation (Brett, 1979; Perrin & Rubin, 1990). Such processes depend on species-specific life-history traits, but also on species-specific and size-specific optima and tolerance in environmental gradients. Abiotic factors include water temperature, pH, oxygen, light, spawning substrate and shelter, and important biotic factors are food availability, predators and competitors. According to Arranz et al. (2016), there are negative correlations between mean length and intraspecific and interspecific fish density, indicating that competition for resources is a key driver for the size structure. Some case studies report changes in mean size and growth over time, interpreted as at least partly influenced by a warming climate (e.g. Jeppesen et al., 2012).

Coldwater species, for example salmonids, are decreasing in abundance or disappearing in southern parts of their distribution area due to warming temperatures (e.g. Hein et al., 2012; Jeppesen et al., 2012), but changes may also involve size distributions of more widespread and tolerant species. Time-series data indicate dominance shifts from larger to smaller species in a warming climate, as well as increased dominance of young and small fish within populations (Daufresne et al., 2009). Such patterns have been explained by the temperature-size rule (Atkinson & Sibly, 1997), where individuals are expected to mature at a smaller size in a warmer climate, and sacrifice growth to larger adult body sizes to ensure reproductive success. In recent years, relationships between fish size and temperature have often been studied by using a space-for-time substitution approach (e.g. Arranz et al., 2016; Emmrich et al., 2014; Jeppesen et al., 2010; Van Dorst et al., 2019), facilitated by standard sampling of fish in many lakes within gradients of temperature, nutrients, watercolour and other lake characteristics. Such studies revealed significant relationships between different measures of size (size metrics) and environmental gradients. Most notably, the mean length of fish generally decreases in warmer lakes, both for the total fish community (Emmrich et al., 2014) and within some of the most commonly occurring species (Arranz et al., 2016), including European perch (*Perca fluviatilis* L.), hereafter perch.

Besides water temperature, several anthropogenic stressors currently affect freshwater ecosystems and size distributions of fish, for example eutrophication, acidification, resource exploitation, habitat alterations, spread of invasive species and global warming (Dudgeon et al., 2006; O'Reilly et al., 2015; Vörösmarty et al., 2010). These stressors are intertwined; for example international agreements to reduce emission of sulphur and nitrogen (causing acidification of lakes in some regions; c.f. Grennfelt et al., 2020) was followed by decreased weathering, sometimes leading to critically low calcium concentrations in lakes in North America and Europe (Jeziorski et al., 2008). In addition, increased concentration of dissolved organic matter and browner water in some northern lakes have been explained by recovery from acidification, afforestation or a wetter climate (De Wit et al., 2016; Kritzberg, 2017; Monteith et al., 2007).

Perch has its native distribution in large parts of Europe and northern Asia (Kottelat & Freyhof, 2007), and it is the most commonly occurring fish species in Swedish lakes (Tammi et al., 2003). This species can be categorised as a cool water fish (sensu Magnuson et al., 1979), that is with preference for intermediate temperatures (21°C–25°C). Juvenile growth of perch, and other percid fish species, generally increases with temperature, along latitudinal gradients (Galarowicz & Wahl, 2003; Heibo et al., 2005) or between years in the same lake (Tolonen et al., 2003; Uphoff et al., 2013); however, total biomass can decrease with increasing temperatures (Van Dorst et al., 2019). Perch feed predominantly on increasingly larger prey, from zooplankton and benthic invertebrates to fish during different life stages (Mittelbach & Persson, 1998). In order to grow large, it also needs good light conditions to efficiently feed on other fish (Radke & Gaupisch, 2005). Slower growth in browner water might be due to less efficient feeding on small zooplankton and larger invertebrates (Estlander et al., 2012). Along with pike (*Esox lucius* L.), perch is the most frequent species in catches of recreational freshwater fisheries in Sweden (Sande, 2020). If the fishery removes substantial amounts of perch from a lake, the size structure will shift towards a higher dominance of smaller fish (Olin et al., 2017). On the contrary, a higher mean and maximum size of perch have been observed after decreased landings by anglers (Skov et al., 2017).

Sweden has a long history of extensive monitoring of lake fish by using gillnets (Holmgren et al., 2016). The current European standard (CEN, 2015), that is sampling of fish with Nordic multimesh gillnets, was introduced in some Swedish lakes in 1993. It has increasingly been used, for example for assessment of ecological status according to the European Water Framework Directive (European Commission, 2000). During 1996–2021, more than 150 Swedish lakes where sampled with Nordic multimesh gillnets every single year (Holmgren, 2021). Geometric mean length of perch is one of the metrics used as part of a multi-metric index for fish in lakes (Holmgren et al., 2018), but so far no metric focussing on the largest fish in the catch has been used in the large-scale programmes for monitoring and assessment of fish in Swedish lakes.

The present study aimed at testing whether perch are generally becoming larger or smaller in Swedish lakes, and whether average trends differ between lakes in southern and northern regions. The approach was to test for temporal trends in different size metrics of perch, calculated from catches in extensive monitoring with standard gillnets. Metrics represented mean size and occurrence or relative abundance of both the smallest and the largest individuals, and for some lakes also perch size in two age groups. Based on previous space-for-time studies, we expected a decrease in mean length of perch, related to the observed average increase in air temperature (SMHI, https://www.smhi.se/en/climate/climate-indicators/climate-indicators-temperature-1.91472). Decreased mean size was expected to be reflected by an increased proportion of small individuals (<100 mm), due to increased early growth and survival of young fish. Expectations were less clear about general trends in occurrence or proportion of very large perch (≥350 mm), due to complex interactions influencing growth to large size. The question was whether extensive data from standard sampling would support reports from anglers, that is on recently more very large perch in lakes of northern Sweden. We primarily analysed overall yearly average values from many lakes sampled in 1996 to 2021, and then, we used 40 time-series lakes to see whether large-scale trends could also be observed when repeatedly sampling in the same lakes.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and lake data selection

This study relied on extensive data from sampling of fish with Nordic multimesh gillnets (CEN, 2015), more specifically data from Swedish lakes stored in the National Register of Survey test-fishing (NORS, Kinnerbäck, 2022). We primarily selected data from 1996 to 2021, a period when perch was caught and individual length was measured in more than 100 lakes each year. Sampling was performed during summer, using standard benthic gillnets (1.5 m height, 12 3 m long panels with 5–55 mm mesh bar). The benthic gillnets were set overnight (ca 12 hours including dusk and dawn) in different depth strata to represent the whole lake. The number of gillnets per lake and year depended on lake area and depth (CEN, 2015). Some of the deeper lakes were also sampled with pelagic gillnets (6 m height, 11 3 m long panels with 6.25–55 mm mesh bar), set at the deepest part of the lake.

In total, perch were caught in 4714 fish sampling events in 2121 lakes. More than half of the lakes (1276) were sampled only once, 40 lakes for at least 10 years and 12 lakes annually for 26 years. In general, the same gillnet locations were used from year to year in the time-series lakes. Each lake was assigned to one of two geographical regions (Figure 1), to reveal any difference in trends of perch size between southern and northern parts of Sweden. The division between south and north is at latitude 60°N in the western part until this latitude reaches the catchment of River Dalälven. Then, it follows the southern limit of the catchment until it reaches the Baltic Sea, according to the regulation used in Swedish water management (HaV, 2017). A few southern lakes in our large data set were situated in a lowland area north of 60°N, overlapping in latitude with some of the inland lakes at higher elevation of the northern region, but there was no such overlap for the time-series lakes (Figure 1). In every single year, more lakes were sampled in the south, but at least 19 lakes per year were sampled in the northern region (Figure 2).

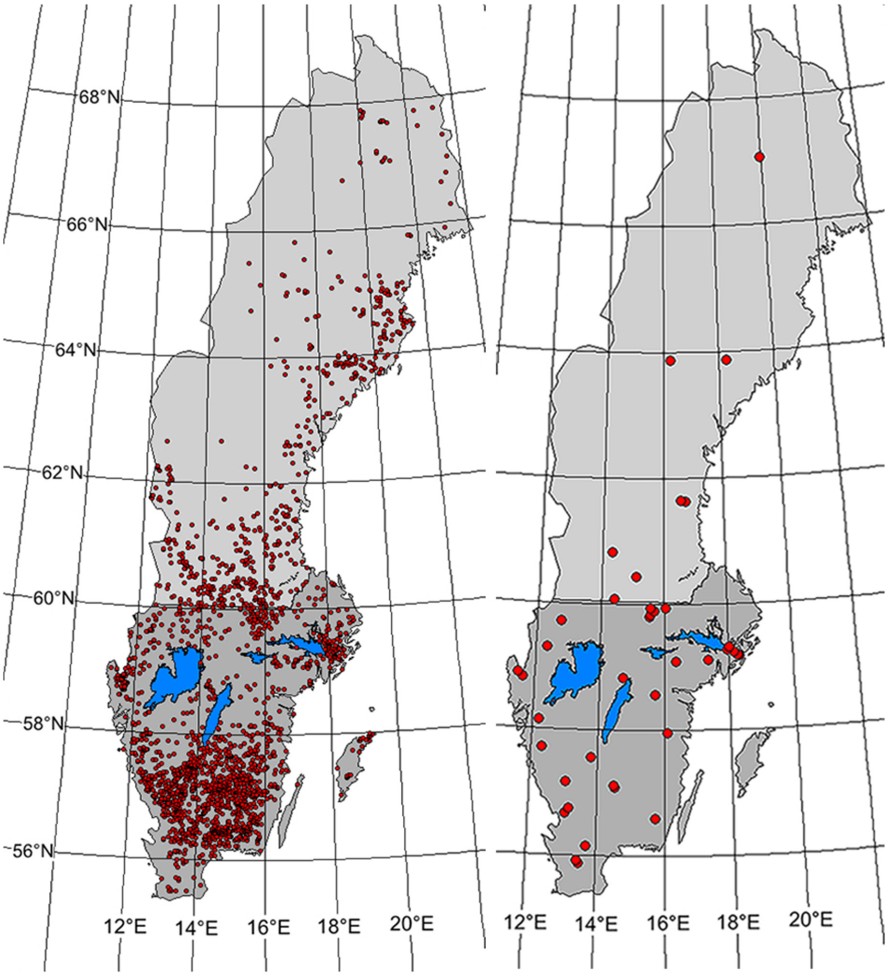

**FIGURE 1** Spatial distribution of the studied perch lakes in Sweden, in a southern (dark grey) and a northern region (light grey). The red dots represent all 2121 lakes sampled in 1–26 years during 1996–2021 (left panel), and 40 lakes sampled in at least 10 years (right panel).

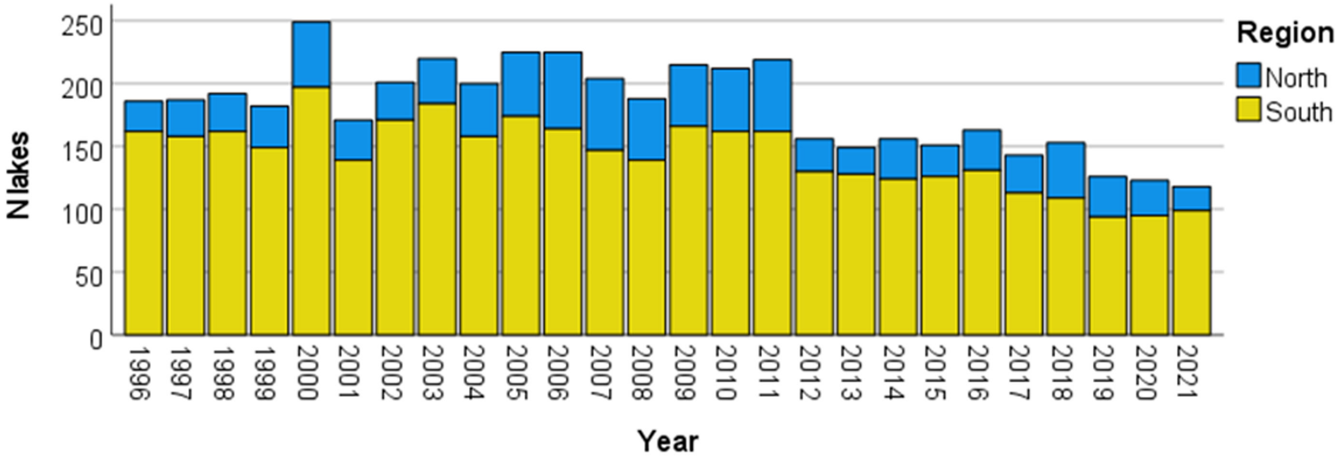

FIGURE 2 Number of perch lakes sampled per year, in the south and north regions.

TABLE 1 Characteristics of the perch lakes sampled during 1996–2021 (1580 lakes in the south and 541 lakes in the north), shown as mean, minimum and maximum values.

| | Southern region | | | Northern region | | |
|---|---|---|---|---|---|---|
| Lake descriptor | Mean | Min. | Max. | Mean | Min. | Max. |
| (1) Latitude (WGS84-N) | 57.62 | 55.49 | 60.40 | 62.34 | 60.01 | 67.88 |
| (2) Longitude (WGS84-E) | 14.64 | 11.27 | 19.22 | 16.72 | 12.22 | 23.48 |
| (3) Elevation (m) | 135 | 0 | 336 | 264 | 1 | 832 |
| (4) Lake area (ha) | 206 | 1 | 17,863 | 191 | 1 | 6531 |
| (5) Maximum depth (m)[a] | 11.2 | 1 | 75 | 13.9 | 1 | 71 |
| (6) Highest coastline (1 = above, 0 = below) | 0.71 | 0 | 1 | 0.58 | 0 | 1 |
| (7) Mean air temperature (°C) | 6.4 | 4 | 8 | 2.9 | −1 | 6 |
| (8) *N* fish sampling dates | 2.4 | 1 | 26 | 1.8 | 1 | 26 |
| (9) Npue-Total (*N* per gillnet and night) | 43.7 | 0,1 | 608 | 29.1 | 0,8 | 297 |
| (10) Bpue-Total (g per gillnet and night) | 1543 | 10 | 9993 | 1545 | 20 | 7311 |
| (11) *N* fish species | 5.0 | 1 | 15 | 4.2 | 1 | 13.5 |
| (12) Npue-Perch (*N* per gillnet and night) | 19.8 | 0.1 | 466 | 16.1 | 0.1 | 106 |
| (13) Bpue-Perch (g per gillnet and night) | 634 | 6.5 | 5505 | 924 | 0.5 | 6553 |
| (14) Mean length (mm) | 116 | 56 | 366 | 142 | 59 | 456 |
| (15) % Occurrence of perch ≥350 mm | 55.6 | | | 52.8 | | |
| (16) % Individual perch <100 mm | 35.4 | 0 | 94,64 | 21.4 | 0 | 100 |
| (17) % Individual perch 100–199 mm | 54.5 | 0 | 100 | 57.6 | 0 | 100 |
| (18) % Individual perch ≥200 mm | 10.1 | 0 | 100 | 21.0 | 0 | 100 |
| (19) % Individual perch ≥350 mm | 1.1 | 0 | 100 | 1.5 | 0 | 100 |

*Note*: Descriptors 1–7 are based on one fixed value per lake, and descriptors 8–19 are based on mean values of one or more sampling years per lake.

[a] Maximum depth was available only for 1571 lakes in the south and 534 lakes in the north.

All lakes had records of some lake characteristics available in the NORS database, that is latitude, longitude, elevation, lake area, position above or below the highest coastline after the last glaciation and mean air temperature during the standard period 1961–1990 (Table 1). With a few exceptions, there was also a record of lake maximum depth. The air temperature represented climatic differences between lakes rather than temperature levels experienced by the fish in specific years. Data on surface water temperature were available for most studied years in 14 of the time-series lakes, covering most of the latitude range of lakes in the large dataset. From the year 2000, temperature loggers set at 1–1.5 depth recorded temperature four to six times per day. Temperature was measured at 0.5 m depth, in the middle of each month from May to September, at least until year 2012. By calculating mean temperature during May–September for both types of measurement, mean temperature at 1–1.5 m depth could be estimated for years without, or with malfunctioning, temperature loggers.

Lakes in both regions covered similarly large ranges in lake area, maximum depth and local species richness, but the northern lakes were on average situated more east, at higher elevation and in a colder climate (Table 1, Figure A1 in Appendix 1). The subsets of time-series lakes of both regions were on average similar to other lakes in the large data set. A few perch lakes in the large dataset were however smaller and larger, and shallower and deeper, than any time-series lakes, probably explaining a higher range in observed fish species richness in the large dataset. On average, the surface water temperature during May–September increased about 1°C (from 16 to 17°C) during 1994–2021 (Figure A2), but differences between years sometimes exceeded 2°C within the same lake.

For all lakes and years when perch was caught, we extracted records of numbers and biomass (g) per unit effort (Npue and Bpue) in benthic gillnet catches, for perch and for the total of all species caught. Npue and Bpue were simply expressed per gillnet and night, because the area of the standard gillnet is fixed at 45 $m^2$. The numbers of species in the total catch, of benthic and pelagic gillnets were taken as a measure of fish diversity. Data on individual length of all perch were also extracted, from the combined catch in benthic and pelagic gillnets. Individual mass (g) was generally not measured. Exceptions were 64 lakes (including 33 time-series lakes) where subsamples (ca 70 perch) were weighed and samples were taken for age determination, using sagittal otoliths and operculum bones, and for back-calculation of length after completed growth seasons according to Holmgren and Appelberg (2001).

## 2.2 | Perch size metrics

For each lake and year, six different metrics were calculated to represent different aspects of perch size structure (no. 14–19 in Table 1). The average size of perch was expressed as mean geometric length (mm), hereafter mean length. As an arbitrary size limit of very large individuals, we chose 350 mm to roughly represent perch larger than 500 g. This was based on a length–weight relationship [weight (g) = $2.975 \times 10^{-6} \times$ length (mm)$^{3.238}$], based on 24,803 aged perch in the database. For each fish sample, perch was recorded as present or absent, and it was used for calculation of % of samples with very large perch within each year and region. The remaining four metrics were % of perch individuals within the following size groups: <100 mm, 100–199 mm, ≥200 mm and ≥350 mm (a subset of ≥200 mm).

Two additional growth-related metrics were calculated for 33 of the time-series lakes with regular ageing of ca 70 perch per year of sampling; back-calculated length after the first and the fifth completed growth seasons. Here, we selected individuals with estimated ages between 1 and 6 (caught in the middle of their second to seventh growth seasons), to avoid older individuals with potentially less accurate age. All selected individuals allowed estimation of length at age 1 ($L_{\text{age1}}$), but back-calculated length at age 5 ($L_{\text{age5}}$) was only used for perch caught at age 5 or 6. Mean values of $L_{\text{age1}}$ and $L_{\text{age5}}$ were taken for each lake and year of birth.

## 2.3 | Data analysis

Temporal trends on perch size metrics were tested by using two datasets, differing in geographical coverage and analysis approach. Firstly, a large dataset (4714 samples in 2121 lakes during 1996–2021) was used to test for general trends over time. With fairly high numbers of lakes within each year and region (94–198 in the south and 19–61 in the north), we assumed that within-region estimates of annual mean values were approximately normally distributed. Secondly, a smaller time-series dataset (40 lakes sampled in 10–26 years during 1996–2021) had only one estimate per size metric and year, and we made no assumption on their error distributions.

For the large dataset, we ran linear regression analyses to test for temporal trends within regions (south or north), in seven perch metrics (no. 12–14 and 16–19 in Table 1) and eight other lake- or sampling-specific descriptors (no. 3–7 and 9–11 in Table 1) that might potentially confound conclusions on observed trends for perch. Each of the metrics (one at a time) was used as dependent and year as independent variable. Most of the dependent variables were transformed (see footnotes in Table 2 and Table A1) before analysis, in order to normalise residuals of the regressions. Logistic regression was used for the binomial metric occurrence of perch ≥350 mm. Raw *p*-values were Bonferroni-adjusted, that is multiplied with the number of metrics compared within each region. Adjusted *p*-values < .05 were interpreted as significant trends. The estimated annual means and their 95% confidence limits were also visually explored in graphs.

For time-series lakes, all available years sampled with Nordic gillnets were included in tests for temporal trends, including lakes sampled in 10–28 years during 1994–2021. Back-calculation of $L_{\text{age1}}$ and $L_{\text{age5}}$, by definition revealed some estimates for completed growth seasons before the first sampled year, and no estimates for the last years with aged subsamples. For harmonisation with other time series, we used only mean values of estimated $L_{\text{age1}}$ and $L_{\text{age5}}$ for years 1994 and later. Trends for metrics of perch size and fish density were analysed lake-by-lake. The non-parametric Kendall's correlation test was used to test for monotonic trends over time. Results were summarised by numbers of positive, negative and insignificant

**TABLE 2** Average trends in perch size metrics during 1996–2021, in most cases after transformation of values according to the footnote.

| Perch size metric | Region | Regression (a + b[d]year) | $F_{1:\text{df res.}}$[d] | Raw *p*-value | Adj. *p*-value |
|---|---|---|---|---|---|
| Mean length (mm)[a] | North | 2.130 + 0.0016[d]year | 11.61 | <.001 | **.0054** |
| | South | 2.074–0.00022[d]year | 37.27 | <.001 | **<.001** |
| Occurrence of ≥350 mm[b] | North | −0.70 + 0.061[d]year | 40.44 | <.001 | **<.001** |
| | South | −0.16 + 0.032[d]year | 47.49 | <.001 | **<.001** |
| % Individuals <100 mm[a] | North | 1.11–0.0012[d]year | 0.24 | .623 | 1.000 |
| | South | 1.35 + 0.0048[d]year | 24.3 | <.001 | **<.001** |
| % Individuals 100–199 mm | North | 64.23–0.53[d]year | 25.45 | <.001 | **<.001** |
| | South | 58.45–0.26[d]year | 26.85 | <.001 | **<.001** |
| % Individuals ≥200 mm[a] | North | 1.005 + 0.013[d]year | 43.79 | <.001 | **<.001** |
| | South | 0.895–0.003[d]year | 9.8 | .002 | **.014** |
| % Individuals ≥350 mm[c] | North | 0.29 + 0.0208[d]year | 58.42 | <.001 | **<.001** |
| | South | 0.46 + 0.0081[d]year | 42.31 | <.001 | **<.001** |

*Note*: Year 1996 was set to year 0 in the regression analyses. The estimated intercept (a), or its back-transformed value, then represents the estimated metric year 1996, and the slope (b) estimates the annual rate of change. *F*-values of the ANOVAs are given along with raw and adjusted *p*-values (Bonferroni, $m = 6$ comparisons per region). Significant tests are marked in bold.

[a] Log-transformed before analysis.

[b] Logistic regression was used and the value in column 'F1:df res' shows Wald chi-squared value.

[c] Transformed by fourth root before analysis.

[d] 969 Residual degrees of freedom in the north and 3741 in the south, respectively.

trends (significance when $p < .05$). Any predominance of negative or positive trends was evaluated by testing the null hypothesis that the median value of Kendall's tau ($N = 40$ lakes) was equal to 0, by using one-sample Wilcoxon rank sign test and Bonferroni adjustment for number of tested metrics.

Data selection, graphs and analyses were performed using IBM® SPPS® Statistics (version 27, release 27.0.1.0), except for regression models and transformations, which were run in SAS 9.4 TS level 1 M6.

## 3 | RESULTS

### 3.1 | Large data set—based on 2121 lakes

Each of six perch size metric appeared to increase or decrease significantly over time in the large data set (Table 2), except for the proportion of the smallest perch in the northern region. Mean length of perch was generally larger in the northern than in the southern region (Figure 3a), and there was an increasing trend over time in the north but a decreasing trend in the south. The proportion of small perch (<100 mm) was higher in the southern region (Figure 3b). The annual mean values increased in the southern region, but there was no trend over time in the northern region. The occurrence of very large perch (≥350 mm) was on average lower in northern than in southern lakes in the earlier years (Figure 3c). The average occurrence of very large perch increased in both regions. During the first half of the study period, the average occurrence of very large perch was always below 60% in both regions, and most often less than 40% in the northern regions. In contrast, at least one very large perch was caught in more than 60% of the lakes sampled in both regions in the most recent years. The overall average proportion of large individuals was only 1.1% in the southern and 1.5% in the northern region (Table 1), but the proportion of large individuals increased over time in both regions (Figure 3d), although less clearly in the south. Intermediate-sized perch (100–190 mm) on average made up more than 50% of the perch catch (Table 1), with significantly deceasing trends in both regions (Table 2). Larger perch (≥200 mm) generally contributed more to the catch in the north than in the south, and this size group increased in the north while it more slowly decreased in the south.

There were also some apparent trends in other lake characteristics (Table A1). Compared with the perch size metrics, there were relatively fewer trends in lake elevation, area, maximum depth and mean air temperature. However, significant slopes in regressions for air temperature in the north, and for lake area in the south, indicated some artificial differences between years, depending on how lakes were selected for fish sampling. In addition, there was a weak positive trend in observed species richness in the southern region, and positive trends in perch numerical densities in both regions, and for perch biomass in the north. Numerical density of all fish also increased in both regions, while no trends appeared for total fish biomass. Just as for the perch size metrics, the trends in the other biological metrics might reflect real trends in average values over time, which in this study approach cannot be disentangled from possible effects of not sampling the same set of lakes in all years.

### 3.2 | Time-series data—based on 40 lakes

Most of the lakes with time-series data were situated in the southern region (32 lakes) and only eight in the northern region (Figure 1).

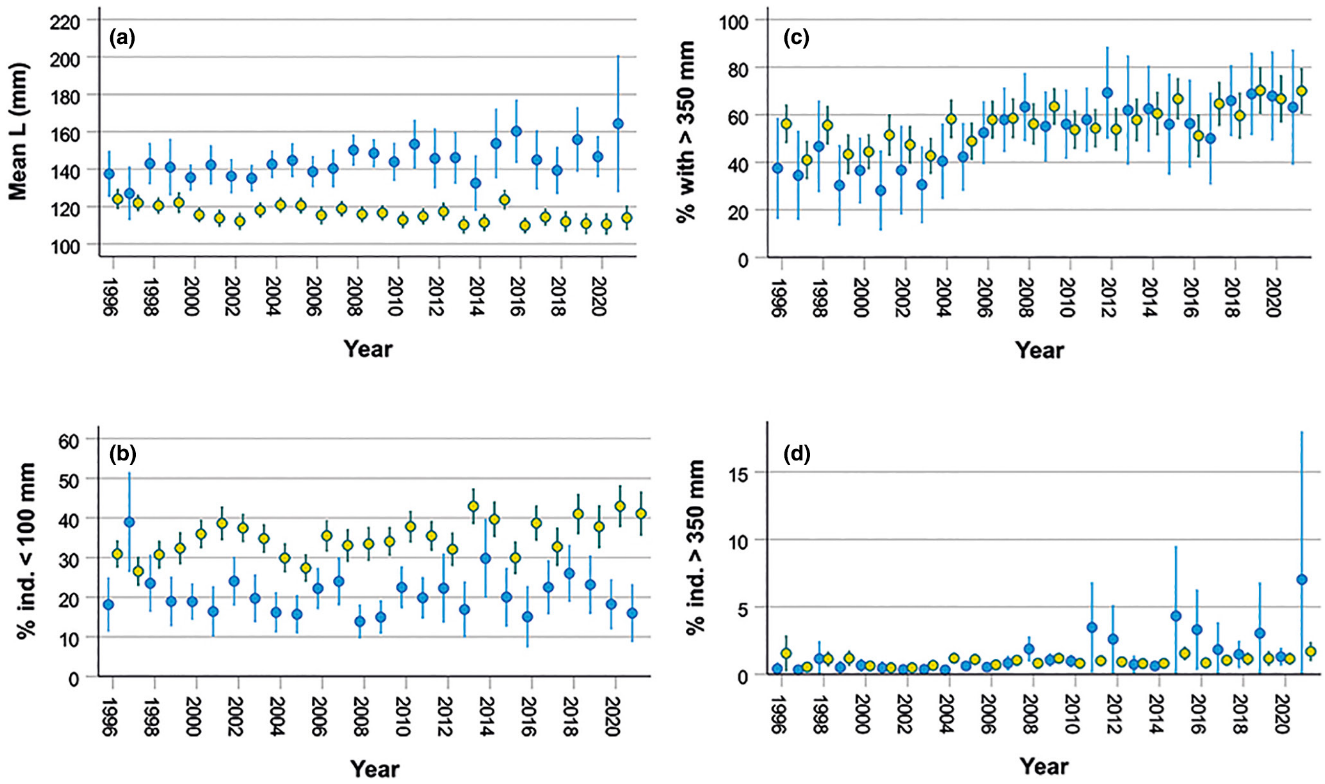

**FIGURE 3** Annual mean values ± 95% confidence intervals of perch size metrics within the southern (yellow) and northern (blue) regions; (a) mean length (mm); (b) % individuals <100 mm; (c) % of lakes with at least one individual ≥350 mm; and (d) % individuals >350 mm.

**TABLE 3** Number of trends over time for five perch size metrics and four fish density metrics (Kendall's tau, significance when $p < .05$), within 40 time-series lakes (32 in southern and eight in northern regions, 10–28 years per lake).

| Perch size or density metric | Negative | Positive | Insignificant | Median tau | Raw *p*-value | Adjusted *p*-value |
|---|---|---|---|---|---|---|
| Mean length of perch | 10 (10; 0) | 4 (4; 0) | 26 (19; 8) | −0.123 | .048 | .432 |
| % Individual perch <100 mm | 2 (1; 1) | 7 (5; 2) | 31 (26; 5) | 0.149 | **.003** | **.027** |
| % Individual perch 100–199 mm | 3 (3; 0) | 1 (1; 0) | 36 (28; 8) | −0.056 | .085 | .765 |
| % Individual perch ≥200 mm | 11 (9; 2) | 6 (5; 1) | 23 (17; 6) | −0.124 | .098 | .882 |
| % Individual perch ≥350 mm | 1 (1; 0) | 10 (8; 2) | 29 (23; 6) | 0.123 | **<.001** | **<.001** |
| Npue-Perch | 2 (1; 1) | 7 (6; 1) | 31 (25; 6) | 0.153 | **.001** | **.009** |
| Bpue-Perch | 5 (3; 2) | 8 (8; 0) | 27 (21; 6) | 0.053 | .285 | 1.000 |
| Npue-Total | 6 (5; 1) | 4 (4; 0) | 30 (23; 7) | 0.062 | .455 | 1.000 |
| Bpue-Total | 9 (8; 1) | 6 (5; 1) | 25 (19; 6) | 0.004 | .732 | 1.000 |

*Note*: Figures within brackets are lakes in the southern and northern regions, respectively. Median tau, raw and adjusted *p*-values (Bonferroni, $m = 9$ comparisons) are given for tests of $H_0$: median trend = 0 (one-sample Wilcoxon signed rank test, $N = 40$ lakes).
Significant *p*-values are highlighted in bold.

Both negative and positive trends were found in at least one lake each, for each of five perch size metrics and four fish density metrics (Table 3, Figure 4), although no significant monotonic trends were found in most of the lakes. There were more negative than positive trends for mean length of perch, and all significant trends occurred in lakes in the southern region. In contrast, positive trends more frequently occurred for the relative contributions of both the smallest (<100 mm) and the largest (≥350 mm) perch, and the positive trends were found in lakes in both regions. Positive trends were also more frequent than negative trends for the numerical density (Npue) of

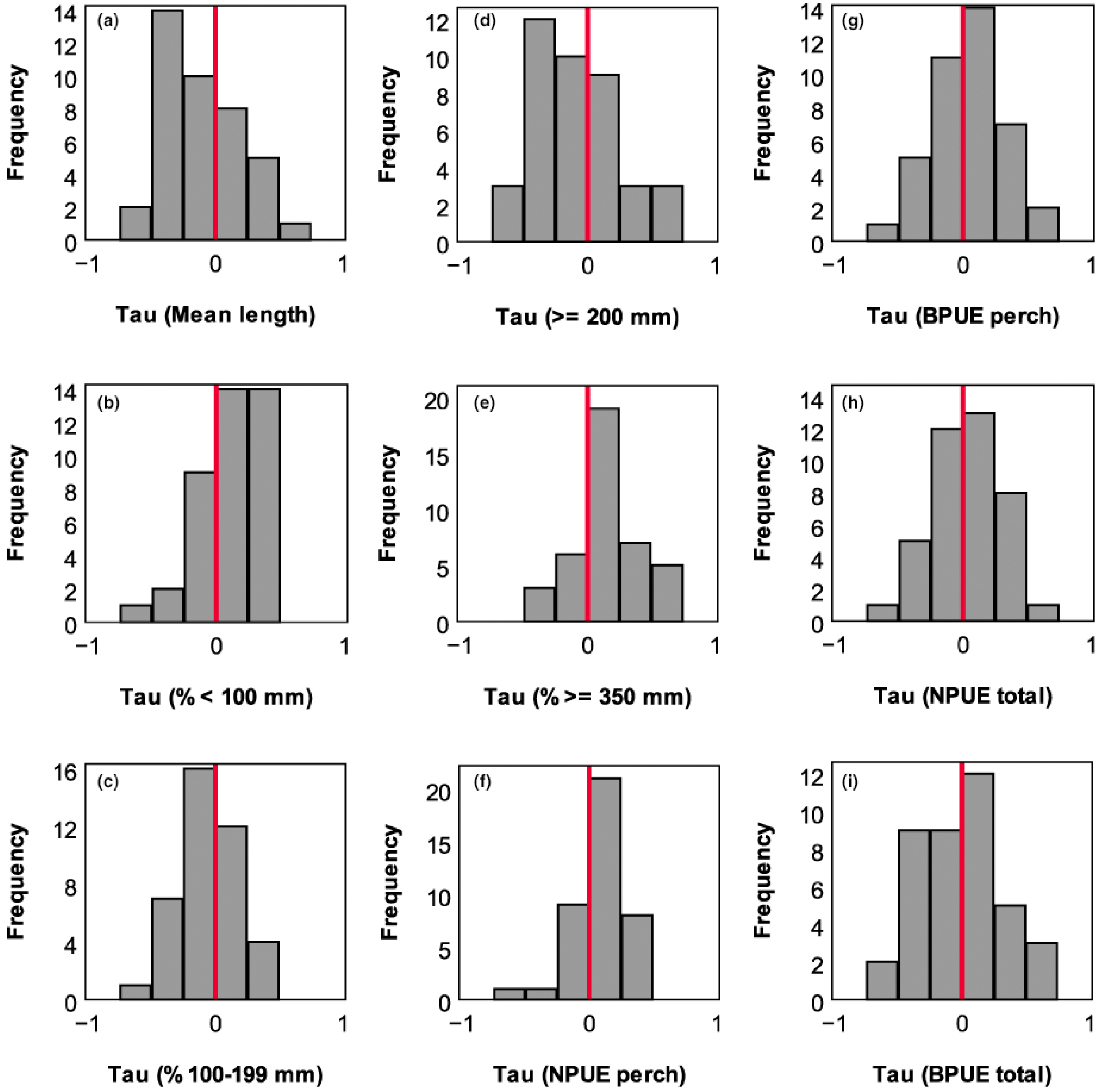

FIGURE 4 Distributions of the test statistic tau in trend tests within 40 times-series lakes ($N = 10–28$ years per lake, median 22), for perch size metrics; (a) mean length, (b) % individuals < 100 mm, (c) % individuals 100–199 mm, (d) % individuals ≥ 200 mm and (e) % individuals ≥ 350 mm, and for density metrics; (f) Npue of perch, (g) Bpue of perch, (h) total Npue and (i) total Bpue. The red vertical line separates negative and positive values. Tau is significant ($\alpha = .05$) at values above $|.265–.551|$, depending on $N$.

perch, but median trends were not significantly different from zero for perch biomass (Bpue), or for number or biomass of the total fish catch.

Age and back-calculated length at previous ages were available for perch in 25 of the time-series lakes in the southern region and for all of the eight lakes in the northern region. Mean length at age 1 ($L_{\text{age1}}$) tended to increase over time in most of the lakes, with a significant increase within 12 lakes and only one lake of the northern lakes had a decreasing trend (Figure 5a, Table 4). In contrast, there was no general trend in mean length at age 5 ($L_{\text{age5}}$, Figure 5b). Most lakes had insignificant trends, but some positive and some negative trends appeared in lakes of both the southern and the northern regions.

## 4 | DISCUSSION

Our primary focus was on revealing any general or predominating temporal trends in the size structure of perch, by using a unique

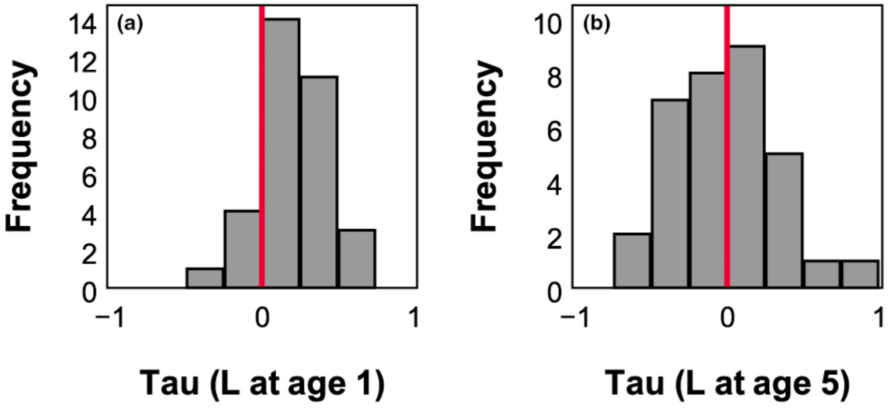

**FIGURE 5** Distributions of the test statistic tau in trend tests within 33 times-series lakes, for (a) mean length at age 1 ($N = 13–28$ years per lake, median 27) and (b) mean length at age 5 ($N = 8–28$ years, median 23). The red vertical line separates negative and positive values. Tau is significant ($\alpha = .05$) at values above $|.265–.643|$, depending on $N$.

**TABLE 4** Number of trends over time in back-calculated length of perch at ages 1 and 5 (Kendall's tau, significance when $p < .05$), within 33 time-series lakes (25 in southern and 8 in northern regions, 8–28 years per lake).

| Perch length metric | Negative | Positive | Insignificant | Median tau | Raw *p*-value | Adjusted *p*-value |
|---|---|---|---|---|---|---|
| Mean length at age 1 | 1 (0; 1) | 12 (10; 2) | 20 (15; 5) | 0.232 | **<.001** | **<.001** |
| Mean length at age 5 | 7 (3; 4) | 6 (4; 2) | 20 (18; 2) | −0.020 | .454 | .908 |

*Note*: Figures within brackets are lakes in the southern and northern regions, respectively. Median tau, raw and adjusted *p*-values (Bonferroni, $m = 2$ comparisons) are given for tests of $H_0$: median trend = 0 (one-sample Wilcoxon signed rank test).
Significant *p*-values are highlighted in bold.

large dataset of many Swedish lakes sampled one or more times during a period of 26 years. With a subset of far fewer time-series lakes, we found that some of the general trends in the large data set were also prevailing within lakes sampled in at least 10 years. One main result was that the expected decrease in mean length of perch and increase in the numerical proportion of small perch (<100 mm) were observed in the southern, but not in the northern region. The most general overall trend was an increasing occurrence and proportion of the largest-sized perch (≥350 mm) in both regions in the large dataset. The average trends in the southern region of the large dataset also appeared as predominant trends within time-series lakes, although opposite trends were observed within some lakes in each region. This study also revealed that perch size at age 1 generally increased within lakes over time, while more variable trends were found for size at age 5.

The ongoing global warming has already increased water temperatures and other thermal characteristics in European lakes (e.g. Arvola et al., 2009). Our data from some of the Swedish perch lakes confirm increasing water temperature as a general trend, although with large between-year variation compared with the average trend during 1994–2021 (Figure A2). The general idea that global warming benefits the small species and individuals in aquatic ecosystems was previously supported by a meta-analysis of time series of fish in French rivers, in the North Sea and in the Baltic Sea (Daufresne et al., 2009). Such observations inspired several studies using fish sampling with standardised methods and large-scale temperature derived from gridded maps of sea surface temperature for marine fish (e.g. Audzijonyte et al., 2020) or air temperature for freshwater fish (e.g. Arranz et al., 2016; Emmrich et al., 2014). The marine study relied on standard diving surveys with reef fish size observations at large scales for both space and time. They found that 55% of the species were smaller in warmer water, while the rest were larger, and that the temperature response through space was generally consistent with the temperature response with time at any given site (Audzijonyte et al., 2020). To our knowledge, there is so far no similar study for freshwater fish in lakes. Sampling of lake fish with multimesh Nordic gillnets has been a European standard method since 2005. The standard has been used in many European lakes, and data were collated in a joint database for development of fish-based assessment methods (Argillier et al., 2013). This dataset was used in several research studies using a space-for-time approach (see e.g. Mehner et al., 2017), because most lakes were sampled only once and most of them within a relatively short period of about 10 years. Our present study on perch size in Swedish lakes fills some of the previous gap, by covering a fairly large geographical variation (Figure 1, Table 1) and many different lakes sampled in any year during a period of 26 years.

Here, we focused entirely on temporal changes in perch size, in order to search for general trends in as many Swedish lakes as possible, independent of what environmental changes (except for the general climate change) were actually occurring over time in specific lakes. We know that many lakes were sampled for physical and chemical parameters, but in most cases not consistently measured and at the same frequency through space and time. Many of the perch lakes have been treated with limestone to mitigate negative effects of acidification (Holmgren et al., 2016), but liming status was not known for all lakes in the present study. Concentrations of sulphate have decreased as response to decreasing airborne acidification, along with increasing trends in pH and total organic carbon (Futter et al., 2014). The previous brownification of Swedish lakes has possibly levelled off in recent years, as recently reported for running waters (Eklöf et al., 2021). Total phosphorous has generally decreased, and relatively more in already nutrient-poor ecosystems (Huser et al., 2018). Just a few of the present perch lakes were previously severely affected by eutrophication, with some of them biomanipulated as one of the tools to mitigate nuisance algal blooms (Bernes et al., 2015). Introduction and range expansion of exotic and translocated species is an increasing problem in many European lakes and reservoirs, although fish species non-native to Sweden are rarely occurring in Swedish lakes (Trochine et al., 2018). Translocation of native species to new lakes is more often reported in northern Europe (Tammi et al., 2003), but most translocations occurred many decades before the first year of fish sampling in the present study. Most of the lakes may be used for recreational fishing to some extent, in most cases by private fishing rights owners. They have no obligation to document and report their catches, and it was hard to get quantitative information on catches, even for the most intensively studied time-series lakes (Holmgren, 2003). However, most Swedish lakes do not achieve good chemical status (EEA, 2018), mainly because mercury concentrations exceed critical thresholds. This fact might have reduced the public interest for fishing of perch for human consumption in most of the lakes in the present study.

Based on the large dataset, the mean length of perch decreased over time in the southern region, and also in many of the time-series lakes, as expected in a warming climate. A previous space-for-time analysis of European lakes found a negative correlation between mean length of perch and air temperature, and an even stronger negative effect of perch density on the mean size (Arranz et al., 2016). In this study, we found increasing abundance of perch in both datasets, and of all fishes in the large dataset, indicating that increased competition might contribute to the decreasing size. A lower mean size of perch and a higher total fish abundance might also indicate more eutrophic conditions, for example when using a Swedish-Norwegian fish index for assessing ecological status (Holmgren et al., 2018). This seems to be a less probable explanation for the presently observed trends over time, as oligotrophication is more generally occurring in Swedish lakes (Huser et al., 2018). Our results also revealed higher proportions of small perch (<100 mm) over time in the southern region, indicating a higher recruitment or higher survival of young-of-the-year fish possibly resulting from less predation from larger predatory fish, including cannibalistic perch (Persson et al., 2000). The predominance of increasing perch size at age 1 indicated improved growth conditions for young perch, perhaps related to longer periods with near optimum temperature for growth. Increasing trends in perch size at age 1 were already indicated in shorter time series for a subset of the present lakes (Jeppesen et al., 2012), where the size at age 1 was positively correlated with the mean surface water temperature from May to September.

Perch lakes in the northern region displayed a somewhat unexpected increasing trend in mean length of perch (opposite to the southern region), and there was no significant change in the proportion of small perch (<100 mm) in the large data set. Instead, there was a high variation between adjacent years in the average proportion of small perch in the north. Such a pattern might appear if strong year classes occur due to synchronised occurrence of more favourable weather conditions, especially in the northern region. We have previously found higher between-year variation in recruitment of perch in the northern compared with the southern region, in some of the present time-series lakes (Appelberg et al., 2020; Holmgren, 2007). The proportion of intermediate-sized perch (100–199 mm) decreased in both regions, while the proportion of larger sizes (≥200 mm) increased in the northern and decreased in the southern regions. In combination with increasing perch density over time, in both numbers and biomass, the changed size structure in northern lakes might indicate improved conditions for survival to higher age and more individuals growing to larger size. The causes and consequences of winter mortality differ between fish species, size classes and local environmental conditions in complex ways (Hurst, 2007). Differences in winter mortality might contribute to the diversity of observed trends in perch size metrics within time-series lakes in both regions. Searching for lake-specific reasons is, however, out of the scope of the present study. In winter times lakes in northern Sweden are covered by ice and snow for considerably longer periods than in the southern region (Hallerbäck et al., 2022), but ice break-up date has become earlier during the time period of the present study. Shorter periods in dark and cold water will probably favour all sizes of cool water species like perch, but the smallest individuals suffer more from winter starvation than larger fish (Heermann et al., 2009).

The most novel result of the present study was the increasing occurrence and proportion of very large perch (≥350 mm) over time in both regions. Larger perch is highly evaluated by anglers (e.g. Lott & Sundvall, 2010), but they are usually not used as indicators in assessment of ecological status in lakes (Ritterbusch et al., 2022). According to the Water Framework directive (European Commission, 2000), an acceptable high or good status is achieved when age structure of the fish community is not indicating failure in reproduction of particular species. Assessment is therefore based on age or size metrics related to occurrence or abundance of small fish. Larger perch are, however, used as an indicator in coastal fish assessment (Bergström et al., 2016), because of their high value in recreational and commercial fisheries. In that case, larger perch is defined as those above 250 mm, that is below, our present definition of very large perch. It is very challenging to estimate abundance or relative proportion of the largest fish, simply because they occur in much lower numbers than smaller fish. The largest fish in the lakes may also not be efficiently caught in the standard gillnets (Šmejkal et al., 2015), but this issue is probably not relevant when perch is the targeted species. In the present study, one or more very large perch were caught in 55% of the 2121 lakes sampled at least once during 1996–2021, and their numbers were on average 1.2% of the total catch of perch. It is in practice not possible to detect within-lake changes in the largest perch from 1 year to another, or to find significant differences between specific lakes. The detection of positive trends of very large perch in the present study was only possible because many lakes were sampled in each of 26 years in a standardised way, with no serious change over time in the type of lakes sampled. The positive trend was further supported by more positive than negative trends in a reasonably high number of time-series lakes. There is unfortunately a large knowledge gap on trends over time in recreational fishing for very large perch. We might currently just hypothesize that the habit of catch-and-release of trophy fish has increased in many of the Swedish lakes, as in other parts of the world (Sass & Shaw, 2020).

The overall pattern of decreasing mean length along with increasing number of fish might indicate increased intra- and interspecific competition over time, as suggested by Arranz et al. (2016). The growth of one or more life stages will decrease with increasing fish density, unless there is also a sufficiently increased food production during longer growth seasons in a warming climate. We had no data on potential prey for all life stages of perch in our study lakes. In contrast to space-for-time studies (e.g. Arranz et al., 2016; Van Dorst et al., 2019), we could not even include temperature, water colour, acidity or nutrients measured at relevant scales on a lake and year basis in our data sets. The predominance of increasing size at age 1, but no general trend in size at age 5, in the time-series lakes, is possibly indicating a greater influence of warming than of browning (van Dorst et al., 2019). Increasingly browner water was the most plausible explanation for decreasing growth of 1- and 2-year-old perch during a 20-year period in a Finnish lake (Rask et al., 2014). Many Swedish lakes and streams became browner when acidity decreased in the first part of the present time series (Futter et al., 2014), but both of these trends seemed to diminish in more recent years (Eklöf et al., 2021). Our study will hopefully stimulate more research based on our long time series of fish monitoring. We would specifically recommend more directed studies on explanations for the increased occurrence of very large perch in Swedish lakes.

## AUTHOR CONTRIBUTIONS

With input from E.P., K.H. conceived the study and lead the direction and planning. Both authors contributed with analyses, to the writing and revision of earlier drafts, and approved the final version.

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## CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interests.

## DATA AVAILABILITY STATEMENT

The datasets generated and analysed in the study are available from the author on reasonable request.

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## REFERENCES

Appelberg, M., Blass, M., Dahlberg, M., Holmgren, K., Kokkin, M., & Yngwe, R. (2020). *Åldersanalys i fiskövervakningen. Viktig miljöinformation finns i fiskars hårda vävnader. Aqua reports, 2020:19*. Institutionen för akvatiska resurser, Sveriges lantbruksuniversitet, Drottningholm Lysekil Öregrund 64 p. (in Swedish with English summary).

Argillier, C., Caussé, S., Gevrey, M., Pédron, S., de Bortoli, J., Brucet, S., Emmrich, M., Jeppesen, E., Lauridsen, T., Mehner, T., Olin, M., Rask, M., Volta, P., Winfield, F. I. J., Kelly, F., Krause, T., Palm, A., & Holmgren, K. (2013). Development of a fish-based index to assess the eutrophication status of European lakes. *Hydrobiologia*, *704*, 193–211.

Arranz, I., Mehner, T., Benejam, L., Argillier, C., Holmgren, K., Jeppesen, E., Lauridsen, T. L., Volta, P., Winfield, I. J., & Brucet, S. (2016). Density-dependent effects as key drivers of intraspecific size structure of six abundant fish species in lakes across Europe. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*, 519–534.

Arvola, L., George, G., Livingstone, D. M., Järvinen, M., Blenckner, T., Dokulil, M. T., Jennings, E., Nic Aonghusa, C., Nõges, P., Nõges, T., & Weyhenmeyer, G. A. (2009). The impact of the changing climate on the thermal characteristics of lakes. In G. George (Ed.), *The impact of climate change on European Lakes. Aquatic ecology series* (Vol. *4*, pp. 85–102). Springer. https://doi.org/10.1007/978-90-481-2945-4_6

Atkinson, D., & Sibly, R. M. (1997). Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology and Evolution*, *12*, 235–239.

Audzijonyte, A., Richards, R. D., Stuart-Smith, R. D., Pecl, G., Edgar, G. J., Barrett, N. S., Payne, N., & Blanchard, J. L. (2020). Fish body sizes change with temperature but not all species shrink with warming. *Nature Ecology and Evolution*, *4*, 809–814.

Bergström, L., Bergström, U., Olssonc, J., & Carstensen, J. (2016). Coastal fish indicators response to natural and anthropogenic drivers – variability at temporal and different spatial scales. *Estuarine, Coastal and Shelf Science*, *183*, 62–72.

Bernes, C., Carpenter, S. R., Gårdmark, A., Larsson, P., Persson, L., Skov, C., Speed, J. D. M., & van Donk, E. (2015). What is the influence of a reduction of planktivorous and benthivorous fish on water quality in temperate eutrophic lakes? A systematic review. *Environmental Evidence*, *4*, 13.

Brett, J. R. (1979). Environmental factors and growth. In W. S. Hoar, D. J. Randall, & J. R. Brett (Eds.), *Fish physiology* (Vol. *VIII*, pp. 677–743). Academic Press.

CEN. (2015). *Water quality – Sampling of fish with multi-mesh gillnets*. European Standard. European Committee for Standardization. Ref. No. EN 14757:2015.

Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Science of the USA*, *106*, 12788–12793.

de Wit, H. A., Valinia, S., Weyhenmeyer, G. A., Futter, M. N., Kortelainen, P., Austnes, K., Hessen, D. O., Räike, A., Laudon, H., & Vuorenmaa, J. (2016). Current browning of surface waters will be further promoted by wetter climate. *Environmental Science and Technology Letter*, *3*, 430–435.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Leveque, C., Naiman, R. J., Prieur-Richard, A. H., Soto, D., Stiassny, M. L. J., & Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, *81*, 163–182.

EEA. (2018). *European waters – assessment of status and pressures 2018*. EEA Report No 7/2018, 85 p.

Eklöf, K., von Brömssen, C., Amvrosiadi, N., Fölster, J., Wallin, M. B., & Bishop, K. (2021). Brownification on hold: What traditional analyses miss in extended surface water records. *Water Research*, *203*, 117544.

Emmrich, M., Pedron, S., Brucet, S., Winfield, I. J., Jeppesen, E., Volta, P., Argillier, C., Lauridsen, T. L., Holmgren, K., Hesthagen, T., & Mehner, T. (2014). Geographical patterns in the body-size structure of European lake fish communities along abiotic and biotic gradients. *Journal of Biogeography*, *41*, 2221–2233.

Estlander, S., Horppila, J., Olin, M., Vinni, M., Lehtonen, H., Rask, M., & Nurminen, L. (2012). Troubled by the humics – effects of water colour and interspecific competition on the feeding efficiency of planktivorous perch. *Boreal Environment Research*, *17*, 305–312.

European Commission. (2000). Directive 2000/60/EC of the European Parliament and of the council of 23 October 2000 establishing a framework for the community action in the field of water policy. *Official Journal of the European Communities*, *L327*, 1–82.

Futter, M. N., Valinia, S., Löfgren, S., Köhler, S. J., & Fölster, J. (2014). Long-term trends in water chemistry of acid-sensitive Swedish lakes show slow recovery from historic acidification. *Ambio*, *43*, 77–90.

Galarowicz, T. L., & Wahl, D. H. (2003). Differences in growth, consumption, and metabolism among walleyes from different latitudes. *Transactions of the American Fisheries Society*, *132*, 425–437.

Grennfelt, P., Engleryd, A., Forsius, M., Hov, Ø., Rodhe, H., & Cowling, E. (2020). Acid rain and air pollution: 50 years of progress in environmental science and policy. *Ambio*, *49*, 849–864.

Hallerbäck, S., Huning, L. S., Love, C., Persson, M., Stensen, K., Gustafsson, D., & AghaKouchak, A. (2022). Climate warming shortens ice durations and alters freeze and break-up patterns in Swedish water bodies. *The Cryosphere*, *16*, 2493–2503.

HaV. (2017). *Havs- och vattenmyndighetens föreskrifter och allmänna råd om kartläggning och analys av ytvatten enligt vattenförvaltningsförordningen* (*2004:660*). *HVMFS:20*, *18*. https://www.havochvatten.se/vagledning-foreskrifter-och-lagar/foreskrifter/register-vattenforvaltning/kartlaggning-och-analys-av-ytvatten-hvmfs-201720.html

Heermann, L., Eriksson, L.-O., Magnhagen, C., & Borcherding, J. (2009). Size-dependent energy storage and winter mortality of perch. *Ecology of Freshwater Fish*, *18*, 560–571.

Heibo, E., Magnhagen, C., & Vøllestad, L. A. (2005). Latitudinal variation in life-history traits in Eurasian perch. *Ecology*, *86*, 3377–3386.

Hein, C., Öhlund, G., & Englund, G. (2012). Future distribution of Arctic char *Salvelinus alpinus* in Sweden under climate change: Effects of temperature, lake size and species interaction. *Ambio*, *41*, 303–312.

Holmgren, K. (2003). Är små svenska sjöar påverkade av fiske? – Exempel från Integrerad KalkningsEffektUppföljning (IKEU) och nationell miljöövervakning. *Fiskeriverket Informerar*, *2003*, 8, 28 p (in Swedish with English summary).

Holmgren, K. (2007). Fiskfaunans variation inom och mellan sjöar av olika karaktär. *Fiskeriverket Informerar*, *2007*, 1, 44 p (in Swedish with English summary).

Holmgren, K. (2021). *Provfiske i sjöar – historia, nuläge och framtida behov. Aqua reports*, *2021:19*. Institutionen för akvatiska resurser, Sveriges lantbruksuniversitet, Lysekil. 88 p. (In Swedish with English summary).

Holmgren, K., & Appelberg, M. (2000). Size structure of benthic fish communities in relation to environmental gradients. *Journal of Fish Biology*, *57*, 1312–1330.

Holmgren, K., & Appelberg, M. (2001). Effects of environmental factors on size-related growth efficiency of perch, *Perca fluviatilis*. *Ecology of Freshwater Fish*, *10*, 247–256.

Holmgren, K., Degerman, E., Petersson, E., & Bergquist, B. (2016). Long term trends of fish after liming of Swedish streams and lakes. *Atmospheric Environment*, *146*, 245–251.

Holmgren, K., Kinnerbäck, A., Svensson, J., Sandlund, O. T., Hesthagen, T., Saksgård, R., Sandøy, S., & Poikane, S. (2018). Intercalibration of the national classifications of ecological status for northern lakes. In *Biological quality element: Fish fauna. JRC112702, EUR 29335 EN*. Publications Office of the European Union.

Hurst, T. P. (2007). Causes and consequences of winter mortality in fishes. *Journal of Fish Biology*, *71*, 315–345.

Huser, B. J., Futter, M. N., Wang, R., & Fölster, J. (2018). Persistent and widespread long-term phosphorus declines in boreal lakes in Sweden. *Science of the Total Environment*, *613-614*, 240–249.

Jeppesen, E., Meerhoff, M., Holmgren, K., Gonzalez-Bergonzoni, I., Teixeira-de Mello, F., Declerk, S., DeMeester, L., Søndergaard, M., Lauridsen, T. L., Bjerring, R., Conde-Porcuna, J. M., Mazzeo, N., Iglesias, C., Reizenstein, M., Malmquist, H., Liu, Z., Balayla, D., & Lazzaro, X. (2010). Impacts of global warming on fish community structure and dynamics, and potential ecosystem effects. *Hydrobiologia*, *646*, 73–90.

Jeppesen, E., Mehner, T., Winfield, I. J., Kangur, K., Sarvala, J., Gerdeaux, D., Rask, M., Malmquist, H. J., 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.

Jeziorski, A., Yan, N. D., Paterson, A. M., DeSellas, A. M., Turner, M. A., Jeffries, D. S., Keller, B., Weeber, R. C., McNicol, D. K., Palmer, M. E., McIver, K., Arseneau, K., Ginn, B. K., Cumming, B. F., & Smol, J. P. (2008). The widespread threat of calcium decline in fresh waters. *Science*, *322*, 1374–1377.

Kinnerbäck, A. (Ed.). (2022). *National Register of survey test-fishing – NORS*. Swedish University of Agricultural Sciences, Department of Aquatic Resources http://www.slu.se/sjoprovfiskedatabasen [2022-02-28].

Kottelat, M., & Freyhof, J. (2007). *Handbook of European freshwater fishes*. Kottelat.

Kritzberg, E. S. (2017). Centennial-long trends of lake browning show major effect of afforestration. *Limnology and Oceanography Letters*, *2*, 105–112.

Lott, J., & Sundvall, A. (2010). *A study of anglers preferences – valuation of different quality attributes at Lycksele FVO in the north of Sweden*. Master I thesis in economics, 15 ECTS, Umeå University, 22 p.

Magnuson, J. J., Crowder, L. B., & Medvick, P. A. (1979). Temperature as an ecological resource. *American Zoologist*, *19*, 331–343.

Mehner, T., Brucet, S., Argillier, C., Beklioglu, M., Ferreira, T., Hesthagen, T., Holmgren, K., Jeppesen, E., Kelly, F., Krause, T., Rask, M., Volta, P., Winfield, I. J., & Podgornik, S. (2017). Metadata of European Lake fishes dataset. *Freshwater Metadata Journal*, *23*, 1–8.

Mittelbach, G. G., & Persson, L. (1998). The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 1454–1465.

Monteith, D. T., Stoddard, J. L., Evans, C. D., de Wit, H. A., Forsius, M., Høgåsen, T., Wilander, A., Skjelkvåle, B. L., Jeffries, D. S., Vuorenmaa, J., Keller, B., Kopacek, J., & Vesely, J. (2007). Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature*, *450*, 537–540.

Olin, M., Tiainen, J., Rask, M., Vinni, H. M., Nyberg, K., & Lehtonen, H. (2017). Effects of non-selective and size-selective fishing on perch populations in a small lake. *Boreal Environment Research*, *22*, 137–155.

O'Reilly, C. M., Sharma, S., Gray, D. K., Hampton, S. E., Read, J. S., Rowley, R. J., Schneider, P., Lenters, J. D., McIntyre, P. B., Kraemer, B. M., Weyhenmeyer, G. A., Straile, D., Dong, B., Adrian, R., Allan, M. G., Anneville, O., Arvola, L., Austin, J., Bailey, J. L., … Zhang, G. (2015). Rapid and highly variable warming of lake surface waters around the globe. *Geophysical Research Letters*, *42*(24), 773–781.

Perrin, N., & Rubin, J. F. (1990). On dome-shaped norms of reaction for size-to- age at maturity in fishes. *Functional Ecology*, *4*, 53–57.

Persson, L., Byström, P., & Wahlström, E. (2000). Cannibalism and competition in Eurasian perch: Population dynamics of an ontogenetic omnivore. *Ecology*, *81*, 1058–1071.

Radke, R. J., & Gaupisch, A. (2005). Effects of phytoplankton-induced turbidity on predation success of piscivorous Eurasian perch (*Perca fluviatilis*): Possible implications for fish community structure in lakes. *Naturwissenschaften*, *92*, 91–94.

Rask, M., Sairanen, S., Vesala, S., Arvola, L., Estlander, S., & Olin, M. (2014). Population dynamics and growth of perch in a small, humic lake over a 20-year period – Importance of abiotic and biotic factors. *Boreal Environment Research*, *19*(suppl. A), 112–123.

Ritterbusch, D., Blabolil, P., Breine, J., Erős, T., Mehner, T., Olin, M., Peirson, G., Volta, P., & Poikane, S. (2022). European fish-based assessment reveals high diversity of systems for determining ecological status of lakes. *Science of the Total Environment*, *802*, 149620.

Sande, H. (2020). Recreational fisheries - characterization, quantification and biological impact on natural resources. *Aqua introductory research essay 2020:1*. Swedish University of Agricultural Sciences, Department of Aquatic Resources, Drottningholm Lysekil Öregrund. pp. 46.

Sass, G. G., & Shaw, S. L. (2020). Catch-and–release influences on inland recreational fisheries. *Reviews in Fisheries Science & Aquaculture*, *28*, 211–227.

Skov, C., Jansen, J., & Arlinghaus, R. (2017). 62 years of population dynamics of European perch (*Perca fluviatilis*) in a mesotrophic lake tracked using angler diaries: The role of commercial fishing, predation and temperature. *Fisheries Research*, *195*, 71–79.

Šmejkal, M., Ricard, D., Prchalová, M., Říha, M., Muška, M., Blabolil, P., Čech, M., Vašek, M., Jůza, T., Monteoliva Herreras, A., Encina, L., Peterka, J., & Kubečka, J. (2015). Biomass and abundance biases in European standard gillnet sampling. *PLoS One*, *10*, e0122437.

Tammi, J., Appelberg, M., Beier, U., Hesthagen, T., Lappalainen, A., & Rask, M. (2003). Fish status survey of Nordic lakes: Effects of acidification, eutrophication and stocking activity on present fish species composition. *Ambio*, *32*, 98–105.

Tolonen, A., Lappalainen, J., & Pulliainen, E. (2003). Seasonal growth and year class strength variations of perch near the northern limits of its distribution range. *Journal of Fish Biology*, *63*, 176–186.

Trochine, C., Brucet, S., Argillier, C., Arranz, I., Beklioglu, M., Benejam, L., Ferreira, T., Hesthagen, T., Holmgren, K., Jeppesen, E., Kelly, F., Krause, T., Rask, M., Volta, P., Winfield, I. J., & Mehner, T. (2018). Non-native fish occurrence and biomass in 1943 Western Palearctic lakes and reservoirs and their abiotic and biotic correlates. *Ecosystems*, *21*, 395–409.

Uphoff, C. S., Schoenebeck, C. W., Hobacka, W. W., Koupal, K. D., & Pope, K. L. (2013). Degree-day accumulation influences annual variability in growth of age-0 walleye. *Fisheries Research*, *147*, 394–398.

van Dorst, R. M., Gårdmark, A., Svanbäck, R., Beier, U., Weyhenmeyer, G. A., & Huss, M. (2019). Warmer and browner waters decrease fish biomass production. *Global Change Biology*, *25*, 1395–1408.

Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A. A., Green, P., Glidden, S., Bunn, S. E., Sullivan, C. A., Reidy Liermann, C., & Davies, P. M. (2010). Global threats to human water security and river biodiversity. *Nature*, *467*, 555–561.

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## APPENDIX 1

**TABLE A1** Average trends in factors potentially influencing observed trends in perch size metrics during 1996–2021 (see Table 1), after transformation of values according to the footnote. Year 1996 was set to year 0 in the regression analyses. The back-transformed intercept (a) in each linear regression then represents the estimated descriptor in year 1996, and the slope (b) estimates the annual rate of change. *F*-values of the ANOVAs are given along with raw and adjusted *p*-values (Bonferroni, $m = 9$ comparisons per region). Significant tests are marked in bold. Descriptors in italics are fixed values per lake, and any apparent trend therefore indicates a bias over time in the annual selection of sampled lakes.

| Lake descriptor | Region | Regression (a + b[d]year) | $F_{1:\text{df res.}}$[d] | Raw *p*-value | Adj. *p*-value |
|---|---|---|---|---|---|
| *Elevation (m)*[a] | North | 16.26−0.054[d]year | 5.95 | .015 | .134 |
| | South | 11.32−0.015[d]year | 3.51 | .061 | .550 |
| *Lake area (ha)*[b] | North | 3.051−0.004[d]year | 0.58 | .448 | 1.000 |
| | South | 2.75 + 0.014[d]year | 25.15 | <.001 | **<.001** |
| *Maximum depth (m)*[b] | North | 1.15−0.0023[d]year | 3.36 | .067 | .604 |
| | South | 1.03−0.00079[d]year | 1.31 | .253 | 1.000 |
| *Mean air temperature (°C)*[c] | North | 11.29−0.119[d]year | 12.05 | <.001 | **.005** |
| | South | 40.60 + 0.0027[d]year | 0.02 | .880 | 1.000 |
| Npue-Total (*N* per gillnet and night)[b] | North | 1.24 + 0.0066[d]year | 18.49 | <.001 | **<.001** |
| | South | 1.42 + 0.0028[d]year | 10.81 | .001 | **.009** |
| Bpue-Total (g per gillnet and night)[b] | North | 2.91 + 0.011[d]year | 57.12 | <.001 | **<.001** |
| | South | 3.00 + 0.0033[d]year | 20.03 | <.001 | **<.001** |
| *N* fish species[b] | North | 0.694−0.00083[d]year | 1.05 | .305 | 1.000 |
| | South | 0.708 + 0.0017[d]year | 16.14 | <.001 | **<.001** |
| Npue-Perch (*N* per gillnet and night)[b] | North | 1.06 + 0.0052[d]year | 12.2 | <.001 | **.004** |
| | South | 1.14 + 0.0030[d]year | 14.07 | <.001 | **.002** |
| Bpue-Perch (g per gillnet and night)[b] | North | 2.62 + 0.015[d]year | 66.48 | <.001 | **<.001** |
| | South | 2.64 + 0.0016[d]year | 3.77 | .052 | .470 |

[a] Square-root-transformed before analysis.

[b] Log-transformed before analysis.

[c] Square-transformed after conversion to Kelvin.

[d] 969 degrees of freedom in the north and 3741 in the south, except for maximum depth (961 in the north and 3732 in the south).

**TABLE A2** Geographical position and characteristics of 14 time-series lakes, with estimated mean water temperature at 1–1.5 m depth during May–September (WT May–Sep) in all or most years during 1994–2021.

| Lake | Region | Latitude | Longitude | Elevation (m) | Area (ha) | Max. depth (m) | WT May-Sep (°C) | *N* years |
|---|---|---|---|---|---|---|---|---|
| Jutsajaure | North | 67.05897 | 19.94362 | 422 | 112 | 9 | 11.60 | 25 |
| Remmarsjön | North | 63.86204 | 18.27264 | 234 | 131 | 14 | 13.76 | 26 |
| Källsjön | North | 61.63310 | 16.73538 | 232 | 24 | 17 | 14.82 | 27 |
| Tryssjön | North | 60.44061 | 15.08802 | 344 | 30 | 20 | 14.97 | 25 |
| Stensjön | North | 61.64275 | 16.57529 | 268 | 59 | 9 | 15.48 | 28 |
| Övre Skärsjön | South | 59.83709 | 15.55028 | 219 | 169 | 32 | 15.93 | 28 |
| Stengårdshultasjön | South | 57.55778 | 13.80204 | 224 | 489 | 27 | 16.34 | 27 |
| Fiolen | South | 57.09199 | 14.52957 | 226 | 156 | 10 | 17.24 | 26 |
| Fräcksjön | South | 58.14815 | 12.18118 | 56 | 28 | 15 | 17.45 | 28 |
| Stora Envättern | South | 59.11495 | 17.3535 | 62 | 38 | 11 | 17.50 | 26 |
| Brunnsjön | South | 56.59719 | 15.72807 | 98 | 10 | 13 | 17.61 | 28 |
| Allgjutten | South | 57.94794 | 16.09632 | 126 | 17 | 38 | 17.69 | 26 |
| Stora Skärsjön | South | 56.67118 | 13.06582 | 60 | 32 | 12 | 18.06 | 26 |

*Note*: The lakes are sorted from lowest to highest mean values of WT May-Sep throughout all covered years (*N* years). The time series of WT May–Sep are shown in Figure A2.

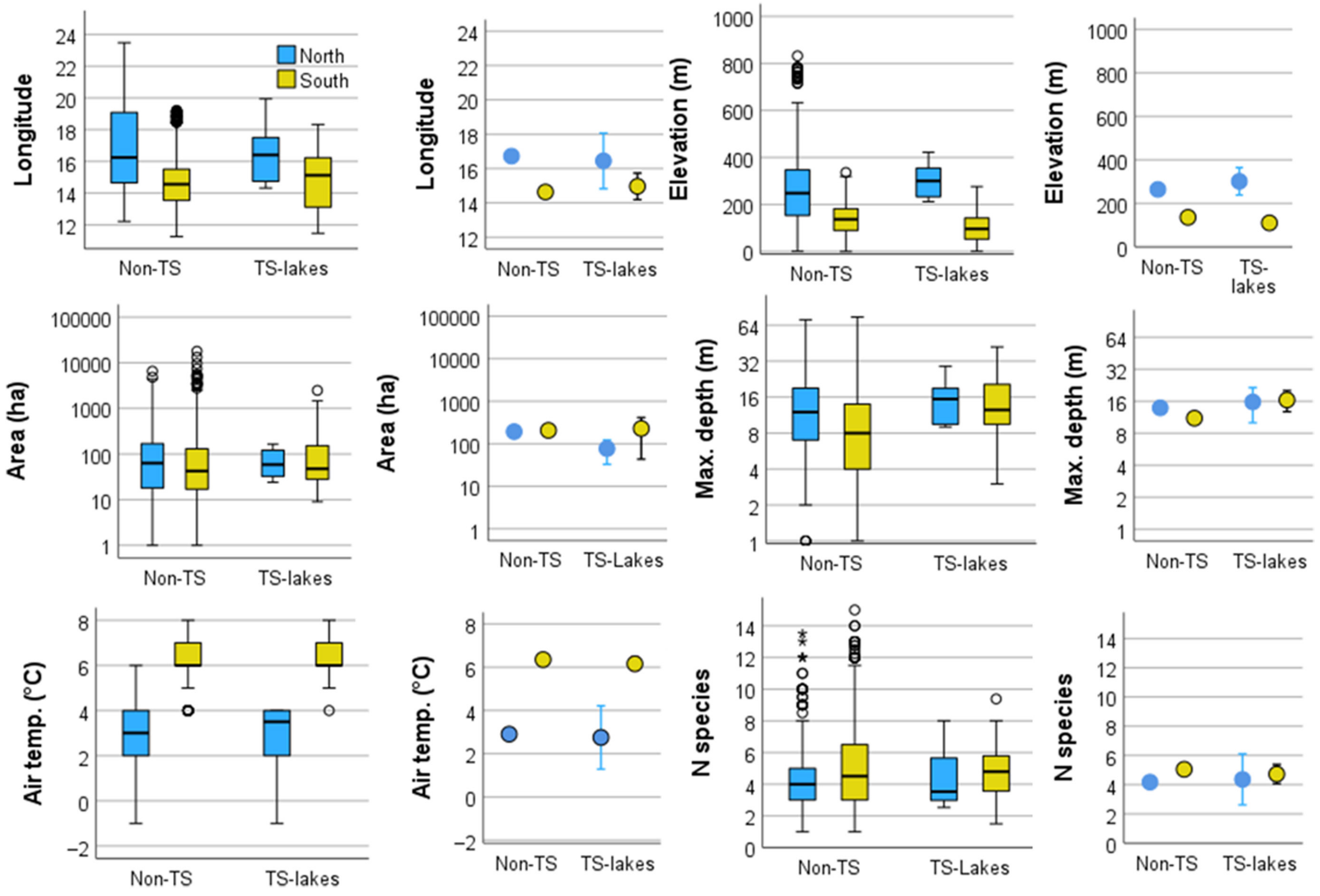

FIGURE A1 Factors potentially influencing observed trends in perch size metrics, within regions (north and south) and groups of lakes sampled in less than 10 years (Non-TS) and time-series lakes (TS-lakes). Selected factors are longitude, elevation, lake area, maximum depth, annual mean air temperature and number of observed fish species. The full range of values within-lake groups is shown as (1) boxplots (left) with boxes representing interquartile range and median value as thick horizontal line and (2) error bars with mean value ± 95% confidence interval.

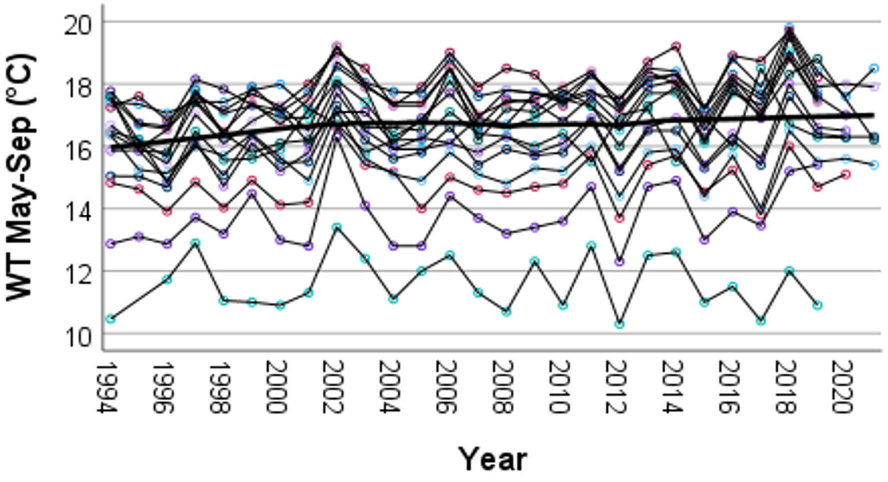

FIGURE A2 Time series of mean water temperature at 1–1.5 m depth during May–September, in 14 of the time-series lakes (see lake description in Table A2). The overall mean trend is indicated by the thick (loess fit) line.