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Temperature-related increase in growth rate in four freshwater lake fish species

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Abstract

Growth is one of the most direct and common ways fish respond to climate change, as fish growth is intimately linked to the temperature of the environment. Observational studies on the effect of shifts in temperature on fish growth are scarce for freshwater fish, and particularly lacking for lake populations. Here, changes in growth rate of bream (*Abramis brama*), perch (*Perca fluviatilis*), pikeperch (*Sander lucioperca*), and roach (*Rutilus rutilus*) over three decades were studied and compared with changes in temperature in the two largest lakes of western Europe: Lake IJsselmeer and Lake Markermeer in the Netherlands. In the autumnal survey catches of bream, perch, and roach, the mean length of YOY increased significantly between 1992 and 2021 in both lakes, but for YOY pikeperch, no temporal changes were found. In a length-stratified dataset of age groups of bream, roach, and perch, the relationship between length and age differed significantly between time periods. In the more recent time periods, indications for higher growth rates across multiple ages were found. Temperature during the growth season increased in the same decades and showed significant correlations with the YOY mean length, for bream, perch, and roach in both lakes, and for pikeperch in Lake Markermeer. These results point toward consistent temperature-induced increases in growth over the age groups for bream, roach, and perch. These increases were found despite the simultaneous process of de-eutrophication in this water system and its potential negative effect on food production. For pikeperch, it is hypothesized that the absence of temporal increase in YOY growth rate is related to its necessary switch to piscivory and subsequent food limitation; the lower thermal range of its main prey smelt, *Osmerus eperlanus*, is hypothesized to have inhibited food availability for YOY pikeperch and its opportunity to achieve higher growth rates.

KEYWORDS

climate change, de-eutrophication, Lake IJsselmeer, Lake Markermeer, northwest Europe

1 | INTRODUCTION

Water temperature is one of the main drivers of life-history traits of fish, such as growth, as the body temperature of these ectotherms is closely linked to the temperature of the environment (e.g., Ficke et al., 2007; Moyle & Cech, 2004). This makes fish communities highly sensitive to changes in water temperature associated with climate change (e.g., Ficke et al., 2007; Jeppesen et al., 2010). Inland fish communities are particularly vulnerable to changes in the environment, due to their limited ability to disperse and the high anthropogenic pressure already exerted on these systems (e.g., Jeppesen et al., 2012; Lynch et al., 2016; Woodward et al., 2010). Still, studies on the effects of climate change on inland fish are scarce (Huang et al., 2021; Lynch et al., 2016; Myers et al., 2017). Observational studies on how directional changes in temperature affect inland fish populations are especially limited (Huang et al., 2021, Lynch et al., 2016, Myers et al., 2017) and tend to focus on salmonids (Lynch et al., 2016).

In Dutch lakes, the water temperature has risen through the past decades (Bolle et al., 2021; Mooij et al., 2008; Rozemeijer et al., 2021) at an above-average speed compared to worldwide trends (Rozemeijer et al., 2021). Four of the key resident fish species in these regions are bream (*Abramis brama*), perch (*Perca fluviatilis*), pikeperch (*Sander lucioperca*), and roach (*Rutilus rutilus*) (Jeppesen et al., 2012). All the four species have optimum growth temperatures between 20 and 25°C (e.g., Hokanson, 1977; Karas & Thoresson, 1992; Kucharczyk et al., 1997; van Dijk et al., 2002; Wang et al., 2009), which are higher than the mean water temperature (17°C) usually attained in the summer in these regions. Increasing water temperatures may have led to increases in growth for these species. Interannual variation in summer temperatures is indeed found to coincide with higher mean length of the YOY of all four species in northwest Europe (e.g., Buijse & Houthuijzen, 1992; Kjellman et al., 2001; Kjellman et al., 2003; Lappalainen et al., 2009; Lappalainen & Malinen, 2022; Mooij et al., 1994; Mooij et al., 2008; Willemsen, 1977). However, no known studies on European inland fish species have identified directional shifts in mean length or other approximations of fish growth across age groups related to shifts in water temperature.

Many possible factors may inhibit a potential increase in growth rate due to increasing water temperatures. For example, higher metabolic rates demand higher food intake. If food availability does not keep pace with individual metabolic demands, or if the availability of food decreases, fish growth will not increase and might even be negatively affected. Such a limiting influence of food availability may have been exacerbated in the Dutch water system due to de-eutrophication. Simultaneously, with increases in temperature, the water system in the Netherlands has undergone strong processes of decreased nutrient loading (Bolle et al., 2021; Rozemeijer et al., 2021). Nutrient levels in the Dutch main rivers and their tributaries were high in the 1970s and 1980s and decreased strongly in the decades afterward (Rozemeijer et al., 2021; van Bennekom & Wetsteijn, 1990; van Beusekom et al., 2019). Nutrient levels are still decreasing, albeit at a slower pace than in the 1980s and early 1990s. This decrease in nutrient influx may have led to lower primary production and decreased food availability at higher trophic levels, although the actual effect of changes in primary production on the food availability for higher trophic levels is complex and often not clear in empirical data (e.g., Bolle et al., 2021; Micheli, 1999; Philippart et al., 2007). Complex interactions between increasing water temperature, food availability, and other factors, such as changes in anthropogenic water use or the fish community, may inhibit the simple, expected physiological response to warming waters to such a degree that no increase in growth rate can be found on a decadal scale (e.g., Lynch et al., 2016).

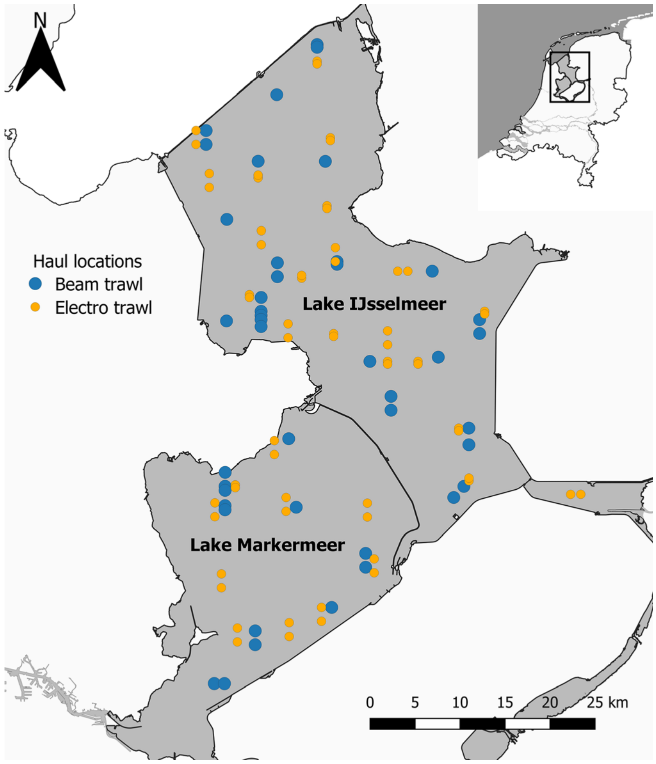

FIGURE 1 Location of Lake IJsselmeer and Lake Markermeer and the haul locations of the autumnal survey.

This study investigated whether decadal shifts in water temperature have led to increases in the growth rate of bream, perch, pikeperch, and roach, despite the strong de-eutrophication before and during the same time period. Changes in growth were studied, using data from a long-standing scientific survey in the two largest freshwater lakes in western Europe: Lake IJsselmeer and Lake Markermeer. Two datasets are available from this survey: one regarding the length distribution of the total survey catch and the other regarding a length-stratified subset of these survey catches with age-at-length information. With these two survey datasets, two separate analyses regarding changes in growth were undertaken. The presence of directional shifts in the mean length of the YOY through the years was investigated, and, for a wider range of age group, changes in the age-at-length relationship across three periods were studied. Subsequently, correlations of interannual variation in YOY mean length and temperature during the growth season were investigated.

2 | MATERIALS AND METHODS

2.1 | Study area

Lake IJsselmeer and Lake Markermeer are large shallow lakes with no stratification, which makes them homomictic and strongly responsive to the prevailing weather conditions (Mooij et al., 2005; Mooij et al., 2008; Willemsen, 1977). Water temperature follows air temperature changes with a delay of c. 7.5 days (Mooij et al., 2008). Both are large lakes, with a surface area of c. 1100 and 700 km^2, and a mean depth of 4.5 and 3.5 m, respectively (Figure 1). They act as water reservoirs and are separated by a dyke with three sluices through which fish can move between the lakes. The area was reclaimed from the sea in 1932 and divided into two lakes in 1975. After the reclamation, an active commercial fisheries with various gears was initiated on these stocks. In the past few decades, the main fisheries on these stocks use gillnets (all four species targeted) and purse seines (bream and roach targeted), whereas eel fykes also affect these stocks in terms of unwanted and discarded by-catch, especially YOY perch (de Leeuw et al., 2008).

2.2 | Field data

The autumnal survey is carried out annually, starting mid-October for 4 to 6 weeks, on board of a research vessel ("Stern"). It is carried out using two gear types, with their own sampling scheme. First, an electric beam trawl survey consists of beams of 3 m wide, with a mesh-size of 36 mm and 250 V, focused on eel. Second, a bottom trawl survey, with a mesh-size of 20 mm in a net weighed down with pieces of chain at the front, focuses on the recruits of the common commercially targeted freshwater fish species bream, perch, pikeperch, and roach. Up to 2012, a 7.4-m-wide bottom trawl was used, which was kept open by an 8-m-wide wooden beam and 1-m-high wooden sticks at both ends. This bottom trawl was replaced in 2013 with a 4-m-wide iron beam trawl. Both gears used a 20-mm mesh in the codend, so no effect on the catch efficiency on the smallest-size classes is expected, and multiple analysis did not found any differences in catch efficiency for different-size classes (Tien & de Leeuw, 2023, van Overzee et al., 2013). The autumnal survey consists of 20/29 hauls in Lake IJsselmeer and 10/14 hauls in Lake Markermeer, with the electric beam trawl and the beam trawl, respectively. Hauls last on average 10 min, with a fishing speed of c. 6.5 km/h with the electric beam trawl and 5.5 km/h with the beam trawl, and have fixed locations (Figure 1). Sampling takes place during daytime. The length of all caught fish is determined on board ("length data"), with total length measured to the centimeter below. The sampling strategy consists of measuring all fish of a species, except for bream, perch, and roach smaller than 20 cm; if these are caught in large numbers, a subsample of minimally 50 individuals is taken for length measurements. The bottom trawl survey and its length sampling have been standardized since 1989 (except for the aforementioned gear change in 2013), and the electric beam trawl survey and its length sampling, and the age data sampling methodology, have been standardized since 1996.

For age determination of bream, pikeperch, and roach, scales are collected and for perch, pectoral fins are clipped. Age is determined by counting growth rings. Sampling for age data is length stratified ("age-length data"), but over both lakes and gears, samples are collected in any haul in either lake and over any gear. The aim is to collect a certain number of fish per length bin: 10 fish for the length bin of 8–10 cm (bream and perch), 6–10 cm (roach), 11–15 cm (bream), or 16–20 cm (pikeperch) and 20 fish for 5-cm length bins for any larger fish (11–15 cm, 16–20 cm, etc.). (Note that YOY fish that are smaller than the smallest length bins are caught in the survey but are not sampled for age determination.) For most lower-length bins in the survey, these numbers are met, but for the higher-length bins, they are often not met (see Appendix S1). However, even for the well-sampled length bins, numbers vary greatly between years, especially for the lowest-length bins (where 10 individuals are targeted), with a decrease in sample size through the years. Especially in the early years, fish smaller than the minimal length class have been collected in relatively large numbers, where these numbers decreased through the years.

2.3 | Data analysis

2.3.1 | Growth changes in YOY

Spawning starts in April and probably continues into May for pikeperch, perch, and roach and into June for bream (Emmerik & de Nie, 2006; Kottelat & Freyhof, 2007), after which the growth season runs into September. Therefore, regarding the YOY, the autumn bottom trawl survey encompasses the individual body length attained after one whole growth season. The length data of the bottom trawl survey from 1992 onward were used to estimate the mean length of the YOY after one growth season. Because the length-frequency distribution of YOY shows a domed shape and in most years overlaps minimally with the length distribution of older age groups, the fish that are YOY can be assigned based on their length in the survey catches. For perch and pikeperch, no overlap in the length distribution between the YOY and older age groups occurred. For bream and roach, overlap in the length distribution of YOY and older age groups only occurred in <15% of the yearly length-frequency distributions. For all species, individuals were assigned as YOY if their body size was below a cut-off length separating the first cohort from older cohorts. The mean length of this group generally coincides with the peak of the length frequency distribution of the first cohort and is therefore a reliable estimate for YOY (Appendix S2). If borders between YOY and older fish were not clearly visible, the age-length key of that year was checked to confirm or improve the choice of cut-off length made. Catches per length bin (centimeter class) were raised to number per fished hectare, and subsequently, the mean length was

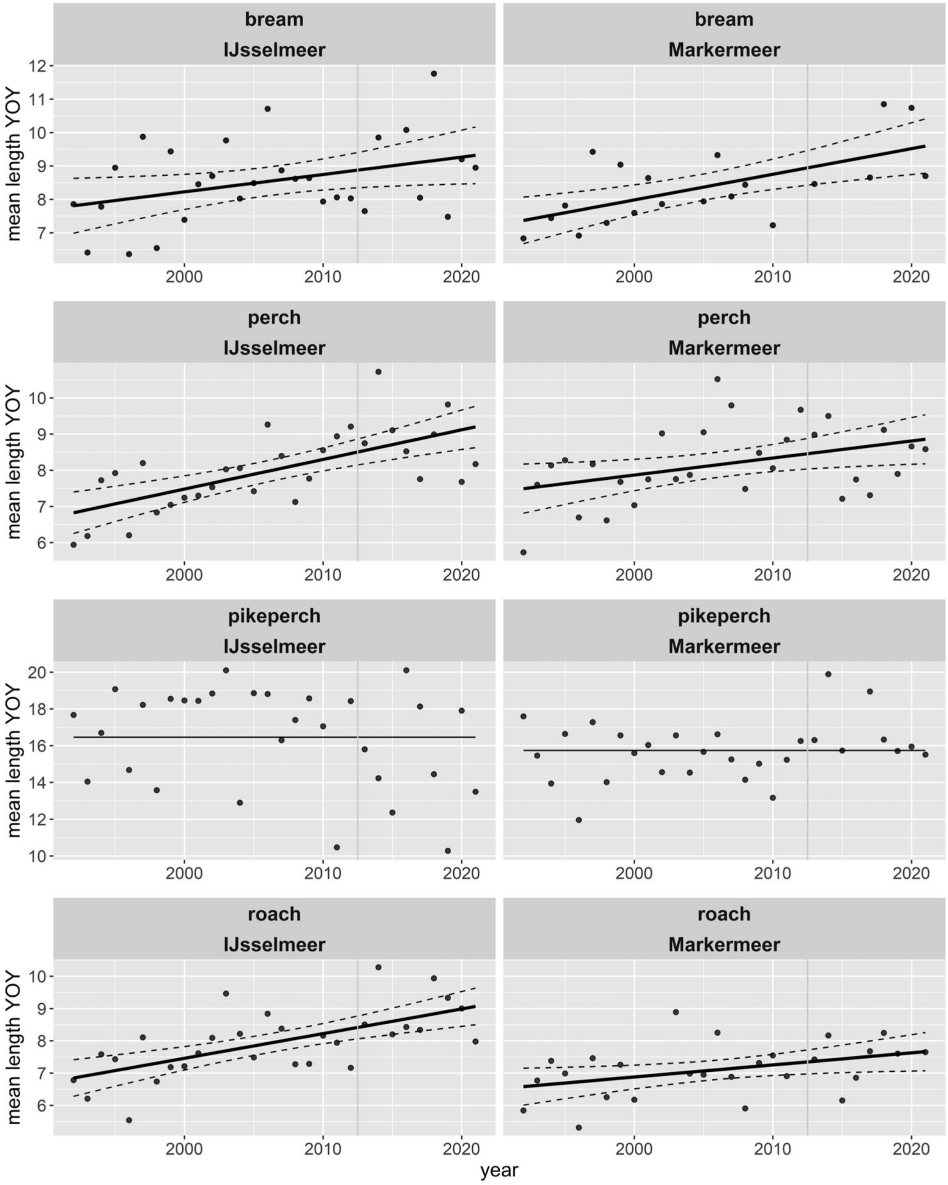

FIGURE 2 Scatterplot between year and mean length of YOY (cm) caught in the bottom trawl survey, per species per lake. For bream (*Abramis brama*), perch (*Perca fluviatilis*), pikeperch (*Sander lucioperca*), and roach (*Rutilus rutilus*) in lakes IJsselmeer and Markermeer in the Netherlands in 1992–2021. Lines: Relationship as estimated in the generalized linear model, with 95% c.i. in dotted lines. Horizontal line: No significant effect of year, line is mean overall years. Light gray vertical line: Switch in bottom gear type.

estimated for all YOY per lake. Year means that were based on fewer than 10 fish were removed from the dataset (for Lake IJsselmeer 1 year of bream and for Lake Markermeer 10 years of bream, 1 year of pikeperch, and 4 years of roach).

Potential changes in growth were analysed with the YOY mean length as dependent variable and year as a continuous explanatory variable in a generalized linear model with a Gaussian error structure and an identity link. Assumptions were checked with diagnostic plots and residuals adhered to both normality and homogeneity. Relations were examined per lake, as YOY are assumed to commute little between the two connected lakes. Gear type (before and since 2013) could not be taken into account in the statistical analyses, as it highly correlated with year. However, no indications were found for consistent changes in mean length before and after the gear change for any of the stocks (Figure 2).

$$\text{length}_i = \alpha + \beta \times \text{year}_i$$

where length_i is the YOY mean length in year i, and α and β are constants.

2.3.2 | Growth changes based on age-at-length estimates

The available age-length data are not suitable for estimating changes in growth via estimates of growth curves such as the von Bertalanffy growth curve. Larger fish are underrepresented in this autumnal recruitment survey, and only a small amount of larger fish is available per year (Appendix S1). This increases the dependency of the parameter estimates on the sparsely sampled older fish. Similarly, age determination was not possible for the smallest fish, although fish smaller than the smallest length bins were caught in the bottom trawl survey. However, changes in growth rate for a range of age classes can be examined without estimating growth rate parameters by focusing on changes in the relationship between length and age within length bins that are well sampled. To statistically investigate changes in growth rate, the length-conditional age sampling scheme needs to be taken into account. This sampling scheme prohibits the use of statistical models that estimate length as being dependent on age, because a key assumption in statistical models is that the explained variable consists of independent samples. A related problem is that when estimating length-at-age relationships with length-conditional age samples, growth rate can be easily overestimated (Goodyear, 2019): with yearly decreasing numbers within a cohort, combined with skewed and overlapping length ranges of adjacent ages, the older ages will be underrepresented within a sampled length bin, which leads to overestimation of the average length within an age class. Therefore, age as being dependent on length was investigated, considering that the samples are age-independent, allowing us to explore the probability that a fish of a given length has a certain age. This method means the growth rate itself was not estimated, but potential presence of temporal changes in growth rate could be estimated. It was then assumed that the level of underrepresentation of older ages within a length bin remains constant through the years.

Years were divided into periods to reach adequate numbers per length class. Three non-adjoining 5-year periods (with 4/5 years in between) were chosen, running from 1996 to 2001 (with 1999 missing in the dataset), 2006 to 2010, and 2016 to 2020. From the entire sampled length range, a subset was selected based on two criteria: (1) all fish smaller than the minimal length as defined in the survey methodology were removed: bream and perch < 8 cm, pikeperch < 16 cm, and roach < 6 cm; (2) if any of the three periods did not contain minimally 10 samples within a length bin of 5 cm, the bin was removed from the analysis. These criteria led to a length range used in this analysis of 8–40 cm for bream, 8–30 cm for perch, 16–40 cm for pikeperch, and 6–30 cm for roach. This selected length range corresponds with an age range of age 0, up to age 14 for bream, up to age 4 for perch, up to age 2 for pikeperch, and up to age 13 for roach.

Potential changes in growth rate were analysed with a generalized linear model with age as dependent variable, using a Poisson error distribution and a log link function (thus assuming exponential growth). Length, the interaction between length and period, and lake were used as explanatory variables. The samples of the two lakes were analysed in the same model, as sampling stratification took place over both lakes, and migration between the lakes took place for the older age groups. Explanatory variables were dropped based on a χ^2 test (Zuur et al., 2019). For pikeperch, the selected length groups contained mostly two age groups (YOY and 1+), with a scarcity of older age groups. These data do not comply with the assumptions of a Poisson error distribution, and pikeperch was dropped from the analysis.

$$\log(\mu i) = \alpha + \beta_1 \times \text{length}i + \beta_2 \times \text{length}i \times \text{period}i + \beta_3 \times \text{lake}i$$

where μ_i is the age of fish i; length$_i$ is the length of fish i; period$_i$ is the period in which fish i is caught; lake$_i$ is the lake in which fish i is caught; and α and $\beta_{1,2,3}$ are constants.

2.3.3 | Temperature during growth season

Temporal changes in water temperature during the growth season were derived from air temperature measurements from meteorological data produced by the Royal Netherlands Meteorological Institute (KNMI) from station Lelystad airport bordering the two lakes (KNMI, 2022). This time series is not corrected for changes in methodology but is highly related to the corrected time series at De Bilt ($R^2 = 0.999$ and $p < 0.0001$ in a linear regression). The degree days were estimated using the Lelystad airport time series: the cumulated degrees Celsius (T) for all days that have a mean day temperature (calculated as $\frac{\max(T) - \min(T)}{2}$) higher than 10°C ($T_0 = 10$°C). Air temperatures are highly correlated with water temperature in Dutch shallow lakes (Mooij et al., 2008). To eliminate the effect of timing of spawning and hatching as much as possible, the time period was adjusted to begin after the main spawning season. For the early spawners, perch, pikeperch, and roach, the period between May 1 and November 15 was chosen; and for the late spawner, bream, the period between June 1 and November 15 was chosen. To estimate the mean temperature during the growth season for older fish, the average temperature between June and September was taken. Spawning season roughly continues until June, and fish are assumed to spend little energy on growth during spawning season. Therefore, June is set as the beginning of the growth season. Temperature is highest between June and September (on average 15°C or higher) and drops afterward.

2.3.4 | Growth of YOY by temperature

The correlation between YOY mean length and growth season temperature expressed as degree days was analysed per lake per species, using a generalized linear model with a Gaussian error structure and an identity link. Assumptions were checked with diagnostic plots, and residuals adhered to both normality and homogeneity.

$$\text{Length}_j = \alpha + \beta \times \text{degree days}_j$$

where length$_j$ is the YOY mean length in degree days j, and α and β are constants.

2.4 | Ethics statement

The care and use of experimental animals complied with Dutch animal welfare laws, guidelines, and policies as approved by the Central Authority for Scientific Procedures on Animals under license number ADV40100202215730.

TABLE 1 Details of the final model for the generalized linear models (GLMs) for YOY mean length ~ year.

Species	Lake	Estimate	S.E.	*t* value	*p*-value(>|*t*|)
Bream	IJsselmeer				
(Intercept)		−95.73	50.57	−1.893	0.0691
Year		0.0520	0.025	2.062	0.0489
	Markermeer				
(Intercept)		−145.47	45.44	−3.201	0.005
Year		0.078	0.023	3.385	0.0033
Perch	IJsselmeer				
(Intercept)		−156.35	34.74	−4.500	0.0001
Year		0.0819	0.0173	4.731	<0.0001
	Markermeer				
(Intercept)		−86.32	41.17	−2.097	0.045
Year		0.0471	0.0205	2.295	0.029
Pikeperch	IJsselmeer				
(Intercept)		181.97	114.65	1.587	0.124
Year		−0.0825	0.0571	−1.444	0.160
	Markermeer				
(Intercept)		−66.74	68.30	−0.977	0.337
Year		0.0411	0.034	1.208	0.238
Roach	IJsselmeer				
(Intercept)		−145.25	34.39	−4.224	0.0002
Year		0.0764	0.017	4.455	0.0001
	Markermeer				
(Intercept)		−67.83	35.2	−1.927	0.066
Year		0.0374	0.018	2.129	0.044

Note: For bream (*Abramis brama*), perch (*Perca fluviatilis*), pikeperch (*Sander lucioperca*), and roach (*Rutilus rutilus*), as caught in the bottom trawl survey in lakes IJsselmeer and Markermeer (the Netherlands).

3 | RESULTS

3.1 | Growth changes in YOY

The directional change in mean length of YOY was studied over the time period 1992–2021 in four species in two lakes. Each dataset contained 30 yearly means, except bream in Lake IJsselmeer (29) and Lake Markermeer (20) and pikeperch (29) and roach (26) in Lake Markermeer. The mean length of YOY bream, perch, and roach increased significantly through the years in both lakes (Figure 2; Table 1). These increases were relatively large for all three species; the estimated average length increased with 1.1–2.4 cm from 1992 to 2021, which is roughly a 25% increase for these YOY with an average length of roughly 8 cm. Pikeperch YOY showed no increase in mean length in either lake.

3.2 | Growth changes from age-at-length

For the three studied fish species with satisfying age data (bream, perch, and roach), all added explanatory variables had a similar effect. As expected, age increased significantly with length. There were significant differences in the length-age relationship between the three periods: the increase in age with length decreased between the periods 1996–2001 and 2016–2020 (Figure 3; Table 2). In both 2006–2010 (mean temperature during growth season: 16.7°C) and 2016–2020 (mean temperature: 17.3°C), fish reached a certain length at a younger age than in 1996–2001 (mean temperature: 16.0°C). Although the estimated slope per period decreased through the three periods, these slopes did not show significant differences between all three periods, but there was always a significant difference between the latter two periods and 1996–2001. Therefore, bream, perch, and roach showed significant increases in growth rate; a length was reached at an earlier age in the latter periods than in the first period (1996–2001). In addition, estimated age was significantly higher in Lake Markermeer than in Lake IJsselmeer for all three species.

3.3 | Temperature effect on YOY growth

The temperature conditions during the growth season increased significantly through the decades (Figure 4; Pearson's correlation tests for year and degree days with T0 = 10°C for the Lelystad time series between May 1 and November 15 [$r = 0.50$, $p = 0.005$] for perch,

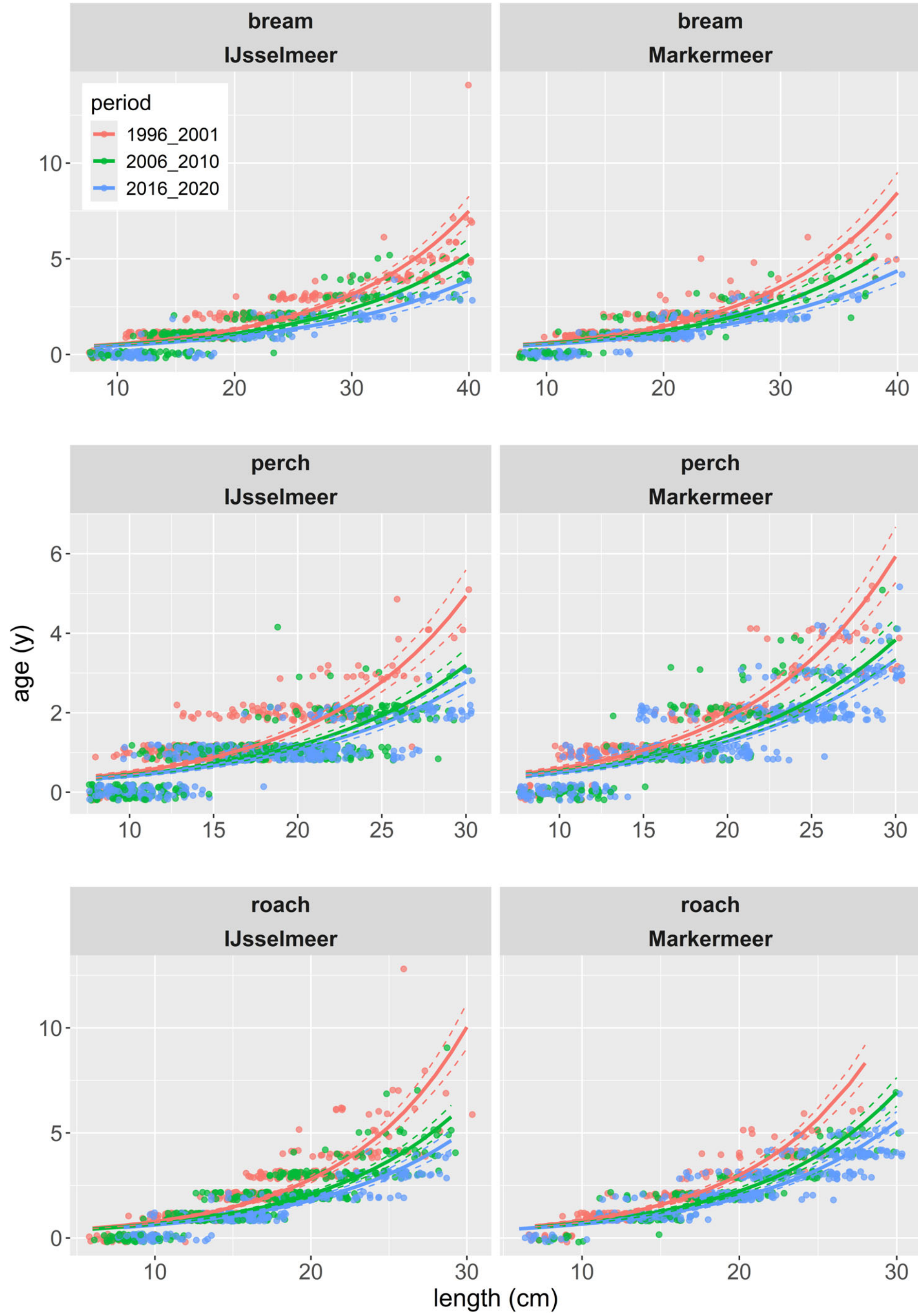

FIGURE 3 Scatterplot between the age and length (cm) of individual fish, per species per lake. For bream (*Abramis brama*), perch (*Perca fluviatilis*), and roach (*Rutilus rutilus*) in lakes IJsselmeer and Markermeer in the Netherlands, sampled in the bottom trawl survey in 1996–2020. Age and length are determined for a length-stratified subset of fish caught in the autumnal survey (see Appendix S1). Data are clumped for three time periods. Data have been jittered for visual clarification. Lines: Relationship as estimated in the generalized linear model, with 95% c.i. in dotted lines, separated for the two lakes.

pikeperch, and roach and between June 1 and November 15 [$r = 0.57$, $p = 0.001$] for bream).

Mean length of the YOY of that year increased significantly with degree days for bream, perch, and roach in both lakes and for pikeperch in Lake Markermeer (Figure 5; Table 3).

4 | DISCUSSION

This study found increases in growth rate through the decades in all analyses for bream, perch, and roach. Mean length of new recruits at the end of the growth season increased through the years in both lakes, and growth rate through the age groups increased over the time periods from 1996 to 2021. For pikeperch, no temporal increase in growth rate was found for new recruits in either lake. Pikeperch growth rate over the age groups could not be analysed due to low variability in age in the dataset. Therefore, for bream, perch, and roach, growth rate seems to have increased through the decades, whereas there was no indication for such an increase for pikeperch.

Temperature during the growth season has also risen in this area. For bream, perch, and roach, the consistent signs of temporal increases in growth rate were accompanied by consistent correlations between interannual variation in YOY mean length and growth season temperature in both lakes. Positive correlations between the

Species	Estimate	S.E.	z value	p-value(>|z|)
Bream				
(Intercept)	−1.4707	0.0771	−19.065	<0.0001
Length	0.0871	0.0026	32.974	<0.0001
Lake Markermeer	0.1208	0.0454	2.662	0.0078
Period 2006–2010	−0.0089	0.0020	−4.444	<0.0001
Period2016–2020	−0.0165	0.0021	−7.948	<0.0001
Perch				
(Intercept)	−1.8433	0.0805	−22.894	<0.0001
Length	0.1147	0.0040	28.457	<0.0001
Lake Markermeer	0.1835	0.0409	4.488	<0.0001
Length: Period 2006–2010	−0.0145	0.0024	−5.954	<0.0001
Length: Period 2016–2020	−0.0192	0.0022	−8.798	<0.0001
Roach				
(Intercept)	−1.5301	0.0655	−23.357	<0.0001
Length	0.1279	0.0035	36.310	<0.0001
Lake Markermeer	0.0691	0.0349	1.982	0.0475
Length:Period2006–2010	−0.0147	0.0019	−7.639	< 0.0001
Length:Period2016–2020	−0.0222	0.0020	−11.011	<0.0001

TABLE 2 Details of the final model for the generalized linear models (GLMs) for age ~ length + length × period + lake for bream (*Abramis brama*), perch (*Perca fluviatilis*), and roach (*Rutilus rutilus*), where age and length are determined for a length-stratified subset of fish caught in the autumnal survey in lakes IJsselmeer and Markermeer (the Netherlands).

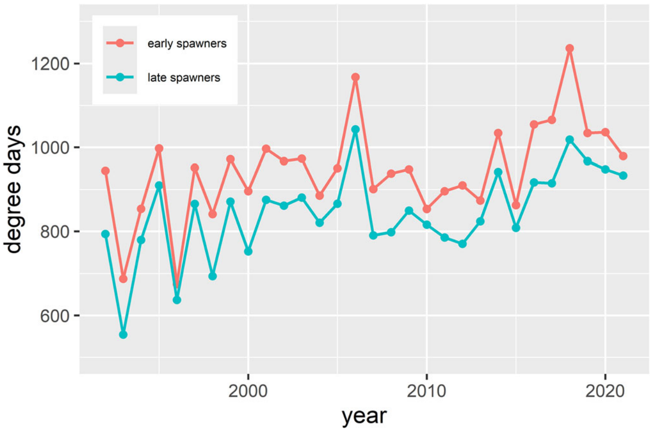

FIGURE 4 Temporal changes in air temperature during the growth season. Degree days with $T_0 = 10°C$ between May 1 and November 15 (blue) and between June 1 and November 15 (red) in the time series at Lelystad, the Netherlands.

interannual variation in summer temperature and YOY length of these three species have also been found in neighboring lakes (Mooij et al., 1994; Mooij et al., 2008) and in other studies in northwest Europe for perch (Kjellman et al., 2001; Kjellman et al., 2003). For the three species, bream, perch, and roach, the temporal increases in YOY growth rate seem likely to be related to increases in water temperature during the growth season.

Although pikeperch showed no signs of increased YOY mean length through the years in either lake, the YOY mean length did correlate significantly with interannual variation in growth season temperature in Lake Markermeer. For pikeperch, a positive correlation of temperature with YOY growth rate has been found in various other studies in northwest Europe (e.g., Kjellman et al., 2001; Lappalainen & Malinen, 2022; Mooij et al., 1994). This apparent dependency on temperature elsewhere and in Lake Markermeer has not translated into a significant increase in growth rate through the years in our study. A possible explanation is the dependency of YOY pikeperch growth on its switch to piscivory. In lakes such as Lake IJsselmeer and Lake Markermeer, pikeperch initially consume a diet of zooplankton and may switch to macrofauna, but within its first growth season (at a length of around 10 cm) the majority of YOY individuals switch to piscivory. After this switch to piscivory, growth rate increases steeply (Buijse & Houthuijzen, 1992; Mooij et al., 1994; van Densen, 1985; van Densen et al., 1996). The growth rate of YOY pikeperch at the end of the growth season will, therefore, depend heavily on the availability of prey fish of the right size. More specifically, growth rate may be related to the availability of its preferred prey fish smelt (*Osmerus eperlanus*). In the past, smelt has been shown essential in the switch to piscivory (Buijse & Houthuijzen, 1992; Mooij et al., 1994). Smelt numbers in both lakes vary greatly between years, and numbers significantly decreased over the study period in both lakes (de Leeuw, van Donk et al., 2020). Smelt has a lower optimal thermal range for growth than pikeperch (Buijse & Houthuijzen, 1992). This may have led to suboptimal conditions and lower densities of smelt with the increasing water temperatures, as has been found for other cold-water species in European freshwater lakes (Jeppesen et al., 2012). This may have reduced the opportunity for pikeperch to switch to piscivory and to consistently increase growth rates with increasing temperatures. Therefore, we hypothesize that the minor temperature effects on the growth of pikeperch in our study may be related to the indirect impact temperature has had on the food availability for this specialized piscivorous species. There are, however, no systematic annual observations

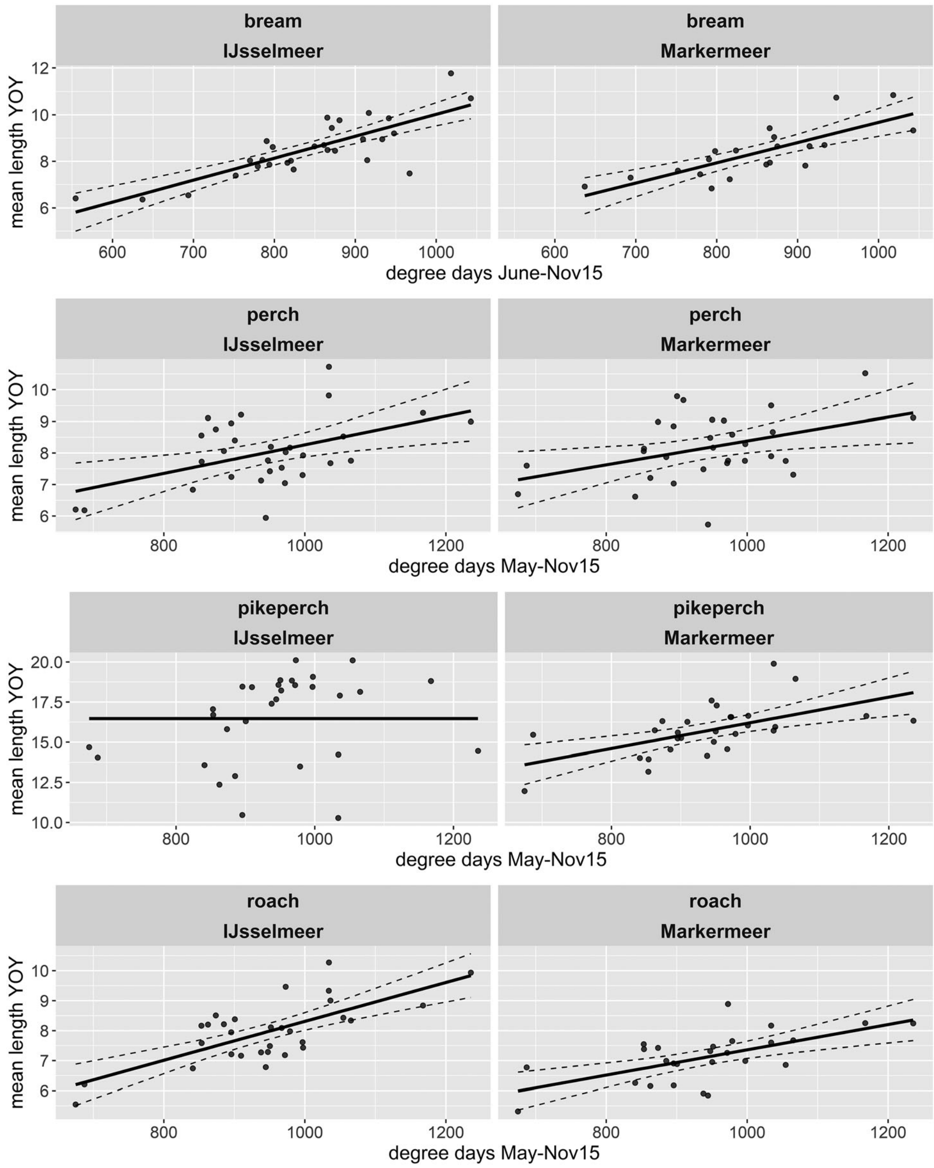

FIGURE 5 Scatterplot between degree days (T0 = 10°C) in the Lelystad time series and mean length of YOY (cm) caught in the bottom trawl survey, per species per lake. For bream (*Abramis brama*), perch (*Perca fluviatilis*), pikeperch (*Sander lucioperca*), and roach (*Rutilus rutilus*) in lakes IJsselmeer and Markermeer in the Netherlands in 1992–2021. Degree days between May 1 and November 15 for the early spawners perch, pikeperch, and roach, and between June 1 and November 15 for the late spawner bream.

on prey choice in recent decades that can be directly related to growth of this species. Future research could include retaining stomachs from the autumnal survey for diet analysis to further substantiate the role of prey availability on the growth of predatory species such as pikeperch.

Food availability does not seem to have prevented temperature-induced growth increases for bream, perch, and roach, despite the strong de-eutrophication before and during the same time period. Also, pikeperch growth has not significantly decreased through the years. The shallow coastal area of the Dutch Waddensea, which is connected to Lake IJsselmeer, has been influenced by the same process of de-eutrophication, although showing no evidence for reduced growth for four resident marine fish species (Bolle et al., 2021). Despite the strong de-eutrophication in the Dutch main rivers, their tributaries, and the connected shallow coastal waters, there are no signs that this has led to decreased growth in resident fish species in these waters.

Observational studies on the impact temperature increases have on growth rate (or other life-history traits) of freshwater fish are scarce (e.g., Huang et al., 2021; Lynch et al., 2016). Here, directional shifts in growth rate of YOY and across age groups are accompanied by significant correlations between interannual variation in temperature and YOY growth in three species and two lakes. The consistent trend across lakes, species, and age groups points toward a dominant influence of an overarching factor, such as temperature, on the increasing growth rates of these fish species. The species and intraspecific age groups belong to various trophic levels. New cohorts of all three species start on a diet of zooplankton and switch to macrofauna after which bream and roach switch to omnivory with a focus on benthos, and perch becomes an omnivore with a focus on piscivory (Buijse & Houthuijzen, 1992; Cowx, 1983; de Nie, 1996; Mooij et al., 1994; van Densen, 1985; Willemsen, 1977). Lastly, the increases are found across lakes that differ with regard to many factors such as biochemistry, hydrology, water visibility, species

TABLE 3 Details of the final model for the generalized linear models (GLMs) for YOY mean length ~ degree days.

Species	Lake	Estimate	s.e.	*t* value	*p*-value(>|*t*|)
Bream	IJsselmeer				
(Intercept)		0.588	1.148	0.512	0.613
Degree days		0.009	0.001	6.988	<0.001
	Markermeer				
(Intercept)		0.987	1.445	0.683	0.503
Degree days		0.009	0.002	5.140	<0.001
Perch	IJsselmeer				
(Intercept)		3.729	1.484	2.513	0.018
Degree days		0.0045	0.002	2.908	0.007
	Markermeer				
(Intercept)		4.605	1.482	3.107	0.004
Degree days		0.004	0.002	2.426	0.022
Pikeperch	IJsselmeer				
(Intercept)		10.66	4.174	2.554	0.016
Degree days		0.006	0.004	1.401	0.172
	Markermeer				
(Intercept)		8.198	2.059	3.982	<0.001
Degree days		0.008	0.002	3.689	0.001
Roach	IJsselmeer				
(Intercept)		1.816	1.141	1.592	0.123
Degree days		0.0065	0.001	5.421	<0.001
	Markermeer				
(Intercept)		3.137	1.045	3.002	0.006
Degree days		0.004	0.001	3.832	<0.001

Note: For bream (*Abramis brama*), perch (*Perca fluviatilis*), pikeperch (*Sander lucioperca*), and roach (*Rutilus rutilus*), as caught in the bottom trawl survey in lakes IJsselmeer and Markermeer (the Netherlands). Degree days with T0 = 10°C in the Lelystad time series between May 1 and November 15 for perch, pikeperch, and roach and between June 1 and November 15 for bream.

assemblage, fishing pressure, and temporal changes (Brinkmann et al., 2019; de Leeuw et al., 2008; Rozemeijer et al., 2021).

Growth is arguably the most direct and common way fish respond to climate change; and it is a key life-history trait that has long-lasting effects on many population traits and the ecological interaction with other species (e.g., Huang et al., 2021, Rountrey et al., 2014). Predicting the effect of climate change on aquatic ecosystems requires a comprehensive understanding of how fish growth responds to temperature increases. In particular, studies on lake fish populations are scarce (Huang et al., 2021). Surveys targeting multiple species are well suited to investigate several species simultaneously and to compare results across species—and in our case, across lakes. An added benefit is that the absence of a significant finding, such as for temporal changes in YOY pikeperch growth in the Dutch lakes, can be placed in this context and not solely attributed to data quality or analytical tools used.

AUTHOR CONTRIBUTIONS

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