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RESEARCH ARTICLE

Environmental and ecological drivers of eye size variation in a freshwater predator: A trade-off between foraging and predation risk

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Abstract

1. Variations in the size and shape of the eye have been observed in many species of fish. As eye size is positively related to visual acuity, larger eyes should favour foraging and detection of predators.
2. However, few studies have examined the variation in eye morphology in relation to the complexity of lake conditions, including environmental perturbation and spatial variation in predation and competition. Such tests are especially important as the degrading of the visual climate is expected due to climate change, where browning, turbidity and variations in structural complexity should set different demands for visual acuity of foraging fish under predation risk.
3. In this study, we tested the variation of the eye size among 667 individuals of an aquatic predator perch, *Perca fluviatilis*, from littoral and pelagic habitats of 14 lakes. We used Secchi depth to assess the effects of the visual climate of our lake systems, as fish foraging is highly related to visual conditions, and studied eye size variation in relation to the contribution of the pelagic resources to an individual's diet and the risk of predation.
4. Secchi depth, the pelagic contribution to the diet and the percentage of piscivores had significant effects on eye size.
5. These variable outcomes suggest that the lake environment in terms of visual climate, predation landscape and diet are major factors of eye size variation in this generalist predator. As many fish species trade off foraging against predation risk, future studies will show whether the complexity of intra- and interspecific interactions contribute to the variation in eye size in freshwater fish.

KEYWORDS
diet, eye size, habitat, *Perca fluviatilis*, plasticity, risk of predation, water transparency

1 | INTRODUCTION

There is a large variation in the expression of phenotypic traits of organisms in response to varying environmental and ecological conditions (West-Eberhard, 2003). Variation in eye size and shape is not an exception, where navigating the environment, finding food and avoiding predators are essential drivers of eye evolution (Beston & Walsh, 2019; Hall & Ross, 2007; Land & Nilsson, 2012). Several studies have described the general aspects of vision including the variation of physiological and morphological traits of eye adaptations (e.g. Cronin et al., 2014; Land & Nilsson, 2012), but few studies have examined the variation in eye morphology in relation to the complexity of conditions in the natural environment including spatial variation in predation and competition (but see Hammerschlag et al., 2018). One reason to focus on the complexity of variables in the natural environment when examining the eye as an adaptive trait is that the selection of an organism's traits varies spatially (Hook et al., 2021; Schluter & Mcphail, 1992). In particular, variation in adaptive traits can be driven by intraspecific interactions with an expression of multiple trophic polymorphic traits resulting from foraging on habitat-specific resources (Rainville et al., 2021; Schluter, 1995; Svanbäck & Eklöv, 2003). Different habitats also offer differing protection against predators, with variability in expressed phenotypic traits often being the result of trade-offs between foraging and predation risk (Eklöv & Svanbäck, 2006; Vamosi & Schluter, 2002). As vision is highly related to both foraging and the ability to detect predators, organisms are likely to respond to such trade-offs with a variation in the size of the eye.

There are several aspects of an organism's ecology that are relevant to the requirements of spatial acuity (Caves et al., 2017). The size of the retinal image increases with the size of the eye and therefore visual acuity improves with increasing size of the eye. A larger eye can increase an animal's fitness by improving its ability to find food and potential mates, and detect predators (Cronin et al., 2014; Land & Nilsson, 2012). Open and structured environments have very different conditions with respect to light levels and the taxa of available food, requiring different visual acuity (Ausprey, 2021; Lisney et al., 2020). Several studies have also found that eye size increases with predation risk as it increases the ability to detect predators (Beston et al., 2019; Hammerschlag et al., 2018; Vinterstare et al., 2020). However, other studies show the opposite pattern that eye size decreases with predation risk (Beston et al., 2017; Svanbäck & Johansson, 2019). The primary explanation suggested is that predators target pigmented structures such as eyes to more effectively attack and subdue prey, driving the evolution towards smaller eyes (Beston et al., 2017). The lack of consistency in suggested mechanisms can be because animals may trade off variation in eye size with multiple factors, such as increasing efficiency in foraging at the same time as avoiding predators. The trade-off in eye size is likely reinforced by the high energetic maintenance cost of the neural tissue, as the eye is one of the most energetically expensive organs among vertebrates (Moran et al., 2015; Niven & Laughlin, 2008). Therefore, plasticity and investment in the eye should be adjusted to the relative risk of being targeted by predators and the benefits of finding food.

In aquatic environments, climate change, recovery from acidification and intensification of land use are modifying ecosystem productivity leading to browner and more turbid lakes with decreased light availability (Kang et al., 2018; Larsen et al., 2011), which may substantially change the outcomes of predator–prey interactions (Ortega et al., 2020; Ranåker et al., 2014). As these changes in the visual environment can impact prey selection or cause decreases in capture rate, changes in the visual climate could further lead to effects at the community level if prey selection is species or size selective (Bartels et al., 2012; van Dorst et al., 2020). Increases in turbidity and water colour also change the habitat structure and accessibility of different resources, emphasizing the importance of including the complexity of natural ecosystems when assessing adaptive responses of eye morphology. Therefore, plastic and genetic responses to environmental variation are also likely to operate simultaneously shaping the variation of adaptive traits in populations (Hendry, 2017; Richardson et al., 2014).

In this study, we used individual fish data from 14 lakes to test whether environmental variation in visual conditions (i.e. Secchi depth), pelagic diet contribution, predation risk and intraspecific competition are associated with differences in the size of the eyes of a common fish predator perch (*Perca fluviatilis*) in littoral and pelagic habitats of freshwater lakes. The perch shows a polyphenic trophic pattern and habitat-specific niche differentiation (Svanbäck & Ekläv, 2003), where littoral fish primarily feed on macroinvertebrates in the littoral zone and pelagic fish mainly feed on zooplankton in the pelagic zone (Marklund et al., 2019; Quevedo et al., 2009). We selected lakes along a water colour gradient from brown to clear (low to high Secchi depth) while minimizing other variables such as lake size and mean depth, to focus on the effects of our focal variables.

We predicted that: (1) Predation affects eye size variation, with fish reducing eye size in relation to increased predation risk, but we predicted a habitat difference in eye size due to a higher conspicuousness of the eye and with this a higher predation risk in the pelagic than in the littoral habitat, as suggested by a previous study (Svanbäck & Johansson, 2019). (2) Independent of habitat, fish in more turbid and less transparent lakes (i.e. lower Secchi depth) will express larger eye size. This builds on the assumption that lower light conditions favour adaptations of larger eye size (Warrant & Locket, 2004). (3) There is a positive association between the contribution of pelagic resources to diet and eye size. This hypothesis assumes that foraging on pelagic resources requires higher visual acuity and thereby larger eye size (Olson et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Field sampling

The study adhered to all applicable international, state and national guidelines regarding ethics approvals. No specific animal ethical permit was necessary, as the study used data from monitoring organizations in Sweden and Germany (see below) and Bartels et al. (2016). To assess eye size variation in perch we used data from Andersson (2021). In summary, fish were collected in 2017 and 2018 from 2 lakes located in Germany (Wuckersee and Großer Vätersee) and 10 lakes located in Sweden (Figure 1), where sampling was carried out in collaboration with the monitoring teams of the National Environmental Monitoring Program (NM) and the Integrated Studies of the Effect of Liming Acidified Waters (IKEU) in Sweden and IGB, Leibniz Institute of Freshwater Ecology and Inland Fisheries, in Germany. We further extended our dataset with perch from two lakes (Oppsveten and Långsjön) that were sampled in 2008 (Bartels et al., 2016). Thus, our data set consists of perch populations from 14 lakes in total. All lakes were small (ranging from 0.1 to 2.5 km^2) and oligo- to mesotrophic (total phosphorus ranging from 3.8 to 27 μg L^{-1}) (see Table 1 for lake characteristics). Sampling in littoral and pelagic zones took place between July and September using benthic multi-mesh gillnets (30 × 1.5 m) and pelagic multi-mesh gillnets (27.5 × 3 m) according to the European standard EN 14757:2015. In the field, fish species were determined and measured to the nearest 1 mm (total length) and weighed to the nearest 0.1 g. The perch were individually photographed on the left lateral side and a piece of dorsal muscle tissue was dissected for stable isotope analyses and frozen at −20°C. The benthic and pelagic resources were sampled and analysed for stable isotopes to estimate the contribution of the resource to the diet of the perch (see below). Pelagic resources were sampled by collecting zooplankton from the pelagic zone using a 25 cm opening zooplankton net with a 60 μm mesh size, by vertical tows at the deepest part of the lake from 1 m above the sediment to the surface and by towing the plankton net along the surface of the pelagic zone behind the boat. Benthic resources were sampled by collecting invertebrates from shallow littoral areas using a net with a kick-sampling method. The biomass of perch per unit effort (BPUE) was used as a proxy for the level of intraspecific competition (e.g. Olsson et al., 2006) and was estimated for each lake by summing the mass of all perch caught divided by the total number of nets. The Secchi depth was used as a proxy for water transparency and was estimated by lowering a white disc into the water at the deepest point in the lake and recording the depth at which the disc could no longer be seen.

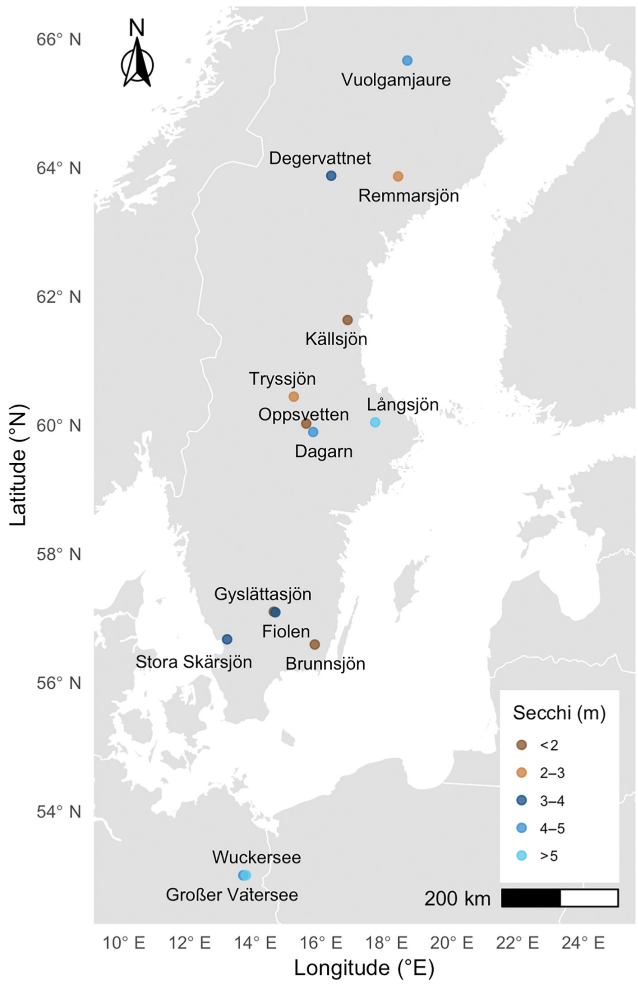

FIGURE 1 Map indicating the locations of lakes in Sweden and Germany and the water transparency (Secchi depth).

2.2 | Stable isotope analyses and estimates of pelagic contributions in perch

Samples for stable isotope analyses of δ^{13}C were oven-dried at 60°C for 48 h, packed in tin capsules and sent to the UC Davis Stable Isotope Facility, Davis, California, USA. To estimate the contribution of pelagic resources (expressed in %) to the diet of individual perch, we used a two-source mixing model (Post, 2002):

$$\text{pelagic contribution}\,(\%) = \frac{\left(\delta^{13}\text{C}_{\text{Consumer}} - \delta^{13}\text{C}_{\text{littoral resources}}\right)}{\left(\delta^{13}\text{C}_{\text{pelagic resources}} - \delta^{13}\text{C}_{\text{littoral resources}}\right)}$$

$\delta^{13}\text{C}_{\text{littoral resources}}$ is the average value of benthic invertebrates (mainly snails) of each lake, while $\delta^{13}\text{C}_{\text{pelagic resources}}$ is the average value of pelagic resources (i.e. mussels and zooplankton) of each lake. See (Andersson, 2021) for stable isotope data and biplots.

2.3 | Estimation of predation pressure

We estimated predation pressure by calculating the percentage of the fish community made up by the abundance of piscivorous fish in each lake. We classified piscivorous perch based on the assumption that perch start to become piscivorous at 120 mm and then linearly increase in their degree of piscivory until a size of 180 mm when they are fully piscivorous (Svanbäck et al., 2015). Other fish species were classified as piscivorous above the stated size threshold: pike *Esox lucius*: from juvenile stages and larger, burbot *Lota lota*: 220 mm (Kahilainen & Lehtonen, 2003), smelt *Osmerus eperlanus*: 90 mm (Vinni et al., 2004) and brown trout *Salmo trutta*: 130 mm (L'Abée-Lund et al., 1992).

TABLE 1 Characteristics of lakes used in this study.

					Perch (*N*)		Mean pelagic contribution (%)	
Lake	Area (km^2)	Mean depth (m)	Secchi depth (m)	Piscivorous fish (% of abundance)	Littoral	Pelagic	Littoral perch	Pelagic perch
Brunnsjön	0.1	5.3	1.1	2.7	30	31	35	44
Dagarn	0.32	3.9	5.6	9.1	30	14	45	60
Degervattnet	1.56	3.9	4	47.3	29	4	30	58
Fiolen	0.32	2.8	3.9	18.1	29	29	1	28
Großer Vätersee	0.12	5.2	4.2	11.6	29	30	35	37
Gyslattasjön	1.72	5.1	1.8	4.2	29	28	51	44
Källsjön	0.3	7.2	0.9	31	30	–	38	–
Långsjön	2.5	6.3	5.6	5.1	30	29	48	65
Oppsveten	0.65	3.3	1.8	7.4	27	29	76	80
Remmarsjön	0.24	7.1	2.6	27.1	30	8	34	33
Stora Skarsjön	1.66	6.7	3.8	5.8	30	29	40	36
Tryssjön	1.4	5	2.6	40.5	28	11	34	32
Vuolgamjaure	2.09	4.1	4.5	45.3	30	–	15	–
Wuckersee	0.23	5.98	5.5	5.6	30	15	49	49

TABLE 2 Replication statement.

Scale of inference	Scale of which the factor of inference is applied	Number of replicates at the appropriate scale
Lake	Lake	14 lakes
Habitat	Habitat	14 littoral and 12 pelagic habitats

2.4 | Statistical analysis

The size of the eyes (in mm) was measured from the photographs of perch, using tpsDig2 (Rohlf, 2015) and used as a response variable in the analyses according to the replication statement (Table 2). We used a generalized additive mixed model (GAMM) from the package mgcv (Wood et al., 2017) to test the effects of 'Secchi depth', 'pelagic contribution to diet', percentage of 'piscivores', 'habitat' and 'BPUE' on perch eye size. All models included the 'lake' as a random smoother to account for multiple fish being sampled from each lake. 'Fish length' was included as a smoother term since fish eye size scales non-linearly with length (Howland et al., 2004), and accounts for a large proportion of variance in fish eye size. The homogeneity of the model residuals was verified by visual inspection of diagnostic plots produced by gam.check (Wood et al., 2017). Plots were created using visreg (Breheny & Burchett, 2017) and ggplot2 (Wickham, 2016) and depict partial residuals showing the change in eye size as the focal variable increases, while holding co-variates constant at their median. All analyses were performed using R version 4.4.0. (R Core Team, 2024).

3 | RESULTS

In total, we analysed 667 perch individuals from 14 lakes. We found that Secchi depth, pelagic contribution to the diet and the percentage of piscivores all had significant effects on perch eye size, indicating that multiple factors contribute to the variation in eye size of perch (Table 3). Habitat and BPUE did not affect the perch eye size. We found that perch eye size decreased in clearer waters (i.e. with increasing Secchi depth) and as the percentage of predators in the lakes increased (Table 3, Figures 2 and 3). On the contrary, the perch eye size increased with increasing pelagic contribution to the individual's diet (Table 3, Figure 4).

4 | DISCUSSION

Our results suggest that environmental and ecological factors contribute to the variation in perch eye size. The Secchi depth, contribution of pelagic resources to the diet and the percentage of piscivores were all significantly correlated to the variation in the eye size of the perch across lakes. Below, we evaluate the different factors contributing to eye size variation and outline major mechanisms behind the evolution of eye size in a generalist freshwater predator.

4.1 | Adaptations to risk of predation

The risk of predation has been suggested to be a major driver of eye size variation (Svanbäck & Johansson, 2019). Interestingly, this can

TABLE 3 Summary of the generalized additive mixed model testing the fixed effects of: The percent of the fish population made up of piscivores (percent piscivore), Secchi depth, pelagic contribution to the individual's diet (percent pelagic diet), habitat where the fish was caught, and perch biomass per unit effort (BPUE).

	β	SE	*t*-value	*p*-value
Linear terms				
Percent piscivores	−0.016	0.005	−3.260	0.001
Secchi depth	−0.158	0.047	−3.359	0.001
Percent pelagic diet	0.003	0.001	2.192	0.029
BPUE	0.000	0.000	0.543	0.587
Habitat	0.026	0.046	0.572	0.567
	Effective df		F-value	p-value
Smooth terms				
Fish length	6.564		815.81	0.000
Lake (random effect)	8.788		12.24	0.000
Adjusted R^2: 0.925 Deviance explained: 92.7%				

Note: Fish length was included as a smooth term and lake was included in the model as random effect. β represents the estimates of the fixed effects.

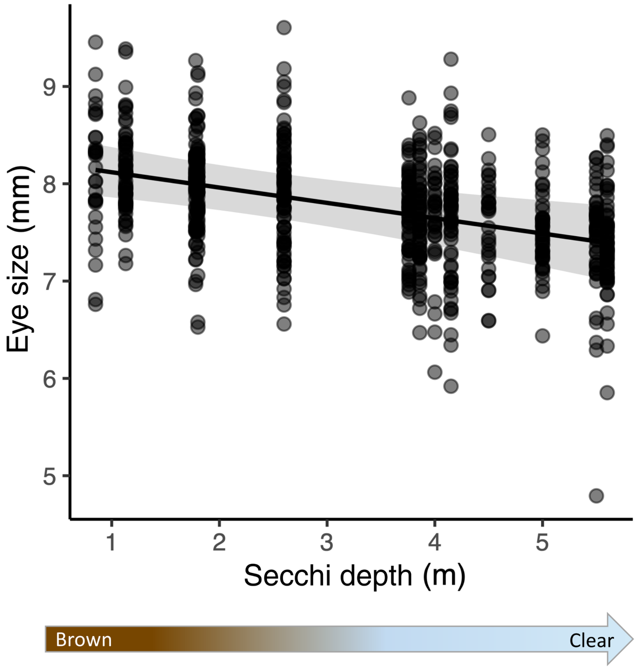

FIGURE 3 Relationship between eye size and Secchi depth (m). Points are partial residuals and show the change in eye size as water transparency increases, while holding co-variates constant at their median. Wald confidence intervals are depicted in grey.

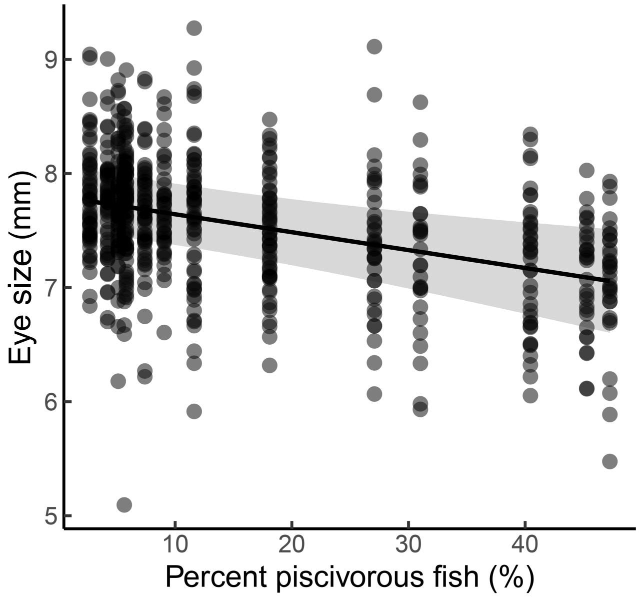

FIGURE 2 Relationship between eye size and percentage of piscivorous fish (% of abundance). Points are partial residuals and show the change in eye size as the percent piscivorous fish increases, while holding co-variates constant at their median. Wald confidence intervals are depicted in grey.

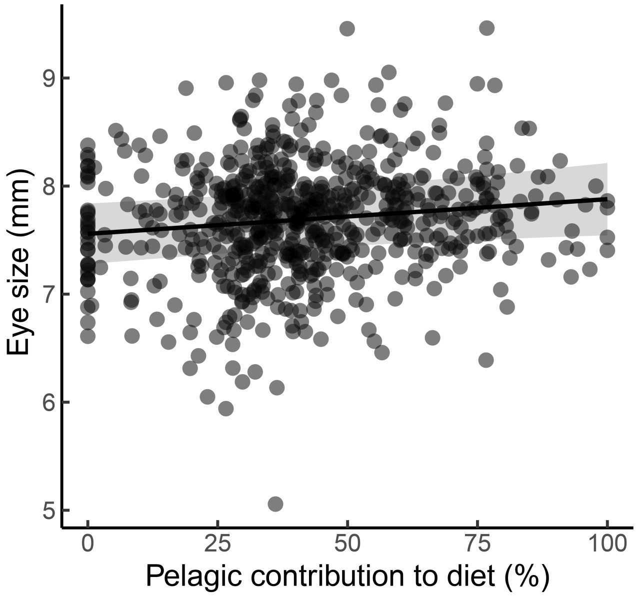

FIGURE 4 Relationship between eye size and the pelagic contribution to the diet (%). Points are partial residuals and show the change in eye size as the pelagic contribution to an individual's diet increases, while holding co-variates constant at their median. Wald confidence intervals are depicted in grey.

drive either an increase or a decrease in eye size (Beston et al., 2017; Glazier & Deptola, 2011). The underlying mechanism suggested to explain increased eye size in relation to predation risk is that larger eyes increase the probability of predator detection (Nilsson et al., 2012), while the alternate mechanism is that a decrease in eye size reduces an individual's conspicuousness to predators (Svanbäck & Johansson, 2019). The eye is a conspicuous morphological feature and vital organ for organisms, and under predation risk this can drive the evolution of false eyespots to attract predator attacks to less vital parts, for example, the tail of a prey's body (Kjernsmo & Merilaita, 2013). The selective pressure of predation risk in reducing eye size was supported by our results, as eye size was negatively correlated with the percentage of piscivores. However, we hypothesized a negative correlation of eye size with predation risk in the pelagic but not the littoral habitat based on previous findings by Svanbäck and Johansson (2019), who suggested that the reflection of the eye contribute to lower survival in open but not complex habitats. Our results did not support a habitat difference in eye size and it is possible that a combination of factors at the whole system scale of our study played into the different outcomes. For example, we do not know whether the risk of predation differed between littoral and pelagic habitats, but a clear negative relationship between eye size and percentage of piscivores showed that predation was a major factor for eye size variation in both habitats.

4.2 | Adaptations to light conditions

The difference in Secchi depth across lakes contributed to the variation in perch eye size, likely due to differences in light regimes. Our results showed that eye size was negatively related to increasing Secchi depth, suggesting that more turbid and darker waters select for larger eye size due to lower light conditions. This result supported our hypothesis and also previous studies showing that lower light conditions favour adaptations of larger eye size (Schmitz & Wainwright, 2011; Warrant & Locket, 2004). Furthermore, it has been shown that perch eye size is positively correlated with lake browning as a result of increased total organic carbon (Bartels et al., 2016) (but see Jokela-Määttä et al. (2019), who found no relationship). Changes in eye size can be one adaptation to reduced light climate but foraging in dim light or changes in spectral properties could also be associated with more subtle adaptations in the visual system through the expression of variation in spectral sensitivities and visual pigments (Carleton et al., 2020). However, we did not examine this aspect of adaptations in this study. We hypothesized that the littoral vegetation could also be a driver of eye size variation as complex environments require larger eye size promoting higher visual acuity and ability to resolve spatial detail (Caves et al., 2017); however, our results did not support this theory as we did not find any habitat differences in eye size. A larger eye seems to be a general adaptation to lower light conditions, but the cost of maintaining a larger eye needs also to be measured against other costs, and the expression of phenotypic traits often results from a trade-off between competition for food and avoiding predation (Eklöv & Svanbäck, 2006). Interestingly, in Mexican cave fish, individuals with a reduced visual system are favoured. Living in complete darkness and experiencing low food resource levels renders vision unnecessary for feeding and predator evasion, and a reduced visual system reduces overall energy expenditure (Moran et al., 2015; Protas et al., 2007). Therefore, individuals can respond adaptively by changing eye size as long as light is available and reduce expensive tissues when they are no longer needed (Caves et al., 2017).

4.3 | Adaptation to resource acquisition

Another suggested factor of eye size variation is variation in resource acquisition. Previous studies have concluded that zooplanktivory is related to enlarged eyes, since foraging on small food items requires high visual acuity (e.g. Cooper & Westneat, 2009; Mcphail, 1984). The gradient in visual climate we examined with varying transparency and scattering of light due to fluxes of organic carbon and turbidity, likely had substantial changes in the visual environment with potential consequences for consumer-resource interactions (e.g. Jonsson et al., 2013). Being part of the sensory system that is costly to produce, eye size has also been shown to be reduced under lower resource conditions (Niven & Laughlin, 2008). As a result, resource competition has been observed to be a major factor of eye size variation in killifish when other potential factors such as predation were absent (Beston & Walsh, 2019). When competition for resources was high within this species, growth and survival of individuals with larger eyes was favoured, as they had a higher foraging rate than individuals with smaller eyes (Beston & Walsh, 2019). In our systems, larger eyes were correlated with higher zooplanktivory indicating differences in the strength of selection, plasticity or both on eye size. However, (Beston & Walsh, 2019) showed that in the presence of predators, the relationship between eye size and competition was absent, which was also supported by our results: sampled perch biomass per unit effort (BPUE), which was used as a proxy for intraspecific competition in our study, was not related to the variation in eye size.

4.4 | Mechanisms of intraspecific eye plasticity

An additional aspect of the variation of eye size is whether this variation is related to phenotypic plasticity or genetic differences. Although we did not test for genetic differences in this study, previous studies have shown that the resource polymorphic patterns within this species are largely related to phenotypic plasticity (Faulks et al., 2015). We have mostly interpreted eye size variation as an adaptive response to environmental and ecological variables. However, it is also possible that variation in eye size or eye morphology can drive changes in foraging behaviour that, in turn, feedback on ecological processes. For example, variation in pupil size in crucian carp caused a shift from diurnal to nocturnal activity (Vinterstare et al., 2020). Previous studies have shown different fish activity patterns between littoral and pelagic habitats and strong relationships between foraging behaviours and capture rate on habitat-specific resources (Andersson et al., 2022; Svanbäck & Eklöv, 2003). Therefore, it is possible that the variation in eye size between individuals in this study, in addition to an adaptive response, could be selected for different perch foraging behaviours resulting in differences in prey selection that correspond with eye size (e.g. Svanbäck & Eklöv, 2003).

5 | CONCLUSIONS

Here, we have shown that predation and Secchi depth are strongly correlated to eye size variation in perch, where a higher water clarity and increasing abundance of predators correspond to smaller eyes in potential prey. Although the pelagic resource contribution to diet play a major role in affecting the variation of perch eye size, predation and the clarity of water driven by turbidity and DOC levels in lakes, emerge as primary factors influencing eye size variation across lakes. Recent studies highlight the importance of predation risk in fish eye size variation (e.g. Beston et al., 2017; Svanbäck & Johansson, 2019; Vinterstare et al., 2020), albeit with somewhat contrasting results. Our study, encompassing a complexity of factors at the whole system scale across 14 different lakes, suggests that predation and water clarity are two key factors influencing fish eye size. Still, our study does not include how the complexity of factors interacts with intra- and interspecific interactions, which would be relevant for future studies.

AUTHOR CONTRIBUTIONS

MLA, KS and PE conceived the ideas and designed the methodology. MLA collected the data. MLA and KS analysed the data. PE and KS led the writing of the manuscript. All authors contributed critically to the drafts and gave the final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they do not have any conflict of interest.

DATA AVAILABILITY STATEMENT

Raw data and code are available at Zenodo, dataset: https://doi.org/10.5281/zenodo.13208408.

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