

Lake depth alters the trajectory of ontogenetic niche shifts in Eurasian perch (*Perca fluviatilis*) in small lakes

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Abstract

The trophic niche of aquatic generalist predators is influenced by ontogeny, habitat characteristics, availability and type of prey, and competitive interactions. Many inter-related lake characteristics influence the availability of prey and may thereby impact foraging niches and the trajectory of ontogenetic niche shifts. Our work uses Eurasian perch (*Perca fluviatilis*) as a model species to examine the correlation of multiple lake and fish community characteristics with the size-dependency of perch populations' realised trophic niche. We used carbon and nitrogen stable isotopes to correlate the changes in perch trophic position across a gradient of total lengths in seven gravel pit lakes that differed in lake morphology, habitat heterogeneity, productivity, structural complexity, and fish community composition. Perch populations in lakes with more shallow-water habitat reached a higher trophic position at smaller sizes than perch in deeper lakes. However, the changes in trophic position with increasing size were less pronounced compared to perch from deeper lakes. Large individuals from the latter perch populations ultimately achieved higher mean trophic positions compared to fish from shallow lakes. Perch in lakes with more shallow-water habitat may, therefore, achieve lower rates of piscivory because of higher relative availability of macroinvertebrates or greater competition with zooplanktivores. Our results suggest that large, piscivorous perch are more likely to develop in deeper lakes, and that these changes in perch trophic position across ontogeny are more strongly related to the depth of lakes than to the type of structured habitat in the littoral zone.

KEYWORDS

competition, habitat heterogeneity, littoral zone, stable isotope analysis, trophic niche

1 | INTRODUCTION

Eurasian perch (*Perca fluviatilis*) are generalist fish native to Europe and northern Asia and introduced to Australia, New Zealand, and South Africa (Collette & Bănărescu, 1977; Weatherley, 1977). The diet of perch tends to change with increasing length and gape size, starting with zooplankton before transitioning to benthic macroinvertebrates

and then fish (Allen, 1935) but considerable variation in this trajectory exists depending on differences in lake habitat and fish community interactions (e.g. Diehl, 1993; Persson & Greenberg, 1990a). The plasticity of the foraging niche of Eurasian perch, therefore, render the "ontogenetic omnivore" perch as suitable model to study the foraging ecology of generalist predators as a function of their abiotic and biotic environment (Persson et al., 2000).

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The ontogenetic niche shifts of perch are well described as a size-dependent shift in main prey type and foraging habitat (Thorpe, 1977b). The previously described zooplanktivorous stage of young perch typically takes place in pelagic habitat before mid-sized perch transition to foraging for benthic macroinvertebrates in the littoral zone (Eklöv, 1997). Perch typically then transition to piscivory, including consumption of conspecifics, as they grow beyond 100 mm in total length. (Allen, 1935; Mittelbach & Persson, 1998; Thorpe, 1977a). These transitions among different prey types vary substantially among ecosystems and are affected by complex interactions of habitat structure and prey availability (Diehl, 1993), predation risk, (Persson & Eklöv, 1995) and intra- and interspecific competition (Persson & Greenberg, 1990a, 1990b). But as a general rule, very large-sized perch (giant cannibals in the terminology of Persson et al., 2003) form when perch become piscivorous early in life (Claessen et al., 2000) and have ample access to suitable fish prey or large and energy-rich macroinvertebrates such as crayfish (Haertel-Borer et al., 2005; Linzmaier et al., 2018). Eurasian perch can, therefore, function as prey or as top-down controlling predators, depending on life stage and body size (Allen, 1935; Persson et al., 2000; Thorpe, 1977b). Depending on ecological context, however, perch foraging niche may deviate from the commonly accepted trajectory. For example, adult perch often continue to consume macroinvertebrates (Linzmaier et al., 2018), and piscivory has been documented in young-of-year perch of less than 50 mm in total length (Beeck et al., 2002; Mehner et al., 1996; Svanbäck & Eklöv, 2003). Although the classical ontogenetic niche shift in perch may be broadly true (e.g. Craig, 1978), there is considerable variation in the trajectory of this change in different environments (e.g. Beeck et al., 2002; Deelder, 1951; Diehl, 1993; Rask, 1983; Treasurer, 1993). Differences in growth and abundance of perch among lakes may be associated with differences in perch foraging niches affected by lake productivity (e.g. Persson et al., 1991), habitat heterogeneity and complexity (Höhne et al., 2020; Vejříková et al., 2017), lake depth (Kahl & Radke, 2006), and/or prey community characteristics (e.g. Persson, 1993), but studies that quantify environmental effects on size-dependency of foraging niche in perch across lakes are rare (but see Karus et al., 2022).

Disentangling the effects on perch foraging niche of lake primary productivity, community composition, and abiotic lake characteristics is difficult because many factors are interrelated. Increased primary productivity may influence perch trophic niche through its bottom-up effects on resource availability, visibility, and interspecific competition (Diehl, 1988). Although increased primary productivity may increase the availability of zooplankton for small perch, cyprinids such as roach (*Rutilus rutilus*) are superior foragers for zooplankton (Persson & Greenberg, 1990b). Moderate lake productivity, therefore, favours high-perch biomass in many lakes, while highly eutrophic lake ecosystems are usually associated with cyprinid dominance (Jeppesen et al., 2000; Mehner et al., 2005; Persson, 1991). However, depth of lake can moderate the competition among roach and perch and lead to stable co-existence as roach and perch segregate in the vertical dimension as juveniles (Kahl & Radke, 2006). In fact, at equal primary productivity, differences in

lake morphology and habitat complexity have been shown to drive differences in perch foraging niche that facilitate coexistence with competitors. For example, shallow lakes can support extensive growth of submerged aquatic vegetation, which can stabilise clear water conditions that favour perch over roach (Scheffer et al., 1993) as perch is more effective than roach at foraging in structurally complex habitats (Diehl, 1988; Persson & Eklöv, 1995; Winfield, 1986). Therefore, complex littoral structure may alleviate bottlenecks in perch recruitment that are associated with interspecific competition (Boll et al., 2012). For example, larger patches and increased structural complexity of submerged vegetation has been associated with increased diversity and abundance of benthic macroinvertebrates (Matias et al., 2010), and perch have been found to outcompete roach and other cyprinids in their search for macroinvertebrates in macrophyte stands and other structures (Diehl, 1988). Because of this increase in resource availability and their superior foraging ability in littoral structure, increased growth of submerged aquatic vegetation has been associated with improved recruitment of piscivorous perch (Hargeby et al., 2005). Along the same lines, increasing depth of lakes can allow co-existence of predation of juvenile perch and roach on zooplankton, and allow larger piscivorous perch to exploit fish prey effectively (Kahl & Radke, 2006). Disentangling the effects of productivity, competition, lake morphology, and littoral habitat requires comparison of perch trophic niche among many lakes with different characteristics in a space for time replication approach or experimental manipulations, which are rarely possible.

Gravel pit lakes provide an ideal ecological laboratory for investigating perch trophic niche across gradients of habitat complexity, productivity, and abundance of competitors and predators because the lakes are abundant and of similar origin and age, but they vary in trophic state and depth (Matern et al., 2022; Seelen et al., 2021; Søndergaard et al., 2018). We used nitrogen and carbon stable isotopes and a statistical model-based approach to understand how these lake variables have affected the feeding ecology of this generalist predator. Because the study lakes are described by many correlated characteristics, we used model selection to rank the importance of lake variables as predictors of mean perch trophic position and change in perch trophic position with increased length. We hypothesized that higher habitat heterogeneity (in terms of lake depth) and complexity (in terms of coverage by aquatic vegetation) in a gravel pit lake would reduce the potential for competitive bottlenecks and allow perch populations to achieve higher average trophic positions.

2 | METHODS

2.1 | Study system

We initially sampled 12 gravel pit lakes in Lower Saxony, northern Germany. All lakes were managed by angling clubs and contained large perch populations. For more details on lake selection, see Matern et al. (2019). Of the 12 lakes, five were removed from the analysis due to insufficient sampling of littoral baselines necessary

to estimate perch trophic position. This study, therefore, examines differences in perch ontogenetic niche shifts in seven lakes (Table 1, Figure 1).

Limnological and morphometric measurements of each of these lakes were completed between September of 2016 and 2017 (Table 1). Echosounding and geolocation data were used to produce depth maps and to calculate surface area and maximum depth as described in Matern et al. (2019). The percentage of lake area occupied by shallow water was also estimated based on these depth maps. The shallow-water zone was defined as the lake depth stratum between 0 and 3 m. The shoreline development factor (SDF) was calculated based on the shoreline length (L) and surface area (A) by the formula $SDF = L / (2\sqrt{\pi A})$. Chlorophyll a ($\mu\text{g/L}$), total phosphorus concentration ($\mu\text{g/L}$), and Secchi depth (m) as indicators of lake productivity were measured four times in all individual lakes within 12 months (autumn 2016, spring, summer, and fall 2017). We used mean values of each of these measurements to describe the trophic state of each lake.

The procedure for quantifying woody littoral structure was adapted from Kaufmann and Whittier (1997). Woody structure was quantified by counting the number of pieces of complex woody structure (CWS) per square meter of littoral area in equidistant sampling units surrounding the shoreline of each lake. CWS was defined as woody debris longer than 50 cm with a minimum diameter of 5 cm and at least 10 cm of three-dimensional structure. The first sampling unit was randomly selected, and subsequent units were placed every 100 to 150 m along the shoreline until a circuit of the lake was completed. Woody structure was counted by snorkelling, and the average density of CWS was calculated for the entire littoral zone of each lake.

Aquatic vegetation coverage (both submerged and emergent) of each lake was estimated between June and August of 2016 using snorkel surveys along equidistant transects following Schaumburg et al. (2014) and described in detail in Nikolaus et al. (2021). Surveys were completed on equidistant sampling units surrounding the shoreline of each lake and then transformed into percent of the lake area covered by vegetation (hereafter, percent vegetation coverage).

2.2 | Fish sampling

Depth-stratified random sampling with benthic multimesh gill nets was completed between August and October of 2016 according to modified European standards for gill net sampling (CEN, 2015) and in compliance with fisheries law in Lower Saxony. These standards, however, were written for lakes larger than 20 ha. A large gravel pit lake, Meitzer See, with a surface area of 19.5 ha, was, therefore, designated as a reference lake. This lake was not sampled for this analysis, but it was one of a full set of 16 lakes sampled for a wider project (see Höhne et al., 2020; Matern et al., 2019, 2022; Nikolaus et al., 2021; Radinger et al., 2023). On this reference lake, 16 nets were deployed to correspond with the standards for 20 ha lakes. The ratio of nets to surface area (0.82) was then multiplied by the

TABLE 1 Lake variables describing lakes' morphology, productivity, shoreline structure, and metabolic biomass of predators, cyprinid interspecific competitors, and intraspecific competitors for small (<120 mm) perch.

Lake name	Lake area (ha)	Max depth (m)	Mean chl a ($\mu\text{g/L}$)	Mean TP ($\mu\text{g/L}$)	Mean Secchi depth (m)	Prop. Macrophyte cover	CWS density (N/m^2)	Prop. Shallow	SDF	Length ² predators (mm^2/m^2 net)	Length ² interspecific competitors (mm^2/m^2 net)	Length ² intraspecific competitors (mm^2/m^2 net)
Donner Kiesgrube 3	1.03	5.2	8.86	39.75	1.78	0.11	0.09	0.309	1.16	4890	576	3692
Kiesteich Brelingen	8.48	8.7	6.5	31.25	1.38	0.04	0.03	0.431	2.2	8000	3829	4293
Kolshorner Teich	4.27	16.1	4.8	10.5	3.8	0.19	0.08	0.219	1.5	3137	298	526
Saalsdorf	9.04	9.2	14.95	20.25	1.65	0.02	0.07	0.169	1.33	1539	670	3339
Steinwedeler Teich	10.35	9.1	5.78	10.25	2.78	0.17	0.03	0.198	1.97	6465	534	1038
Weidekampsee	2.95	4.3	3	9.25	3.65	0.73	0.03	0.583	1.58	5664	575	349
Wiesedermeer	2.93	9.2	6.67	16.25	2.1	0.18	0.01	0.341	1.74	3746	2864	610

Note: TP refers to total phosphorus, CWS to coarse woody structure, and SDF to shoreline development factor. Length² is the sum of lengths squared, an index of metabolic biomass.

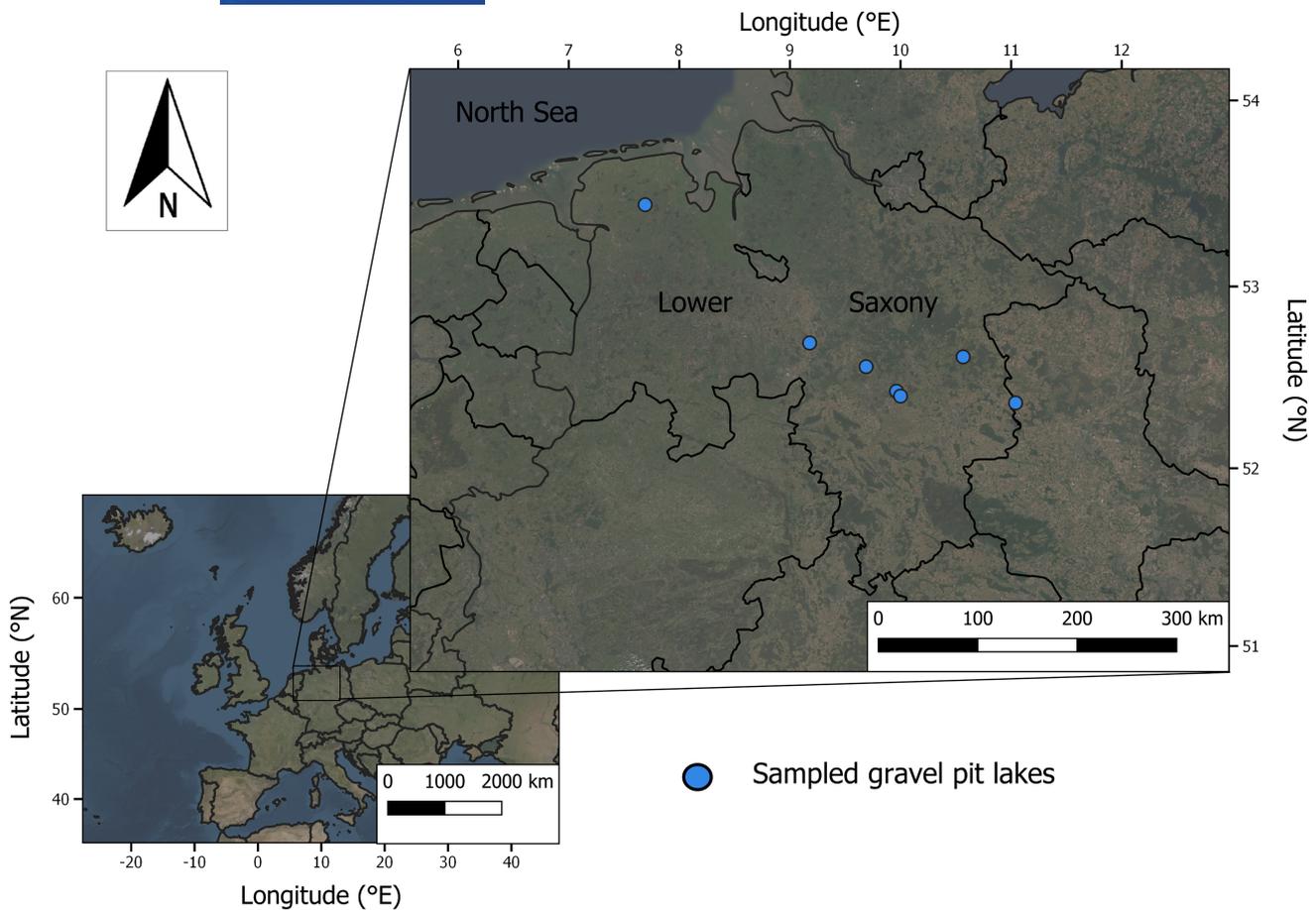


FIGURE 1 Map illustrating the locations of the seven gravel pit lakes in Lower Saxony, Germany sampled for this analysis.

surface area of the remaining lakes to assign a representative number of gill nets for each lake size. Gill nets were then placed according to a depth-stratified random sample design. Further details can be found in Höhne et al. (2020) and Matern et al. (2019). Nets were 40m in length with mesh sizes of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, 55, 70, 90, 110, and 135mm and were placed overnight. Additional sampling was completed in the littoral zone using electrofishing. The total length of each sampled fish was recorded. The samples from both fishing methods were used for stable isotope analysis, but only gill net samples were used for estimates of relative metabolic biomass of predators and inter- and intraspecific competitors.

Interspecific competition, predation, and intraspecific competition within each lake was quantified as relative fish metabolic biomass as proposed by Post et al. (1999). Metabolic biomass, calculated as the sum of squared fish total lengths, provides an index of competitive or predatory interactions that accounts for both fish density and the higher consumption rate of larger individuals. Cyprinids and perch less than 120mm in length were classified as interspecific competitors and intraspecific competitors, respectively. Roach were the most frequently caught cyprinid among these lakes (Matern et al., 2019), and their reliance on zooplankton is expected to decrease after they pass this size threshold, reducing their competition with smaller perch (Hjelm et al., 2003).

Perch greater than 120mm in length, as well as pikeperch (*Sander lucioperca*) and northern pike (*Esox lucius*) greater than 100mm in length were classified as predators based on their size at piscivory in the literature (Mittelbach & Persson, 1998). Individual lengths were weighted by the representation of their depth strata in the stratified random sampling of the lake. Lake-specific relative metabolic biomass was then estimated as the sum of these squared lengths per m^2 gill net ($Length^2/m^2$).

2.3 | Stable isotope analysis

Subsamples for stable isotope analysis were collected from the total electrofishing and gill net catches to represent each lake-specific range of perch total lengths collected through each sampling method (Figure S1). We collected at least five samples per lake, fishing method, and 5cm size class for stable isotope analysis. A minimum of 27 perch individuals from each lake were analysed. Dorsal muscle tissue above the lateral line was dissected out, rinsed with distilled water, and examined under a dissection microscope to remove any bones or scales that remained.

Littoral and pelagic baselines were sampled once from each lake between September and October, 2016, to estimate perch individuals' trophic positions. As a pelagic baseline, zooplankton was

sampled by horizontal tows with a 55 µm plankton net. These samples were left overnight in lake water to allow gut clearance of organisms and then stored at -20°C until processing. Samples were then filtered through 200 µm sieves, rinsed with distilled water, and separated from debris by hand. Submerged aquatic vegetation was used as a shared littoral baseline. Although epiphyton samples are more commonly used as littoral baselines, epiphyton was not systematically sampled in all lakes. The most common sampled littoral resource was submerged vegetation, *Elodea* spp. and *Myriophyllum spicatum*, which was shared by the seven lakes analysed in this study. Submerged aquatic vegetation has been demonstrated as an important contributor of carbon to food webs of shallow lakes and so was accepted as a substitute for epiphyton (Mendonça et al., 2013). In addition, perch $\delta^{13}\text{C}$ values were less negative than those of epiphyton samples in two lakes (Saalsdorf and Steinwedeler Teich), suggesting the epiphyton samples may have been mixed with other biota or that macrophytes formed the base of those lakes' littoral food webs. Macrophyte samples were collected manually from each lake. Samples were stored at -20°C before processing, and debris was later removed under a dissecting microscope with distilled water.

All perch and pelagic and littoral baseline samples were dried at 60°C and ground with a mortar and pestle to a homogeneous powder. Samples were shipped to the Cornell Isotope Laboratory where 1 mg subsamples were packaged in tin capsules and analysed with a Thermo Delta V isotope ratio mass spectrometer interfaced to a NC2500 elemental analyser. Atmospheric nitrogen and Vienna Pee Dee Belemnite were used as $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ standards, respectively (International Atomic Energy Agency, 1993). Analytic precision was tested every 10 samples against an in-house standard, and a chemical methionine standard was used to calculate accuracy of sample measurements for a gradient of amplitude intensities. The standard deviation of the in-house standard runs was 0.09‰ for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. The error of the methionine standard measurement across a range of amplitudes was 0.59‰ for $\delta^{15}\text{N}$ and 0.23‰ for $\delta^{13}\text{C}$. Corrections to isotope values were performed based on these results using a two-point normalisation with two more in-house standards. All C:N values for fish samples fell below 3.5, so correction for lipid content was not necessary (Skinner et al., 2016). Since mathematical lipid correction techniques show inconsistent results for invertebrates (Kiljunen et al., 2006), lipid correction was not completed for zooplankton.

2.4 | Trophic position of perch

Trophic positions (TP) of individual perch were estimated relative to the lake-specific mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of zooplankton and submerged aquatic vegetation (*Elodia* spp. and *M. spicatum*) using the two end-member mixing model adapted from Post (2002). The proportion of carbon coming from the littoral food web for each perch is alpha (α), which is then used to estimate the trophic position of the perch relative to the $\delta^{15}\text{N}$ values of the pelagic and littoral baselines, the baselines' trophic positions, and the mean trophic discrimination

factor of nitrogen (3.4) (Minagawa & Wada, 1984). Littoral and pelagic baselines occupied different trophic positions (assumed to be 1 for submerged macrophytes and 2 for zooplankton), so we added 3.4 to the $\delta^{15}\text{N}$ value of the littoral baseline so that perch trophic position could be estimated relative to two baselines of the same trophic position.

$$\alpha = \frac{\delta^{13}\text{C}_{\text{perch}} - \delta^{13}\text{C}_{\text{pelagic}}}{\delta^{13}\text{C}_{\text{littoral}} - \delta^{13}\text{C}_{\text{pelagic}}}$$

$$\text{TP} = 2 + \frac{(\delta^{15}\text{N}_{\text{perch}} - ((\delta^{15}\text{N}_{\text{littoral}} + 3.4) \times \alpha + \delta^{15}\text{N}_{\text{pelagic}} \times (1 - \alpha)))}{3.4}$$

The value of α is constrained to a range between 0 and 1, requiring mean pelagic baseline $\delta^{13}\text{C}$ values to be below each perch $\delta^{13}\text{C}$ value and mean littoral baseline $\delta^{13}\text{C}$ to be higher. The mean pelagic baseline $\delta^{13}\text{C}$ value in Saalsdorf was initially slightly higher than several of the perch individuals (Figure 2). We, therefore, removed two zooplankton samples with high $\delta^{13}\text{C}$ measurements to prevent impossible values of α , i.e., a proportion of littoral carbon in the perch's diet that was less than zero. After this removal, all perch $\delta^{13}\text{C}$ values in the seven analysed lakes were bounded by their littoral and pelagic baselines.

Twelve linear mixed effects models (LMMs) predicting individual perch trophic position from natural log transformed total length (ln TL), and each of 12 lake characteristics were compared to rank the effects of lake morphology, proportion of shallow-water habitat, productivity, littoral structure, and fish community biomass metrics on perch trophic position (Table 1). Interaction effects between lake characteristics and ln TL were tested for differences in the rate of change in trophic position of increasingly large perch under different environmental conditions. Because of the limited number of unique lakes, only one lake characteristic could be included in each model. We, therefore, compared the fit of a "null" model that included only the main effect of ln TL on trophic position (TP) with 12 alternative models containing the main effects of the ln TL of perch individual i , one characteristic (char) of lake j , and their interaction. We compared model fit using Akaike information criterion corrected for small sample sizes (AICc) and Akaike weight, where the threshold for selecting a better fitting model was a ΔAICc of at least 2 (Burnham & Anderson, 2002). Each model included random intercepts for each lake, γ_j , and assumed that unexplained variation in trophic position, ε_{ij} , for each perch at each lake was normally distributed about the mean predicted trophic position.

Null model:

$$\text{Trophic position}_{ij} = \beta_0 + \beta_1 \ln(\text{Total length})_{ij} + \gamma_j + \varepsilon_{ij}$$

Alternative models:

$$\text{Trophic position}_{ij} = \beta_0 + \beta_1 \ln(\text{Total length})_{ij} + \beta_2 \text{Lake char}_j + \beta_3 \ln(\text{Total length})_{ij} * \text{Lake char}_j + \gamma_j + \varepsilon_{ij}$$

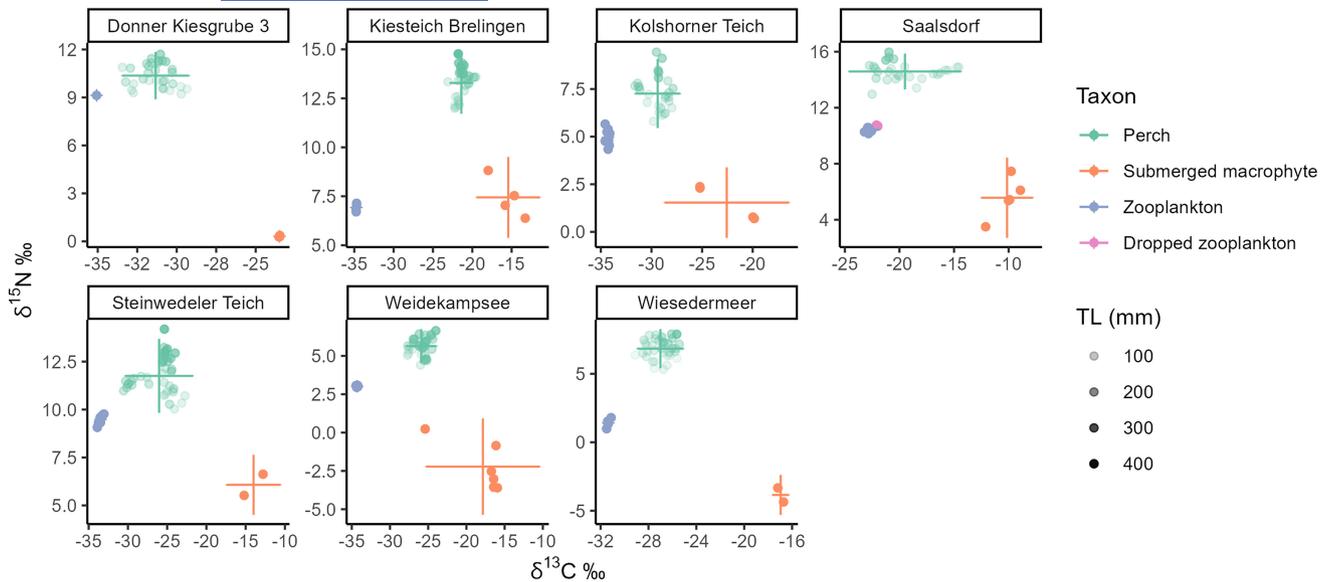


FIGURE 2 Stable isotope ratios for sampled perch, submerged macrophytes (littoral baselines), and zooplankton (pelagic baselines) in seven lakes. Note that points indicating the stable isotope values for larger perch have a higher opacity than those of smaller perch. Points coloured pink from Saalsdorf (Dropped zooplankton) indicate 2 zooplankton samples that were removed from the analysis to allow calculation of perch trophic positions.

LMMs were fit using the lme4 R package (Bates et al., 2015, p. 4). To assist model convergence, all lake characteristics were normalised (i.e. centered at 0 and scaled to an SD of 1). Significance of model coefficients was evaluated with log likelihood ratio testing of nested models. AICc, Akaike weights and marginal and conditional r^2 values were calculated using the MuMIn package (Bartoń, 2020).

2.5 | Sensitivity analysis

Our stable isotope analysis used point estimates of baseline trophic position and trophic discrimination factor of nitrogen that are actually associated with significant uncertainty. We, therefore, investigated the sensitivity of our statistical modelling results to lake-specific variations in (1) pelagic baseline trophic position and (2) nitrogen trophic discrimination factor.

We assumed that our bulk zooplankton samples had a trophic position of 2. However, predatory zooplankton, which would have an expected trophic position of 3, may have also been present in our samples. The difference in $\delta^{15}\text{N}$ values between pelagic zooplankton and littoral submerged vegetation suggests that several lakes' zooplankton samples occupied a higher trophic level than 2. We, therefore, first tested the sensitivity of our best fit model to differences among lakes in the trophic position of zooplankton as a pelagic baseline. We completed 100 iterations of the linear mixed effects model containing the predictors that were the best fit to perch trophic positions in the original analysis. In each iteration, we drew zooplankton samples' assumed trophic position (Zoop TP) for each lake from a uniform distribution between 2 and 3. We then estimated each perch individual's trophic position within each iteration. The

proportion of carbon derived from the littoral food web, α , was calculated the same way as in the main analysis. Trophic position (TP) of perch was estimated relative to the $\delta^{15}\text{N}$ values of the littoral and pelagic baselines. Because the littoral baseline was a primary producer, we adjusted the littoral baseline $\delta^{15}\text{N}$ values upwards by the trophic discrimination factor of 3.4 multiplied by the difference in trophic positions between the pelagic and littoral baselines in each lake in each iteration.

$$\text{TP} = \text{Zoop TP} + \frac{(\delta^{15}\text{N}_{\text{perch}} - ((\delta^{15}\text{N}_{\text{littoral}} + 3.4 * (\text{Zoop TP} - 1)) \times \alpha + \delta^{15}\text{N}_{\text{pelagic}} \times (1 - \alpha)))}{3.4}$$

To test the effect of different lake-specific trophic discrimination factors (TDF) for ^{15}N , we generated 100 iterations of new trophic position estimates for each lake. For each of these iterations, we drew a TDF value from a uniform distribution between 2 and 5. This range was selected to encompass the range in TDF values reported among carnivorous fish while also accounting for the greater uncertainty in trophic position estimates associated with averaging TDF values across relatively few food chain links (Vander Zanden & Rasmussen, 2001). Using these alternative TDF values for each lake, we produced new estimates of trophic position according to the following formula:

$$\text{TP} = 2 + \frac{(\delta^{15}\text{N}_{\text{perch}} - ((\delta^{15}\text{N}_{\text{littoral}} + \text{TDF}) \times \alpha + \delta^{15}\text{N}_{\text{pelagic}} \times (1 - \alpha)))}{\text{TDF}}$$

Then, for the linear mixed effects model that was selected as the best fit in the original analysis, we fit 100 iterations of the model to these new estimates of trophic position and compared our model output to the original coefficient estimates.

3 | RESULTS

The surveyed gravel pit lakes were oligo- to mesotrophic, with chlorophyll *a* concentrations ranging from 3 µg/L in Weidekampsee to 14.95 µg/L in Saalsdorf and corresponding variations in total phosphorus and Secchi depth (Table 1). Lakes were on average small, but they varied in depth and extent of shallow-water habitat. Lake size varied between 1 and 10 ha, and the maximum depth ranged from 4.3 to 16.1 m. The shoreline development factor varied from a nearly circular 1.2 for the gravel pit lake Donner Kiesgrube 3 to 2.2 for Kiesteich Brelingen. Coverage by emergent and submerged macrophytes ranged from 2% coverage in Saalsdorf to 73% coverage in Weidekampsee. CWS density ranged from 0.01 to 0.09 pieces per m². Proportion shallow-water habitat ranged from less than 20% in the case of Saalsdorf to over 70% in the case of Weidekampsee. Lakes also showed substantial variation in their degree of interspecific competition, intraspecific competition, and predation. Relative metabolic biomass of cyprinid competitors (length² interspecific) differed by 3531 mm²/m² between the lakes with lowest (Kolshorner Teich) and highest (Kiesteich Brelingen) metabolic biomass. The lake with the highest relative metabolic biomass of small (<120 mm) perch (Kiesteich Brelingen) differed from the lowest intraspecific competition lake (Weidekampsee) by 3944 mm²/m². The greatest variation was found in relative metabolic biomass of predators, with a difference of 6461 mm²/m² between the lowest (Saalsdorf) and highest (Kiesteich Brelingen) lakes.

Larger perch tended to have higher $\delta^{15}\text{N}$ values, as expected for a species that tends to shift towards piscivory as they grow

(Figure 2). This pattern was more evident in some lakes than others. For example, a more distinct shift in $\delta^{15}\text{N}$ among larger perch was evident in Donner Kiesgrube 3 and Kiesteich Brelingen than in Weidekampsee. Perch populations varied in their mean trophic position and their change in trophic position with length between lakes (Figure 3). Perch in Wiesedermeer had the highest average trophic position across all total lengths. Perch in Steinwedeler Teich, in contrast, had the lowest trophic position at small sizes but showed the greatest increase in trophic position as they grew. Saalsdorf and Weidekampsee perch populations showed the least positive change in trophic position, with both small and large perch occupying moderate trophic positions.

3.1 | Model selection and estimates

The model that predicted trophic position from ln TL and proportion shallow-water habitat emerged as the best fitting model with 90.7% of the Akaike weight (Table 2). This model estimated that an increase of 10% in total length was associated with an increase in trophic position of 0.04 ($\chi^2 = 168.4$, $p < .0001$; Table 3). Proportion of shallow habitat did not significantly affect mean trophic position of perch, but we found a significant negative interaction effect of ln TL and proportion shallow habitat, meaning that trophic position had a less positive relationship with body size in lakes with a greater proportion of shallow waters ($\chi^2 = 17.10$, $p < .0001$). Perch size and proportion shallow habitat explained 17% of the variation in trophic position, and random intercepts by lake explained an

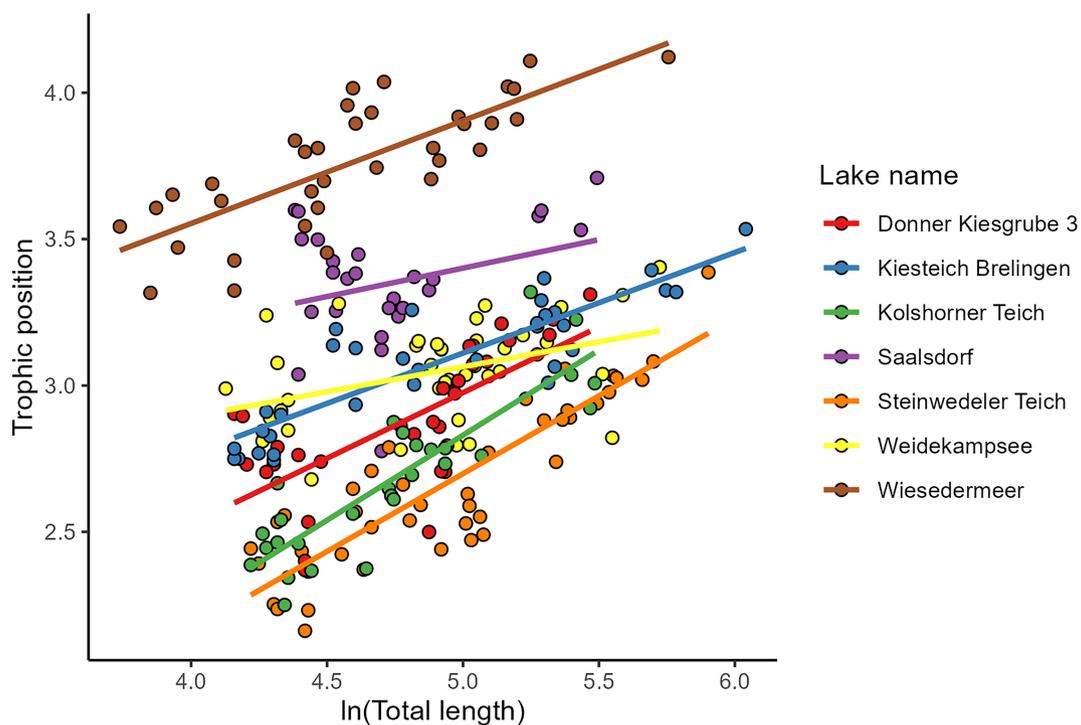


FIGURE 3 Trophic position of perch across natural log transformed total lengths (mm) as estimated by two end-member mixing models at seven lakes. Linear model fits summarise differences in trajectory of these ontogenetic niche shifts among perch populations in different lakes.

Model	Log likelihood	AICc	Δ AICc	Weight
TP ~ ln TL*Prop shallow water	86.6	-160.79	0	0.907
TP ~ ln TL*Max depth	84.2	-155.96	4.83	0.081
TP ~ ln TL*Prop macrophyte	81.5	-150.72	10.07	0.006
TP ~ ln TL*Length ² Interspecific	80.1	-147.90	12.89	0.001
TP ~ ln TL	78.0	-147.78	13.01	0.001
TP ~ ln TL*CWS density	80.0	-147.55	13.24	0.001
TP ~ ln TL*Lake area	79.2	-146.09	14.7	0.001
TP ~ ln TL*Secchi depth	79.0	-145.70	15.09	0
TP ~ ln TL*Mean Chl a	78.6	-144.75	16.04	0
TP ~ ln TL*Length ² Predators	78.6	-144.75	16.04	0
TP ~ ln TL*Length ² Intraspecific	78.2	-143.98	16.81	0
TP ~ ln TL*SDF	79.0	-143.85	16.94	0
TP ~ ln TL*Mean TP	78.1	-143.82	16.97	0

Note: All lake predictors have been normalised, with a mean of 0 and SD of 1. The model in bold is the likely best fit based on Akaike weight. CWS refers to coarse woody structure, SDF to shoreline development factor, and Mean TP to mean total phosphorus. Length² is the sum of length squared, an index of metabolic biomass.

TABLE 3 Model parameter estimates for the model predicting perch trophic position (TP) from natural log transformed total length (ln TL), the proportion of the lake surface in shallow-water habitat, and their interaction.

Parameter	Coefficient estimate (SE)	Chi squ	p value
Intercept	1.18 (0.19)		
ln TL	0.39 (0.02)	168.35	<.0001
Prop shallow water	0.55 (0.19)	0.11	.74
ln TL*Prop shallow water	-0.10 (0.02)	17.10	<.0001
SD of lake random intercept	0.39		
Conditional r^2	0.89		
Marginal r^2	0.17		

Note: Bold coefficients indicate significance at an alpha of .05.

additional 72% of the variation in trophic position. The remaining 11% of variation in trophic position was unexplained residual variance. In lakes with more shallow-water habitat, trophic position of small perch was higher than perch in more pelagic lakes. Trophic position in shallower lakes did not increase as much as perch grew, so these populations reached on average a lower maximum trophic position at larger sizes than would be expected in deeper lakes (Figure 4).

Among models that were not selected as the best fit to the data, ln TL was always a strong positive predictor of trophic position (Table S1). In the second-best fit model with 8.1% of the Akaike weight, the interaction between ln TL and maximum depth was positive, supporting the conclusion from the best-fit model that lake depth was the primary predictor of perch foraging niche among these lakes. The remaining lake characteristics were not relevant predictors of perch trophic niche in these lakes.

TABLE 2 All candidate models explaining perch change in trophic position (TP) with natural log-transformed total length (ln TL).

3.2 | Sensitivity analysis

After fitting the best fit model to each iteration of the data with different trophic position values for the zooplankton pelagic baseline, we found very little variation in the interaction effect of ln TL and proportion shallow-water habitat. The effect size of the interaction effect was slightly more negative than the results of the original model with a mean value of -0.13 compared to the original value of -0.10 (Figure A1 in Appendix A). Variation among lakes in ¹⁵N trophic discrimination factor had a stronger effect on this interaction effect. The sign of the interaction effect between ln TL and proportion shallow-water habitat was always negative (Figure A2 in Appendix A), but the coefficient was only significant in 91 out of 100 iterations of the sensitivity analysis. The effect of shallow-water habitat on perch trophic niche is therefore somewhat sensitive to assumptions about variation in trophic discrimination factor.

4 | DISCUSSION

We found that the proportion of shallow-water habitat, not habitat complexity, best predicted differences in perch populations' ontogenetic niche shifts between the seven lakes. The proportional of shallow water had greater predictive power than any individual habitat structure (e.g., degree of vegetation or coarse woody habitat), perhaps because it aggregated many smaller effects of individual habitat types that are typically elevated in shallow water. Small perch in lakes with more shallow-water habitat occupied higher trophic levels than small perch in lakes with more deep-water habitat, suggesting that young perch in deeper lakes relied more on zooplankton than on benthic macroinvertebrates. However, larger perch in shallow lakes achieved a lower trophic position on average than those in deeper lakes, suggesting that shallow-water perch populations continued

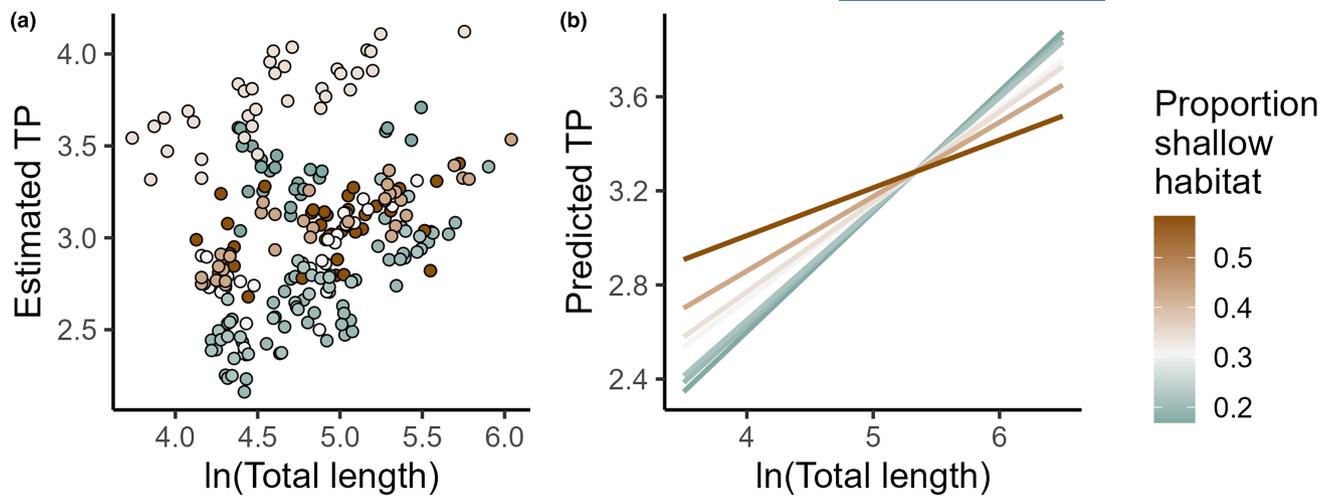


FIGURE 4 Estimates of perch trophic position (TP) versus natural log transformed total length (mm) (a) and marginal effects of the model predicting trophic position from ln TL across a range of proportions of shallow-water habitat represented in the data (b). Perch in lakes with less shallow-water habitat tended to have a lower TP at smaller body sizes, and TP increased more rapidly and reached a higher maximum value with increased body size than perch in shallower lakes.

to consume lower trophic level benthic macroinvertebrates as a major component of their diet as they grew while perch in deeper lakes transitioned to a greater degree of piscivory. Maximum depth of gravel pit lakes was a distant second-best predictor of this difference among perch populations. Abundance of littoral structures such as macrophytes and coarse woody structure, however, were not selected as important predictors of perch trophic position, suggesting that habitat heterogeneity, and specifically heterogeneity in lake depth, was driving the differences in perch foraging niche.

Interpretation of these results is limited to the trajectory of change in trophic position with increasing total length rather than the absolute or mean trophic position of perch populations. Our individual estimates of perch trophic position may be biased because of seasonal changes in carbon and nitrogen stable isotope ratios of zooplankton. Although stable isotope ratios of submerged vegetation show little seasonal variation (Syväranta et al., 2006), zooplankton $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values within lakes have been demonstrated to show seasonal trends (Syväranta et al., 2006; Yoshioka et al., 1994). Because fish muscle tissue integrates carbon and nitrogen from the previous several months of feeding, the stable isotope ratios of the littoral and pelagic baselines that were collected in September and October were most likely different from those of the basal resources integrated into perch muscle tissue in the months prior to sampling. The bias in trophic position estimates may have varied depending on fish size because smaller, fast-growing fish tend to exhibit higher turnover rates for carbon and nitrogen in their muscle tissue (Thomas & Crowther, 2015; Weidel et al., 2011). Larger perch, therefore, integrated zooplankton carbon and nitrogen from earlier in the summer compared to smaller perch. If zooplankton $\delta^{15}\text{N}$ values increased throughout the summer as demonstrated by Syväranta et al. (2006), the trophic position estimates of smaller perch may have been negatively biased. This potential bias would have influenced the slope of the relationship between trophic position and log transformed total

length within each lake, but would not, to our knowledge, influence the correlation of this slope with environmental characteristics between lakes. If, however, shallower lakes in our study also tended to be warmer, the additional increase of carbon and nitrogen turnover caused by warmer water in shallower lakes may have confounded the relationship between the trajectory of ontogenetic niche shifts in perch and the effects of water depth. When the surface temperature of the study lakes was monitored in 2017 as detailed in Höhne et al. (2020), very little variation in mean daily temperature between lakes was detected. When we compared the mean daily surface temperatures of Saalsdorf and Weidekampsee (i.e. the lakes with the least and greatest proportion of shallow-water habitat, respectively) the maximum difference in temperature was 1.84°C in early April, 2017 (Figure S2). The effect size of temperature on stable isotope turnover in animal tissue has also been demonstrated to be small (Vander Zanden et al., 2015). We, therefore, do not believe that our observations of the trajectory of perch populations' ontogenetic niche shifts were confounded by differences in water temperature among study lakes.

In the lakes we sampled, the classic perch ontogenetic niche shift, where small perch consume pelagic zooplankton before transitioning to benthivory and then piscivory (Allen, 1935), probably relied on the availability of sufficient pelagic habitat. Larger and deeper lakes with more heterogeneity in depth are associated with greater biomass of large fishes (Holmgren & Appelberg, 2000), including perch (Blindow et al., 1993; Persson et al., 1991), most likely because the perch can exploit pelagic prey more efficiently than prey that refuges in littoral habitat (Eklöv & Diehl, 1994). Similarly, among the full set of gravel pit lakes that we sampled, habitat heterogeneity, including shoreline development factor and maximum depth, were important predictors of perch growth (Höhne et al., 2020), revealing that large-sized perch are more likely to develop in deeper mesotrophic lakes. The reduced mean trophic position of large perch in gravel pit

lakes with more shallow-water habitat suggests that reduced piscivory in shallower lakes may be a mechanism driving a reduction in growth rates as perch feed longer on abundant macroinvertebrates. Prey fish in shallower lakes may have also been better at evading predation by large perch (Eklöv & Persson, 1996) further reducing both growth rates and trophic position of large perch.

That heterogeneity in lake depth, rather than littoral complexity, was the most closely associated lake characteristic with changes in perch trophic niche was initially unexpected. A greater abundance of submerged vegetation was expected to increase the abundance and diversity of benthic macroinvertebrates (Matias et al., 2010), stabilise macroinvertebrate populations in the presence of predation (Diehl, 1993), and potentially improve recruitment of piscivorous perch (Hargeby et al., 2005). Among the models that were not selected, the significant negative effect of macrophyte cover on changes in perch trophic position with increased length (Table S1) was most likely driven by differences in abundance of shallow-water habitat rather than the three-dimensional habitat complexity provided by vegetation. Kahl and Radke (2006) have previously outlined how water depth is a major structuring factor in the vertical dimension that reduces habitat overlap of roach and juvenile perch. Lake depth may, therefore, support perch survival under high levels of competition and later support the transition to piscivory through availability of open waters for cannibalism and interspecific predation (Eklöv & Diehl, 1994). The direct relationship of perch ontogenetic niche shifts to depth heterogeneity rather than structural complexity suggests that the change in foraging niche was driven by a lack of pelagic resources (i.e. zooplankton and pelagic forage fish) in shallow lakes rather than an abundance of littoral benthic macroinvertebrates.

The increased consumption of macroinvertebrates by perch in shallow lakes may also have been related to higher degrees of interspecific competition for zooplankton in shallow but structurally simple lakes. Shallower lakes tend to support higher populations of zooplanktivores such as roach (Mehner et al., 2005), resulting in perch populations experiencing higher inter- and intraspecific competition as smaller and larger age classes of perch are forced into competition for benthic macroinvertebrates (Persson, 1987a, 1987b). Littoral structure is expected to mediate this effect by providing three-dimensional foraging habitat where perch are competitively superior foragers (Diehl, 1988; Persson & Eklöv, 1995; Winfield, 1986). However, the proportion of shallow-water habitat, rather than interspecific competition or productivity, was the best predictor of the trajectory of perch ontogenetic niche shifts. Although interspecific competition, productivity, and littoral structure may have had additional effects on perch foraging niche in these lakes, our analysis did not have sufficient degrees of freedom to investigate these potential interactions.

Our limited number of study lakes additionally raises the possibility that our model selection result was a statistical artefact. The measurements of lakes' proportions of shallow-water habitat may have integrated many small effects on perch ecology associated with littoral zones. Proportion of lake habitat that is shallower

than 3 m would remain constant over time, but other characteristics associated with littoral habitat, such as coverage by vegetation and density of interspecific competitors, would show seasonal and annual variation. Although proportion of shallow-water habitat emerged as the best predictor of perch trophic position among these lakes, temporally varying characteristics, therefore, may have influenced perch trophic niche, with their aggregate effect evident in the response of perch trophic position to proportion of shallow-water habitat. The trajectory of perch ontogenetic niche shifts within each lake was also strongly influenced by the estimated trophic position of a small number of large individuals (Figure S1, Figure 3). Because only a small number of lakes could be included in this analysis, chance omission of large individuals (i.e. large individuals being present but not sampled in apparently size-truncated lakes such as Donner Kiesgrube 3) may have had an outsized effect on our final result compared to that of a study analysing a greater number of water bodies.

Another unexpected result was the lack of a response of perch trophic niche to predator abundance (Table S1). Predator relative metabolic biomass was the strongest predictor of perch growth rates among the full set of 13 gravel pit lakes from which the seven lakes in this analysis were selected (Höhne et al., 2020). This effect, however, may stem from selective predation on slower growing perch, leaving behind the faster growing conspecifics rather than being caused by bottom-up effect of increased prey availability. Many lake ecosystems are bottom-up controlled, with limited top-down impact of fish predators on fish prey in German lakes (Mehner, 2010). The fact that all lakes likely hosted cyprinid and perch populations at carrying capacity probably reduced the predictive effect of prey and predator biomass to zero. To isolate the effect of competition and predation, exploitation experiments may be necessary.

Our study examined a relatively small sample size of small, structurally simple gravel pit lakes, and so had several additional limitations. Littoral structures concentrate food sources for fish communities and provide refuges and spawning habitat (Radinger et al., 2023), but the effects on fish populations of adding woody structure to lakes vary depending on lake characteristics (Maday et al., 2023; Sass et al., 2022). Littoral structure may, therefore, have more influence on perch trophic niche in larger or more complex lakes. Macrophyte biomass has also been demonstrated to increase food chain length in small, shallow lakes (Ziegler et al., 2015). Unfortunately, our limited number of study lakes prevented us from investigating the effects of structural complexity while controlling for the effects of depth heterogeneity. Observed variation in mean trophic position among perch populations may be the result of the previously described temporal mismatch between the sampled baselines and the baselines that were actually integrated into perch muscle tissue over the several months pre-sampling. Alternatively, these variations could be associated with our use of point estimates of baseline trophic position and $\delta^{15}\text{N}$ trophic discrimination factor. In our sensitivity analysis, we found that variation in the assumed trophic position of zooplankton as a pelagic baseline had no effect on our model results (Appendix A) However, model results were

somewhat more sensitive to variations in $\delta^{15}\text{N}$ trophic discrimination factor (TDF). Although TDF has been demonstrated to be relatively consistent among carnivorous fish (Caut et al., 2009; Sweeting et al., 2007), greater variation in TDF among herbivorous consumers, such as the benthic macroinvertebrates linking perch to our submerged macrophyte littoral baseline, would introduce error into estimates of trophic position (Vander Zanden & Rasmussen, 2001). The most uncertainty in trophic position estimates would therefore be associated with highly littoral perch. Perch littoral reliance, summarised as alpha in our analysis, showed considerable variation within and between the seven gravel pit lakes (Figure S3). However, mean alpha values for each population, which were not affected by uncertainty in TDF, were positively associated with the proportion of shallow-water habitat in each lake (Figure S4), further supporting our conclusion that larger perch reached lower trophic levels because of increased consumption of littoral macroinvertebrates.

5 | CONCLUSIONS

Large-bodied perch, which are usually piscivorous, have been described as having a structuring role in lake ecosystems (Persson et al., 2003) and are desired targets of anglers (Beardmore et al., 2014). Our work supports the conclusion that greater water depth is associated with greater recruitment of piscivorous perch (e.g. Holmgren & Appelberg, 2000), and that the impact of lake morphology may override the effects of specific littoral habitat structures in driving piscivory. Although creating shallow-water habitat and structural complexity may increase fish abundance by providing foraging and refuge habitat for fish communities (Radinger et al., 2023), these activities will not necessarily increase the number of large, piscivorous perch.

AUTHOR CONTRIBUTIONS

AT—Investigation, Methodology, Formal analysis, Visualisation, Writing—Original draft preparation and review and editing. TM—Methodology, Supervision, Writing—Review and editing. TK—Conceptualization, Resources, Writing—Review and editing. SM—Investigation, Data curation, Visualisation, Writing—Review and editing. RN—Investigation, Data curation, Writing—Review and editing. RA—Conceptualization, Funding Acquisition, Project administration, Supervision, Writing—Review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to report.

DATA AVAILABILITY STATEMENT

Data sets from this study are openly available in the repository "Stable isotope data and analysis for perch populations in German gravel pit lakes" at <https://doi.org/10.6084/m9.figshare.13000103.v5> (Trudeau, 2020).

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SUPPORTING INFORMATION

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APPENDIX A

Sensitivity analysis

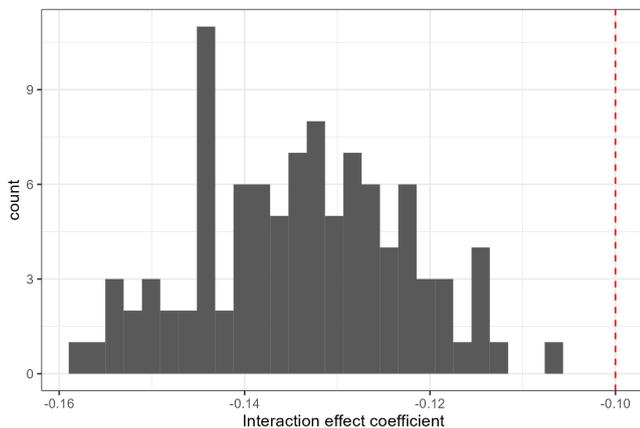


FIGURE A1 Coefficient estimates for the interaction of natural log transformed total length and proportion shallow water area when predicting perch trophic position. Pelagic baseline trophic position was randomly drawn from a uniform distribution between 2 and 3, resulting in different values for individual perch trophic position estimates, but similar relationships between lake habitat, perch size, and trophic position. The red dashed line indicates the estimate of the interaction effect in the main analysis, where a zooplankton trophic position of 2 was assumed.

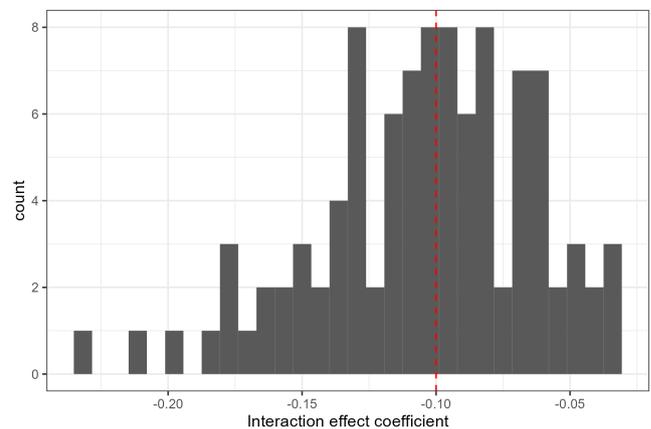


FIGURE A2 Coefficient estimates for the interaction of natural log transformed total length and proportion shallow water area when predicting perch trophic position. Trophic discrimination factor for each lake was randomly drawn from a uniform distribution between 2 and 5. Variation in TDF had a stronger effect on interaction effect estimates than did variation in pelagic baseline trophic position. The red dashed line indicates the estimated interaction effect in the main analysis, where we assumed a trophic discrimination factor of 3.4.