








ORIGINAL ARTICLE

Environmental determinants of perch (*Perca fluviatilis*) growth in gravel pit lakes and the relative performance of simple versus complex ecological predictors

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Abstract

Growth of fish is an important contributor to individual fitness as well as fish production. Explaining and predicting growth variation across populations is thus important from fundamental and applied perspectives, which requires knowledge about the ecological factors involved in shaping growth. To that end, we estimated environment-dependent von Bertalanffy growth models for 13 gravel pit lake populations of Eurasian perch (*Perca fluviatilis*) from north-western Germany. To identify the main drivers of perch growth, we evaluated the performance of 16 different biotic or abiotic lake variables in explaining growth variation among lakes. In addition, we compared growth predictions from the best-performing model incorporating “complex” variables that require intensive sampling effort, with a model using only “simple”, easily measurable lake variables (e.g. shoreline development factor). The derivation of a simple model aimed at future applications in typically data-poor inland fisheries, predicting expected growth potential from easily measurable lake variables. A model combining metabolic biomass of predators, maximum depth and shoreline development factor performed best in predicting perch growth variation across gravel pits. All three parameters in this model were positively related to perch growth. The best-performing simple model consisted only of the shoreline development factor. Length-at-age predictions from both models were largely identical, highlighting the utility of shoreline development factor in approximating growth potential of perch in gravel pits similar to our study lakes. Our results can be used to inform fisheries management and restoration efforts at existing or newly excavated gravel pit lakes.

KEYWORDS

Bayesian hierarchical model, environmental effects on fish growth, Eurasian Perch, gravel pit lakes, predation, shoreline development

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1 | INTRODUCTION

Identifying and understanding biotic and abiotic drivers of fish growth is of fundamental importance in ecology and is also relevant to inform effective conservation and fisheries management (Beverton & Holt, 1957; Campana & Thorrold, 2001). In the presence of typically gape-limited predators, fast growth can reduce natural mortality and is thus a key fitness component in fishes (Werner, Gilliam, Hall, & Mittelbach, 1983). Fast growth is also crucial for fish production and yield in fisheries (Beverton & Holt, 1957).

The growth of fishes is a function of consumption and metabolism, two processes that are prone to biotic and abiotic influences related to thermal environment, availability of food and presence of predators (van Poorten & Walters, 2016). The local biotic and abiotic conditions vary greatly across inland lakes and may account for a significant proportion of variation in fish growth within ecoregions (Wagner et al., 2007). A good understanding of the relative importance of different ecological factors impacting consumption and metabolism is necessary to explain and predict variation in growth across populations. Knowledge about the environmental dependencies of growth for fishes can in turn help identifying potentially fast- or slow-growing populations and inform fisheries management actions, such as the design of harvest restrictions (FAO, 2012).

We examined biotic and abiotic influences on growth patterns of Eurasian perch (*Perca fluviatilis*) in artificially created gravel pit lakes in Germany. Gravel pits are formed by the mining of sand, gravel and other mineral resources; they are a dominant lake type in many agricultural and urbanised landscapes (Søndergaard, Lauridsen, Johansson, & Jeppesen, 2018; Zhao, Grenouillet, Pool, Tudesque, & Cucherousset, 2016) and provide important habitats for recreational fisheries (Meyerhoff, Klefoth, & Arlinghaus, 2019). Relative to natural lakes, gravel pits tend to be fairly steeply sloped, are often mesotrophic (Søndergaard et al., 2018) and characterised by limitations in the availability of structured habitat in the littoral (Emmrich, Schällicke, Hühn, Lewin, & Arlinghaus, 2014). Fish ecological research in European gravel pit lakes is scarce (Matern et al., 2019; Søndergaard et al., 2018; Zhao, et al., 2016). Specifically, there is a lack of research on the environmental determinants of fish growth, including perch growth as a prime target of many inland fisheries in lakes (Heermann et al., 2013; Jacobsen, Berg, & Skov, 2004).

Perch fulfil key ecological roles in lakes, as they are often the dominant piscivore of the pelagic zone under mesotrophic conditions (Mehner, Diekmann, Brämick, & Lemcke, 2005; Persson, Diehl, Johansson, Andersson, & Hamrin, 1991) and can exert a large impact on lake food webs through predation (Persson et al., 2003). Perch typically undergo two ontogenetic diet shifts as they grow in length (Amundsen et al., 2003). In the larval stage, perch feed on zooplankton in the pelagic zone, before they move to the littoral zone within the first year of life, where they mainly feed on zooplankton and later on benthic invertebrates (Amundsen et al., 2003).

After a second ontogenetic niche shift, perch become piscivorous (Amundsen et al., 2003; Hjelm, Persson, & Christensen, 2000). The occurrence and timing of ontogenetic niche shifts depend on a number of environmental conditions, habitat availability, and degree of intraspecific and interspecific food competition (Hjelm et al., 2000; Persson & Greenberg, 1990). This ontogenetic complexity and its plasticity imply that growth of perch can be affected by a broad range of factors related to both abiotic and biotic drivers including density-dependent population feedback (Ylikarjula, Heino, & Dieckmann, 1999).

Biotic drivers are known to affect growth of perch via food availability, competition and predation (Holmgren & Appelberg, 2001; Persson & Greenberg, 1990; Persson et al., 2003). Increasing nutrient availability alters the amount, species composition and size structure of the prey base available to higher trophic levels, supporting food webs from the bottom-up (Ask et al., 2009). Lake eutrophication benefits growth and biomass of perch up to a maximum under mesotrophic conditions, whereupon further eutrophication usually has negative effects on perch production (Hartmann & Nümann, 1977; Persson et al., 1991). For a given nutrient level, the degree of interspecific competition limits the amount of food available to the individual perch, with implications for growth. In particular, higher densities of zooplanktivorous cyprinids, such as roach (*Rutilus rutilus*), can force juvenile perch to shift to macroinvertebrate feeding (too) early in life. This in turn can increase intercohort competition with older conspecifics and ultimately reduce individual growth rates (Hjelm et al., 2000; Persson & Greenberg, 1990). In the piscivorous stage, however, perch growth may profit from increased biomass of zooplanktivores serving as prey (Hjelm et al., 2000). Relatedly, the relevance of intraspecific competition in shaping perch growth has been documented for both juvenile (Byström & Garcia-Berthou, 1999) and adult stages (Arranz et al., 2015).

Accelerated growth has been observed for perch that switch diet to piscivory early in life, possibly even as age-0 fish (e.g. Urbatzka, Beeck, Van der Velde, & Borcharding, 2008). Yet, increasing predation pressure may negatively affect feeding activity and risk-taking of inferior, usually small-bodied juvenile perch (Magnhagen & Borcharding, 2008). These changes might depress growth of juveniles (Ahrens, Walters, & Christensen, 2012) with knock-on effects on adult growth if the switch to piscivory is delayed. Alternatively, greater predator biomasses might evolutionarily select for fast growth in juveniles, to outgrow gape-limited predators more rapidly (Biro, Post, & Abrahams, 2005). The presence of large cannibals in perch can also thin out juveniles, thereby releasing them from food competition and stunting, facilitating growth of the survivors (Persson et al., 2003). Thus, the top-down impacts of predation on growth of perch could both be negative or positive, depending on local conditions, justifying further research.

In addition to competition for food and predation, habitat structure also affects growth of perch. In particular, the density and quality of physical habitat such as macrophytes and dead wood are known to correlate with the amount and diversity of zoobenthic organisms, which are an important food source for young perch (e.g. Watkins,

Shireman, & Haller, 1983). Beside food provision, physical habitat can indirectly facilitate growth, as perch are known to be particularly efficient feeders in physical structures compared to cyprinid competitors, while sufficient refuge from predation is provided (Diehl, 1988; Hargeby, Blom, Blindow, & Andersson, 2005; Persson & Eklöv, 1995).

Among the abiotic drivers of growth, water temperature is one of the most broadly recognised factors that affects the development of all ectothermic animals via physiological and metabolic effects (Fry, 1971; Magnuson, Crowder, & Medvick, 1979) and through lower trophic level responses shaping prey availability and abundance (Yvon-Durocher, Jones, Trimmer, Woodward, & Montoya, 2010). A time series analysis from Lake Windermere (U.K.) has found that growth of Eurasian perch can be positively related to summer water temperature (Le Cren, 1958), yet more recent meta-analyses predict shrinking mean sizes of perch with further increases in temperature due to climate change (van Dorst et al., 2019; Ohlberger, Edeline, Vøllestad, Stenseth, & Claessen, 2011). In addition, water transparency, which is coupled to changing nutrient loads and temperature, has implications for feeding efficiency and resource utilisation of visual predators, such as perch, thereby affecting growth (Bartels, Hirsch, Svanbäck, & Eklöv, 2012; Diehl, 1988; van Dorst et al., 2019; Horppila et al., 2010; Jacobsen, Berg, Baktoft, Nilsson, & Skov, 2014).

Among the morphological factors, surface area, lake depth and shoreline length constitute indicators of resource and habitat heterogeneity and are positively correlated with the species richness of zooplankton (Dodson, 1992), macrophytes (Thomaz, Souza, & Bini, 2003), macroinvertebrates (Heino, 2000) and fish (Barbour & Brown, 1974; Eckmann, 1995). A high availability of diverse food sources and physical habitats may be of particular relevance for the "ontogenetic omnivore" perch that regularly moves among pelagic and littoral habitats and diets depending on local food competition (Persson, Byström, & Wahlström, 2000).

The objective of this study was to examine the biotic and abiotic correlates of perch growth specific to small gravel pit lakes with water areas below 20 ha. We computed nested (individuals within populations) von Bertalanffy growth models for 13 perch populations across Lower Saxony (Germany) and compared the performance of 16 different in-lake variables to explain the observed growth variation across lakes. To improve the application potential of the growth models to typically data-poor inland fisheries management, we specifically explored the relative performance of easily measurable predictors (e.g. lake depth or shoreline development factor). We asked whether the models with simple variables performed similarly in predicting growth variation of perch among lakes compared to more complex ecological predictors.

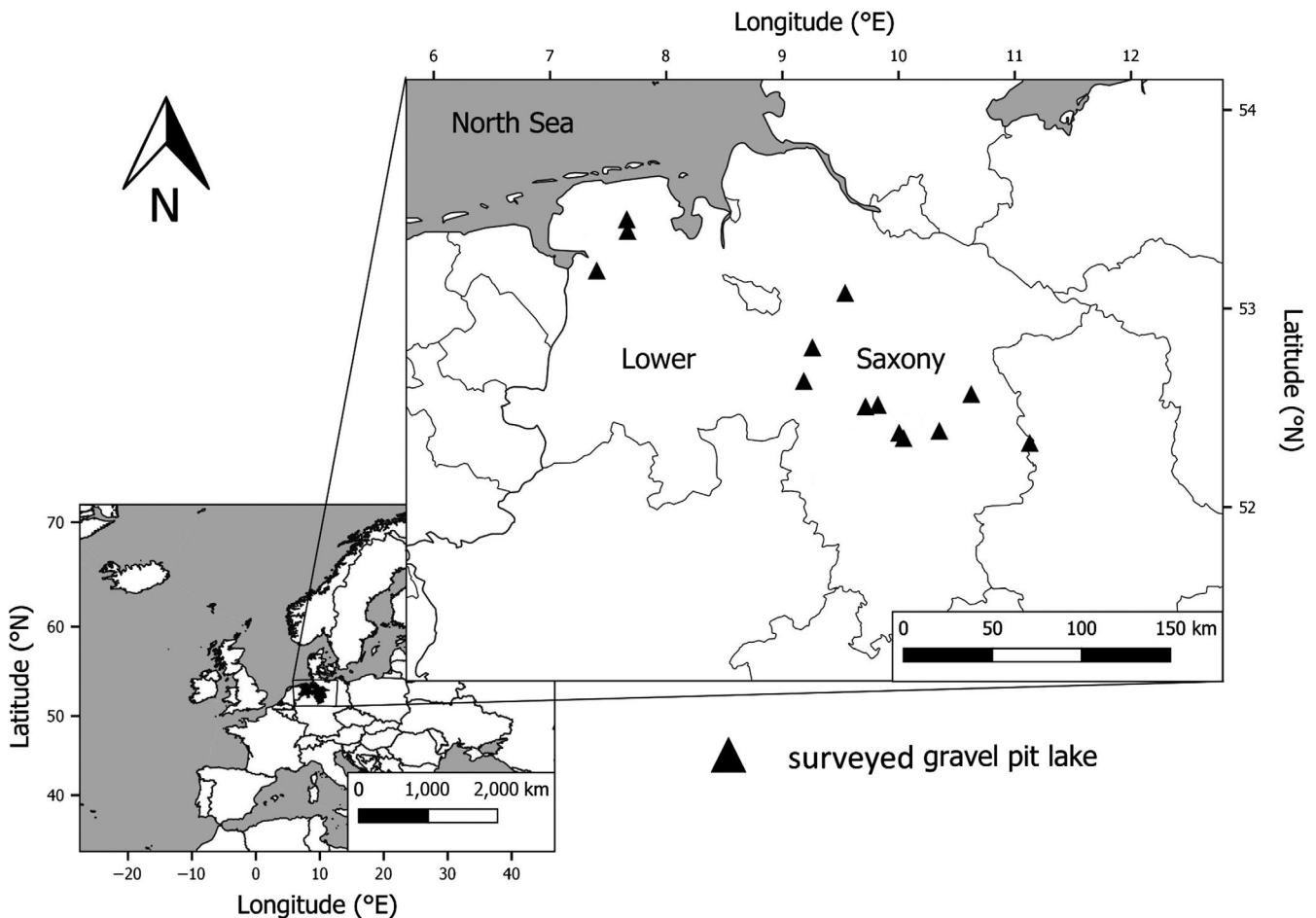


FIGURE 1 Location of surveyed gravel pit lakes ($N = 13$) in Lower Saxony, Germany (modified from Matern et al., 2019)

Our work addressed the following research questions:

1. Which biotic and abiotic environmental factors serve best in predicting growth variation of perch across gravel pit lakes in north-western Germany?
2. How well does a growth model consisting of just easily estimable environmental variables perform relative to models that additionally use complex ecological variables?

2 | MATERIALS AND METHODS

2.1 | Study lakes and collection of size-at-age data

Our fish sampling complied with fisheries law in Lower Saxony and included permission for electrofishing (# 34.4-65434-IV). Fish

communities and environmental descriptors of 13 gravel pit lakes (<20 ha) located in the lowlands of Lower Saxony, north-western Germany, were surveyed in autumn 2016 (Figure 1; Tables 1 and 2). Fish community surveys used benthic multi-mesh gillnets and daytime electrofishing, both conducted in autumn when epilimnion temperature was above 15°C. We used an adapted CEN (2015) standard for benthic multi-mesh gillnets. As the CEN (2015) standard provides depth-stratified gillnet numbers only for lakes of 20 ha or larger, and because all our study lakes were smaller than this threshold, we adjusted the gillnet number to the lake size to achieve a similar gillnet pressure in all gravel pit lakes. The largest lake (Meitzer See, 19.6 ha) was the designated reference lake, where 16 benthic gillnets were set as the CEN (2015) standard recommends for 20 ha lakes. The gillnet pressure of Meitzer See was calculated as the ratio of gillnets to lake size. Afterwards, this quotient was multiplied by the lake size of each (smaller) gravel

TABLE 1 Overview of sampled lake descriptors

Lake	Lake area (ha)	Mean depth (m)	Max. depth (m)	SDF	Mean Chlorophyll a (µg/l)	Mean Secchi depth (m)
Chodhemster Kolk	3.26	5.55	10.1	1.10	3.99 ± 1.86	1.8 ± 0.96
Collrunge	4.71	3.95	8.61	1.09	5.86 ± 1.84	2.7 ± 0.7
Donner Kiesgrube	0.97	3.32	5.16	1.19	10.86 ± 4.31	1.53 ± 0.55
Kiesteich Brelingen	9.36	3.21	8.71	1.85	5.93 ± 2.41	1.43 ± 0.25
Kolshorner Teich	4.75	6.38	16.1	1.09	5.81 ± 3.56	3.23 ± 1.42
Meitzer See	19.6	11.9	23.5	1.31	2.2 ± 0.32	4.5 ± 0.7
Pfütze	11.4	4.26	7.35	1.72	3.64 ± 1.54	3.23 ± 1.14
Plockhorst	15.1	3.18	8.19	1.6	25.31 ± 5.38	0.9 ± 0.36
Saalsdorf	9.03	5.33	9.21	1.28	13.59 ± 4.38	1.77 ± 0.84
Stedorfer Baggersee	2.12	1.67	2.81	1.2	10.93 ± 1.08	1.63 ± 0.55
Steinwedeler Teich	11	5.29	9.06	1.72	6.45 ± 3.67	2.7 ± 1.04
Weidekampsee	3.23	2.25	4.29	1.57	3.2 ± 0.54	3.93 ± 0.42
Wiesedermeer	3.27	3.73	9.23	1.67	6.93 ± 1.73	2.1 ± 0.89
	Mean TP (µg/L)	Macrophyte coverage (%)	CWS density (N/m ²)	Pelagic area (%)	Mean GDD (°C*day)	
Chodhemster Kolk	15.9 ± 3.5	22.9	0.01	73.6	1,531	
Collrunge	14.9 ± 1.1	45.4	0.035	67.3	1,807	
Donner Kiesgrube	47.3 ± 19.6	11.3	0.087	63.8	1,818	
Kiesteich Brelingen	34.3 ± 25.8	4.21	0.031	51.1	1,671	
Kolshorner Teich	13 ± 4.6	19	0.082	79.6	1,954	
Meitzer See	7 ± 3.6	5.22	0.061	91.2	1,616	
Pfütze	12.3 ± 0.6	62.9	0.049	67.2	1,913	
Plockhorst	45.3 ± 10	19.9	0.08	47.9	1,841	
Saalsdorf	22.7 ± 7.5	22.4	0.071	84.4	1,664	
Stedorfer Baggersee	31.3 ± 7.6	59.8	0.024	0	1,700	
Steinwedeler Teich	11.3 ± 4.2	16.7	0.029	82.5	1,820	
Weidekampsee	11.3 ± 3.2	72.7	0.026	41.7	1,837	
Wiesedermeer	19 ± 1	17.8	0.005	57.1	1,707	

Note: Mean ± Standard Deviation is given for variables with repeated measurements.

Abbreviations: CWS, coarse woody structure; GDD, growing degree-days; TP, total phosphorous; SDF, Shoreline development factor.

TABLE 2 Overview of sampled community descriptors

Lake	Length ² Perch (mm ² /m ² net)	Length ² Predators (mm ² /m ² net)	Length ² Intraspecific (mm ² /m ² net)	Length ² Interspecific (mm ² /m ² net)	Piscivory (MTL at age-2 and -3)
Chodhemster Kolk	2,746	1,768	1,377	508	3.51 ± 0.11
Collrunge	7,527	3,198	4,328	733	3.20 ± 0.26
Donner Kiesgrube	8,582	4,890	3,692	576	3.98 ± 0.17
Kiesteich Brelingen	11,348	8,000	4,292	3,829	3.96 ± 0.12
Kolshorner Teich	3,015	3,137	526	298	2.97 ± 0.39
Meitzer See	1,743	1,579	225	307	3.70 ± 0.13
Pfütze	6,218	3,057	3,161	0	3.71 ± 0.21
Plockhorst	6,631	7,080	2,685	1,057	3.50 ± 0.23
Saalsdorf	4,113	1,539	3,339	670	4.62 ± 0.18
Stedorfer Baggersee	7,717	3,273	4,444	358	3.46 ± 0.1
Steinwedeler Teich	7,463	6,465	1,038	534	2.63 ± 0.25
Weidekampsee	5,931	5,664	349	575	2.91 ± 0.44
Wiesedermeer	2,626	3,746	610	2,864	3.70 ± 0.14

Note: Standard deviation is given for Piscivory.

Abbreviation: MTL, Mean trophic level.

pit lake to define the number of gillnets to be set in each lake. The total number of benthic gillnets was then distributed according to the extension of the depth strata (0–2.9, 3–5.9, 6–11.9 and 12–19.9 m) as recommended in the CEN (2015) standard to guarantee an equal sampling effort per lake size. Gill nets were set following a depth-stratified random sample design (see CEN, 2015 and Matern et al., 2019 for details). Multi-mesh gillnets of 40 m length and 1.5 m height, with mesh sizes of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, 55, 70, 90, 110 and 135 mm (panel length of each mesh size was 2.5 m) were deployed once per lake for approximately 12 hr overnight in the benthic zone. After the nets were retrieved, littoral electrofishing was conducted along the entire shoreline of each lake from a boat using an 8 kW fuel-driven generator (EFKO Fischfanggeräte GmbH Leutkirch “FEG 8000”) and an anode diameter of 40 cm. The purpose of the electrofishing was to capture the smallest size classes representatively, which are often strictly littoral-bound and might thus not be fully vulnerable to the gill nets. We pooled all captured perch from both gears for ageing, as the combined use of two complementary gears reduces bias in ageing studies (Wilson et al., 2015). The total length of each fish (perch and other species) captured was measured to the nearest millimetre, and a subsample of perch was lethally sampled for ageing.

2.2 | Ageing

A maximum of ten individual perch per 20 mm length-class were sampled for the growth analysis. Opercular bones were chosen for age and growth determination, as these structures allow more reliable age estimation compared to other hard structures of perch (Baker & McComish, 1998; Le Cren, 1947). Opercula were removed from the

previously killed fish and prepared for reading following the procedure suggested by Le Cren (1947). One operculum was prepared and analysed for each individual and read by the first author. In addition, for all perch > 250 mm and within each lake for at least the five largest individuals, both opercula were prepared. In these fish, both opercula were analysed and radius/annuli measurements averaged. The rationale was to analyse growth of the (presumably) oldest individuals as accurately as possible, because these fish are usually less frequent in a population, but have a substantial impact when estimating the population growth function (Quist, Pegg, & DeVries, 2012).

To gather age and growth information, distances of annuli from the focus (located in the innermost part of the structure) and the total operculum radius were measured along a consistent axis aligned through the centermost part of the structure (Le Cren, 1947). The measurements were taken using a digital microscope and image analysis software (Quick Scope vision measurement device; QSPAK software; www.mitutoyo.co.jp/eng). Age-0 fish and individuals where the opercula showed no discernible annuli were excluded from the analysis. Moreover, the growth increment of the year-of-capture was omitted from growth analyses because this year was not completed.

The opercula size-at-age data did not exhibit the Rosa Lee phenomenon after an initial inspection following Duncan (1980). Thus, we used all operculum radius-at-age data of each fish, properly accounting for multiple measurements of individual fish in the statistical model fitting (see below).

2.3 | Biotic variables

Indicators of lake trophic status were measured as chlorophyll a and total phosphorous (TP) as described by Matern et al. (2019) for the same study lakes. Secchi-depth measurements represent

both trophic status and water transparency. As these measures are known to fluctuate across seasons, we averaged observations from spring, summer, and autumn 2017 to obtain measures of mean chlorophyll *a* and mean total phosphorous. Secchi-depth data additionally included observations from spring, summer, and autumn 2018.

The variables representing fish community were calculated as metabolic biomass because it has been suggested that raw catch per unit effort measures do not appropriately account for the disproportionately higher consumption by large individuals (Post, Parkinson, & Johnston, 1999; Walters & Post, 1993). Metabolic biomass was calculated as the sum of squared fish lengths per unit fishing effort of m² gillnet area (hereafter abbreviated as “length²”) using a stratified mean across depth strata while taking the depth strata extension of each lake into account (following CEN, 2015). Intraspecific competition measures comprised sum of length² per effort estimates of small perch < 120 mm total length to represent juvenile intraspecific competition (“Length² Intraspecific”) and length² of perch of all sizes to represent juvenile and adult intraspecific competition (“Length² Perch”). The metabolic biomass of nonperch, nonpredatory species < 120 mm represented interspecific juvenile competition (“Length² Interspecific”), because literature suggests that interspecific competition is most strongly affecting growth at this life stage (Persson & Greenberg, 1990). Typical competitor species such as roach are mostly zooplanktivorous at sizes below the chosen threshold of 120 mm (Hjelm et al., 2003). Predation pressure (“Length² Predators”) was represented by the length² estimate of potential predatory species (pike *Esox lucius* > 100 mm, zander *Sander lucioperca* > 100 mm and perch > 120 mm). These length thresholds were chosen to represent the onset of piscivory in the respective species following the meta-analysis by Mittelbach & Persson (1998). The contribution of each species to the pooled variables is given in Supporting Information S1. All fish biomass measures were derived using only gillnet catch data. Multi-mesh gill nets are a standard approach to assess lake biomass in Europe (CEN, 2015) and thus enable comparability with future studies. As an indicator of how early perch switch to piscivorous feeding in any of our study lakes, we calculated a piscivory index as the mean trophic level of age-2 and age-3 perch against a zooplankton baseline. This measure was derived from a previously conducted lake-specific stable isotope analysis of the same individuals that were also sampled for age and growth (Trudeau, 2018).

2.4 | Abiotic variables

Mean lake depth, maximum lake depth and the extension of pelagic zone (area with water depth > 3 m) were derived from bathymetric maps quantified for all lakes using echosounding (see Matern et al., 2019 for details). Geographical waypoints were taken along the shoreline by using open-source maps (<https://www.geoplaner.de>; last visit: 04.11.2019), and lake area and shoreline length were calculated using the software R 3.5.2 (R Core Team, 2018). A shoreline development factor was calculated as the ratio of a lake's shoreline length to the circumference of a circle of equal area to the lake

(Osgood, 2005). A higher shoreline development factor indexes a larger, more irregular shoreline length for a given lake size.

Macrophyte coverage (submergent and emergent) was estimated from snorkel surveys conducted between late June and late August 2016 on equidistant transects, using the protocol of Schaumburg et al. (2014) and then transformed into per cent coverage per lake as described in Nikolaus et al. (2019). Coarse woody structures (CWS) in the littoral were surveyed between mid-June and mid-July 2017 along equidistant transects of 10 m length and 4 m width perpendicular from the shore (or to a maximum of 3 m water depth). The number of coarse woody items found in these transects was summed over all transects and divided by the area that was covered by the transects to obtain a wood density index (further details in Nikolaus et al., 2019). Dead wood was categorised as coarse woody item if one of three criteria was true: bulk diameter > 5 cm, length > 50 cm, or at least secondary branching (as described in DeBoom & Wahl, 2013) was present.

As a measure of the temperature experienced by the perch, we calculated the cumulative growing degree-days (Neuheimer & Taggart, 2007) as derived from temperature logger data (Onset “HOBO Pendant Temp” dataloggers). Two loggers were fixed at 0.5 m water depth in each lake, usually on opposite shore sites of the lake. These loggers measured water temperature every two hours. First, daily degree-days were calculated as the integral of mean daily temperature above a base threshold of $T_0 = 10^\circ\text{C}$ (Chezik, Lester, & Venturelli, 2014). A T_0 of 10°C was chosen because it has been used in previous growth analyses in perch (Mooij, Lammens, & Van Densen, 1994). The daily values were then summed per year to yield the cumulative growing degree-days. Temperature data from August 2016–July 2018 were analysed, averaging repeated observations of daily degree-days across years.

2.5 | Modelling growth

Growth models were based on operculum radii-at-age instead of fish length-at-age data to reduce possible bias introduced through back-calculation of total length, where a joint intercept is derived from a regression of operculum radius on fish total length (Francis, 1990). This intercept is then applied to all fish, which reduces among-individual variance in backcalculated length-at-age in dimensions of the fish length. This issue is avoided by working in operculum length units. We fitted an integrated von Bertalanffy growth function to operculum radius-at-age data, as this model has been recognised to fit observed data of *Perca* spp. well (Chen, Jackson, & Harvey, 1992). We used pooled data from both gears (gillnetting and electrofishing) across all study lakes in a Bayesian hierarchical mixed-effects model. Length L at a given age t was predicted by.

$$L_{t,i} = L_{\infty,i} \left(1 - e^{-K_{i,l}(t - t_{0,i})} \right),$$

where $L_{t,i}$ is the predicted operculum radius of fish i in lake l at age t , $L_{\infty,i}$ is the theoretical maximum operculum radius of fish i in lake l ,

$K_{i,l}$ is the Brody growth coefficient (expressing the rate at which L_{∞} is approached as 1/year, which is also a proxy for juvenile growth rate) of fish i in lake l , $t_{i,l}$ is the estimated age of fish i in lake l , and $t_{0,i}$ is the theoretical age at length zero of fish i in lake l .

The data structuring followed a three-level hierarchical approach. Repeated measurements of operculum radius-at-age (in mm) were nested within individual fish, individual fish were nested within lakes, and lake-specific von Bertalanffy parameters $L_{\infty,l}$ and K_l were associated with a unique set of environmental characteristics as described below.

Though opercula radii constituted the response variables of our environmental models, we illustrate final predictions of size-at-age at the body length scale to facilitate interpretation (e.g. Figure 2). To that end, we regressed opercula size at capture on observed fish's total length at capture, which followed a linear relationship ($y = 21.8 + 15.6x$; $R^2 = 0.981$). Parameter estimates of this linear function were used to transform operculum lengths to body length.

2.6 | Explaining growth variation along environmental gradients

To identify key mechanisms shaping perch growth, lake-specific $L_{\infty,l}$ and K_l estimates were modelled as a function of different linear combinations of environmental variables. Following the arguments of van Poorten and Walters (2016), environmental variables relate to different mechanisms of metabolism and consumption, thereby differentially affecting the parameters of the von Bertalanffy growth model. Asymptotic length L_{∞} was assumed to be a ratio of anabolism q (approximately proportional to consumption) and standard metabolic rate M per body length L ($\frac{q}{M}$) (van Poorten & Walters, 2016). This suggests that external factors that affect consumption alone, either directly through foraging rate or efficiency, or indirectly through food availability, will impact L_{∞} (van Poorten & Walters, 2016). By contrast, mechanisms affecting consumption and metabolism simultaneously will cancel out. Consequently, we decided to model covariates affecting consumption alone on $L_{\infty,l}$, while environmental covariates affecting both consumption and metabolism were modelled on K_l in line with arguments by van Poorten and Walters (2016).

Variables modelled on $L_{\infty,l}$ included measures of lake productivity, such as chlorophyll a and total phosphorous concentration through bottom-up effects on prey availability, and Secchi depth through additional effects on foraging efficiency. Habitat structural variables such as the proportion of pelagic zone, shoreline development factor, macrophyte and dead wood density, may be related to macroinvertebrate abundance and diversity (e.g. Watkins et al., 1983), thereby impacting consumption. Competition measures, that is, metabolic biomass of intra- and interspecific competitors (<120 mm), and perch of all sizes, were modelled on $L_{\infty,l}$ as they ultimately affect the per capita consumption. Water temperature, measured as the annual growing degree-days (GDDs), affects consumption through

activity and energy demands, and metabolism through enzyme activity (Fry, 1971). Hence, GDD was modelled using K_l as response variable. Mean depth, maximum depth and lake area were also modelled on K_l , because other studies showed a correlation between these lake morphometry measures and water temperature (e.g. Arai, 1981) and may in addition affect nutrient availability through mixing. Piscivory was assumed to influence consumption through the consumed prey type, and metabolism through increased activity when chasing mobile prey fish. Finally, predator biomass was modelled on K_l , as high predation pressure may induce reduced risk-taking, thus decreasing activity and food uptake of prey individuals (Magnhagen & Borchering, 2008).

To assure positive values for the growth coefficient K_l , all covariates affecting consumption and metabolism were implemented in the following linear form using a log-link function (following Varkey et al., 2018):

$$K_l = Ke^{\sum \alpha_j X_{(CM)j}}$$

where $X_{(CM)j}$ is an observed covariate affecting consumption and metabolism (CM), and α_j represents the estimated variable-specific effect size. The same applied to covariates that were assumed to affect consumption exclusively and were thus modelled on $L_{\infty,l}$

$$L_{\infty,l} = L_{\infty} e^{\sum \beta_j X_{(C)j}}$$

with $X_{(C)j}$ being a covariate that affects consumption (C), and β_j being the corresponding effect size. All covariates were z-transformed (mean-subtracted and divided by standard deviation) prior to application of the model.

Concerning the stochastic components of the hierarchical model, up to three levels were considered. For the lowest level, size-at-age observations were assumed to be normally distributed around the expected value ($L_{t,l,i}$) with a common (within and across fish) standard deviation (σ_{obs}). At the between-fish level of the same lake, the three parameters of the von Bertalanffy model were assumed to be gamma-distributed with a lake-specific mean and standard deviation. Note that these gamma distributions were parameterised by a rate and a scale, the latter being the product of the expected mean and the rate. The lake-specific values of the von Bertalanffy parameters were in turn assumed to be gamma-distributed with a mean given by a lake-specific expected value and with a between-lake standard deviation. For L_{∞} and K , the lake-specific expected values were given by the linear combination of environmental variables described above. Conversely, the expected value for the theoretical age at length zero, t_0 , was assumed to be environmentally independent, but lake-specific (values are reported in Supporting Information S2).

A principal component analysis was conducted for lake variables affecting L_{∞} and K , respectively, to recognise potentially correlated variables (Supporting Information S3). Axes with Eigenvalues > 1 were interpreted (Kaiser–Guttman criterion), and variables with high loadings on the same axis (>0.4) were not included in the same model to avoid multicollinearity issues (Chatfield & Collins, 1980).

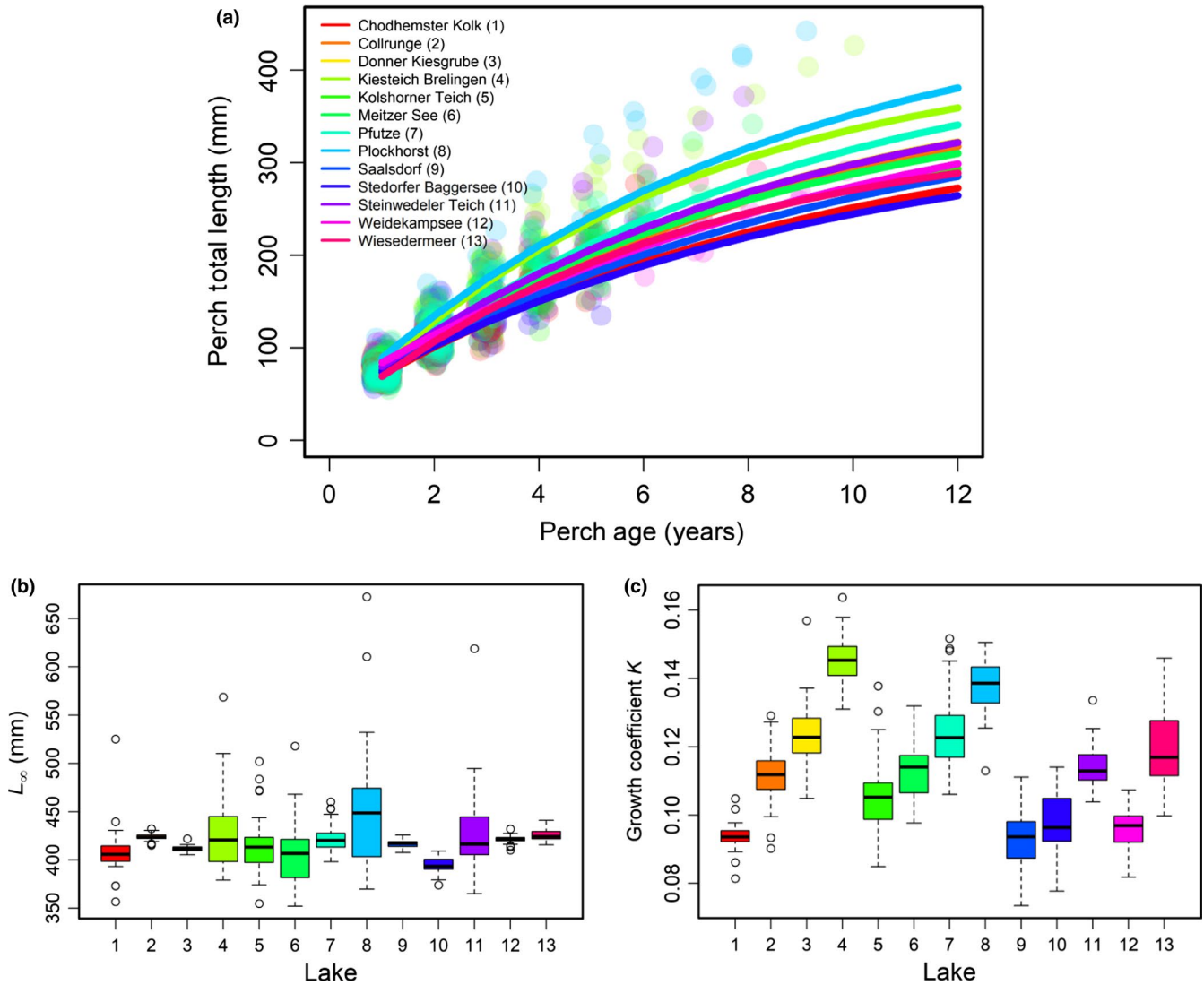


FIGURE 2 Results of the basic growth model without environmental covariates. (a) Predicted lake-specific von Bertalanffy growth functions with observed data points at the body-length scale. Lake numbers to interpret the x-scale of (b) and (c) are given in parentheses. (b) Boxplots of lake-specific Bayesian posterior probability distributions of L_{∞} . (c) Boxplots of lake-specific posterior probability distributions of K

We computed multiple nested models using forward variable selection (Heinze, Wallisch, & Dunkler, 2018) to ultimately find a combination of predictor variables that performed best in predicting growth of perch. Starting from a base model without environmental covariates, each of the considered covariates was modelled in a univariate manner on the respective response variable (L_{∞} or K); it was previously assigned to (Table 3, models #1–#16). Only significant factors were combined on the next level of complexity (model #17). In a Bayesian context, any variable is considered *significant*, if the 95% credibility interval of its posterior distribution does not include zero (Royle et al., 2013). When no more variables were significant, nonsignificant ones that performed better in a single-variable model than the base model (see model evaluation strategy below) were included. This step was repeated as long as inclusion of further variables improved model goodness. As suggested by Quince, Shuter, Abrams, and Lester (2008), the deviance information criterion (DIC)

was used to assess and compare all tested models (Tables 3 and 4). This measure evaluates the quality of a model based on its explanatory power, while rewarding lower numbers of effective parameters (= “law of parsimony”). A smaller value of DIC thus corresponds to a more parsimonious model and increased prediction power. Consequently, the model with the lowest DIC was retained as the most suitable model to describe perch growth in gravel pits based on environmental covariates (Tables 3 and 4).

After having identified the best available model to describe perch growth, the set of covariates was reduced to only those that were assumed to be easily obtainable by local fisheries managers (Table 4). The previously described variable selection process was then repeated in the same way to find the “best simple” model, similar to the overall best available growth model. Variables considered “easily measurable” were Secchi depth, mean and maximum depth, proportion of pelagic zone (derivable from echosounder surveys), lake area,

TABLE 3 Results of the model selection process considering all available covariates

Model	L_{∞}	K_1	DIC	Δ DIC
Base	L_{∞}	K_1	4,180.5	158.1
#1	L_{∞}	$K_1 e^{\text{Lake area}}$	4,176.9	154.5
#2	L_{∞}	$K_1 e^{\text{Mean depth}}$	4,163.7	141.3
#3	L_{∞}	$K_1 e^{\text{Max. depth}}$	4,116.2	93.8
#4	L_{∞}	$K_1 e^{\text{Growing degree-days}}$	4,159.2	136.8
#5	L_{∞}	$K_1 e^{\text{Piscivory}}$	4,095	72.6
#6	L_{∞}	$K_1 e^{\text{Length2 Predators}^*}$	4,057.9	35.5
#7	$L_{\infty} e^{\text{Proportion Pelagic}}$	K_1	4,182.6	160.2
#8	$L_{\infty} e^{\text{Shoreline development factor}^*}$	K_1	4,059.2	36.8
#9	$L_{\infty} e^{\text{Total phosphorous}}$	K_1	4,202.1	179.7
#10	$L_{\infty} e^{\text{Secchi depth}}$	K_1	4,288.2	265.8
#11	$L_{\infty} e^{\text{Chlorophyll } a}$	K_1	4,166.6	144.2
#12	$L_{\infty} e^{\text{Coarse woody structure}}$	K_1	4,096.4	74
#13	$L_{\infty} e^{\text{Macrophyte coverage}}$	K_1	4,099.3	76.9
#14	$L_{\infty} e^{\text{Length2 Interspecific}}$	K_1	4,080.9	58.5
#15	$L_{\infty} e^{\text{Length2 Intraspecific}}$	K_1	4,093.7	71.3
#16	$L_{\infty} e^{\text{Length2 Perch}}$	K_1	4,075.9	53.5
#17	$L_{\infty} e^{\text{Shoreline development factor}}$	$K_1 e^{\text{Length2 Predators}}$	4,035.2	12.8
#18	$L_{\infty} e^{\text{Shoreline development factor}}$	$K_1 e^{\text{Length2 Predators} + \text{Lake area}}$	4,142.4	120
#19	$L_{\infty} e^{\text{Shoreline development factor}}$	$K_1 e^{\text{Length2 Predators}^* + \text{Mean depth}}$	4,057.2	34.8
#20	$L_{\infty} e^{\text{Shoreline development factor}}$	$K_1 e^{\text{Length2 Predators}^* + \text{Max. depth}}$	4,022.4	0
#21	$L_{\infty} e^{\text{Shoreline development factor}}$	$K_1 e^{\text{Length2 Predators} + \text{Growing degree-days}}$	4,164.8	142.4
#22	$L_{\infty} e^{\text{Shoreline development factor}}$	$K_1 e^{\text{Length2 Predators}^* + \text{Piscivory}}$	4,081.5	59.1
#23	$L_{\infty} e^{\text{Shoreline development factor} + \text{Chlorophyll } a}$	$K_1 e^{\text{Length2 Predators}}$	4,162	139.6
#24	$L_{\infty} e^{\text{Shoreline development factor} + \text{Coarse woody structure}}$	$K_1 e^{\text{Length2 Predators}}$	4,243.4	221
#25	$L_{\infty} e^{\text{Shoreline development factor} + \text{Macrophyte coverage}}$	$K_1 e^{\text{Length2 Predators}}$	4,070.6	48.2
#26	$L_{\infty} e^{\text{Shoreline development factor} + \text{Length2 Interspecific}}$	$K_1 e^{\text{Length2 Predators}}$	4,133.3	110.9
#27	$L_{\infty} e^{\text{Shoreline development factor} + \text{Length2 Intraspecific}}$	$K_1 e^{\text{Length2 Predators}}$	4,212.1	189.7
#28	$L_{\infty} e^{\text{Shoreline development factor}^* + \text{Length2 Perch}}$	$K_1 e^{\text{Length2 Predators}}$	4,166.3	143.9

Note: Given are the implemented variables in any respective model, and the Deviance Information Criterion (DIC) as the ranking criterion. Best performing model's DIC is highlighted in bold (#20). Δ DIC corresponds to the numerical difference of any model's DIC to that of the best performing model. Bold letters and a * indicate a significant covariate. Models with more covariates had increased DIC estimates, and are reported in Supporting Information S6.

and shoreline development factor (both determinable with open-access geographical programs). These are all abiotic variables, as none of the available community variables were considered easily obtainable.

The parameters of the models described above were estimated using a Bayesian approach. The posterior probability distribution for each model was inferred using Markov chain Monte Carlo (MCMC) simulation, implemented in JAGS 4.3.0 (Plummer, 2003). The model, data and MCMC settings were implemented with an ad hoc R routine (R 3.5.2; R Core Team, 2018) that used the "R2Jags" package (Su & Yajima, 2012). Priors and other modelling details are fully described in the R routine, which is provided as Supporting Information S4 and S5. Posterior probability distributions were estimated from 100,000 iterations, a burn-in period of 50,000 iterations, a thinning factor of 10, and three Markov chains. Convergence

was then evaluated through visual examination of trace plots of MCMC chains. Moreover, when the estimated R.hat value (a statistic that compares within- and between chain variability) of any covariate in a model exceeded 1.1, additional sets of 50,000 iterations each were run until the R.hat values were < 1.1 (Gelman & Shirley, 2011). In doing so, former iterations were burnt-in. This step ensured comparability of goodness measures across models.

3 | RESULTS

In total, $N = 704$ perch contributed to the cross-lake growth analysis. Total length of the observed fish ranged from 48 to 434 mm. The estimated age of the oldest individual in the sample was 10 years.

TABLE 4 Results of the model selection process using only variables that were considered obtainable by local fisheries managers

Model	$L_{\infty l}$	K_l	DIC	Δ DIC
Base	$L_{\infty l}$	K_l	4,180.5	121.3
#1	$L_{\infty l}$	$K_l e^{Lake\ area}$	4,176.9	117.7
#2	$L_{\infty l}$	$K_l e^{Mean\ depth}$	4,163.7	104.5
#3	$L_{\infty l}$	$K_l e^{Max.\ depth}$	4,116.2	57
#7	$L_{\infty l} e^{Proportion\ Pelagic}$	K_l	4,182.6	123.4
#8	$L_{\infty l} e^{Shoreline\ development\ factor^*}$	K_l	4,059.2	0
#10	$L_{\infty l} e^{Secchi\ depth}$	K_l	4,288.2	229
#38	$L_{\infty l} e^{Shoreline\ development\ factor}$	$K_l e^{Lake\ area}$	4,138.6	79.4
#39	$L_{\infty l} e^{Shoreline\ development\ factor}$	$K_l e^{Mean\ depth}$	4,090.1	30.9
#40	$L_{\infty l} e^{Shoreline\ development\ factor^*}$	$K_l e^{Max.\ depth}$	4,067.6	8.4

Note: Given are the implemented variables in any respective model, and the Deviance Information Criterion (DIC) as the ranking criterion. Best performing model's DIC is highlighted in bold (#8). Δ DIC corresponds to the numerical difference of any model's DIC to that of the best performing model. Bold letters and a * indicate a significant covariate.

Of the sampled perch, 66% were captured by gillnets, whereas 34% were caught by electrofishing.

3.1 | Growth models without covariates

The von Bertalanffy growth curves for all lakes on the basis of length-at-age data without any covariates are shown in Figure 2a. Medians of posterior probability distributions of $L_{\infty l}$ derived from this base model ranged from 393 mm (Stedorfer Baggersee) to 457 mm (Plockhorst; Figure 2b). Median estimates of K_l ranged from 0.095/year (Stedorfer Baggersee and Chodhemster Kolk) to 0.146/year (Kiesteich Brelingen; Figure 2c). The base model was assigned a DIC of 4,180.5, which was 158.1 points greater than the DIC from the best model that included explanatory covariates (Table 3). The base model was thus not the best-fitting model.

3.2 | Growth models including biotic and abiotic variables

On a univariate level, the effects of predator metabolic biomass (modelled on K_l) and shoreline development factor (modelled on $L_{\infty l}$) were found to be significant and positive (Table 3). Among all models examined in our forward selection approach, a model consisting of

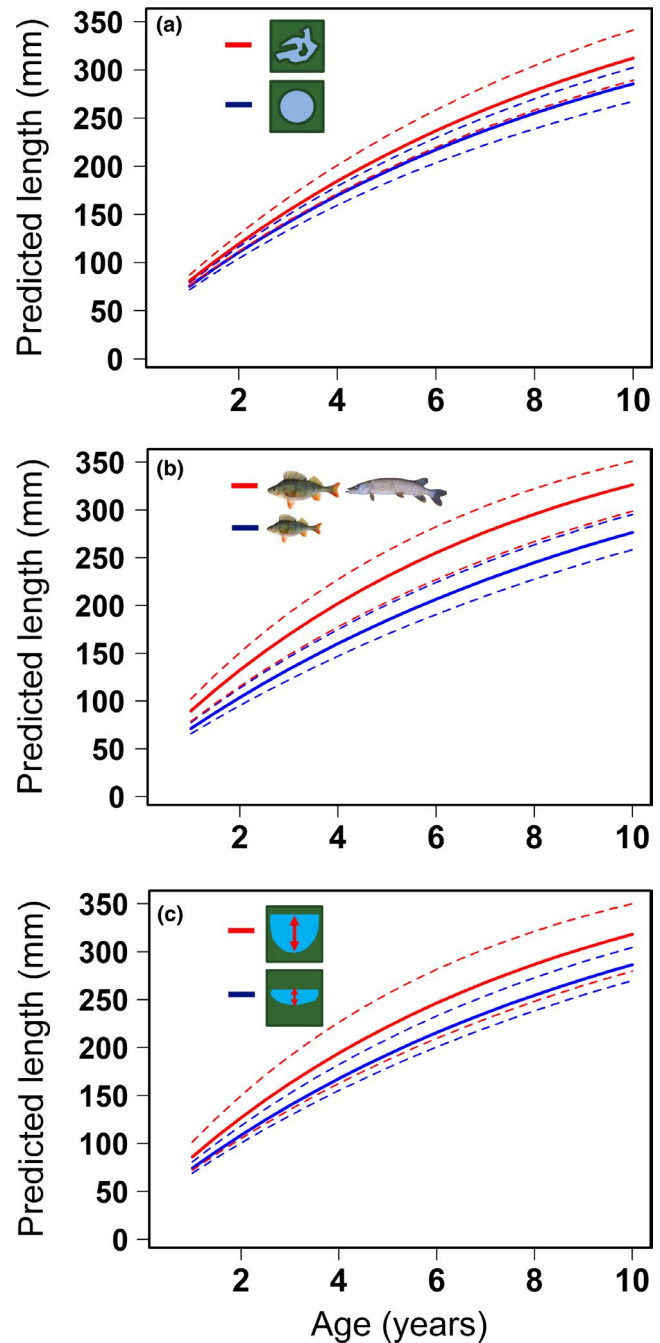


FIGURE 3 Effect sizes of (a) shoreline development factor, (b) predator metabolic biomass and (c) maximum depth, as predicted from the best-performing model to explain growth variation (#20). Red lines represent a predicted growth curve when the respective covariate is set to its upper quantile value (97.5%). At the same time, other covariates in the model are fixed at their mean across lakes. Blue lines represent a growth curve predicted from the lower quantile of the respective covariate (2.5%). Dashed lines indicate the credibility interval of the projected growth curve

predator metabolic biomass, maximum depth (modelled on K_l) and shoreline development factor (modelled on $L_{\infty l}$) received the lowest DIC estimate (Table 3, model #20). The positive median estimates

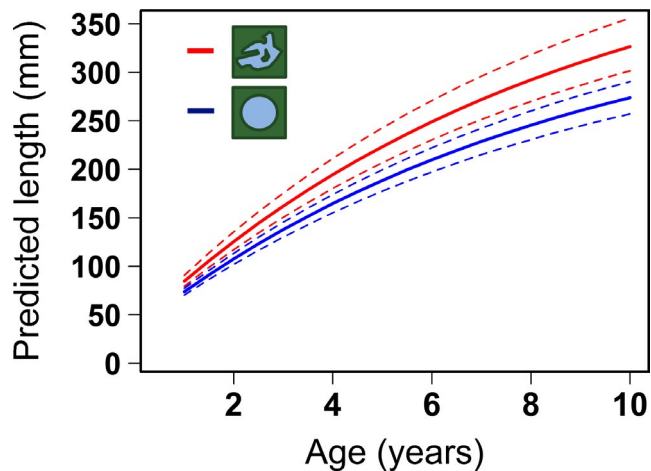


FIGURE 4 Effect size of shoreline development factor on growth predictions as predicted from the best model of “simple” variables (#8). Red lines represent a predicted growth curve when the covariate is set to its upper quantile value (97.5%). Blue lines represent a growth curve predicted from the lower quantile of the covariate (2.5%). Dashed lines indicate the credibility interval of the projected growth curve

of the posterior distributions indicate a positive effect direction for each covariate in this model, but the confidence intervals of maximum depth and shoreline development factor overlapped zero, suggesting weak effects (Supporting Information S6). Accordingly, the effect size of predictors, as indicated by the distance between a projected growth curve from the lower and upper quantile of the parameter, was larger for predator biomass than for shoreline development factor and maximum depth (Figure 3). Neither intraspecific nor interspecific competition (as indexed by metabolic biomasses) significantly improved model performance, and the only biotic variable exerting strong effects was a top-down measure—predator biomass.

A results table of the model selection process using only easily obtainable environmental variables is given in Table 4. In the single-covariate models (#1–#13), shoreline development factor (model #8) received the lowest DIC estimate and was the only significant variable, with a positive effect on L_{∞} . On the next level of complexity (two predictors; models #38–40), all models had larger DIC values compared to model #8. We thus retained model #8 as the best-performing simple model, implying that K was not predicted by any environmental covariate in this model. The univariate effect size of shoreline development factor on growth curves is visualised in Figure 4. Extensive results of the model selection process including Bayesian credibility intervals of parameter estimates are provided as Supporting Information S6 and S7.

When comparing growth predictions from the best complex model #20 with predictions from the best simple model #8, it became apparent that there were only minor and biologically negligible differences between the two growth projections. The credibility interval of length-at-age predictions of model #8 was slightly larger for some lakes, especially at younger fish ages (e.g. Figure 5b). Comparison plots of the two models for selected lakes are shown in Figure 5 and predicted lengths at some representative

ages are given in Table 5. As the lake-specific models represented the average growth trajectory of a population, growth models fitted the observed length-at-age data poorer in lakes where growth of perch showed strong variation among extremely poor and very fast-growing individuals. Lakes with substantial within-population variation in growth consequently had larger uncertainties in von Bertalanffy parameter estimates (e.g. Lake “Plockhorst”; Figures 2b and 5c).

4 | DISCUSSION

Growth of perch in gravel pits of north-western Germany was best predicted from a model combining the metabolic biomass of predators, maximum depth (both describing growth coefficient K) and shoreline development factor (describing maximum length L_{∞}). The top-down force of predation was found to induce the greatest variation in growth within our set of predictors, with higher predator biomasses promoting increases in the Brody growth coefficient K as a proxy of juvenile growth rate. This result is in line with previous studies finding a positive link between predation pressure and juvenile growth rates (or K) of perch (Heibo & Magnhagen, 2005; Persson et al., 2003). The inclusion of maximum depth as a predictor in the best model moreover substantiates the previously described role of lake morphometry for perch performance (Kahl & Radke, 2006; Jeppesen, Peder Jensen, SØndergaard, Lauridsen, & Landkildehus, 2000; Mehner et al., 2005), although the effect of lake depth on perch growth was smaller than the effect of predator biomass (Figure 3b,c). Additionally, the positive association of higher shoreline development factors with increased theoretical maximum lengths (L_{∞}) suggests the importance of shoreline habitat diversity and availability for growth prospects of the “ontogenetic omnivore” perch. Throughout different life stages, perch are reliant on a functioning littoral shoreline serving both as forage habitat and as refuge from predation (Diehl, 1988; Persson & Eklöv, 1995). A more pronounced shoreline development factor typically correlates with a greater diversity of habitats and prey types, which according to our study benefits perch growth in gravel pits.

The shoreline development factor, describing L_{∞} , produced the best-performing growth prediction when only easily obtainable variables were considered. This model delivered similar lake-specific growth projections as those derived from the top-ranked complex model with a difficult to enumerate measure of metabolic biomass of predators. The simple model we identify might thus constitute a promising application when information about lake-specific fish communities is lacking (as is often the case in the management of small, artificial lakes), but fisheries managers are interested in prescreening lakes that promise to offer good (or poor) growth for perch. Information on the growth potential of gravel pit lakes may also inform decisions about introductions when gravel pits are formed and fish communities are about to be established.

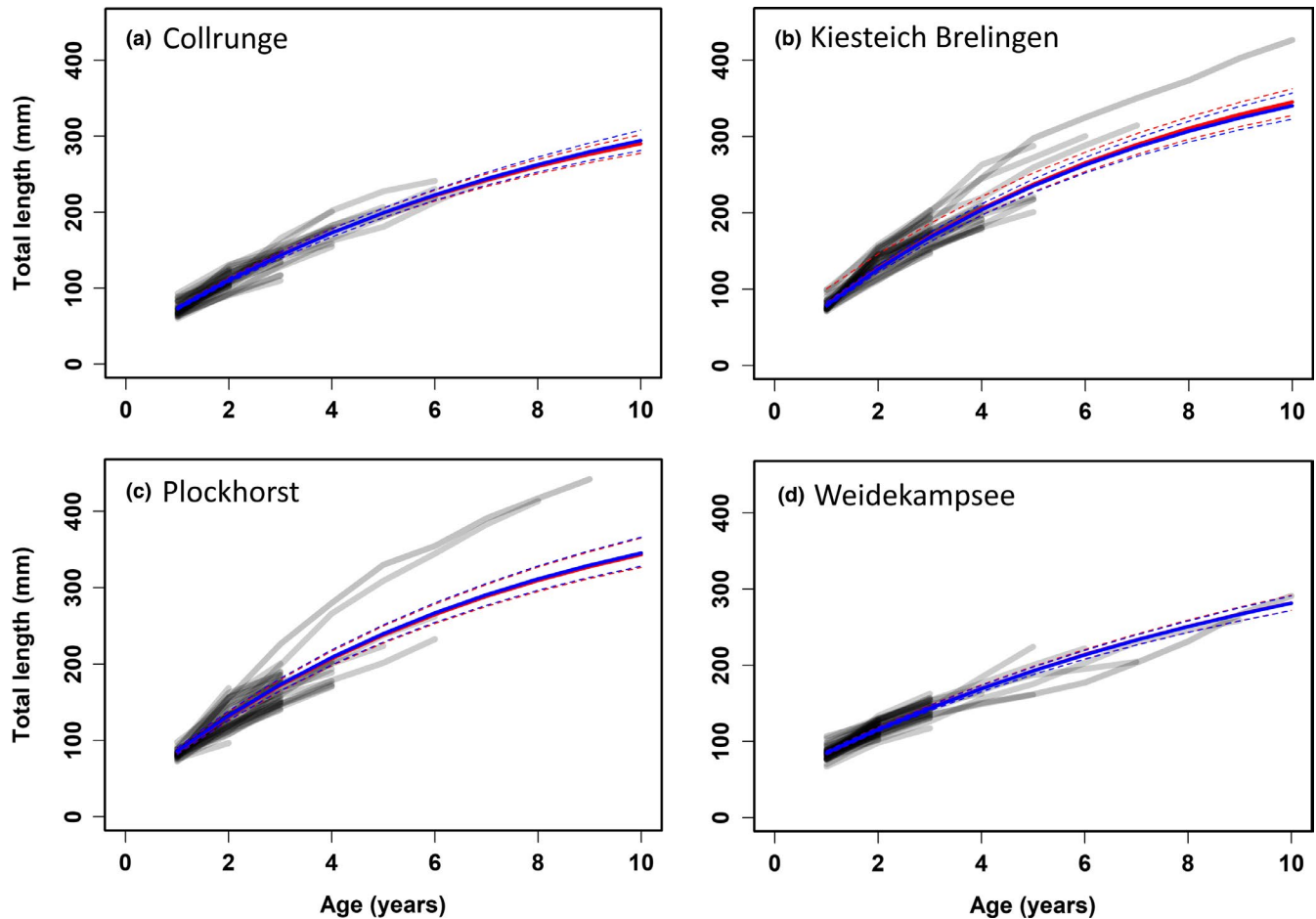


FIGURE 5 Comparison plots of von Bertalanffy growth curves predicted by “best complex” model #20 (blue lines) versus growth curves predicted by “best simple” model #8 (red lines) for four exemplary lakes. Dashed lines indicate the Bayesian credibility interval of the respective growth model. Grey lines in the background indicate the body length-at-age trajectories of individual fish

4.1 | Best prediction of perch growth from “complex” variables

There are several mechanisms that may underlie the observed positive link between metabolic biomasses of predators and juvenile growth rate K , and its strong contribution to between-lake variation in growth. Similar to our work, Heibo and Magnhagen (2005) found a positive association of relative predator density and perch growth rates and concluded that this was likely a result of thinning effects through predation leading to elevated prey availability for the surviving animals. Similar evidence has been presented elsewhere (Persson, Andersson, Wahlström, & Eklöv, 1996; Persson et al., 2003). However, in our study we did not detect a relation of competitive (intra- and interspecific) indices with perch growth. Similarly, there was no evidence for stunting in our study populations as the final length of fish was rather high across all lakes. Thus, a possible thinning effect of high predation biomass seems unlikely as an explanation for our study findings.

A further reason could relate to growth-selective predation. High predation risk has been found to select for faster growing individuals who are able to grow more rapidly into a size refuge,

where they are safe from gape-limited predators (Biro et al., 2005). As we failed to find evidence for the Rosa–Lee phenomenon (which would suggest slower-growing fish living longer) in our data, we suggest that high predator biomass may have fostered growth through selective predation of more slowly-growing individuals. More specifically, as large perch were the main contributor to our measure of predator metabolic biomass (Supporting Information S1), we propose that the correlation between predator biomass and juvenile growth rates K largely stemmed from cannibalistic interactions. Our study thus supports earlier findings that intercohort cannibalism controls perch growth rates within populations (Persson et al., 2003). However, our results suggest that this process may involve top-down control through selective predation of slower-growing individuals rather than being exclusively driven by cannibalistic thinning of stunted juvenile populations by cannibals.

A related explanation could be that populations with low predator biomass might also be more intensively fished (Lewin, Arlinghaus, & Mehner, 2006). Except for one lake, all the study lakes are managed for recreational fisheries, yet the actual exploitation rate of perch is unknown. It is, however, safe to assume that in particular larger perch are regularly targeted and removed

TABLE 5 Lake-specific L_{∞} , lake-specific K (as medians of the posterior probability distributions), and body length-at-age (in mm) at three exemplary ages (age-1, age-3, age-5) as predicted from the best overall model including “complex” variables (#20) versus the “best simple” model (#8), shown for four sample lakes

Lake	Model	Age-1 (mm)	Age-3 (mm)	Age-5 (mm)	L_{∞} (mm)	K_i
Weidekampsee	#20	85.1	143.7	192.5	428.7	0.094
	#8	85	144	192.9	437.2	0.091
	Δ	-0.01	+0.03	+0.04	+8.5	-0.003
Kiesteich Brelingen	#20	79.1	168.2	235.5	442.4	0.141
	#8	79.6	169.2	237.5	454.8	0.136
	Δ	+0.5	+1	+2	+12.4	-0.005
Plockhorst	#20	85.6	173.1	239.8	448.1	0.137
	#8	85.5	171.8	238	459.9	0.131
	Δ	-0.01	-1.3	-1.8	+11.8	-0.006
Wiesedermeer	#20	73.2	147.1	206.4	441.6	0.111
	#8	73.2	147.5	206.9	447.1	0.110
	Δ	+0	+0.4	+0.5	+5.5	-0.001
Mean difference \pm SD		0.13 \pm 0.25	0.68 \pm 0.57	1.09 \pm 0.96	9.5 \pm 3.2	0.004 \pm 0.002

for consumption across our study lakes. Fisheries selectively capture bold and fast-growing individuals (Biro & Post, 2008; Klefoth, Skov, Kuparinen, & Arlinghaus, 2017), which in turn would mean that more intensively fished populations could host slower-growing, less vulnerable individuals. These effects stemming from fisheries selection would also contribute to a positive correlation of predatory biomass and growth rate, assuming that fishing pressure caused different biomasses of predators.

Finally, it has been shown experimentally that predation may elicit behavioural and habitat-use responses of perch. Juvenile perch have been found to reduce risk-taking when exposed to a higher size-specific predation pressure (Magnhagen & Borcharding, 2008). Reduced risk-taking may imply less time spent foraging, possibly leading to slower growth (Ahrens et al., 2012). However, although Persson and Eklöv (1995) also showed that higher predation risk forces juvenile perch into refuge habitats (e.g., physical structures), this habitat shift accelerated the shift from planktivorous to benthivorous feeding, and ultimately growth rates were independent of predator presence and refuge use. This might be facilitated by the fact that perch are able to feed efficiently also in refuge habitats (Diehl, 1988; Persson & Eklöv, 1995). Collectively, our results suggest that the benefits of predation (probably through selective predation of slowly-growing perch) outweigh the potential growth-impairing effects of high predator biomass.

In combination with predator biomass, maximum depth improved model performance, indicating that morphometry may be relevant for perch growth in gravel pits as well, with a tendency for increased lake depths to be associated with faster growth rates K . Associations of lake depth with the performance of perch in lake ecosystems are broadly recognised in the literature. For example, it is common that perch are a dominant species in deeper, mesotrophic lakes (Jeppesen et al., 2000; Mehner et al., 2005). Lake depth may shape opportunities of niche separation between

perch and competing cyprinids and thereby shapes food competition independent of densities (Kahl & Radke, 2006). An increased lake depth can thus facilitate widening of the initially described “juvenile competitive bottleneck” between perch and cyprinids, allowing better growth opportunities for perch (Kahl & Radke, 2006; Persson & Greenberg, 1990).

The positive relation of maximum length L_{∞} with the shoreline development factor univariately and in the best-performing model emphasises the involvement of habitat-related factors in shaping perch growth. In general, longer shoreline lengths relative to a lake's surface area may provide a higher quantity and diversity of habitats and resources (Barbour & Brown, 1974). Availability of diverse littoral habitats serving as refuge and foraging habitats might reduce bottlenecks across different niches and may thus be of particular importance for an ontogenetically complex species such as perch. Persson (1983) reported that habitat homogeneity in lakes (as is more likely the case in lakes with low shoreline extension) hinders niche segregation among age-classes of perch, thus increasing intraspecific competition and reducing size diversity in perch populations. Importantly, an isolated relationship of growth potential with the densities of specific physical habitat features (i.e., macrophyte coverage or dead wood density) was not supported by our data. We thus suppose that the overall diversity of shoreline habitats and resources, rather than the density of one physical habitat type, may be more important in determining growth of perch in gravel pits.

4.2 | Best prediction of perch growth from “simple” variables

The shoreline development factor (affecting L_{∞}) turned out to constitute the best-performing “simple” variable to explain

growth variation in perch. When comparing growth curves for our study lakes as predicted from the best available model with curves from the best “simple” model, both delivered similar predictions with biologically negligible deviations (Figure 5, Table 5). In a few lakes, model predictions of the simple model showed wider uncertainties at low ages compared to the best “complex” model, likely due to the lack of a useful predictor for juvenile growth rate K (Figure 5b). Combining results of the two presented models, we conclude that biotic interactions (through predation) are relevant for explaining perch growth in gravel pits, but if no information on fish community is available, our simple model using only shoreline development has utility for approximations of expected growth. However, it remains to be seen whether the findings of our simple model apply beyond lakes that are ecologically similar to our study lakes. Moreover, the similarities in predictions of the two presented models have to be seen against the background that variation in estimated L_{∞} of our study lakes was rather low (Figure 2b). Our models would therefore profit from validation in other gravel pit lakes. Code for the complex- and simple-variable model for application to new lakes is provided as Supporting Information S4 and S5.

4.3 | Limitations

There are a few limitations to this study that need to be stressed. One has to be careful with generalisations of the results beyond the environmental gradients and geographical region on which our analysis was based. Mainly, this constraint applies to covariates related to trophic status, with the majority of lakes in our work being mesotrophic. However, nutrient-scarcity seems to be common particularly in young gravel pit lakes (Søndergaard et al., 2018). Similarly, while temperature did not relate to perch growth in our lakes located within a geographically narrow study region, it is well known that temperature affects perch growth in lakes from a larger geographical range (e.g. Arranz et al., 2015; van Dorst et al., 2019). Importantly, it should be noted that growth was calculated back in time from 2015 (after the uncompleted sampling year 2016 was excluded), but lake and community variables were only available for 2016 and subsequent years. We used repeated measurements of lake variables where possible to represent average conditions of a lake as best as possible. This study thus assumes temporal stability of environmental conditions in the study lakes, but there is no possibility in the scope of our analysis to verify this assumption. A final limitation relates to the absence of information about the sex of the individuals we sampled, but sex-specific dimorphic growth has been documented for perch (Mooij, Van Rooij, & Wijnhoven, 1999). Either sexual size dimorphism or bimodal growth through early piscivorous individuals (Urbatzka et al., 2008) could be explanations for the large between-fish variability in observed length-at-age data of some lakes (e.g. Figure 5c), but unlikely biases our results, because representation of the different sexes by gear should be equal among lakes.

5 | CONCLUSION

Among the environmental variables examined in this study, the best model to explain cross-lake variation of perch growth in gravel pits consisted of the metabolic biomass of predators, maximum depth (both positively related to K) and shoreline development factor (positively related to L_{∞}). The large effect size of the relationship between predator biomass and juvenile growth rates provides support for the strong role of predation and cannibalism in shaping perch growth. Lakes that offer good growth potential for perch should thus be carefully managed for controlling fishing mortality of adult and predatory perch if the aim is to maintain fast growth and large-sized fish in the stock (Johnston, Arlinghaus, & Dieckmann, 2013). Our results additionally emphasise the importance of certain morphometric properties in determining growth of perch in gravel pits, in particular lake depth and shoreline complexity. Extensive shorelines, which typically scale with habitat and resource heterogeneity, seem to be particularly beneficial for the growth potential of species with a complex ontogeny and food niche differentiation such as perch.

When detailed information on a lake's fish community is lacking, our work highlights the utility of the shoreline development factor for growth prediction, yielding similar results as models with “complex” variables. Local fisheries managers can apply our models to identify lakes likely hosting fast- or slow-growing perch stocks. This information can in turn be used to inform fisheries management decisions in newly created gravel pit lakes (e.g. where to introduce perch) and inform habitat-related restoration efforts (e.g. how to design shorelines to foster perch growth).

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CONFLICT OF INTEREST

The authors confirm that this article content has no conflict of interests.

AUTHOR CONTRIBUTIONS

LH, MP and RA conceived and designed the investigation. LH, SM, RN and AT performed field and/or laboratory work. LH, MP and CTM analysed the data. LH wrote the article. MP, CTM, SM, RN, AT and RA edited the manuscript.

DATA AVAILABILITY STATEMENT

The data sets analysed in this study are openly available in the repository "figshare" at <https://doi.org/10.6084/m9.figshare.9340712.v7> (Höhne, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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