

# The role of predation risk in structuring life-history traits of crucian carp (*Carassius carassius*) in a series of small boreal lakes

Ilaria de Meo<sup>1</sup>  | Kjartan Østbye<sup>1,2</sup> | Kimmo K. Kahilainen<sup>3</sup> | Antonio B. S. Poléo<sup>1</sup>

<sup>1</sup>Department of Forestry and Wildlife Management, Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, Inland Norway University of Applied Sciences, Campus Evenstad, Koppang, Norway

<sup>2</sup>Department of Bioscience, Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, Oslo, Norway

<sup>3</sup>Lammi Biological Station, University of Helsinki, Helsinki, Finland

## Correspondence

Ilaria de Meo, Department of Forestry and Wildlife Management, Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, Inland Norway University of Applied Sciences, Campus Evenstad, Koppang 2480, Norway.

Email: [ilaria.demeo@outlook.it](mailto:ilaria.demeo@outlook.it)

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## Abstract

Predation is a major evolutionary force determining life-history traits in prey by direct and indirect mechanisms. This study focuses on life-history trait variation in crucian carp (*Carassius carassius*), a species well known for developing a deep body as an inducible morphological defence against predation risk. Here, the authors tested variation in growth and reproductive traits in 15 crucian carp populations in lakes along a predation risk gradient represented by increasingly efficient predator communities. Lakes were located in south-eastern Norway and were sampled in summer 2018 and 2019. The authors expected crucian carp to attain higher growth rate, larger size, and later age at maturity with increasing predation risk. In the absence of predators, they expected high adult mortality, early maturity and increased reproductive effort caused by strong intraspecific competition. They found that the life-history traits of crucian carp were clearly related to the presence of piscivores: with increasing predation risk, fish grew in body length and depth and attained larger asymptotic length and size at maturity. This growth was evident at young age, especially in productive lakes with pike, and it suggests that fish quickly outgrew the predation window by reaching a size refuge. Contrary to the authors' predictions, populations had similar age at maturity. High-predation lakes also presented low density of crucian carp. This suggests that fish from predator lakes may experience high levels of resource availability due to reduced intraspecific competition. Predation regulated life-history traits in crucian carp populations, where larger size, higher longevity and size at maturity were observed in lakes with large gaped predators.

## KEYWORDS

gape-limited predators, growth, intraspecific competition, predation risk, reproductive effort, size refuge

## 1 | INTRODUCTION

Predation is considered one of the main ecological factors affecting freshwater communities, influencing not only prey population

dynamics but also individual growth and behaviour (Lima & Dill, 1990; Sih, 1987; Werner et al., 1983). Predation has a central role in structuring prey life-history traits, and shifts in prey growth or size and age at maturation have usually been attributed to

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predator selectivity (Abrams & Rowe, 1996; Belk & Hales Jr, 1993; Endler, 1986). In general, increased mortality in adult individuals selects for early maturation and high reproductive investment, whereas the opposite occurs with increased mortality in young individuals (Reznick et al., 1990; Stearns, 1992). Nonetheless, several other aspects can influence the direction of prey energy allocation such as predator density, size structure or optimal foraging strategy (Stein, 1977; Zandoná et al., 2011). For example, piscivorous fish such as pike *Esox lucius* L. are gape-limited predators which usually select prey below a certain size that maximizes their capture and handling ability (Hambricht, 1991; Mittelbach & Persson, 1998; Nilsson & Brönmark, 2000). This size-selective mortality on small individuals may favour prey species growing rapidly into a “size refuge” (Lundvall et al., 1999; Taborsky et al., 2003). Therefore, prey reaching a size refuge to elude gape-limited predators are subject to higher juvenile mortality, and a rapid somatic growth at young age may be achieved by postponing reproduction. This strategy was observed among populations of bluegills *Lepomis macrochirus* (Rafinesque 1819), which grew faster and reached sexual maturity at a relatively larger size and older age when occurring with high abundance of large predators (Arendt & Wilson, 1999). Other studies showed that different populations of guppies changed their life-history patterns depending on the type of predation. In streams with gape-limited predators, guppies matured at a later age and larger size, and had lower reproductive effort when compared to guppies occurring with large predators feeding mostly on adult individuals (Reznick & Endler, 1982).

Predation mortality can also increase individual growth rate of prey by reducing fish density and thus lowering intraspecific competition (Persson et al., 1996; Tonn et al., 1994; Van Buskirk & Yurewicz, 1998). Moreover, predation risk can induce shifts in prey behaviour, such as a reduction in foraging activity or a switch to unsuitable habitats, resulting in lower growth or reproductive allocation (Werner et al., 1983; Heins et al., 2016). Alternatively, prey can increase foraging activity and undergo higher predation risk at small sizes in return for faster growth and low mortality as soon as they outgrow the predation window (Urban, 2007; Werner & Hall, 1988). The choice of a certain behaviour is highly dependent on predation strategy (Van Buskirk, 2001; Wood & Moore, 2020) and resource availability, because scarce food generally forces individuals to increase foraging activity or use of risky habitats (Anholt & Werner, 1995; Werner & Hall, 1988). Life-history strategies may also differ between males and females due to sex-related differences in energy acquisition and assimilation in response to predation risk (Rennie et al., 2008).

Crucian carp *Carassius carassius* (L.) is a widespread cyprinid fish particularly vulnerable to gape-limited predators (Brönmark et al., 1995; Brönmark & Miner, 1992) and develops a deep body when exposed to cues from predators feeding on conspecifics, representing an inducible morphological defence against predation risk (Nilsson et al., 1995). In natural populations, crucian carp has usually been described as occurring with a distinctive dichotomy in morphology, biology, and population structure, depending on piscivore presence (Holopainen, Aho et al., 1997). The species has physiological adaptations to survive anoxic conditions under ice cover during winter. In autumn, it builds up a

glycogen storage that can be used for anaerobic metabolism (Blažka, 1958; Piironen & Holopainen, 1986). Because most other fish species are sensitive to oxygen depletion, a lake may change from a multispecies assemblage to a single-species assemblage of crucian carp under severe winter conditions (Holopainen, Aho et al., 1997). In lakes without predators, crucian carp can reach very high densities and have low relative body depth (RBD) and small size. By contrast, in lakes with piscivores, crucian carp have greater RBD and typically occur in low density and large sizes (Brönmark et al., 1995; Poléo et al., 1995). Experimental studies have shown that this change in body depth (BD) could be associated with resource availability and fish behaviour rather than with predation cues only (Andersson et al., 2006). High densities of crucian carp in predator-free lakes are subject to strong intraspecific competition, eventually leading to a stunting of populations (de Meo et al., 2023; Tonn et al., 1994). Moreover, crucian carp respond to alarm cues by decreasing swimming activity, implying an alteration in energy use with allocation to somatic growth in the presence of predators (Holopainen, Tonn, & Paszkowski, 1997; Johansson & Andersson, 2009; Pettersson & Hedenström, 2000). Whether these changes in growth and morphology are directly or indirectly mediated by predation, a deep body and large size seem to be the result of better growth conditions (Vøllestad et al., 2004). Nonetheless, to the authors' knowledge, there are no studies testing the effect of different predation regimes on the structuring of life-history traits of crucian carp in the wild.

In this study, the authors wanted to test variation in life-history traits of crucian carp from 15 lakes along a gradient of predation risk. Studies on growth and reproductive traits of crucian carp populations in northern Europe are currently limited to predator-free populations (Tarkan et al., 2016, and references therein). Here, the authors contrasted life-history traits of crucian carp from lakes without predators with lakes presenting increasingly efficient piscivore communities represented by brown trout *Salmo trutta* L., perch *Perca fluviatilis* L. and pike as main predators. Brown trout and perch have a generalist diet and can undergo shifts to piscivory late in life (Jensen et al., 2012), whereas pike is strictly piscivore and usually grows to a large body and gape size (Mittelbach & Persson, 1998). Experimental and field studies have also shown that the presence of pike induced a stronger anti-predator defence response in crucian carp compared to the other predator species (Brönmark & Pettersson, 1994; de Meo et al., 2021). The author hypothesized that (a) crucian carp would gradually attain higher growth rate and larger adult size as predation risk on small individuals was increasing; (b) this increase in growth may be achieved by delaying age and size at maturity of both sexes; (c) in the absence of predators, high population density and strong intraspecific resource competition would determine early age and size at maturity.

## 2 | MATERIALS AND METHODS

### 2.1 | Study lakes and data collection

The 15 study lakes were located in south-eastern Norway and were surveyed between June and August in 2018 and 2019 (see

Supporting Information Table S1). All lakes were small (0.25–11 ha) and had a high proportion of littoral zone and variable productivity (TotN, 312–1985  $\mu\text{g l}^{-1}$ ; TotP, 8–164  $\mu\text{g l}^{-1}$ ). Abiotic parameters included lake surface area (ha), maximum depth (m), total nitrogen ( $\mu\text{g l}^{-1}$ ), total phosphorus ( $\mu\text{g l}^{-1}$ ) and total organic carbon ( $\text{mg l}^{-1}$ ). The authors collected these parameters directly in the field or retrieved them from the Norwegian Environment Agency and the Norwegian Institute for Water Research (for details, see de Meo et al., 2021). Lakes presented different communities of piscivorous fish. Six lakes were completely predator free (Forkerudtjern, Mottjernet, Langmyrtjern, Nordre Sætertjern, Skråtjernet and Brynitjernet), whereas nine lakes had different predators: brown trout (Karussputten, Småvanna, Posttjernet), perch (Bjørnmyrdammen), perch + brown trout (Svartkulp, Øvresetjern) or perch + pike (Nusttjernet, Bugårdsdammen, Stomperudtjern). The authors caught fish using various sets of gillnets, baited traps and kick nets to maximize the chance to capture small crucian carp for age determination. They assessed the relative fish density using Nordic multimesh gillnets 1.5 m deep and 30 m long, consisting of 12 equidistant panels with mesh sizes of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm from knot to knot. They calculated CPUE (catch per unit of effort,  $n$  fish/net-h) for littoral and pelagic habitats (de Meo et al., 2021). After capture, they euthanized fish with an overdose of the anaesthetic MS-222 using prolonged immersion and transported them to the laboratory, and the fish were frozen for subsequent analysis. The Norwegian Environmental Agency (2018/4155) gave permission to catch fish which were sampled after oral approval by the local landowners.

## 2.2 | Laboratory work

The authors measured crucian carp for total length ( $L_T$ ) and BD to the nearest millimetre and wet mass ( $M_W$ ) to the nearest 0.1 g. They measured BD from the anterior insertion of the dorsal fin to the insertion of the pelvic fin. They determined sex and maturation stage of crucian carp by gonad inspection. They considered females mature when gonads were turgid and presented visible oocytes. For age determination, they took a sample of scales ( $n \sim 6$ ) from the area between the dorsal fin and the lateral line. Scales were cleaned manually to remove any skin remains and let completely dry. Age was determined by counting the number of annuli (*i.e.*, the narrow, dark zones formed during winter months) along the primary radius of scales (Steinmetz & Müller, 1991) using a Microfiche Reader (Eyecom 1000). The authors excluded damaged or regenerated scales from the reading. In addition, they measured total length (mm) and gape height (mm) of brown trout, perch and pike. They present data on predator populations caught using Nordic multimesh gillnets (Supporting Information Table S2). Gape height was the maximum distance between the tip of the upper jaw and the mandible. They calculated the mean maximum gape size (MaxGS) for each lake considering only the predators with the largest gape height ( $n = 10$ ), irrespective of the species (Supporting Information Table S2). Because a large proportion of brown trout and perch in the study lakes was small sized and probably did not undergo

ontogenetic shifts to piscivory (Jensen et al., 2012), the authors selected MaxGS over mean gape height to avoid potential underestimation of maximum predation window.

## 2.3 | Data analysis

### 2.3.1 | Total length and RBD

The authors calculated individual crucian carp RBD as the ratio of BD to  $L_T$ . They tested differences in mean  $L_T$  and RBD among crucian carp from different lakes using Kruskal–Wallis test because data departed significantly from normality (Shapiro–Wilk test;  $W = 96$ ,  $P < 0.001$  and  $W = 86$ ,  $P < 0.001$ , respectively). They tested differences in mean  $L_T$  and RBD between males and females from each lake using Wilcoxon test. They used  $\chi^2$  test to test significant deviations from the expected male-to-female sex ratio (1:1). They used data only from Nordic gillnets to avoid sampling bias in sex ratio, as females entering a trap may attract several males, with the exception of Skråtjernet and Nordre Sætertjern, where sex data on crucian carp collected from Nordic gillnets were not available.

### 2.3.2 | Growth

The authors estimated growth parameters fitting Bayesian growth models with informative priors using the “BayesGrowth” package (Smart & Grammer, 2021) in R statistical software. The “BayesGrowth” package uses the “Stan” computer programme (Carpenter et al., 2017) to build Markov–Chain Monte Carlo (MCMC) models via the “rstan” R package (Stan Development Team, 2020). Growth models are commonly fit using a frequentist approach; however, not all length or age classes can be always effectively sampled, introducing bias in growth estimation. When estimating growth using a Bayesian approach, additional information can be easily incorporated into length-at-age modelling by creating informative priors on known length-at-birth and species maximum length. In this study, fish sampling was biased towards large individuals in lakes with predators, as small crucian carp show an elusive behaviour (Supporting Information Figure S1). On the contrary, in predator-free lakes larger individuals may be undersampled. In this case, Bayesian models can be particularly useful because they can account for underrepresentation of the smallest and largest size classes. First, the authors determined the growth model that was the best fit for the data among three common models: the von Bertalanffy growth function (VBGF), the logistic function and the Gompertz function (Table 1). They fitted the three models to the data from each lake, considering males, females and all fish separately. They used informative priors on  $L_0$  and  $L_\infty$  parameters using a normal distribution.  $L_0$ , which represents length-at-birth, was set at 0.5 cm for all lakes (Laurila et al., 1987).  $L_\infty$ , which represents asymptotic length at which growth is zero, was set at 38.1 cm, the maximum individual length recorded from all lakes. Standard error on priors was set at 10%, resulting in  $L_0 \sim N(0.5, 0.05)$  and  $L_\infty \sim N(38.1, 3.81)$ . The growth parameter ( $k$ ) and the residual standard

**TABLE 1** Equations of the candidate growth models used in leave-one-out-cross-validation (LOOCV) procedure

Model	Growth function
von Bertalanffy	$L_a = L_\infty - (L_\infty - L_0)e^{-ka}$
Logistic function	$L_a = (L_\infty L_0 e^{ka}) / (L_\infty + L_0 (e^{ka} - 1))$
Gompertz function	$L_a = L_\infty e^{(\log(L_\infty/L_0)(1-e^{-ka}))}$

Note:  $L_a$  is the length-at-age  $a$ ,  $L_0$  is the length-at-birth,  $L_\infty$  is the asymptotic length at which growth is zero and  $k$  is the growth coefficient parameter.

error ( $\sigma$ ) represent non-informative prior with a uniform distribution, and their upper bound was set at values of  $k \sim U(0, 1)$  and  $\sigma \sim U(0, 100)$ , respectively, well above the expected estimates of these parameters. The authors used identical priors for the three candidate growth models. They ran four MCMC chains with 10,000 iterations and a burn-in period of 5000 iterations. Model selection was achieved through the leave-one-out-cross-validation (LOOCV) method using the “loo” R package (Vehtari et al., 2017). LOO weights were calculated for each model, and the candidate model with the highest LOOICw (LOOIC weights) was considered the most appropriate, similar to the AIC weights in the frequentist approach. In subsequent multivariate analyses, the authors considered only the growth parameters estimated from the best growth model. They checked for model convergence using the Gelman and Rubin test and with diagnostic plots using the “Bayesplot” R package (Gabry, 2020).

### 2.3.3 | Reproductive biology

The mean total length ( $L_{50}$ ) and age ( $A_{50}$ ) at which 50% of sampled individuals were sexually mature was determined by fitting a logistic regression model to the proportion of mature vs. immature. Confidence intervals for the model parameters of the logistic regression were estimated via bootstrapping ( $n = 1000$ ). In predator-free lakes (Forkerudtjern, Motttjernet, Langmyrtjern, Skrätjernet and Brynitjernet) and in brown trout lake Karussputten, sample sizes were large, and it was possible to determine  $L_{50}$  and  $A_{50}$  for males, females and both sexes combined. In the other lakes, most of the fish were mature, and the authors were able to estimate length and age at maturity only for combined sexes for Stomperudtjern and Svartkulp.

### 2.3.4 | Relating predation risk with life-history traits

The authors explored patterns of association among life-history traits of crucian carp from lakes with different predation risk by performing PCA on log-transformed growth and reproductive parameters (Winemiller & Rose, 1992). Growth parameters included asymptotic body length ( $L_\infty$ ), growth coefficient ( $k$ ), length at age 1 ( $L_1$ ) and maximum life span ( $T_{Max}$ ). They chose length at age 1 ( $L_1$ ) as a representative parameter to estimate YOY growth (i.e., growth during the first year after hatching). They

calculated  $T_{Max}$  as the average of maximum ages observed in each population ( $n = 10$ ). Reproductive parameters comprised length ( $L_{50}$ ) and age ( $A_{50}$ ) at maturity and sex ratio. RBD and relative crucian carp density (CPUeC) were also included in the analysis. Because data were lacking  $L_{50}$  and  $A_{50}$  values for some lakes, they performed PCA using the package missMDA (Josse & Husson, 2016), which allowed them to handle missing entries in principal components (PC) methods by estimation of missing values. The authors assessed credibility of the results obtained by visual inspection of uncertainty associated to predicted values using the function plot.MIPCA. They conducted all statistical analyses using R version 4.0.1 (R Core Team, 2020).

## 3 | RESULTS

### 3.1 | Total length and RBD

Crucian carp mean RBD differed significantly among lakes ( $\chi^2 = 1473.7$ ,  $df = 14$ ,  $P < 0.001$ ) and ranged from 0.27 in the predator-free lake Langmyrtjern to 0.40 in Bugårdsdammen, Nusttjernet and Stomperudtjernet, where both perch and pike were present (Table 2). Mean  $L_T$  was also significantly different among lakes ( $\chi^2 = 1467.7$ ,  $df = 14$ ,  $P < 0.001$ ). Maximum  $L_T$  ranged from 11.7 cm in Politihøgskolen to 38.1 cm in Bugårdsdammen. In all lakes without predators and brown trout-lakes Karussputten and Småvanna, females were significantly larger than males, but RBD did not differ between sexes (Figure 1; Supporting Information Table S3). In the other lakes, females had similar mean  $L_T$  or were slightly larger than males (Bjørnmyrdammen and Nusttjernet). Males had similar or higher RBD than females, with the exception of Øvresetetjern (Figure 1). Sex ratio was significantly different among lakes ( $\chi^2 = 91.97$ ,  $df = 14$ ,  $P < 0.001$ ). Females were always dominant in predator-free lakes, with the exception of Motttjernet. In the presence of predators, sex ratio was generally in favour of males, with the highest values in lakes Bugårdsdammen and Stomperudtjernet (Table 2).

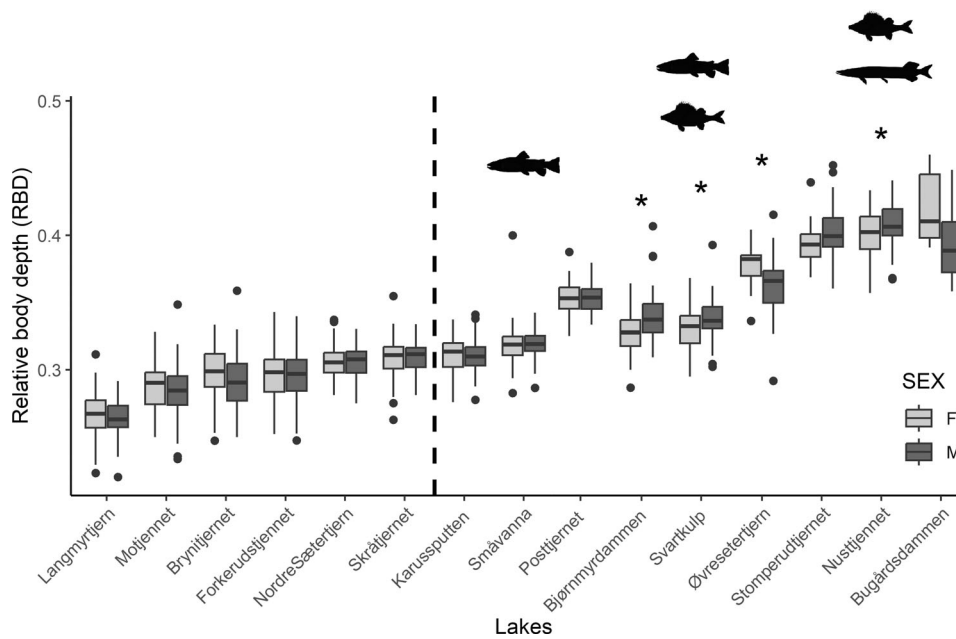
### 3.2 | Growth

The VBGF was the best-fit growth model for age estimation (LOOICw  $\sim 1$ ) of males, females, and all fish from each lake (Supporting Information Table S4), whereas there was no support for the logistic and the Gompertz growth functions (LOOICw  $\sim 0$ ). Thus, all growth parameters used in the following multivariate analyses were estimated from the VBGF. Mean parameter estimates varied greatly among the lakes (Table 2; Figure 2).  $L_\infty$  ranged from 12.6 cm in the predator-free lake Nordre Sætertjern to 42.0 cm in the pike-lake Bugårdsdammen. The growth coefficient was the highest in Nordre Sætertjern ( $k = 0.32 \text{ year}^{-1}$ ) and lowest in Brynitjernet ( $k = 0.07 \text{ year}^{-1}$ ). It has to be noted that in lake Brynitjernet fish reached very large asymptotic length compared to other predator-free lakes ( $L_\infty = 31.9 \pm 4.1$ ). Nonetheless, large s.d. suggests that adult fish might have been under-sampled in this lake. Maximum life span ranged from  $7.9 \pm 1.6$  years in lakes without predators to  $12.1 \pm 2.6$  years in lakes with predators.

**TABLE 2** Life-history characteristics of 15 populations of *Carassius carassius* from southern Norway with different predators (*Esox lucius*, *Perca fluviatilis*, *Salmo trutta* and no predators)

Lakes	Predators	RBD	n	$L_{\infty}$	k	$L_1$	$T_{Max}$	SexR	$L_{50}$	$A_{50}$	CPUE <sub>c</sub>
Nustjernet	<i>E. lucius</i> , <i>P. fluviatilis</i>	0.40	86	38.3 (0.6)	0.16 (0.01)	6.0	15.2	1.02	-	-	0.45
Bugårdsdammen	<i>E. lucius</i> , <i>P. fluviatilis</i>	0.40	31	42.0 (0.9)	0.12 (0.01)	5.5	16.2	7.00	-	-	0.10
Stomperudtjern	<i>E. lucius</i> , <i>P. fluviatilis</i>	0.40	99	38.9 (1.2)	0.13 (0.01)	5.3	12.6	6.33	11.6 (11.2–11.9)	3.0 (2.5–3.5)	0.42
Øvresetetjern	<i>P. fluviatilis</i> , <i>S. trutta</i>	0.37	49	37.0 (1.0)	0.15 (0.01)	5.7	13.3	1.23	-	-	0.42
Svartkulp	<i>P. fluviatilis</i> , <i>S. trutta</i>	0.33	124	33.5 (1.5)	0.12 (0.01)	4.3	11.4	1.11	12.8 (11.4–13.9)	3.2 (2.1–4.0)	0.30
Bjørnmyrdammen	<i>P. fluviatilis</i>	0.33	179	21.1 (0.4)	0.22 (0.01)	4.5	11.1	1.82	-	-	2.11
Posttjernet	<i>S. trutta</i>	0.35	47	33.6 (2.5)	0.10 (0.01)	3.7	11.8	2.81	-	-	0.19
Småvanna	<i>S. trutta</i>	0.32	95	19.7 (0.5)	0.23 (0.01)	4.5	9	1.14	-	<4	1.03
Karussputten	<i>S. trutta</i>	0.31	112	27.5 (2.4)	0.13 (0.02)	3.8	8.3	1.27	10.6 (9.8–11.4)	3.6 (3.1–4.0)	0.99
Skråtjernet	-	0.31	143	15.2 (0.5)	0.25 (0.02)	3.7	6.5	0.58	7.9 (7.7–8.2)	2.9 (2.7–3.1)	1.83
Nordre Sætertjern	-	0.31	105	12.6 (0.5)	0.32 (0.03)	3.8	6.1	0.74	-	-	7.93
Forkerudtjern	-	0.30	192	16.1 (0.6)	0.20 (0.01)	3.4	9.6	0.55	7.0 (6.4–7.8)	2.6 (2.3–2.9)	10.63
Brynitjernet	-	0.30	107	31.9 (4.1)	0.07 (0.01)	2.6	7	0.83	8.1 (7.4–8.7)	3.9 (3.3–4.3)	4.08
Mottjernet	-	0.29	185	21.0 (1.0)	0.14 (0.01)	3.2	9.9	1.29	9.0 (8.7–9.3)	4.0 (3.8–4.2)	7.80
Langmyrtjern	-	0.27	179	21.3 (2.3)	0.11 (0.02)	2.6	8.8	0.51	7.2 (7.0–7.5)	3.7 (3.5–4.0)	2.07

Note: Relative body depth (RBD) and total number of individuals for length-at-age estimation ( $n$ ). Mean asymptotic length ( $L_{\infty}$ ), growth coefficient ( $k$ ) and length at age 1 ( $L_1$ ) estimated from the von Bertalanffy function, where values in parentheses are the s.d. of the respective parameters from their posterior distributions. Maximum life span ( $T_{Max}$ ) and sex ratio (SexR; males:females). Mean length ( $L_{50}$ ) and age ( $A_{50}$ ) at maturity, where numbers in parentheses are the 95% bootstrapped c.i. Crucian carp relative density [CPUE<sub>c</sub> (catch per unit of effort)]. Sample distribution and size prevented some of the maturity calculations and are marked with “-”. All lengths ( $L$ ) refer to total length ( $L_T$ ) in centimetres.  $T_{Max}$  and  $A_{50}$  are in years, and  $k$  is in year<sup>-1</sup>.



**FIGURE 1** Variation in relative body depth (RBD; *i.e.*, ratio of body height to total length) between female (F) and male (M) *Carassius carassius* from the 15 study lakes. Asterisks (\*) denote significant differences ( $P < 0.05$ ). Dashed line separate lakes without predators (left side) from lakes with *Salmo trutta* (Karussputten, Småvanna, Posttjernet), *Perca fluviatilis* or *P. fluviatilis* (Bjørnmyrdammen, Svartkulp, Øvresetjern) and *Esox lucius* and *P. fluviatilis* (Stomperudtjern, Nusttjernet, Bugårdsdammen).

### 3.3 | Reproductive traits

The authors found no significant differences in  $L_{50}$  or  $A_{50}$  between males and females from the predator-free lakes and Karussputten as confidence intervals were largely overlapping (Supporting Information Table S3). Thus, they considered only combined males and females for subsequent analysis. Overall,  $A_{50}$  for both sexes combined averaged  $3.4 \pm 0.6$  years in lakes without predators and  $3.3 \pm 0.3$  years in lakes with predators.

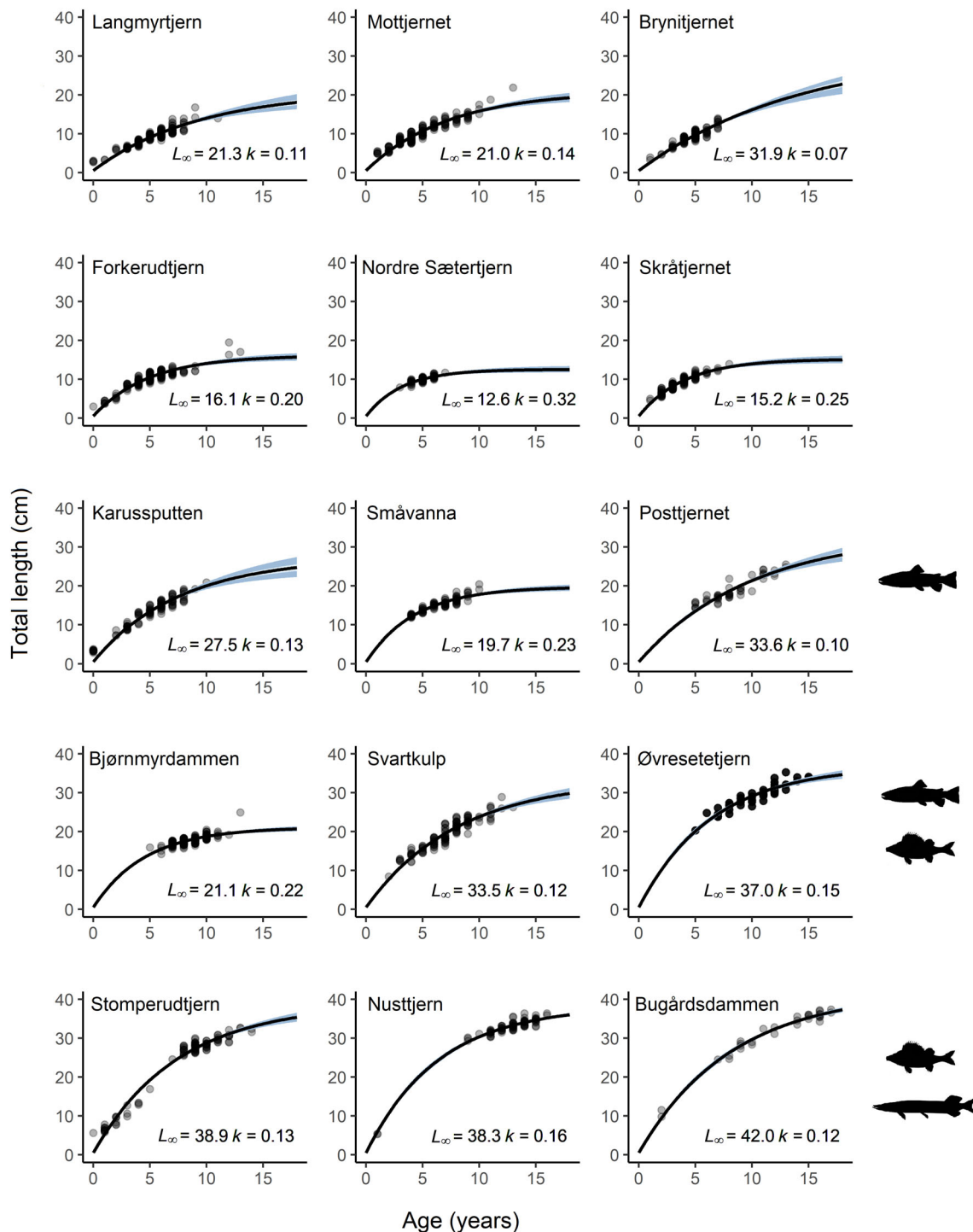
### 3.4 | Relating predation risk with life-history traits

The first two PCs explained 87.4% of the total variation in the data (Figure 3). The first axis accounted for 61.5% of the variation, and positive values were strongly associated with crucian carp RBD (eigenvector = 0.910), growth traits  $L_{\infty}$  (0.889) and  $L_1$  (0.774), MaxT (0.889), reproductive traits  $L_{50}$  (0.958) and sex ratio (0.813; males:females), whereas negative values were associated with CPUE<sub>c</sub> (−0.899). The second axis accounted for 25.9% of the total variation and was strongly associated with  $k$  (eigenvector = 0.899) and  $A_{50}$  (−0.955). Lakes were grouped along the first PC axis based on the different predation categories. Lakes where predators were not present were grouped clearly on the left of the PCA plot, thus consisting of abundant shallow-bodied and small-sized individuals with small length at maturity and short life span and dominated by females. The opposite pattern was found in the presence of pike, whereas growth traits of crucian carp showed intermediate characteristics in the presence of trout and perch. The second axis explained variation mainly within predation categories, in particular within no predators and trout lakes.

## 4 | DISCUSSION

The population structure and life-history traits of crucian carp were clearly related to the presence of piscivorous fish. As expected, fish gradually achieved larger size, older age and higher RBD, with increasing predation risk represented by different predator communities. This size increment was evident at young age, especially in productive lakes with pike. Contrary to the authors' hypotheses, populations had similar age at maturity and growth coefficient with increasing predation risk. Crucian carp also showed small differences in growth between sexes. Predator-free lakes were largely dominated by females.

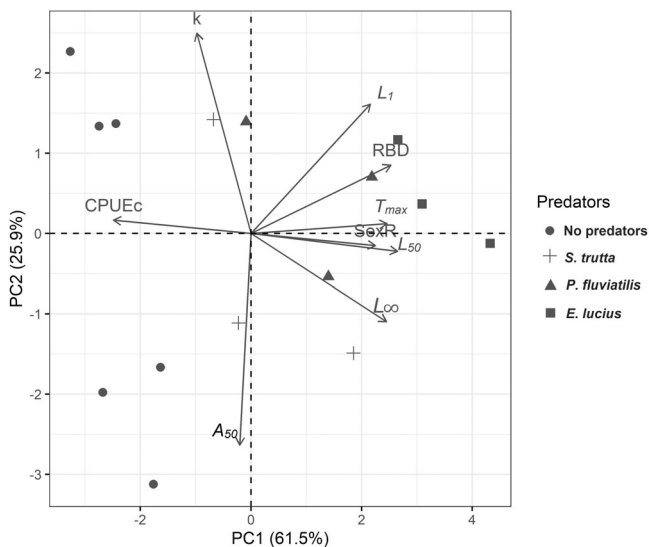
Young crucian carp attained larger body length with increasing predation risk. This overall increase in body length in the presence of predators occurred concurrently to an induced change in BD. Trout, perch and pike represented a gradient in predation efficiency, presenting increasingly deeper gape size, and crucian carp may quickly outgrow the predator window by reaching a size refuge. Nonetheless, growth coefficient was not associated with predator community and was generally low in lakes with piscivores, which indicates continuous growth to reach large size. Fish had also longer life span with increasing predation risk. It is to be noted that the relative density of pike in lakes Stomperudtjern, Nusttjernet, and Bugårdsdammen was lower with respect to predator density from the other lakes. Nonetheless, a great proportion of trout and perch presented small body size and may have not undergone a shift to piscivory (Mittelbach & Persson, 1998). Moreover, several factors such as the coexistence of different predator species with specific foraging strategies may directly or indirectly influence prey fish growth (Heynen et al., 2017), making it difficult to separate the effect of predator community from gape size.



**FIGURE 2** von Bertalanffy growth curves for *Carassius carassius* from 15 lakes without predator fish (first and second rows from the top), with *Salmo trutta* (third row), *Perca fluviatilis* or *S. trutta* and *P. fluviatilis* (fourth row) and *Esox lucius* and *P. fluviatilis* (fifth row). Shaded areas around the growth curves correspond to the 95% credibility intervals. Values indicate asymptotic length ( $L_{\infty}$ ) and growth coefficient ( $k$ ).

In predator-free lakes, two main constraints could prevent fish from growing to older age: a food constraint and a seasonality constraint. Dense allopatric populations suffer high intraspecific competition and adult mortality, with a few or no fish reaching large sizes (Tonn et al., 1994). This food constraint might be lowered by the thinning of population in the presence of increasingly efficient predators.

Thus, predation can have an indirect positive effect on prey growth by reducing the density of prey population and releasing survivors from resource competition (Van Buskirk & Yurewicz, 1998). These mechanisms are expected to be highly dependent on resource availability (Day et al., 2002). Interestingly, in trout lakes Posttjernet and Karussputten, crucian carp had the lowest first-year length compared



**FIGURE 3** Scatterplot of PCA of life-history traits of *Carassius carassius* from 15 lakes. Lakes are coded based on predation category, i.e., *Esox lucius*, *Perca fluviatilis*, *Salmo trutta* and no predators. Percentages indicate how much of the variation is explained by the first two principal component axes. Mean asymptotic length ( $L_{\infty}$ ), growth coefficient ( $k$ ), length at age 1 ( $L_1$ ), maximum life span ( $T_{Max}$ ), sex ratio (SexR; males:females), mean length ( $L_{50}$ ) and age ( $A_{50}$ ) at maturity, relative body depth (RBD) and *C. carassius* relative density [CPUEc (catch per unit of effort)].

to the other predator lakes, including Småvanna, which had a similar fish community. Lakes Posttjernet and Karussputten also had the lowest nutrient values among all lakes, suggesting that growth might be limited by resource availability. By contrast, all pike lakes were very productive and supported diverse fish communities. These lakes presented a great proportion of complex vegetated littoral habitats, which may provide fish with a habitat refuge from predators. Resource and refuge availability may favour crucian carp body growth even after fish have outgrown predator gape size. Predator-free lakes with high productivity such as Forkerudtjern and Mottjernet supported dense crucian carp populations. In the absence of predators, however, growth and reproductive traits were particularly variable and may depend on other factors in addition to resource availability. Lake size and depth are particularly important as small ponds at northern latitudes are subject to extreme seasonal changes, such as abruptly rising temperatures during summer and anoxic conditions during winter. Water temperature regulates crucian carp growth (Tarkan et al., 2011) and spawning (Aho & Holopainen, 2000), and interannual changes in temperatures likely have strong effects on life-history traits of fish living in small systems (Dembski et al., 2006). In addition, whereas the main growth period for crucian carp is summer, in autumn fish need to build up reserves for overwintering (Piironen & Holopainen, 1986). Small crucian carp from allopatric populations have been observed to store a significantly higher proportion of glycogen reserves compared to large fish from multispecies communities (Vornanen et al., 2011). Liver was also the main glycogen store for small fish, whereas large fish used white muscle as main deposit

(Vornanen et al., 2011). Fish from allopatric populations might invest more energy and time for building up winter reserves, as they inhabit ponds with harsh environmental conditions. Moreover, energy reserve requirements are expected to vary greatly even among predator-free populations because of different lake depths, and thus oxygen availability during winter, with consequences on fish mortality, growth and population dynamics (Fox & Keast, 1990).

Age at sexual maturity was variable among lakes, with values ranging between 3 and 4 years. These results were comparable to values of populations from similar latitudes (Holopainen & Pitkänen, 1985), although studies on length and age at maturity of crucian carp are rare in Fennoscandia. Contrary to the authors' predictions, age at maturity was not increasing with predation risk. By contrast, crucian carp reached length at maturity at larger sizes with predators, as a result of increased growth at young age. These results seem to contrast with life-history theory, because maturation should happen at the expense of growth or survival (Stearns, 1992). Small fish from predator lakes may grow fast to reach a size refuge from predation, with a larger initial energy investment into body growth compared to reproduction.

Moreover, the authors observed slight differences in growth between sexes. In some predator lakes females had lower RBD with respect to males, suggesting a potentially higher investment in reproduction. Similarly, Vinterstare et al. (2023) found that male crucian carp had significantly deeper bodies than females in the presence of predators, both in the wild and under experimental conditions. Interestingly, the authors found that adult sex ratio was female biased in lakes without predators and male biased in lakes with predators. Because sexes did not differ in their age at maturity, it is possible to exclude the effect of higher density of the sex that matures earlier. Sex ratio can be the result of differences in adult mortality where females are preferentially selected by predators (Arendt et al., 2014). Males at the onset of maturity may reduce feeding activity to reduce predation risk, whereas females need to move to gain energy and nutrients for egg production (Rennie et al., 2008; Trudel et al., 2000). Experimental studies showed that female crucian carp lose the typical predator avoidance behaviour just before spawning (Lastein et al., 2008). This bolder behaviour might increase predation risk for females but was displayed for a short time (Lastein et al., 2008). On the contrary, as observed in perch, females might be less active and take refuge in the littoral vegetation compared to males (Estlander & Nurminen, 2014), which also may have reduced their catchability. In lakes without predators, males had generally smaller body size than females, suggesting that they might have lower competitive edge and higher early mortality, so that females would eventually result in more abundance.

Crucian carp displays specific morphological adaptations to elude predation risk (Brönmark & Miner, 1992). The present study shows that fish can achieve a size refuge by increasing both BD and size. Fast growth is evident at young age when fish are most vulnerable to predation, especially in the presence of predators with large gape size such as pike. Crucian carp allocate more energy to growth and reproduction and live longer in the presence of



predators, which strongly suggests higher food availability in these lakes. Fish from predator lakes experience higher levels of resource availability as an indirect consequence of reduced intraspecific competition caused by predation (de Meo et al., 2023). The study lakes with pike were also very productive systems with structural complexity, which may favour growth even after fish have outgrown predator gape size. Moreover, crucian carp seem to decrease their activity levels, rather undergo risky behaviours, when exposed to piscivores (Holopainen, Tonn, & Paszkowski, 1997). Thus, fish may reduce foraging activity, and the energy saved is then allocated to growth (Rennie et al., 2005, 2008). This energy-saving mechanism is enhanced by the effects of reduced intraspecific competition and increased favourable environmental conditions. On the contrary, high density and thus strong resource competition in allopatric populations will likely force individuals to active foraging to increase survival. In addition, other piscivorous predators such as water birds or otters have a considerable impact on fish communities, and their role could also be investigated (Almeida et al., 2013). Future studies should specifically address variation in energy allocation to reproduction in the presence of predators. Predation intensity modifies life-history traits and size structure of prey populations and should be considered in ecological studies.

#### AUTHOR CONTRIBUTIONS

I.M.: conceptualization (lead), data curation (lead), formal analysis (lead), investigation (lead), methodology (lead), project administration (equal) and writing – original draft (lead). K.Ø.: conceptualization (equal), methodology (equal), resources (equal) and writing – review and editing (supporting). K.K.K.: conceptualization (equal), formal analysis (supporting), methodology (equal) and writing – review and editing (supporting). A.B.S.P.: conceptualization (equal), project administration (lead), resources (lead) and writing – review and editing (supporting).

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#### ORCID

Ilaria de Meo  <https://orcid.org/0000-0003-1433-2017>

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