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Intra- and interspecific predation on Roach larvae (*Rutilus rutilus*) in a eutrophic lake in South-Eastern Norway

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Abstract

In eutrophic lakes, the omnivorous roach (*Rutilus rutilus*) is known to dominate over other species, due to competitive advantages. This study aims to explore the dietary behaviour of roach, rudd (*Scardinius erythrophthalmus*) and perch (*Perca fluviatilis*) in the eutrophic lake Årungen, with a particular focus on the predation and cannibalism exhibited by roach and perch. Field data were collected through gillnet fishing from May 26th to June 27th, followed by examination of gut contents enhanced with Alizarin red S to detect fish larvae remnants in roach and rudd. Additionally, the growth rates of free-swimming fish larvae were assessed to determine the predation window for roach and perch, and to investigate the effect of environmental factors on growth.

Findings from this study indicate no differences in the diets of the three species, suggesting they overlap and compete for resources. Roach engaged increasingly in facultative piscivory as temperatures rose, suggesting temperature as an important factor. Perch also engaged increasingly in piscivory, to a larger degree than roach, but water temperature had no effect on its behaviour. The influence of maximum prey size was not different for roach and perch on the probability of piscivory, but roach had the highest optimum prey size of the two. Further, when analysing the age calculation data there was a significant interaction effect between species, temperature, and delta length (the difference between the empirical length of the predator at capture and its predicted length). Perch demonstrated increased piscivory at lower temperatures for individuals with poor growth, whereas roach piscivory increased at higher temperatures under similar conditions of poor growth. The fish larvae were identified as roach, suggesting roach may have engaged in cannibalism. The study also observed a negative growth rate for larval roach as the temperatures rose, with the empirical weight consequently below the predictions. This trend may align with density-dependent factors, including increased predation and potential competition for, and limitations in, available resources.

Overall, the results from this study highlight the complex interactions among fish species in eutrophic lakes, and the adaptive behaviours of the species in response to environmental shifts. It has revealed that facultative piscivory and cannibalism among cyprinids may be more prevalent than previously anticipated.

Sammendrag

Mort er en allsidig art som er kjent for å dominere i eutrofe innsjøer, grunnet fordeler i konkurranse. Dette studiet tar sikte på å utforske diett hos mort, sørv, og abbor i den eutrofe innsjøen Årungen, med særlig fokus på predasjon og kannibalisme hos mort og abbor. Datainnsamling ble utført ved garnfiske fra 26. mai til 27. juni, etterfulgt av undersøkelser av mageinnhold, farget med Alizarin rødt S for å detektere rester av fiskelarver hos mort og sørv. I tillegg ble veksten til frittsvømmende fiskelarver vurdert for å undersøke effekten av predasjonsvinduet hos mort og abbor, og for å undersøke effekten av miljøfaktorer på vekst.

Funnene i studiet indikerer ingen forskjeller i dietten til de tre artene, noe som tyder på at de overlapper hverandre og dermed konkurrerer om ressurser i Årungen. Det ble funnet piscivore (larvespisende) adferd hos mort, som økte med økende temperaturer, noe som antyder at temperatur kan være en viktig faktor for denne adferden. Det var ingen forskjell i påvirkningen av maksimal byttestørrelse hos mort og abbor, men mort hadde det høyeste optimum for byttestørrelse av de to artene. Videre, ved analyse av aldersberegnende data, var det en signifikant interaksjonseffekt mellom arter, temperatur og delta lengde (forskjellen mellom empirisk lengde til predator ved fangst og dens predikerte lengde). Individer av abbor med dårligere vekst enn forventet økte inntaket av fiskelarver ved lavere temperaturer, mens hos individer av mort med dårligere vekst økte inntaket av fiskelarver ved høyere temperaturer. Fiskelarvene som ble samlet inn ble identifisert til å være mort, noe som antyder at mort kan ha utvist kannibalistisk adferd. Det ble også observert en negativ vekstrate hos fiskelarvene, hvorav den empiriske vekten forble under forventet vekt, noe som samsvarer med høy predasjon og mulig konkurranse og begrensninger for de tilgjengelige ressursene.

Resultatene understreker de komplekse samspillene blant fiskearter i eutrofe innsjøer og ulike arters tilpasninger i respons til miljøendringer. Studiet viser at fakultativ piscivory og kannibalisme blant karpefisker kan være mer utbredt enn tidligere antatt.

1. Introduction

The increasing human population exerts pressure on aquatic ecosystems, primarily through agriculture and urbanization (Smith et al., 1999). Among notable known negative anthropogenic impacts are the input of fertilizers and wastewater into lakes that result in excessive nutrient levels, particularly phosphorus and nitrate, causing rapid eutrophication (Bernes et al., 2015; Schindler, 1974; Smith, 2003). The process of eutrophication often leads to increased phytoplankton, algae, and aquatic plants, and in some cases cyanobacteria blooms, resulting in increased turbidity and anoxic conditions due to increased photosynthetic activity (Akinnawo, 2023; Rathore et al., 2016; Smith et al., 1999). These conditions may influence the biodiversity in lacustrine ecosystems by inducing substantial alterations in structure and function, impacting organisms across taxa, from algae and phytoplankton (Smith et al., 1999) to aquatic plants and fish communities (Akinnawo, 2023; Svärdson & Molin, 1981, p. 151).

Climate change, another major threat to ecosystems worldwide (Rosenzweig et al., 2007), can increase lake eutrophication effects through increased events of extreme precipitation and flooding, leading to increased water flow into lakes (Madsen et al., 2014; Semadeni-Davies et al., 2008; Tabari, 2020). The enhanced influx of nutrients and particles are widely recognized to negatively impact freshwater and marine ecosystems (Arvnes et al., 2019; Semadeni-Davies et al., 2008). Additionally, human alterations of the catchment such as removing natural vegetation or using impervious material, leads to less water retention capacity, which amplifies the negative effects by climate change (Semadeni-Davies et al., 2008). The Oslofjord area is no exception to the worldwide challenges posed by threats of climate change, extensive runoff, and eutrophication. Nutrient runoffs are known to heavily eutrophicate lakes of the Oslofjord catchment (Bernes et al., 2015; Eie & Borgstrøm, 1981), as observed in sediment core studies, which demonstrated rapid and persistent cultural eutrophication during the 20th century (Skogheim & Erlandsen, 1984). Thus, human alterations to ecosystems, coupled with increased precipitation resulting from climate change, amplifies eutrophication processes in both lacustrine and marine ecosystems.

Human alterations and eutrophication often impede the restoration of lakes to their pristine condition as they grapple with the intricate dynamics within their food webs (Bernes et al., 2015; Horppila & Kairesalo, 1990; Persson et al., 1993), particularly the fish community, affecting the water quality (Andersson et al., 1978; Borgstrøm et al., 1980). Hierarchical dynamics within these communities enable adaptable species like Cyprinids roach (*Rutilus*

rutilus) and rudd (*Scardinius erythrophthalmus*) to thrive in nutrient-rich conditions (Lammens & Hoogenboezem, 1991, p. 354; Svärdson, 1976; Vejrik et al., 2016). Roach, with its varied diet including cyanobacteria and macrophytes, exploit a wider array of food sources, and through predation, alter the composition of zooplankton and benthic invertebrates, which increases phytoplankton blooms and thereby sustains the eutrophication processes (Andersson et al., 1978; Brooks & Dodson, 1965; Henrikson et al., 1980). Their diel migrations also contribute to nutrient loading, promoting algal growth (Andersson et al., 1978; Haugen et al., 2019; Henrikson et al., 1980). Consequently, managing roach populations can mitigate eutrophication by reducing nutrient levels and water turbidity (Henrikson et al., 1980), as well as increasing survival chances for less adaptable species.

The domination of roach in eutrophic lacustrine ecosystems is known to affect the perch (*Perca fluviatilis*) population, whose hunting is impaired by the increased turbidity (Bernes et al., 2015; Lessmark, 1983; Svärdson & Molin, 1981, p. 144), giving roach advantages in competition. Fish communities are dynamic, as fish undergo niche shifts throughout their lives with changes in food preferences and niche utilization (Andersson et al., 2007; Persson, 1988, p. 203; Persson et al., 2004), which increases inter- and intraspecific competition (Persson, 1983; Svärdson, 1976). The interspecific competition between sympatric species perch and roach is affected by the size-structured nature of fish communities, allowing smaller species such as roach to outcompete perch individuals during their juvenile stages, when zooplankton is the primary food item for both species (Persson & Greenberg, 1990a; Persson & Greenberg, 1990b; Svärdson, 1976). This early-life resource competition subsequently affects the fish population by altering interactions of perch and roach, diminishing the predatory pressure on roach (Persson, 1983; Persson & Greenberg, 1990b).

Predation is an important regulatory mechanism that can help to restore stability in eutrophic lacustrine ecosystems by reducing the abundance of young fish (Sharma & Borgstrøm, 2008; Tonn et al., 1992). Similar to benthivores influencing water quality from the bottom-up (Meijer et al., 1994; Søndergaard et al., 2008), piscivores have a top-down impact on ecosystems, affecting primary production based on their densities (Carpenter et al., 1985). Therefore, restoration efforts in eutrophic lakes often involve removing dominating planktivorous or benthivorous species (Andersson et al., 1978; Tolonen et al., 2000), and/or stocking piscivores and potential cannibals (Bernes et al., 2015), underscoring the importance of predation in maintaining ecosystem diversity.

Certain piscivorous species engage in cannibalism, reducing the competition by decreasing the number of smaller conspecifics and enhancing resource availability (Claessen et al., 2000; Sharma & Borgstrøm, 2008). Since fish grow continuously (Persson, 1988, p. 203), competition spans various size classes, with smaller individuals often benefiting from their foraging efficiency and higher metabolic rates, leading to asymmetric interactions (Claessen et al., 2000). The interplay between competition and cannibalism influences growth rates, resulting in population cycles and different life history strategies that vary with hatching year (Claessen et al., 2000). Increased cannibalism post-hatching reduces competition within cohorts, potentially enabling growth of larger individuals, whereas less cannibalism heightens competition and suppresses growth (Claessen et al., 2000). Therefore, life history strategies often align with the pace of life syndrome (POLS) (Debecker & Stoks, 2019; Ricklefs & Wikelski, 2002), where faster-growing individuals tend to be bolder and take more risks (Biro et al., 2014), which often coincides with a piscivorous diet (Keast, 1985). The individual growth of fish can therefore indicate whether cannibalism or competition are most prominent as regulatory mechanisms.

Cannibalism, or piscivory in general, is infrequently observed in cyprinids and has not been previously documented in roach, except as an incidental component of their diet (Lammens & Hoogenboezem, 1991; Winfield & Townsend, 1991, p. 560). Yet, previous studies have found presence of facultative piscivory in cyprinid species within lacustrine ecosystems hosting invasive species rudd (Guinan et al., 2015; Kapuscinski et al., 2012) or while experiencing food shortages (Vejrik et al., 2016). Thus, we selected the eutrophic lake Årungen in the Oslofjord catchment where invasive species and cyprinids are present (Eie & Borgstrøm, 1981; Sharma & Borgstrøm, 2008), and where predation and competition are important regulatory mechanisms for the fish community (Borgstrøm et al., 1984). This study aims to explore the dietary behaviour of cyprinids roach and rudd, as well as the perciform perch, with a particular focus on the predation and cannibalism exhibited by roach and perch. The following questions and predictions will be investigated:

- Q1: Are there any apparent differences in the diet of species roach, rudd, and perch?
    - o P1.1 Perch will exhibit higher percentage of piscivory than roach and rudd.
- Q2: Do roach exhibit facultative piscivory, and how is this behaviour influenced by lake abiotic conditions and prey size?
    - o P2.1 Roach will engage in cannibalism behaviour.
    - o P2.2 Amount of piscivory will increase with rising temperatures.
    - o P2.3 There will be a maximum prey length for predation.

- Q3: Do individual characteristics age and growth influence amount of facultative piscivory?
- Q4: How does the growth of free-swimming larvae correlate with increasing water temperatures and the facultative piscivory?
    - o P4.1 Larval growth will be positively correlated with water temperatures.

2. Materials and method

2.1 Study area

The study is carried out in the lake Årungen (Figure 1; Table 1), which is a calcareous on the municipal boundary between Ås and Frogn municipalities in the southeastern Norway (UTM 32: 598201, 6618153) (Borgstrøm et al., 1984; L'Abée-Lund & Vøllestad, 1985). Vollebekken, Fosterudbekken, Storgrava, Bølstadbekken, and Østbybekken are the five tributaries that run into Lake Årungen (Borgstrøm et al., 1984; L'Abée-Lund & Vøllestad, 1985). Bølstadbekken is located in the east, while Smebølbekken and Storgrava are situated in the west. Smebølbekken and Storgrava are the two main sources of runoff into Årungen.
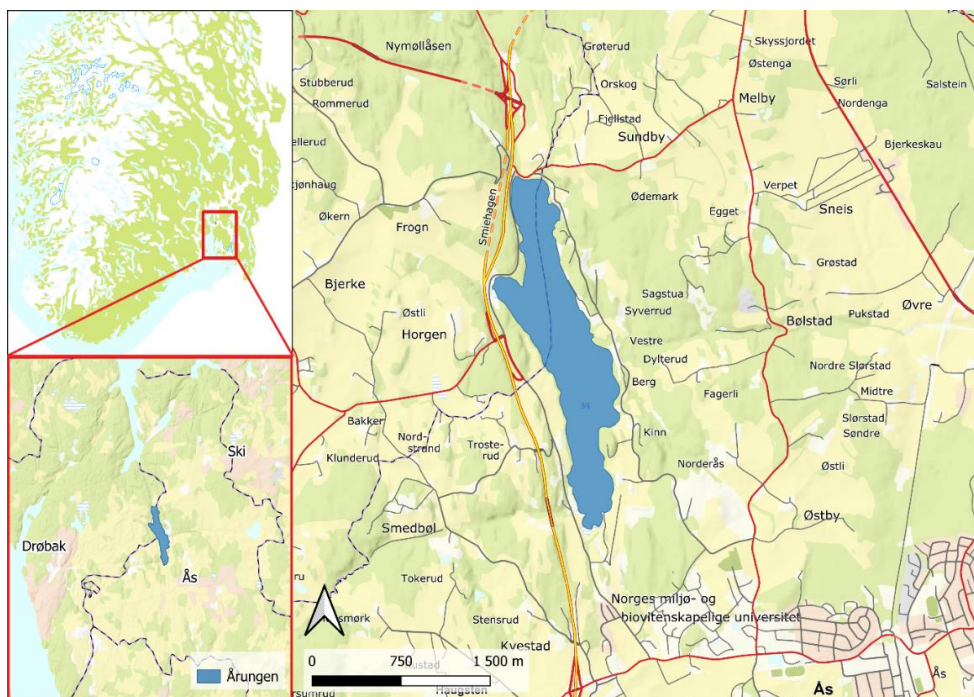
Figure 1 The study area, lake Årungen (highlighted in blue), is situated near the town Ås, as well as in close proximity to the fjord, in the southeastern parts of Norway.

2.1.1 Description of lake Årungen, its catchment and watercourse

Catchment of the eutrophicated lake Årungen encompasses agriculture and urban landscape (Borgstrøm et al., 1984; Eie & Borgstrøm, 1981), leading to very high phosphorus and nitrogen levels in all tributaries feeding into Årungen (Borch et al., 2007; Stabell et al., 2022). The extensive nutrient concentrations often lead to high abundance and domination of cyanobacteria in July and August (Borgstrøm et al., 1984; Sharma & Borgstrøm, 2008), as well as anaerobic

conditions in the bottom layers during thermal stratification (Eie & Borgstrøm, 1981) (Figure 5). Due to excessive blooms of cyanobacteria, algae, and plankton (Borgstrøm et al., 1984), the Secchi depth in Årungen has stayed unchanged since around 1991 when it was between 1-1.5 m, which indicates a persistence of the eutrophication process (Strand et al., 2015).

Table 1 The physical properties are presented for the lake Årungen (1Eie and Borgstrøm (1981); 2 Borch et al. (2007)).

Total area[1]	$1.2\ km^2$
Volume[2]	$9.2 \cdot 10^6\ m^3$
Catchment area[1]	$52\ km^2$
Elevation above sea level[1]	$33\ m$
Mean depth[1]	$8.1\ m$
Max depth[1]	$13.2\ m$
Theoretical retention time[2]	$4.5\ months$

The continuous eutrophication of Årungen is reflected in the amount of phosphorus, which fluctuates seasonally, suggesting rapid recycling of phosphorus in addition to external input (Bernes et al., 2015; Borgstrøm et al., 1984). As a result, the ecological status of Årungen is classified as 'moderate', according to the Water Framework Directive's classification status (Direktoratsgruppen vanndirektivet, 2018; Stabell et al., 2022). Årungen drains into the inner sections of Oslofjorden, Bunnefjorden (Borgstrøm et al., 1984), thereby affecting the marine ecosystem through its runoff (Thaulow & Faafeng, 2014).

2.1.2 Fish community in Årungen

The earleir literature shows that Årungen supports the stocks of perch (*Perca fluviatilis*), Northern pike (*Esox lucius*), European eel (*Anguilla anguilla*), and roach (*Rutilus rutilus*) (Borgstrøm et al., 1984; Eie & Borgstrøm, 1981; L'Abée-Lund & Vøllestad, 1985). There has also been observations of migrating salmonid (*Salmonidae*) individuals from the Oslofjord, as well as a few individuals of the crucian carp (*Carassius carassius*) (Borgstrøm et al., 1984). More recent findings show that invasive species rudd (*Scardinius erythrophthalmus*) and tench (*Tinca tinca*) (Sharma & Borgstrøm, 2008), have been introduced by man during late 1990s and/or early 2000s.

To assess the current composition and abundance of fish species in Årungen, a gillnet survey was conducted from October 10th to October 11th 2023, following the European standard for a minimum effort sampling approach based on lake size and depth (CEN, 2005), using eight

benthic gillnets (1.5x30m) and one pelagic gillnet (5x30m) (Figure 2). The benthic gillnets were randomly deployed to compensate for the uneven distribution of fish (CEN, 2005), while the pelagic gillnet was positioned in the deepest part of the lake (Figure 2). Fish captured with gillnets were identified, and their total length (to the nearest millimetre) and weight (in grams, using Sartorius GMBH type 1219MP) were measured for every individual. Estimates of abundance were expressed as Catch per unit effort (CPUE), accounting for catches per m^2/t, calculated using following equation:

$$CPUE = \frac{Species\ count}{net\ size} \times \frac{100}{Effort\ time}$$

In total, catches yielded 420 roaches (73.7 %), 103 perches (18.1 %), and 47 rudd (8.3 %) sampled in Årungen (See Appendix, Figure A1). Overall, roach was found to be the dominating species, with on average seven individuals per 100 m^2 fishing nets, per night. The pelagic gillnet yielded the highest catch, where roach also dominated with a CPUE of ca. 13 and 39.8 individuals per 100 m^2 fishing nets, per night for depths 0-3 m and 3-6 m respectively, while roach and rudd had a CPUE close to zero. The catches from the benthic gillnets had varying amounts of roaches, perches, and rudd (see Appendix, Figure A2). While roach and perch were present both in pelagic and benthic areas of Årungen, rudd was almost found only in the benthic zone.

The echo sounding was conducted to estimate fish biomass in the pelagic areas of Årungen on the 9th of November 2023, after dark, to coincide with the increased nocturnal activity in the pelagic zone (Bjerkeng et al., 1991) (Figure 2). It was performed in a zigzag manner with a 70 kHz Simrad EY60 echosounder, as described by Gjelland et al. (2019). Working frequency of the echo sounding was 70 kHz, and transmitted pulse was four times per second (per 0.25 second). The estimated biomass (kg/ha) and calculated individuals per hectare is shown in Table 2 Distribution of estimated biomass from echo sounding in Årungen presented in kg per hectare and individuals per hectareTable 2, further indicating a dominance of roach.

Table 2 Distribution of estimated biomass from echo sounding in Årungen presented in kg per hectare and individuals per hectare, for depth layers 0-6 m and 6 m and downwards.

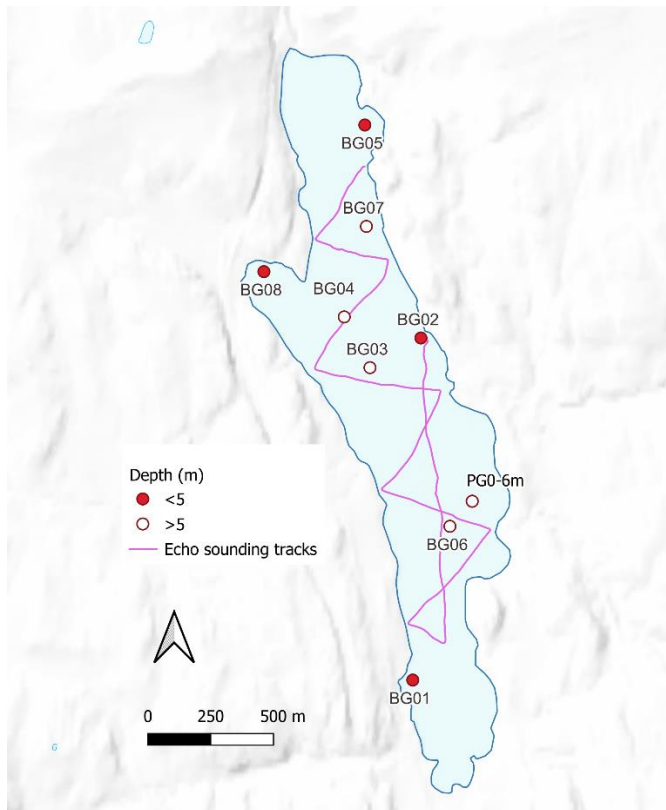| Depth layer	kg/ha	# fish/ha
<6 m	151.89	1983.96
>6 m	55.61	253.37

Figure 2 The benthic (BG) and pelagic (PG) gillnet survey and echo sounding of Årungen were conducted October 10th to October 11th, at nine different locations, using benthic gillnets (BG) and one pelagic gillnet (PG). The nets were placed at either a depth of >5 m (red) or <5 m (white). The pelagic gillnet was set at the deepest parts of Årungen.

2.1.3 Water temperature and climate

During the study period from May 26th to June 27th, the weather was notably warmer and drier than usual (Figure 3). Consequently, the highest water temperature recorded was on June 18th reaching 24.2 °C, while the lowest temperature was 13.2 °C recorded on May 28th. The mean temperature during the study period was 19.3 °C. Water temperature data for the study period were recorded using HOBO temperature and light data loggers (UA-002-64) near the fish larvae sampling location (shoreline), positioned at approximately 1 m deep (Figure 4). Weather and climate data were provided by seklima.met.no (Weather station number: SN17850). Additionally, the water temperature was measured on the deepest parts of the lake to capture temperature of the whole column, using a CB-50 Data Buoy with a submersible data logger (X2-SDL) and temperature string for profiling (TS210). They showed that the lake was thermically stratified from June to October, reaching quite warm temperatures in the upper 5-6 meters in this period (Figure 5).
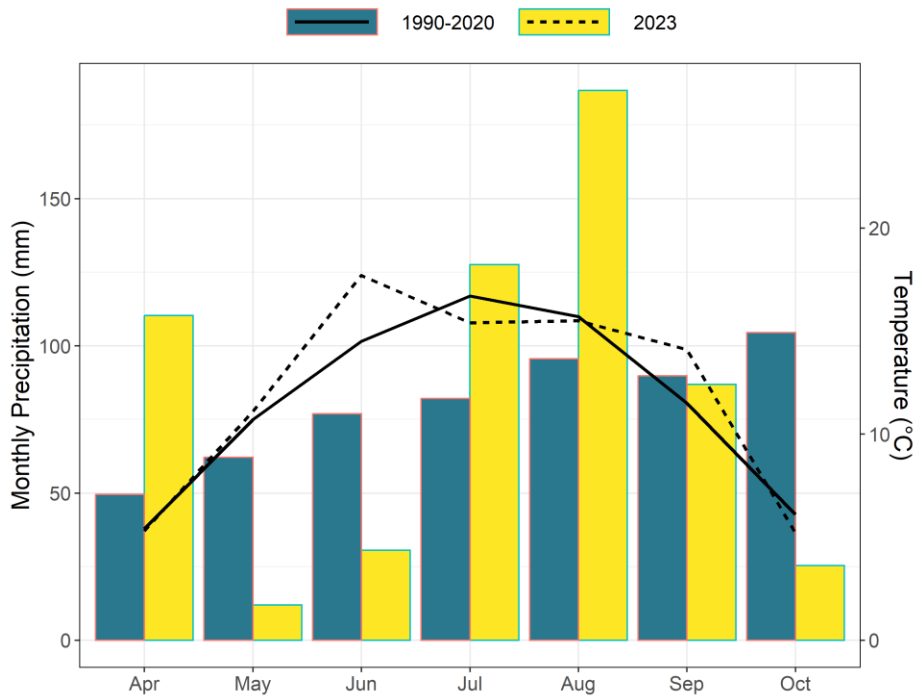
Figure 3 The monthly precipitation is represented by columns and average monthly temperatures are showed by the lines from the weather station in Ås, comparing data from the sampling period in 2023 to the monthly averages between 1990 and 2020.
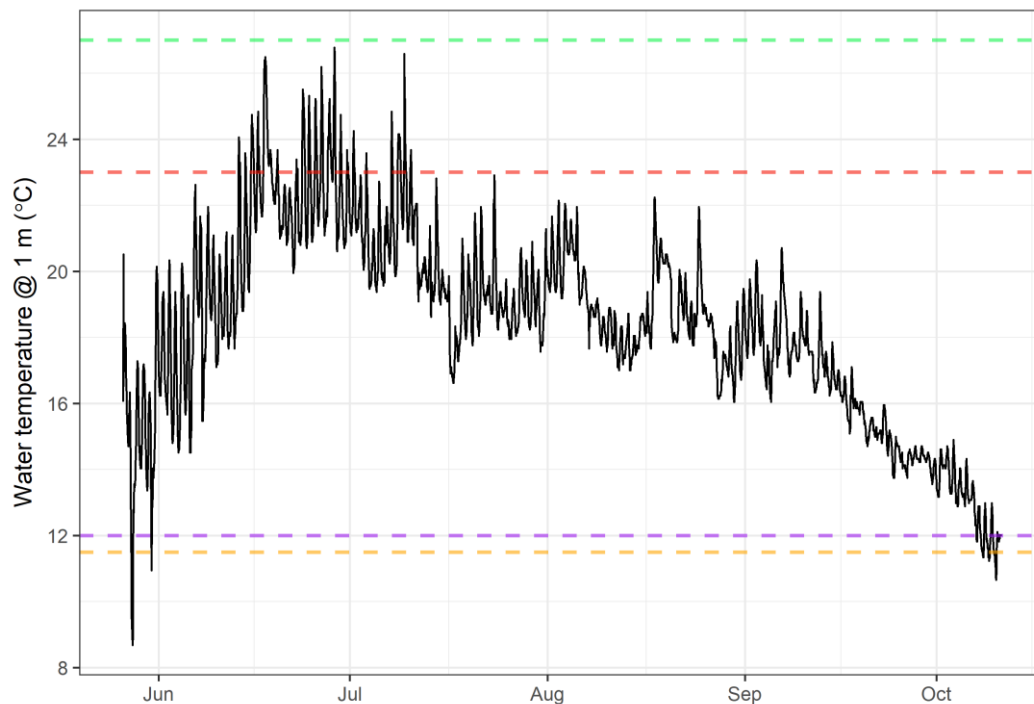
Figure 4 The logged water temperature (°C) at 1 m in Årungen are presented by a black line. The optimum temperature for perch is shown in red (Fiogbé & Kestemont, 2003, while green indicates the optimum temperature for roach (van Dijk et al., 2002). The orange and purple dashed lines show lower temperature limit for perch (Linløkken, 2023) and roach (Mooij & Vantongeren, 1990) respectively.
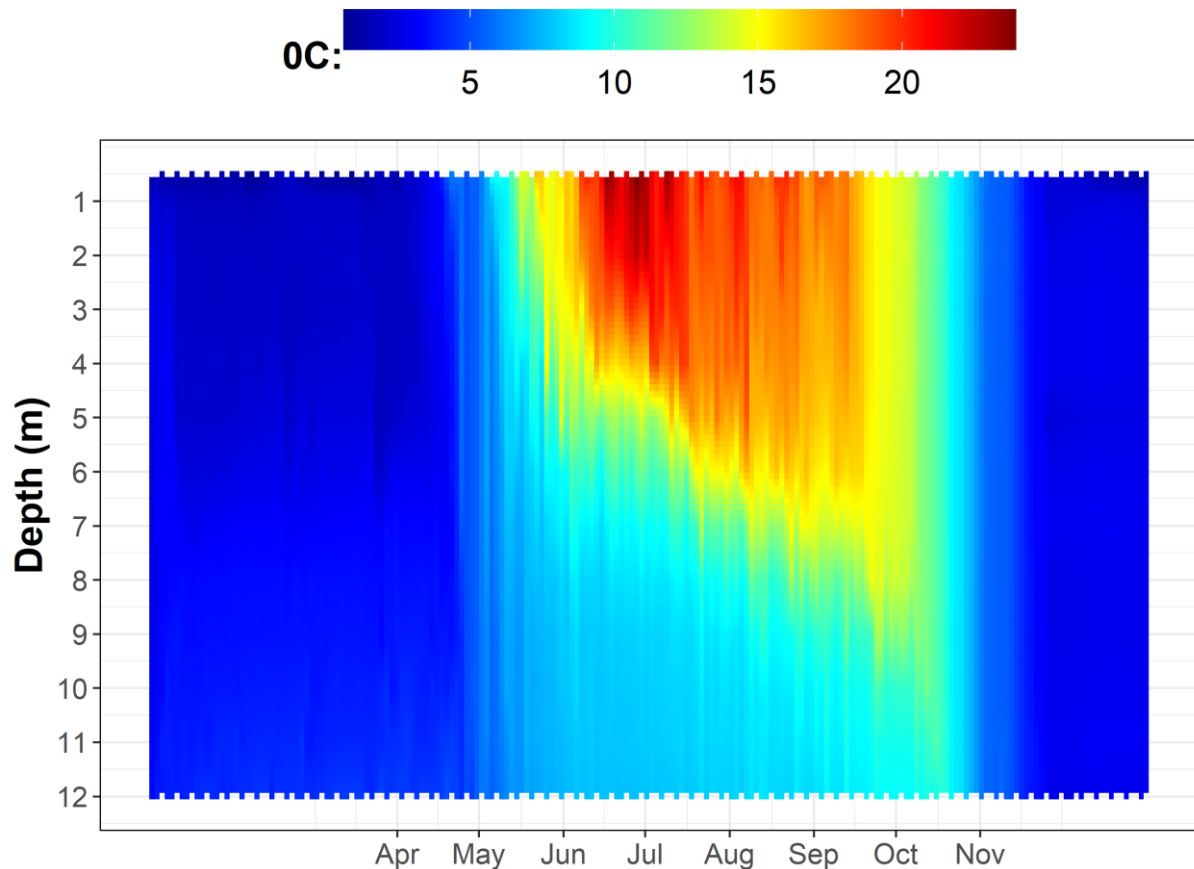
Figure 5 The water temperature in Årungen was measured every 30 minutes through the entire water column, during the period April to November in 2023, showing a thermally stratified lake from June to October.

2.3 Littoral sampling for potential predators and larval roach

Free-swimming roach larvae and their potential predators were sampled in the littoral zone of Årungen every other day for a total of 11 days in the period from May 26th to June 27th, 2023. Focusing on the southern end of the lake, two sampling locations were chosen based on species diel migration patterns and habitat preferences (Bohl, 1980; Eie & Borgstrøm, 1981; Horppila, 1999) (Figure 5). Benthic gillnets (1.5mx30m) were deployed at each location, following the method outlined by Appelberg et al. (1995) to capture a mix of species and sizes representative of a lake's community (CEN, 2005). Gillnetting was conducted between 09:00 and 12:00 h, with nets retrieved after a maximum of 15 minutes in the water. Simultaneously, fish larvae were sampled using a Bongo trawl (25 cm in diameter and 375-micron net) along the gillnet and a dipnet was used from the shore. Fish were promptly frozen for subsequent laboratory analysis to preserve gut contents (Horppila, 1994), while the fish larvae were kept cold for less than 24h before analysis.

Figure 5: The sampling locations (Location 1 and 2), as well as the sampling spot for free-swimming larvae, are located at the southern end of Årungen. GPS tracking was taken May 30th to show approximate sampling route on the lake.

2.3 Laboratory procedures

2.3.1 Extraction and identification of stomach content

To investigate dietary preferences and facultative piscivory, gut contents were collected from 81 perch, 111 roach, and 35 rudd, where 3 perch, 2 rudd, and 19 roach had an empty gut. The fish was weighed (g) and measured lengthwise (mm) as described earlier and classified by sex and stage of maturity by examining the gonads. Due to variations in species composition in the gillnets from day to day, the number of samples taken from each species also varied. Since roach and rudd lack of a stomach, content was extracted from the anterior third of their gut (Horppila, 1994; Horppila, 1999; Vøllestad, 1985). For perch the stomach was utilized. Food items were examined using a stereoscopic microscope. Volumetric analysis was employed to estimate the relative abundance of different food items (Vøllestad, 1985; Windell & Bowen, 1978, p. 221).

Alizarin red S, a sodium salt dye known for its strong affinity to calcium and commonly used to stain bone tissue (Erdoğan et al., 1995; Liao et al., 2020), was used for roach and rudd gut content samples to distinguish fish remnants from other food items. The pharyngeal teeth of cyprinids crush the food (Sibbing, 1991, p. 403), making it harder to separate food items, therefore Alizarin red S is used to highlight bone structure of free-swimming larvae in the gut.

Rountree (2003) recommended adding 0.4 ml of 1 % Alizarin red and allowing it to stain overnight. However, due to the small size of the larvae (8-12mm), higher concentrations resulted in excessive red colouring of the entire specimen, including bones and tissue. Therefore, the solution was diluted to 0.1 % concentration through testing on larvae from the sampling, leaving a pink pigmentation on the specimens (Figure 7). Each petri dish of gut content contained approximately 10 ml of water after rinsing the content from the zip-lock bags (Figure 6). Six drops of 0.1 % Alizarin red solution were then added to the petri dish for approximately 10 minutes before rinsing it over a filter (250µm). After staining and rinsing, various taxonomic levels were used for identification of prey, as described in Vøllestad (1985): genus or class for zooplankton; order, infraorder, suborder, or family for insects and zoobenthos; other items as detritus/algae, macrophytes, fish, or parts. A category named 'pink pigmented remnants' was included, as 0.1 % alizarin red S was used to colour the sample.

To enable testing for probability of piscivory, 'Fish total' category was created by combining 'Fish' and 'Pink pigmented remnants' data. In the context of this study, the term 'piscivory' specifically refers to larval piscivory, as only one perch was found with a juvenile roach in its stomach. The 'insect' category was formed by combining *Ephemeroptera, Anisoptera,* Parts, *Sialidae, Trichoptera, Chironomidae pupae, and Chironomidae larvae*. Mollusca and Asellus aquaticus merged into 'Other' category, and the 'Zooplankton' category included *Daphnia, Bosmina, Ostracoda,* and *Copepoda*
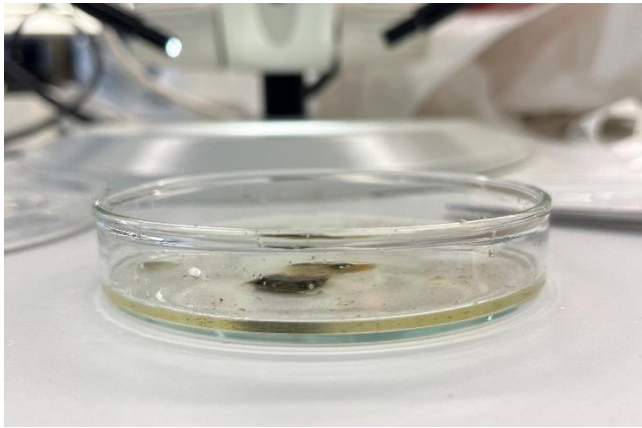
Figure 6 The gut content was put in petri dishes with approximately 10 ml of water, before staining using Alizarin red S.

Figure 7 A test of the Alizarin red S was conducted on fish larvae and insects prior to staining the gut samples. It showed that insects were not affected by colouring, but fish larvae were colored pink.

2.3.2 Measuring roach larvae

Over the study period, a total of 340 larval roach were sampled and measured, with 68 collected using the Bongo net and 272 with the dipnet. All the roach larvae were examined and photographed using a stereoscopic microscope. Total length was measured for all individuals with measurements recorded to nearest millimetre. Anaesthesia was administered to facilitate measurements as the larvae became more mobile. Subsequently, the larvae were preserved in Drams glass containing 70% ethanol.

2.3.3 Age determination of potential predators

Age determination of potential predators were conducted using the operculum (Le Cren, 1947). After removal, the operculum was briefly placed in boiling water to remove skin and blood residues. Each operculum was digitally photographed using a stereoscopic microscope (LEICA S9i) and the program LAS Office 1.4.6 28433, with operculum as enlarged as possible (1x-4x). Based on operculum quality and range of sizes for all three species, 123 individuals were selected for ageing. Growth sones were analysed and measured using Image J software (version 1.54g) on selected individuals (Figure 8)

Back-calculated lengths for previous years were determined using the following formula: $L_1 = \frac{R_1}{R_{tot}} \times L$, where L_1 represented the total length of the fish the first year, R_1 was the radius of the first growth ring, R_{tot} was the total radius of the operculum, and L was the total length of the fish when caught. This back-calculation method relies on the proportional relationship between the operculum length and fish length for roach, rudd, and perch (Horppila, 1999; Le Cren, 1947; Linløkken, 2023).
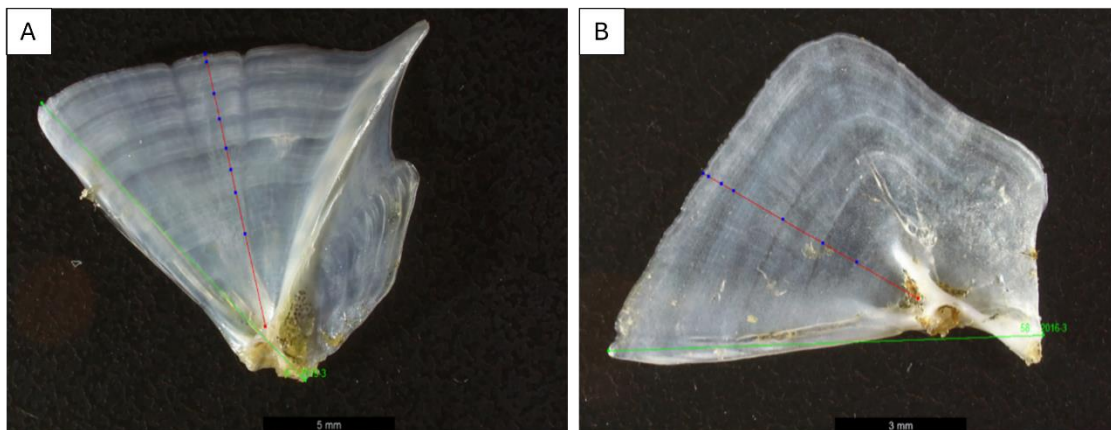
Figure 8 An example of the opercular bones used in age determination, where the winter sones are darker than the summer sones (indicated with a blue dot). The opercular bones presented are from a) a seven winters old female perch, and b) a six winters old female rudd.

2.4 Statistical analyses

2.4.1 Software for data analyses

All preparation and statistical analyses of data were done using R version 2023.06.2. (R Core Team, 2023). The packages 'dplyr' (Wickham et al., 2023a), 'AICcmodavg' (Mazerolle, 2023), 'lubridate' (Grolemund & Wickham, 2011), 'nls2' (Grothendieck, 2022), 'nlstools' (Baty et al., 2015), 'fields' (Nychka et al., 2021), 'viridis' (Garnier et al., 2023), 'scales' (Wickham et al., 2023b), 'reshape2' (Wickham, 2007), 'patchwork' (Pedersen, 2024), 'nnet' (Venables & Ripley, 2002), 'car' (Fox & Weisber, 2019), and 'akima' (Akima & Gebhardt, 2022) were used to analyse data. The 'ggplot2' package (Wickham, 2016) was used to visualise the data. Maps were created with QGIS version 3.34.1, using WMS 'Topografisk Norgeskart'. GPS locations from echo sounding were collected using GPS function in the app 'Norgeskart Friluftsliv'.

2.4.2 Differences in diet of species roach, rudd, and perch

The volumetric analysis of diet based on the extracted gut contents was performed for roach, rudd, and perch to investigate differences in diet and the amount of piscivory. Additionally, a multinomial logistic regression was conducted to assess dietary differences, followed by a Type II Wald chi-square test to determine statistical significance.

2.4.3 Generalized linear model for probability of piscivory

To analyse the probability of piscivory for roach and perch, generalised linear model (GLM) was fitted to binomial diet data. Rudd was excluded from the analyses since there was only one individual registered with 'pink pigmented remnants' in the gut. To analyse, a value of 1 indicated the presence of fish in the gut, while 0 denoted its absence. Further, logit-link function was used to relate the expected probability of piscivory to a linear combination of predictor variables predator length (L1), temperature (T), species (S), and prey length (L2) (McCullagh, 1989). To explore if probability of eating larvae was mostly driven or constrained by temperature or prey size, the highly correlated ($rP = 0.84$) variables temperature and prey length (i.e., mean daily length of larvae caught in dipnet/bongo net) were included in different candidate models and included in the same model selection. A second-degree polynomial for the prey-size effect was incorporated as a candidate model to include a potential non-linear effect, e.g. optimum size of prey for predation (pertinent to predation window concept) (Claessen et al., 2002), on the probability of piscivory. In total 16 candidate GLM models were considered, exploring additive and interactive effects of these variables (see Appendix, Table A1).

The candidate models were evaluated using a corrected version of the Akaike Information Criterion (AIC) for small sample size (Akaike, 1974). The model with the lowest AICc value was designated as the 'top' model (Burnham & Anderson, 2002, p. 62), which best explain the observed data (Zuur et al., 2009, p. 483). Models with values over 2 were not considered as top models (Burnham & Anderson, 2002, p. 72). Once identified as the 'top' model, parameter estimates for the model were summarized, and tested through a variance analysis (ANOVA).

2.4.4 Effect of individual growth and age on probability of piscivory

The back calculation data for roach, perch, and rudd from operculum samples were analysed for Lee-effect (Lee, 1912) using a linear model. Parameter estimates were summarized and tested using an analysis of variance (ANOVA). In order to explore the effect of individual growth performance, growth was fitted to a model, using a non-linear regression (Mann, 1991,

p. 458). The von Bertalanffy model assumes that the length of the fish grows towards an asymptotic maximum length (L_∞) with a growth coefficient (K) and a theoretical age when length is zero (t_0) (Mann, 1991, p. 458; von Bertalanffy, 1957):

$$L_t = L_\infty \cdot (1 - \exp(-K \cdot (age - t_0)))$$

The growth curve was used to determine faster or slower-growing individuals. Additionally, the expected length of each species was calculated using the same formula, with estimated values of each variable from the non-linear regression analysis. Further considering the pace of life and its effect on piscivory, a second model selection was performed based on a the selection of individuals from the age data, using the corrected version of AIC for small sample size (Akaike, 1974). There were in total 123 individuals from the age data.

Candidate GLM-models were fitted to binomial diet data, as described earlier. The top model from the initial selection served as the foundational model for the updated set of models, comprising seven candidate GLM-models (see Appendix,

Table A2). By using a logit-link function (McCullagh, 1989), the relationship between the impact of age and growth on the probability of fish larvae in the diet (π_i) were explored using predictor variables back-calculated length at one year old (L1), age (a), and the difference between empirical length at time of capturing and expected length calculated from the von Bertalanffy (1957) model (ΔL).

2.4.5 Effect of water temperature on growth of free-swimming larvae

To predict the growth rate of free-swimming larvae from May to October, the measured lengths (cm) were converted to weights (grams) following the method described by Mooij and Vantongeren (1990), since the larvae had not been weighed in the lab. The relationship between weight (W) and length (L) was modelled using these two regression equations:

$$W = 6.45 \cdot 10^{-7} \cdot L^{3.87} \text{ (For fish } < 19 \text{ mm)}$$

$$W = 4.46 \cdot 10^{-6} \cdot L^{3.23} \text{ (For fish } > 19 \text{ mm)}$$

Subsequently, the calculated weight of free-swimming roach larvae was utilized to predict growth weight and rate over time. The equation derived from laboratory experiments by Mooij and Vantongeren (1990) on roach growth was employed:

$$\frac{dW}{dt} = a_{max} \cdot W^b \cdot (T - c)$$

16

Here, W represents weight, T represents temperature, and t represents time. Parameters b and c, estimated from growth experiments, were found to be 0.56 and 11.5 °C respectively, representing the increment factor and the lowest temperature for growth (Mooij & Vantongeren, 1990). The parameter a_{max} represents the maximum food value under conditions of excess food, and is calculated to correct for weight and temperature differences experienced in the field (Mooij & Vantongeren, 1990), resulting in a value of 3.54 $g^{0.44} \cdot °C^{-1} \cdot d^{-1} \cdot 10^{-3}$. Predicted growth in weight (g) was determined for both the sampling period and the entire May to October period, to be able to include individuals from the gillnet survey that were of a size which indicated them being in age group 0+ (> 7 cm).

3. Results

3.1 Differences in the diet of species roach, rudd, and perch

The multinomial logistic regression and a following type II Wald chi-square test indicated that the diet of perch, roach, and rudd were not different from each other ($\chi^2_{10} = 16.8, p = 0.079$). Nevertheless, gut content analyses revealed some shifts in the dietary preferences of each species throughout the study period (Figure 9). Perch favoured fish, insects, and zooplankton, with an increasing fish consumption over the study period. There were 38 piscivorous perch, out of the total 81 (46.9 %), in the size range 7.2 to 21.2 cm, with most piscivorous activity in the range 12 to 14 cm (see Appendix, Figure B1). From the piscivorous perch, 28 were female and ten were male. Almost all the fish consumed by perch were free-swimming larvae, except for one which was a 1+ roach. Roach were also observed feeding on fish larvae, noted as 'pink pigmented remnants'. Roach fed mostly on macrophytes, algae, and detritus in the start of the study period, but towards the end of the study, zooplankton and fish larvae were key food items, as well as increase of empty gut. Sixteen male roach individuals, out of the total 111 (14.4 %), ranging from 6.9 to 15.5 cm, consumed fish larvae, with most piscivorous activity in the length interval 9 to 11 cm (see Appendix, Figure B1). For both perch and rudd, the age group with most piscivory were 3+ (see Appendix, Figure B2). Fish consumption increased over the study period for perch and roach, as the insect category decreased. The increase in fish consumption for roach was accompanied by an increase in percentage of zooplankton, while for the perch and rudd percentage of zooplankton fluctuated at lower levels. Rudd primarily relied on macrophytes, algae, and detritus throughout the study period, more than roach. Additionally, rudd fed less on zooplankton and more on insects than roach. The insects found in rudd were mostly adult individuals. Only one rudd individual was found with 'pink pigmented remnants', and some days also lacked rudd data.
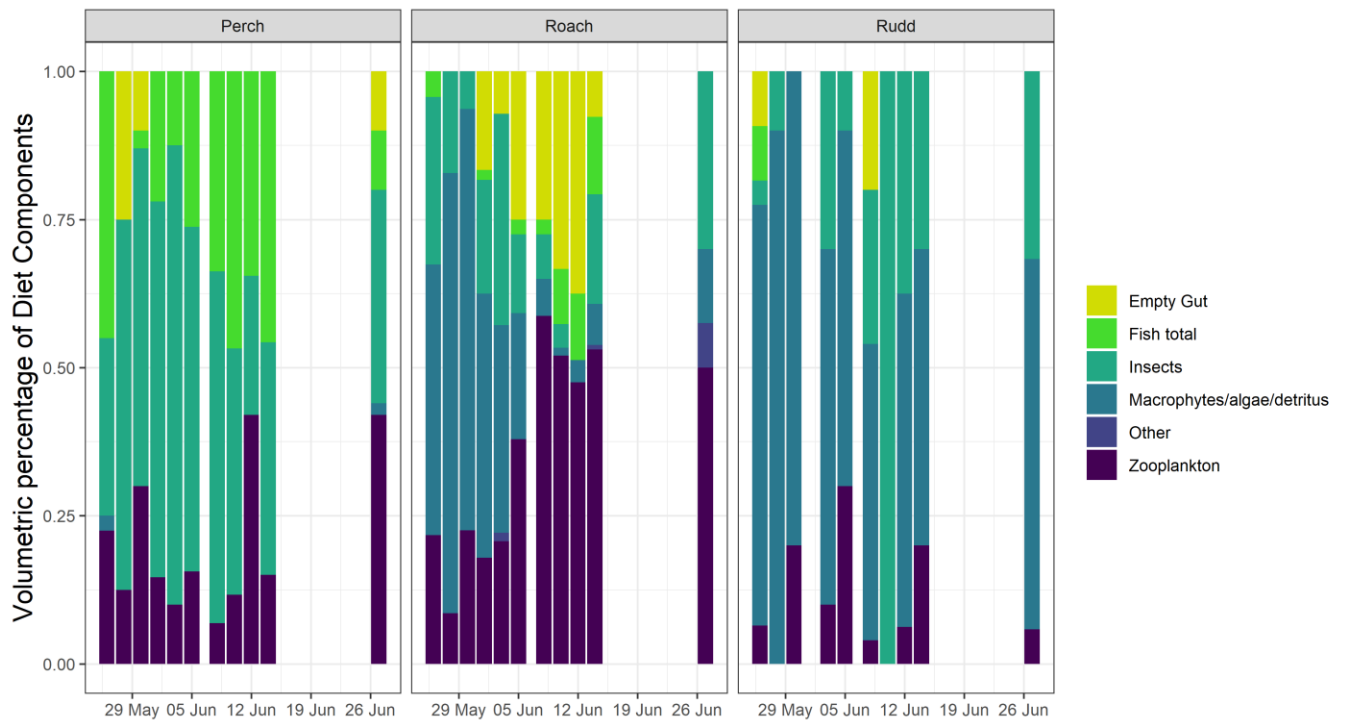
Figure 9 The temporal variation in diet composition represented for perch, roach, and rudd sampled from Årungen. The relative abundance of different food items is characterized in volume (%), and six categories are defined: empty gut, fish total (combined columns fish and pink pigmented remnants), insects, macrophytes/algae/detritus, other, and zooplankton.

3.2 Probability of piscivory in relation to abiotic conditions, prey size, and individual growth

Akaike Information Criterion (AIC) model selection among candidate models fitted to the diet data favoured a predictor structure with additive effects of species and temperature on probability of feeding on fish larvae, with 43 % chance of being top model (AICcWt) (Table 3). The second most supported model favoured a predictor structure with additive effects of second-degree polynomial length of prey and species, with 38 % chance of being top model (AICcWt). Both these models are top models, due to the ΔAICc value being lower than 2.

Table 3 Summary of the Akaike Information Criteria (AIC) model selection are given for the generalised linear models (GLM), where S*T and L2²*S have an ΔAICc lower than 2 indicating that both models have substantial support. The binomial response variable was modeled using species (S), water temperature (T), predator fish length in cm (L1) and prey fish length (L2) as predictor variables. K is the number of model parameters, and AICcWt shows percentage support in the data.

	K	AICc	ΔAICc	Model likelihood	AICcWt	Log likelihood
S*T	4	205.14	0.00	1.00	0.43	-98.46
L2²*S	6	205.37	0.23	0.89	0.38	-96.46
S*T*L1	8	209.33	4.19	0.12	0.05	-96.27
S+T	3	209.75	4.61	0.10	0.04	-101.81
S	2	211.09	5.95	0.05	0.02	-103.51
L2+S	4	211.44	6.29	0.04	0.02	-101.61
S+T+L1	4	211.47	6.32	0.04	0.02	-101.63
S*L1	4	212.18	7.04	0.03	0.01	-101.98
L2*S	3	212.92	7.78	0.02	0.01	-103.40
L1+S	3	213.14	8.00	0.02	0.01	-103.51
L2*S+L1	5	213.20	8.06	0.02	0.01	-101.44
L2*S*L1	8	216.82	11.68	0.00	0.00	-100.02
T	2	229.10	23.96	0.00	0.00	-112.52
Intercept	1	232.02	26.88	0.00	0.00	-115.00
L2	2	232.64	27.49	0.00	0.00	-114.29
L1	2	233.85	28.71	0.00	0.00	-114.89

3.2.1 Effect of species and temperature on probability of piscivory

The candidate model with most support showed that the probability of piscivory increased with increasing temperatures for roach (*Rutilus rutilus*) only (Table 4; Figure 10), while perch remained in the same probability of ~ 50 %. Perch (*Perca fluviatilis*) had an overall higher probability of piscivory than roach. ANOVA test showed that the interaction effect between species and temperature was significant ($\chi^2 = 6.70$, $p < 0.0096$; Table 4)

Table 4 Parameter estimates and ANOVA-results from the generalised linear model (GLM) of the effect of species and water temperature on probability of piscivory are shown. Parameter estimates, standard error (SE), and p-value are represented for every predictor variable in the model including effect of fish species and water temperature on diet. The variable SpeciesPerch is reference and therefore intercept. ANOVA results are presented for every effect considered and interactions between the effects, with significance level set to α = 0.05.

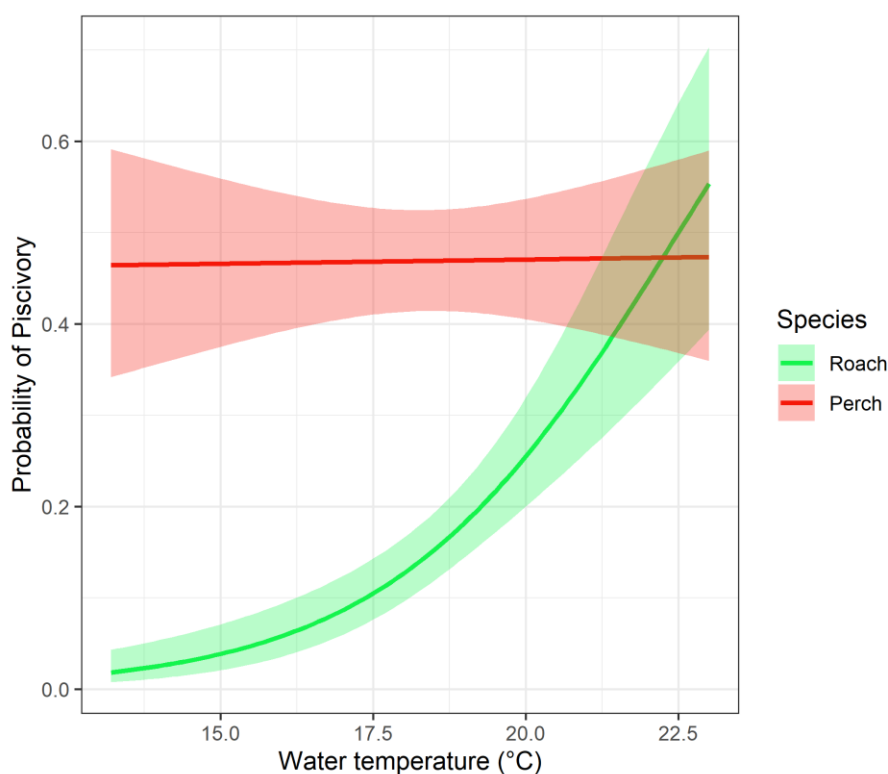| Parameter estimates			ANOVA				
	Estimates	SE	Effect	df	χ^2	df.res	p
Intercept	-0.19	1.66					
SpeciesRoach	-9.46	3.24	Species	1	22.97	190	<0.0001
Temp	0.00	0.09	Temp	1	3.40	189	0.0651
SpeciesRoach:Temp	0.43	0.17	Species:Temp	1	6.70	188	0.0096

Figure 10 The predicted relationship between water temperature and the probability of piscivory are represented for the two species roach in green and perch in red. The plot displays the probability with its uncertainty, represented by shaded ribbons, across the different water temperatures recorded during the sampling period. Temperatures were measured at 1 meter deep.

3.2.2 Effect of species and prey length on probability of piscivory

The candidate model with second most support showed a non-linear relationship between probability of piscivory and length of the prey when captured (Table 5; Figure 11). Perch had an overall higher probability of piscivory, with the highest probability at a prey length of just

below 12.5 mm. Roach, however, had much lower probability of piscivory, and had an optimum of prey length at above 12.5 mm. Through an ANOVA test it was evident that the interaction between species and prey length was non-significant ($\chi^2 = 1.48$, p = 0.48; Table 5).

Table 5 Parameter estimates and ANOVA-results from the generalised linear model (GLM) testing effect of species and prey length on the probability of piscivory. The model incorporated a second-degree polynomial to capture the non-linear effects of prey length (PreyLength2). Parameter estimates, standard error (SE), and p-value are given for every predictor variable in the model including the effect of fish species and prey length on diet. The variable SpeciesPerch is the reference and therefore intercept. ANOVA results are presented for every effect considered and interactions between the effects, with significance level set to $\alpha = 0.05$.

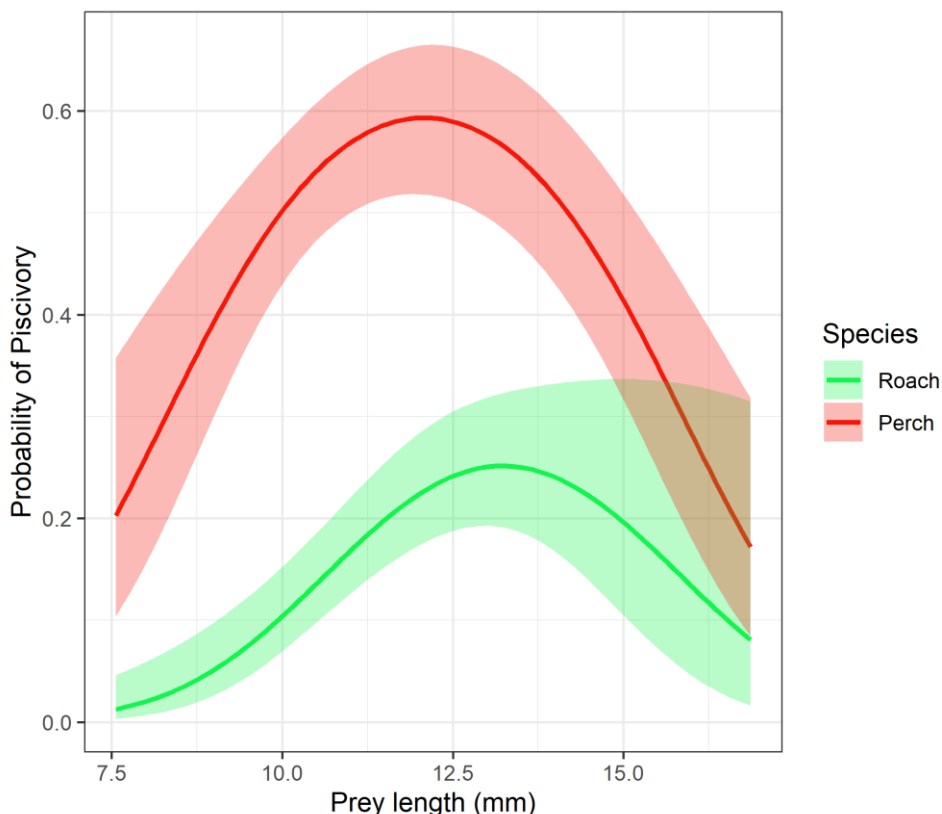| Parameter estimates			ANOVA				
	Estimate	SE	Effect	df	χ^2	df.res	p
Intercept	-12.09	5.41					
PreyLength	2.06	0.89		2	10.08	189	0.0065
PreyLength^2	-0.09	0.04	Species	1	25.51	188	<0.0001
SpeciesRoach	-6.86	10.75	PreyLength:Species	2	1.48	186	0.476
PreyLength:SpeciesRoach	0.64	1.79					
PreyLength^2:SpeciesRoach	-0.02	0.07					

Figure 11 The predicted relationship between prey length (mm) and the probability of piscivory is represented for roach in green and perch in red. The plot displays the 95 % CI represented as shaded ribbons, across the different prey lengths which were measured from sampled fish larvae.

3.2.3 Effect of individual growth on probability of piscivory

Results from the back calculation of length and age showed a range of individuals from different age groups (Figure 12). Roach had the widest range of ages, while perch and rudd (*Scardinus erythrophtalmus*) had individuals up to 7 years of age. There was a significant negative Lee effect in the back-calculated age and length data for roach, where age accounted for approximately 15 % of the variation in first-year growth ($R^2 = 0.1557$, $p < 0.002$) (Lee, 1912). Lee effect for rudd and perch was non-significant ($p = 0.665$, $p = 0.656$).
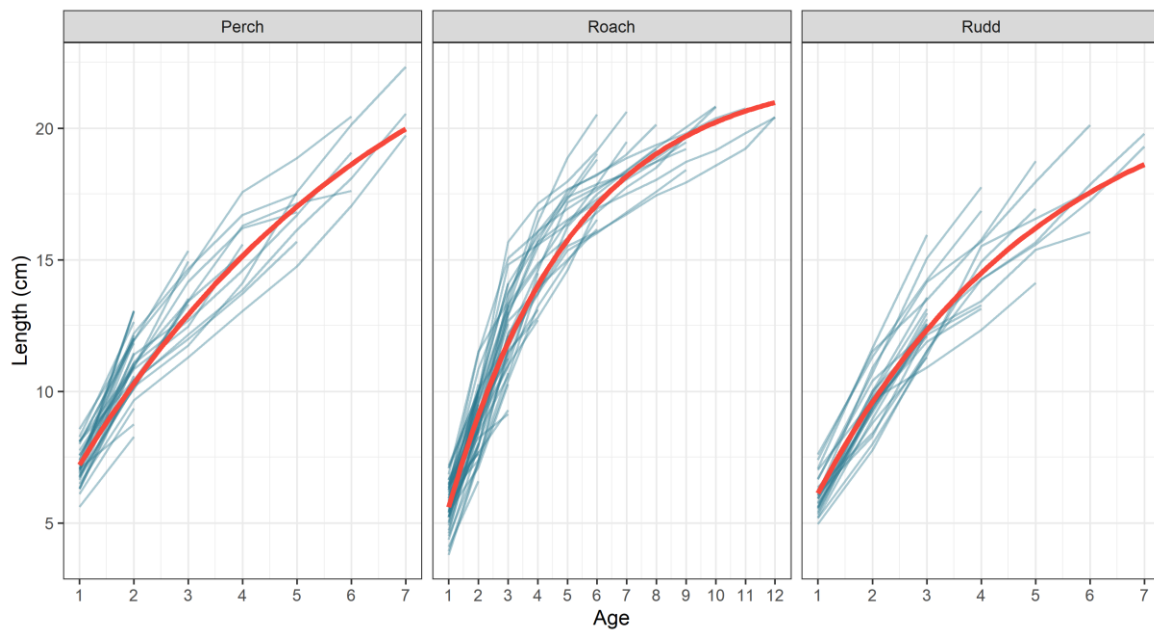

Figure 12 The comparison of the back calculated lengths at different ages for all the individuals are represented in blue and the predicted length at different ages based on von Bertalanffy curve fitting is given in red, for each species.

3.2.3.1 Effect of individual growth and age on probability of piscivory

The second AIC model selection among candidate models fitted to diet data from the selected individuals from the age data favoured a predictor structure with additive effects of species, temperature, and delta length (e.g., the difference between empiric and predicted length of predator (ΔL)) on probability of piscivory (Table 6).

Table 6 Summary of the updated Akaike Information Criteria (AIC) model selection for generalised linear models (GLM) analyzing how age and growth affects the probability of piscivory The binomial response variable was modeled using species (S), temperature (T), age (A), the difference between empiric and predicted length (ΔL), and the back calculated length in the first year (L1). The top model is identified by the lowest AICc value, which is presented first in the table. K is the number of model parameters, and AICcWt shows percentage support in the data.

	K	AICc	ΔAICc	Model likelihood	AICcWt	Log likelihood
S*T*ΔL	8	90.20	0.00	1.00	0.78	-36.26
S*T	4	94.87	4.67	0.10	0.08	-43.21
S*T+A	5	96.26	6.05	0.05	0.04	-42.79
S*T+ΔL	5	96.32	6.11	0.05	0.04	-42.82
S*T*A	8	96.41	6.21	0.04	0.04	-39.37
S*T+L1	5	97.10	6.90	0.03	0.02	-43.21
S*T*L1	8	100.30	10.10	0.01	0.01	-41.31

The model with most support from this model selection based on age data showed that smaller individuals of roach with lower growth than expected (ΔL < 0) had a greater probability of piscivory at higher temperatures (Table 7; Figure 13). Similarily, individuals of roach that exhibited higher growth than expected (ΔL > 0) also showed an increased probability of piscivory at lower temperatures. However, empirical observations for roach were mostly present in areas of lower probability (Figure 12). The model also predicted opposite patterns for perch compared to roach, with higher probability of piscivory with lower growth and lower temperatures. Perch also had an overall increased probability of piscivory under a wider range of conditions, with high probability with better growth and higher temperatures. Additionally, perch empirical observations were more evenly distributed than roach.

The interaction effect between species, temperature, and delta length was significant ($\chi^2 = 8.24$, p < 0.004; Table 7).

Table 7 Parameter estimates and ANOVA-results from the generalised linear model (GLM) testing the effect of species, water temperature, and delta length. Parameter estimates and standard error (SE) are here represented for every predictor variable in the model including effect of species, water temperature, age, and delta length (ΔL) on diet. The variable SpeciesPerch is the reference and therefore the intercept. ANOVA results are presented for every effect considered and interactions between the effects, with significance level set to $\alpha = 0.05$.

| Parameter estimates			ANOVA				
	Estimate	SE	Effect	df	χ^2	df.res	p
Intercept	-0.690	3.183					
SpeciesRoach	-14.645	8.779	Species	1	8.56	93	0.003
Temp	0.027	0.176	Temp	1	4.03	92	0.045
ΔL	-1.748	2.023	ΔL	1	0.01	91	0.906
SpeciesRoach:Temp	0.545	0.440	Species:Temp	1	11.25	90	0.001
SpeciesRoach:ΔL	23.835	12.299	Species:ΔL	1	4.86	89	0.027
Temp:ΔL	0.099	0.108	Temp:ΔL	1	0.01	88	0.924
SpeciesRoach:Temp:ΔL	-1.335	0.666	Species:Temp:ΔL	1	8.24	87	0.004
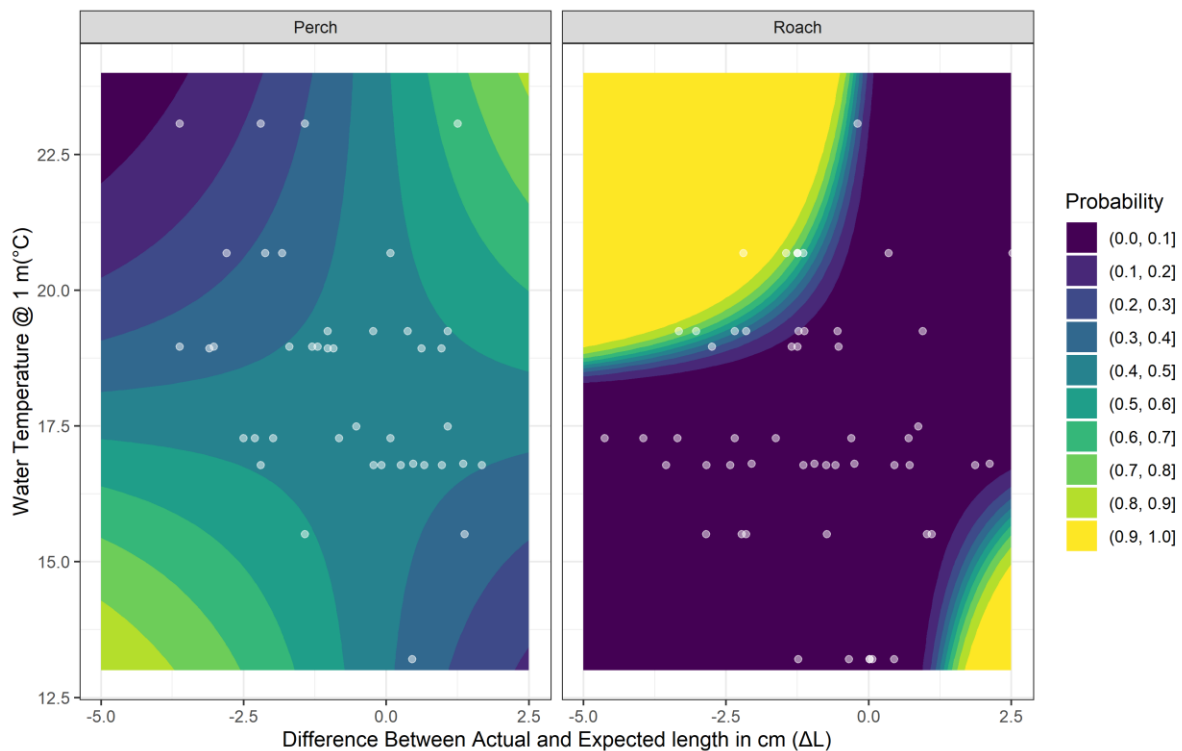
Figure 13 The relationship between water temperature and delta length on the probability of piscivory is represented for roach and perch. The probabilities are characterized as a gradient colouring, with highest and lowest probability in yellow and blue, respectively. The empirical observations of piscivory over different temperatures and delta length are presented by white points.

3.2 Effect of water temperature on growth of free-swimming roach larvae

A minimum of 27 free-swimming roach larvae were sampled every day, and from measuring length there were observed outliers in length in the data, indicating occasional deviations from expected growth patterns. The smallest individual measured 9.1 mm in total length, while the largest reached 28 mm, sampled on the first and last field days, respectively (see Appendix, Table B1; Figure 14). During the first part of the study period, free-swimming pre-larvae (Hammer, 1985) were mainly found around the reed, in addition to unhatched eggs adhered to the reeds, making dipnet the most efficient method due to proximity to the shore. However, as the study progressed, the Bongo net became more effective, particularly from day 3 (May 28th) onwards, as the larvae became more active and left the reed covers, even circling the boat (see Appendix, Figure B3). By day 4 (June 1st), all the eggs attached to the reed had hatched and disappeared. Around the midpoint of the sampling period, the water became increasingly turbid, prompting more active movement around the boat. Day 7 (8th June) had the highest catch from the Bongo net (see Appendix, Figure B3), while day 8 (10th June) displayed similar activity outside the reed. However, in subsequent sampling days, larvae activity decreased, and they remained closer to the reed. Consequently, the last three sampling days resulted in very low catches from the Bongo net (i.e., only 2-3 individuals per day)
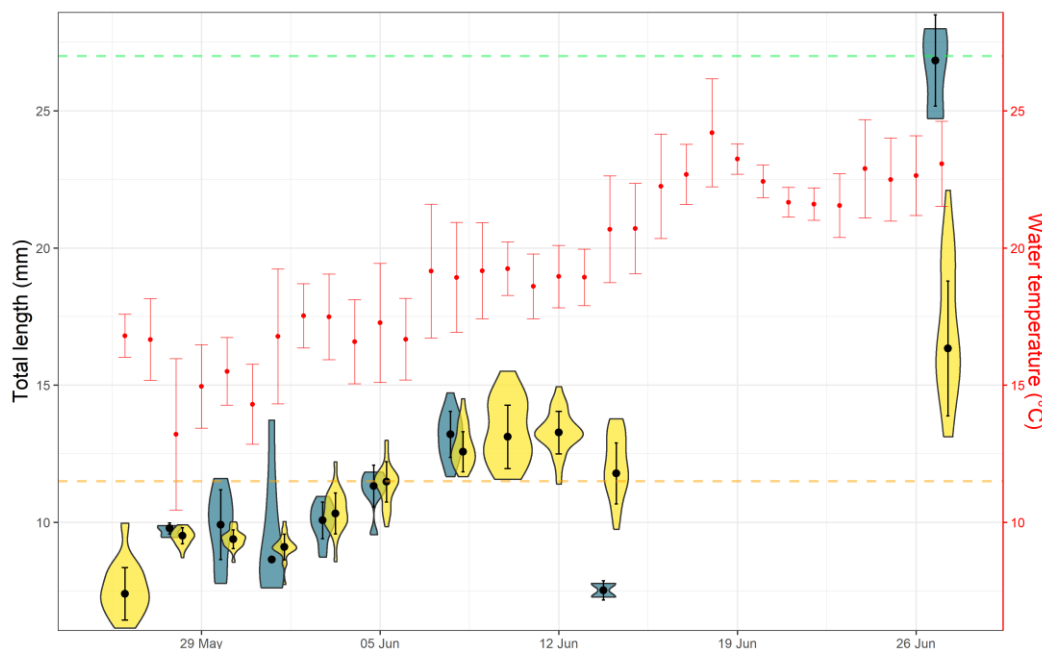

Figure 14 The total length (mm) of the free-swimming fish larvae caught during the sampling period, compared to water temperature during the same period represented in red dots with corresponding standard deviation. The max optimum temperature is represented in green dashed line and minimum temperature represented in orange dashed line for roach. The violins are coloured according to the method used, with blue violins representing Bongo net and yellow violins representing dipnet, and black dot representing median with corresponding standard deviation.

3.2.1 Predicted weight and growth rate of larval roach

Calculations on specific growth rate of the larvae sampled using Dipnet showed a decreasing growth rate associated with increasing water temperatures (Figure 15). For both water temperature and specific growth rate there are considerable error bars, suggesting uncertainty in the specific growth rate measurement. Further, the predicted weight and growth model shows a development as predicted, except for some deviations observed around 1st and 10th of June (Figure 16). Empirical growth was found to be almost consequently below what was predicted. This trend was even more pronounced when two individuals below 7 cm from the gillnet survey were included in the model (Figure 16).
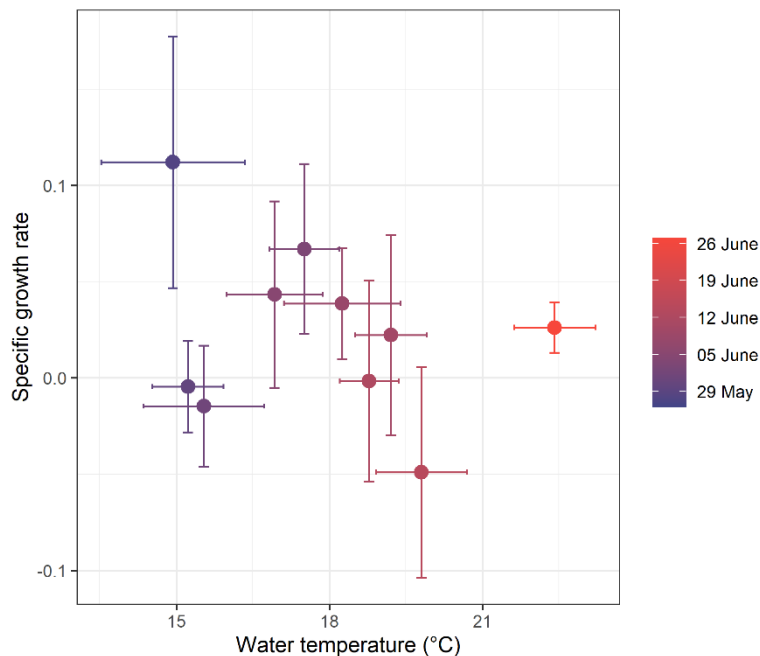

Figure 15 The specific growth rates of the larvae caught using Dipnet is compared to the average water temperature during the sampling period. The standard error (SE) is calculated for both mean temperature and specific growth rate and portrayed using error bars for each point.
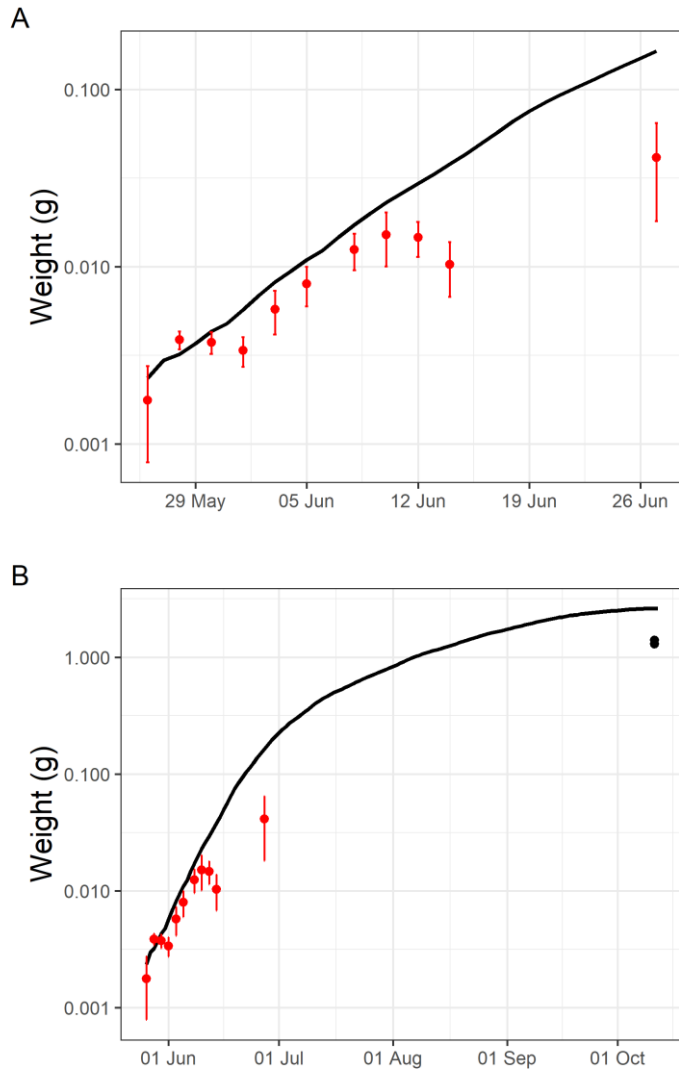
Figure 16 The predicted weight for roach larvae are represented by a black line compared to the empiric weight in red dots from a) the sampling period and b) the period from May to October, with two individuals from the gillnet survey represented as black dots. The predicted weight are calculated weights (Mooij & Vantongeren, 1990) based on measured lengths of the larvae, with corresponding standard deviation.

4. Discussion

This study provides insight into the trophic ecology of roach, rudd, and perch in Lake Årungen, focusing on the piscivory behaviour exhibited by roach and perch. Roach were observed engaging in facultative larval piscivory and cannibalism, with the probability of piscivory increasing with temperatures. Temperature had a greater impact on the probability of piscivory than prey length, and this effect was more pronounced in roach. Further, the individual characteristic growth was found to affect the probability of piscivory. Despite no overall dietary differences among the three species, shifts in dietary preferences were noted during the study. Additionally, the study examined patterns in development of free-swimming roach larvae with increasing temperatures (see Appendix, Figure B7; Figure B8) (Hammer, 1985), which revealed a negative growth rate and empirical weight below what was predicted (Mooij & Vantongeren, 1990).

4.1 The diet of species roach, rudd, and perch

To our knowledge this study is the first to demonstrate that roach in Årungen exhibited facultative piscivory. The 'pink pigmented remnants' found in the guts of roach and rudd are likely fish tissue as indicated by the coloration (see Appendix, Figure B5), which suggest the presence of calcium (Erdoğan et al., 1995; Liao et al., 2020). Though it's conceivable that the 'pink pigmented remnants' could be zooplankton, given that their exoskeletons contain calcium (Nina et al., 1999), the zooplankton exoskeletons discovered in roach guts retained their original colour and integrity, unlike the appearance of the 'pink pigmented remnants' (see Appendix, Figure B5). Additionally, the 'pink pigmented remnants' match the size of fish larvae found in perch guts (see Appendix, Figure B4). Perch displayed cloud-like formations with black pigmentation in their digestive tracts after consuming fish larvae, a contrast to the stomach contents containing only zooplankton (see Appendix, Figure B6). Despite some uncertainty associated with the technique, we are confident that the 'pink pigmented remnants' were fish larvae, indicating larval piscivory.

Since the number of piscivorous roach was low and only one rudd was observed with fish larvae in the gut, this might suggest incidental piscivory, as noted in previous studies (Lammens & Hoogenboezem, 1991). However, Guinan et al. (2015) observed rudd engaging in facultative piscivory before summer, when water temperatures were cooler, and shifting to herbivory as temperatures rose and macrophytes became more abundant, thus providing a superior food source (Behrens & Lafferty, 2007). Roach has the ability to utilize macrophytes when animal

foods are less abundant (Persson, 1991, p. 532). In contrast to rudd, roach utilization of macrophytes, algae, and detritus declined over the study period, suggesting that the shift towards zooplankton and fish larvae was due to food availability. The rise in empty gut occurrences in roach over the study period may support the piscivorous behaviour, aligning with earlier observations where piscivorous individuals frequently had empty guts compared to non-piscivorous individuals (Vinson & Angradi, 2011). However, empty guts could also be explained by food shortages in Årungen, as roach are able to survive on fewer food items (Brabrand, 1985), or due to regurgitation from stress of being captured by gillnets (Le Cren, 1992; Windell & Bowen, 1978, p. 220).

Since roach is an omnivorous species, primarily consuming macrophytes and zooplankton (Eie & Borgstrøm, 1981; Lammens & Hoogenboezem, 1991, p. 354), and perch is a carnivorous, favouring insects, zooplankton, and fish (Eie & Borgstrøm, 1981; Le Cren, 1958; Svärdson, 1976), it was anticipated that perch would exhibit higher levels of piscivory than roach. Indeed, the study found a higher percentage of piscivorous perch (i.e., 46.9 %) compared to roach (i.e., 14.4 %). These findings indicated that piscivory remains a crucial regulatory factor in Årungen (Borgstrøm et al., 1984; Vašek et al., 2013). Additionally, an increase in fish larvae in the diets of both roach and perch was noted during the sampling period. This increase was expected for perch, whose feeding rates rise with increasing prey availability, which in this case was fish larvae (Le Cren, 1958; Linløkken, 2023). The perch individuals exhibiting the highest piscivory were in the age group 3+, which coincides with an ontogenetic shift for the perch (see Appendix, Figure B2). Shifting towards piscivory at this age is beneficial for perch due to a stagnation in growth after reaching maturity (Le Cren, 1992). Given that an ontogenetic shift is linked to prey abundance (Le Cren, 1992), this dietary change likely reflected a shift in the availability of food items, coinciding with a rise in roach larvae presence in the water column during the study.

Contradictory to the predictions, no differences were observed in the overall diets of roach, perch, and rudd, suggesting a dietary overlap. Notably, all three species consume zooplankton, macroinvertebrates, insects, and fish, which could indicate interspecific competition. The interspecific competition for zooplankton between roach and perch may also have affected the changes in dietary preferences over the study period. Particularly, this is evident given the dominance of roach in the lake ecosystem (see Appendix, Figure A1), and its competitive advantages in eutrophic lacustrine ecosystems (Persson et al., 1991; Svärdson & Molin, 1981). Perch has been found to feed less on zooplankton in the presence of dense roach populations (Persson & Greenberg, 1990b), and the results goes along this trend (Figure 9). Larger densities

of roach have previously been found to affect perch juvenile resource utilization, by increasing interspecific competition for zooplankton and leading juvenile perch to switch to macroinvertebrates at an earlier stage (Persson, 1986b; Persson & Greenberg, 1990b). When younger perch undergo an early dietary shift, this can lead to increased intraspecific competition with older perch, who also forage on macroinvertebrates (Persson & Greenberg, 1990b) (see Appendix, Figure B2). Therefore, the intraspecific competition could lead to piscivory being more beneficial for the older perch if fish larvae were a more abundant food source than macroinvertebrates. While there is no growth data confirming an earlier dietary shift in perch, the observed increase in the volumetric percentage of fish larvae and insects in their diet, coupled with generally low zooplankton levels, suggests that the former may be energetically more advantageous and enhance growth (Allen, 1935; Le Cren, 1992).

In addition to competing with perch, roach also engages in interspecific competition with omnivorous rudd (García-Berthou & Moreno-Amich, 2000; Johansson, 1987). While roach efficiently forages on zooplankton (Eie & Borgstrøm, 1981), constituting up to 50 % of its diet on certain days, rudd increasingly relies on insects, particularly those on the water surface. The utilization of neustonic insects minimizes the dietary overlap with roach and drives habitat segregation, because of the interspecific competition (García-Berthou & Moreno-Amich, 2000; Johansson, 1987). Although their diets are similar, rudd favours the littoral zone (see Appendix, Figure A1) and engages more in herbivory compared to roach (García-Berthou & Moreno-Amich, 2000), as roach's efficient foraging on zooplankton outcompetes rudd (Johansson, 1987). The interspecific competition between the three species in Årungen, due to their overlapping diets, could lead to cannibalism being more beneficial as it dampens competition and increases resource availability (Andersson et al., 2007; Hamrin & Persson, 1986).

Cannibalism counteracts the high amplitude dynamics of fish populations by dampening competition, as it removes conspecifics competing for the same resources (Claessen et al., 2000; Persson et al., 2004). Since the larvae sampled during the study period is identified as roach, this could indicate that roach engaged in cannibalism when feeding on fish larvae during this period. While it's conceivable that the roach larvae could be perch, this was considered unlikely as perch typically spawns in egg-ribbons (Gillet & Dubois, 1995), whereas the eggs observed in the field were solitary eggs adhered to reeds, a common spawning behaviour found in roach (Diamond, 1985; Mills, 1991, p. 487) (see Appendix, Figure B9). Roach larvae could also have been rudd, but they usually spawn later in the season than roach (Mark et al., 1987; Rheinberger et al., 1987; Tarkan, 2006). The morphological development of the roach larvae sampled also

resembled larval roach specimens described by Hammer (1985). The piscivorous behaviour of roach coincided with the roach larvae reaching the true feeding stage with organisms resembling the crustaceans Ostracoda in their guts (Hammer, 1985) (see Appendix, Figure B8), indicating they could be competing for resources, which could make cannibalism more beneficial for roach. Additionally, as roach larvae grow, they increase their activity outside the reeds (Rosenzweig et al., 2007). Venturing out from the reed coincides with the crustacean consumption (Mark et al., 1987) (see Appendix, Figure B8), and makes the larval roach more vulnerable to predation from roach and perch. The high predation pressure from roach and perch also indicates that there was a high abundance of roach larvae during the study period (Le Cren, 1992; Linløkken, 2023), which increases the food availability and predation risk.

4.2 Probability of roach and perch piscivory in relation to prey size

The range of prey sizes that a predator can utilize is called the predation window, defined by a minimum and maximum prey size (Claessen et al., 2002). As anticipated, there was a maximum prey length for observed piscivory in both perch and roach, but there was no discernible difference between the species on the impact of prey length on the piscivory probability. However, visually, the data suggests a difference in the optimum prey size for roach and perch. Since maximum prey size is typically determined by the predator's gape size (Nilsson & Brönmark, 2000), and perch has a wider gape more adapted to piscivory than roach (Fish, 1960; Persson, 1983), it would be likely that perch has a higher prey size optimum. Yet, our results showed a higher predicted optimum prey size for roach than for perch (Figure 11). Additionally, the most piscivorous roach were smaller in size (9 to 11 cm) compared to perch (12 to 14 cm) (see Appendix, Figure B1), which should limit the gape size of roach even further. Thus, there was an overlap in the predation windows for perch and roach in terms of prey size, likely influenced by the small size of the larvae at the time of predation (10-12 mm) (Figure *14* The total length (mm) of the *free-swimming* fish *larvae* caught during the sampling period, compared to water temperature during the same period represented in red dots with corresponding standard deviation. The max optimum temperature is represented in green dashed line and minimum temperature represented in orange dashed line for roach. The violins are coloured according to the method used, with blue violins representing Bongo net and yellow violins representing dipnet, and black dot representing median with corresponding standard deviation.Figure 14). Therefore, the fact that roach had the highest optimum prey size could indicate that predator and prey mobility is a more important factor explaining optimum size of larval prey than gape size (Christensen, 1996; Claessen et al., 2002).

Roach having a higher optimum prey size than perch may be due to foraging advantages in eutrophic lacustrine ecosystems. Previous studies have shown that perch forage more efficiently than roach and rudd in the littoral zone when submerged macrophytes are present (Winfield, 1986). Despite the high turbidity in Årungen, which likely has reduced submerged macrophyte abundance (Akinnawo, 2023), reeds are widespread in the study area. The vegetation could therefore influence roach foraging behaviour. Additionally, Christensen and Persson (1993) noted that the presence of vegetation did not affect the speed of the roach prey. In Årungen, this implies that predators must be faster to capture them, regardless of habitat structures. However, when the roach larvae left the reed covers, they become available as food sources in areas where roach is more efficient than perch (Svärdson, 1976; Vøllestad, 1985). When the foraging arena is spatially larger, maximum prey size is often smaller, as it is increasingly difficult for predators to catch the prey (Christensen, 1996). The swimming speed of foraging roach has been found to be higher than perch swimming speed (Johansson & Persson, 1986; Persson, 1991, p. 534). The increased speed of larvae as they grow (Mills, 1982; Mills, 1991; Voesenek et al., 2018), combined with their movement out from the reed into the turbid waters could therefore have increased foraging advantages for roach compared to perch in Årungen.

4.3 Probability of roach and perch piscivory in relation to temperature effects

Fish are highly sensitive to temperature fluctuations (Fry, 1971; Graham & Harrod, 2009). Water temperature affects digestion, energetic demands (Linløkken et al., 2010), assimilation rate (Webb, 1978) and swimming speed (Linløkken et al., 2010), impacting hunting efficiency, growth and recruitment (Linløkken, 2023; Mann, 1991, p. 462) in both perch (Le Cren, 1958) and roach (Britton et al., 2004; Mooij & Vantongeren, 1990). Therefore, a positive correlation between water temperature and piscivory was anticipated. However, the results revealed species-specific responses to temperature changes, showing increased piscivory with rising temperatures only in roach (Figure 10).

Previous studies have shown that roach are eurythermal (Graham & Harrod, 2009; Linløkken et al., 2010), responding more easily to temperature changes than perch (Linløkken et al., 2010), which enhances their competitive advantages over perch (Persson, 1983; Persson, 1986a; Persson & Greenberg, 1990b). Seasonal temperature variations play a crucial role in shaping competitive dynamics among fish species in temperate lakes (Persson, 1986b; Persson, 1987). The study period was unusually warm and dry (Figure 3; Figure 5), and average temperatures

were 19.3 °C, which is below the optimal 23 °C for perch (Fiogbé & Kestemont, 2003) and 27 °C for roach (Hardewig & Van Dijk, 2003; Linløkken, 2023; van Dijk et al., 2002). The highest temperature recorded however, was 24.2 °C on June 18th, exceeding the optimum temperature for perch, a cool water species. Temperatures over the optimum could potentially reduce perch's competitive abilities (Graham & Harrod, 2009; Hokanson, 2011). Additionally, perch hunts visually (Bernes et al., 2015; Lessmark, 1983) and higher temperatures could therefore have decreased its hunting ability as water turbidity increased over the study period. Roach, however, has been found to have higher capture rates and swimming speed (Mittelbach, 1981; Persson, 1986b) at temperatures above 18 °C, and does not rely merely on vision when hunting as it uses suction feeding (Lammens & Hoogenboezem, 1991, p. 356). The disadvantages of perch in combination with roach's advantages, could have tipped the competition in favour of roach.

When analysing based on back calculated aga data, water temperature was still an important factor explaining the probability of piscivory, in addition to the growth of the fish presented as delta length (e.g., the difference between empiric and predicted length of predator). As the life history tactics of fish vary with hatching year (Claessen et al., 2000; Rochet, 2000), the growth of the captured individuals could give indications of the interplay between competition and cannibalism. Our results showed that for both roach and perch, individuals with poor growth had higher probability of piscivory (Figure 13). There were however opposite patterns in temperature responses for the species, as roach had a higher probability at high temperatures, while perch had a higher probability at low temperatures. Additionally, perch had an overall higher probability of engaging in piscivory over a range of temperatures. The temperature responses further suggest that perch piscivory behaviour is not as affected by temperatures increasing as roach piscivory. Individuals engaging in piscivory often tend to be bolder and take more risks (Keast, 1985), which often leads to a faster growth for those individuals (Biro et al., 2014). The individuals experiencing poor growth could therefore have engaged in piscivory to enhance their growth rate. However, in teleost fishes the males are generally smaller than the females (Mann, 1991, p. 471), and since all piscivorous roach were male, this could have skewed the roach results towards poor growth. 10 of 38 piscivorous perch individuals were male, making the size of the males less affecting for perch results. Additionally, it is important to note that the observed data were mostly found in areas of low probability (Figure 13). Even though these results are based on a selection of the individuals, it suggests that roach and perch engaged in larval piscivory to maintain energy to enhance their growth (Keast, 1985). It is also

important to note that the observed data were mostly found in colouring, suggesting low probability. Therefore, it cannot be concluded that there is data present in the areas of higher probability.

4.4 Temperature effect on roach larval growth

Temperature affects the growth and survival of fish larvae, with previous studies suggesting a positive correlation between water temperature and growth of larvae (Mills & Mann, 1985; Mills, 1991, p. 497). Contradictory to expectations, the specific growth rate of roach larvae decreased as water temperatures increased. The rapid specific growth rate of roach larvae post-hatching, however, aligns with previous studies showing that temperature influence larval growth (Mills & Mann, 1985; Wieser et al., 1988). Additionally, there were deviations in the empirical weight compared to the predicted weight, with the actual weights consistently lower than expected. The presence of outliers in the data, potentially from other species like rudd and perch, may have skewed the growth rates; notably, one very small and one very large individual were observed (Figure 15). The lower empirical weights are not unexpected given that the model predictions assume excessive food sources available (Mooij & Vantongeren, 1990). Moreover, the roach population studied by Mooij and Vantongeren (1990) was located further south than Årungen, possibly contributing to the low empirical weights. However, the deviation in growth rate became more pronounces in early June and continued to decline after 10th of June, coinciding with the observed deviations in larval weight (Figure 16).

The observed deviations in weight could be attributed to density-dependent mortality among larval roach, which might explain the negative specific growth rate observed in Årungen (Grenouillet et al., 2001; Linløkken, 2023). High piscivorous pressure during this period suggested a high abundances of roach larvae, potentially leading to reduced resource availability per individual (Mann, 1991, p. 464; Townsend & Perrow, 1989). Unhatched eggs sampled on May 26th and 26th suggest that roach in Årungen hatched just a few days before sampling began (see Appendix, Figure B9), aligning with previous studies on roach spawning and hatching (Diamond, 1985; Mark et al., 1987; Mills, 1991, p. 487). Increased feeding activity and movement away from the reeds typically occur in the second half of June, following late May hatchings (Mark et al., 1987; Rheinberger et al., 1987). Consequently, it is plausible that in this study, roach larvae left the reeds earlier due to the high abundance of larvae and shortage of food. The fish larvae are more sensitive to environmental factors such as food availability in the stage where they develop exogenous feeding (Mills, 1991, p. 496; Sifa & Mathias, 1987). The available food source, likely limited to phytoplankton, which is indigestible for early-stage

roach larvae (Hammer, 1985; Mark et al., 1987; Wieser et al., 1988), could have prompted poor growth and potentially led to an earlier departure from the reed covers. However, without precise observations of the hatching date, we cannot conclude that they left the reeds earlier than usual. Leaving the reeds also increase their vulnerability to predators (Rheinberger et al., 1987). It is therefore possible that smaller individuals remained within the reeds for a longer period, as they are more vulnerable and less adept to avoiding predators (Mills, 1991, p. 497; Voesenek et al., 2018). Consequently, this behaviour might have biased the sample collected with the dipnet from shore towards these smaller individuals and affecting the specific growth rate. Additionally, increasingly active roach larvae might have more effectively avoided capture by bongo trawls (Persson 2004; Noble 1970; Wanzenböck 1997), further skewing growth data towards smaller, less mobile individuals.

4.5 Methodological limitations and suggestions for improvement

This study was performed for only one field season, meaning that a generalization of results should be done with caution. Our results could have been affected by the weather during the study period, considering that 2023 was a warmer and drier year than usual. Because only a small portion of individuals from the lake were analysed, caution should also be applied when using the results to make implications for population level. All the analyses were done on a small sample size; however, this was corrected for during our analyses using the corrected Akaike Information Criteria for small sample sizes. Due to uncertainty of the 'pink pigmented remnants' category based on Alizarin red S colouring (described above), the use of stable isotope analysis of liver tissue could improve the identification of piscivory behaviour (Cowgill & Burns, 1975; Guinan et al., 2015; Myreng, 2013). It could also be combined with DNA metabarcoding to identify taxa of diet components (Snider et al., 2021), or even with a laboratory experiment of roach being fed fish larvae to investigate how it looks in the gut.

For future studies, it would have been an interesting variable to investigate if there were any diel changes in probability of piscivory. Since the gillnetting was performed only during daytime, it could have biased the diet data of roach, as it performs diel migrations based on food availability (Bohl, 1980), leading to zooplankton being overestimated compared to macroinvertebrates, plants and detritus (Horppila, 1999). The difficulty with sampling fish larvae is a common problem, as they become increasingly mobile, and may escape the Bongo net or dip net (Noble, 1970; Persson et al., 2004). An improvement to our used method could therefore be to use a smaller bongo trawl with larger mesh size, which would move faster, since the size used in this study may have been too slow to capture larger individuals. For future

research on larval growth, observations on spawning and hatching could increase the understanding of their development. Additionally, measurements of abundance could have made it possible to investigate if the availability of fish larvae affected amount of piscivory.

4.5 Implications for management

Piscivory and cannibalism by roach could have implications for lacustrine ecosystems affected by eutrophication, potentially triggering trophic cascades throughout the ecosystem and impacting several levels of the food web. With climate change intensifying runoff, managing the water quality of lakes will pose increasing challenges. Advantages for Norwegian roach may grow, given its preference for eutrophic lacustrine ecosystems like Årungen, coupled with potential benefits from warmer field seasons and rising water temperatures. Often targeted for removal, roach management aims to boost zooplankton levels, thereby reducing phytoplankton blooms and enhancing water quality (Andersson et al., 1978; Haugen et al., 2019; Horppila & Kairesalo, 1990). The removal of roach and enhancing of water quality further supports increased populations of predators like northern pike and perch (Bernes et al., 2015; Lessmark, 1983). In lakes such as Årungen and Østensjøvann, where roach is a dominating species (Haugen et al., 2019) (Table 2), a small change in cannibalistic or piscivorous behaviour within the roach population could change the dynamics of the fish population. The cannibalistic behaviour of roach could implicate that roach is partly reducing its own population, and therefore it could also change how many individuals need to be removed in a potential biomanipulation effort to improve water quality. Since Årungen is connected to Oslofjorden, effects of improving the water quality will also affect the marine ecosystem. Further research is therefore needed to investigate how common facultative piscivory in cyprinids is, as it could be valuable when deciding what management strategies to use when restoring eutrophic lacustrine ecosystems.

5. Conclusion

This study found roach engaging in facultative piscivory, and possibly cannibalism, in the eutrophic lake Årungen. However, it is still unsure whether the 'pink pigmented remnants' are fish larvae or not. Although perch were the most piscivorous species observed, contrary to our expectations, there was no overall dietary difference among the three species studied. The effect of temperature on the probability of piscivory was only evident for roach. This species-specific response was probably related to advantages of roach in eutrophic waters, as they are eurythermal and forage more efficiently in turbid waters. While there was no difference in roach

and perch on the effect of prey size on piscivory behaviour, roach had a higher predicted optimum prey size than perch, indicating that gape size is not the primary factor influencing predation window in Årungen. Since roach dominates Årungen, predation or cannibalism behaviour can have a large impact on its population, and consequently for biomanipulation efforts to improve the water quality. Further research is needed on fish larvae piscivory and cannibalism by omnivorous cyprinids in eutrophic lakes, to enable a sustainable management of the ecosystem.

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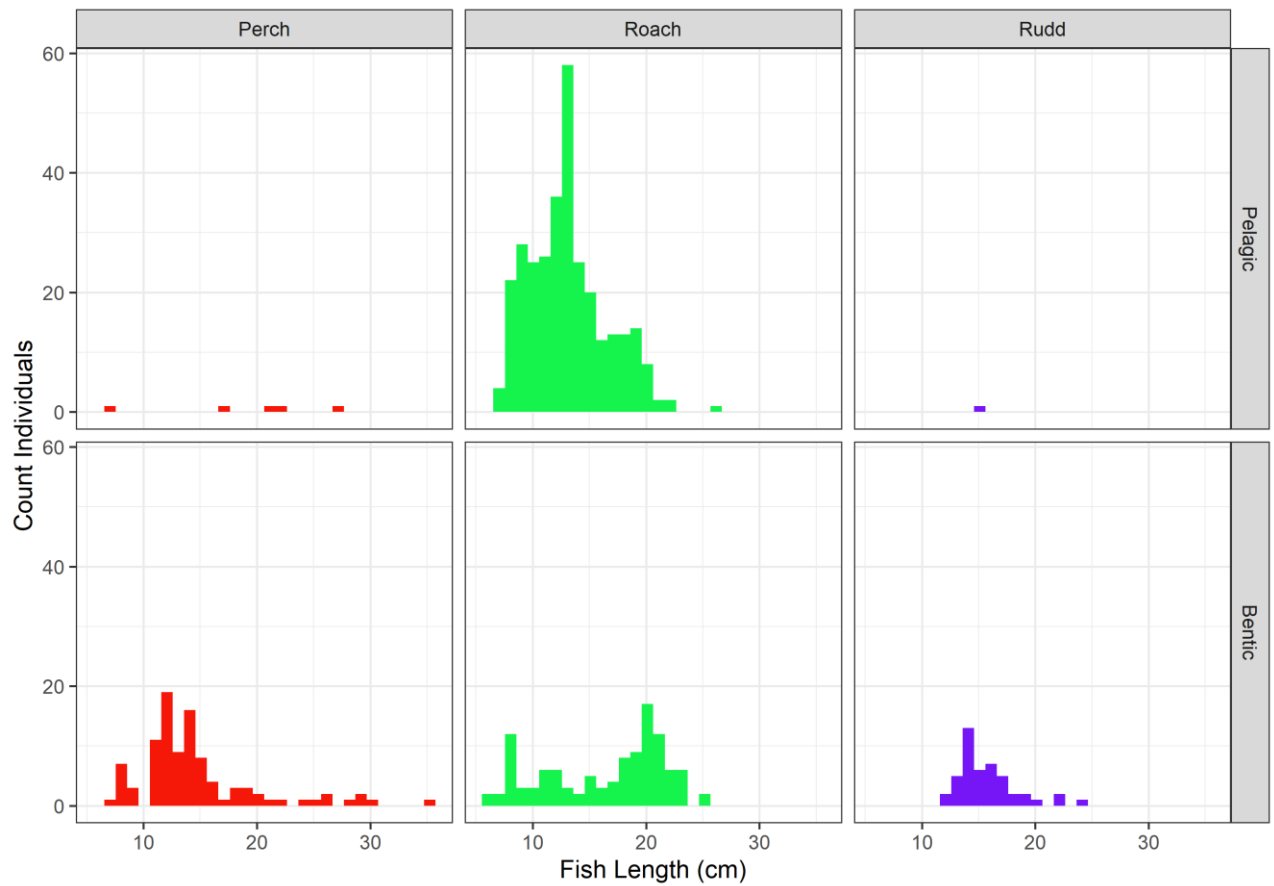
Appendix A

Figure A1 Histogram portraying the counted individuals and length (cm) of each species perch (red), roach (green) and rudd (purple) from the gillnet survey. The plot shows the distribution of fish lengths for the different species in the pelagic zone versus the benthic zone.
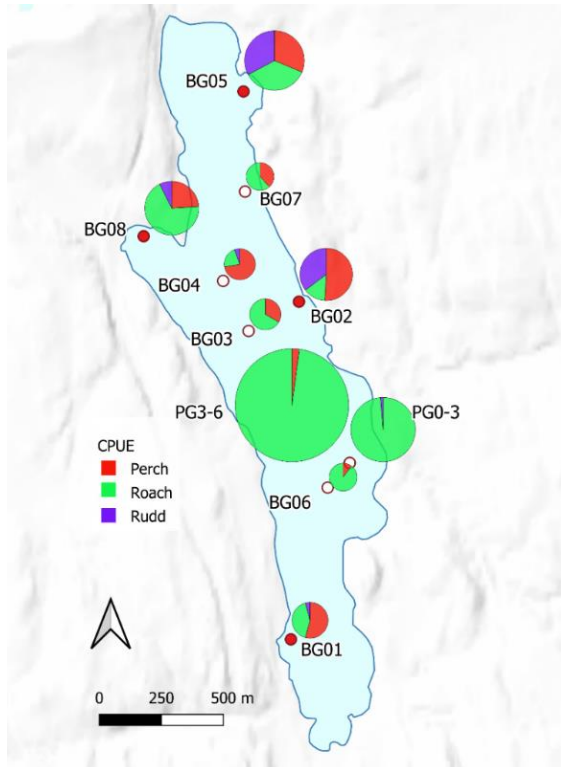
Figure A2 Species distribution for every location during gillnet survey, from calculated CPUE for each species: perch (red), roach (green) and rudd (purple). White dots represent >5 m in depth and red dots represent <5 m in depth. Size of pie chart indicates size of total catch from the gillnet.

Table A1 The generalized linear models (GLM) used when testing probability of piscivory.

Model	Generalized linear model (GLM)
1	glm(PrPPR~Length_cm,filt_dietDataAnalyse, family=binomial(link="logit"))
2	glm(PrPPR~Length_cm*Species,filt_dietDataAnalyse, family=binomial(link="logit"))
3	glm(PrPPR~Length_cm+Species,filt_dietDataAnalyse, family=binomial())
4	glm(PrPPR~Species,filt_dietDataAnalyse, family=binomial())
5	glm(PrPPR~1,filt_dietDataAnalyse, family=binomial())
6	glm(PrPPR~Species*Tem p,filt_dietDataAnalyse, family=binomial())
7	glm(PrPPR~Species+Temp,filt_dietDataAnalyse, family=binomial())
8	glm(PrPPR~Species+Temp+Length_cm,filt_dietDataAnalyse, family=binomial())
9	glm(PrPPR~Species*Temp*Length_cm,filt_dietDataAnalyse, family=binomial())
10	glm(PrPPR~Temp,filt_dietDataAnalyse, family=binomial())
11	glm(PrPPR~Tot.length.mm,filt_dietDataAnalyse, family=binomial())
12	glm(PrPPR~Tot.length.mm*Species,filt_dietDataAnalyse, family=binomial())
13	glm(PrPPR~Tot.length.mm+Species,filt_dietDataAnalyse, family=binomial())
14	glm(PrPPR~Tot.length.mm*Species+Length_cm,filt_dietDataAnalyse, family=binomial())
15	glm(PrPPR~Tot.length.mm*Species*Length_cm,filt_dietDataAnalyse, family=binomial())
16	glm(PrPPR~poly(Tot.length.mm,2,raw=TRUE)*Species,filt_dietDataAnalyse, family=binomial())

Table A2 The generalized linear models used when testing probability of piscivory.

Model	Generalized linear model (GLM)
1	glm(PrPPR~Species*Temp,filt_dietDataAnalyse2, family=binomial())
2	glm(PrPPR~Species*Temp+L1,filt_dietDataAnalyse2, family=binomial())
3	glm(PrPPR~Species*Temp*L1,filt_dietDataAnalyse2, family=binomial())
4	glm(PrPPR~Species*Temp*Age,filt_dietDataAnalyse2, family=binomial())
5	glm(PrPPR~Species*Temp+Age,filt_dietDataAnalyse2, family=binomial())
6	glm(PrPPR~Species*Temp*delta_length,filt_dietDataAnalyse2, family=binomial())
7	glm(PrPPR~Species*Temp+delta_length,filt_dietDataAnalyse2, family=binomial())

Appendix B

A
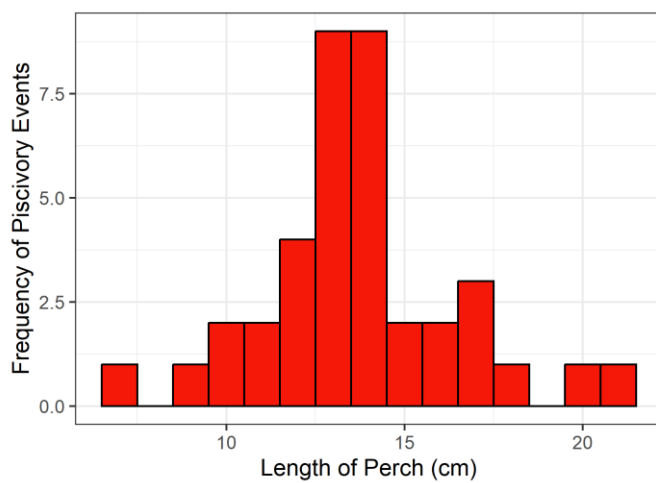
B
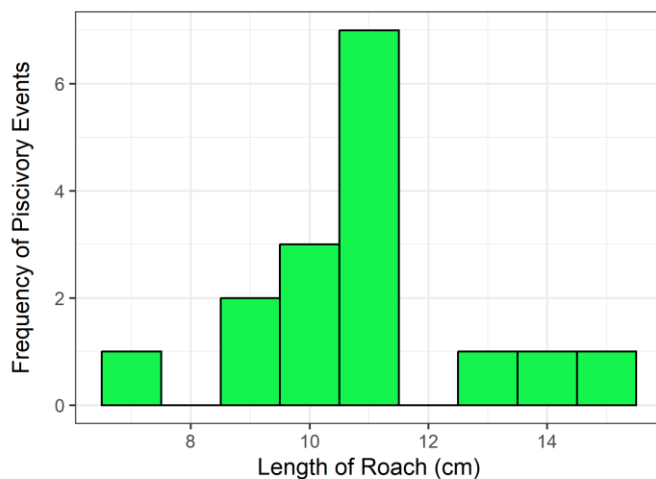
Figure B1 The histograms portray the length of individuals engaging in piscivory, and frequency of piscivory events at different length for a) perch in red and b) roach in green.

A
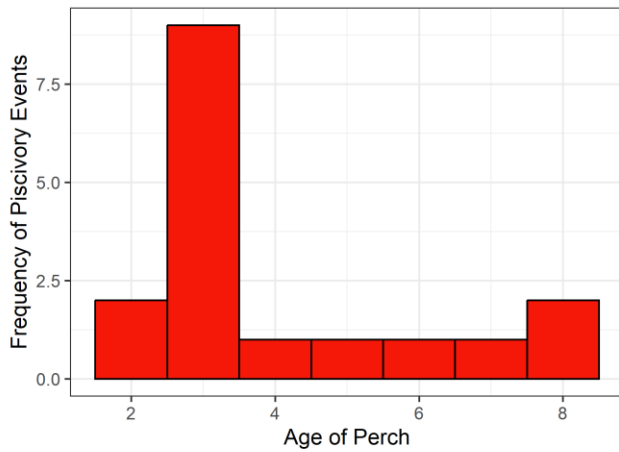
B
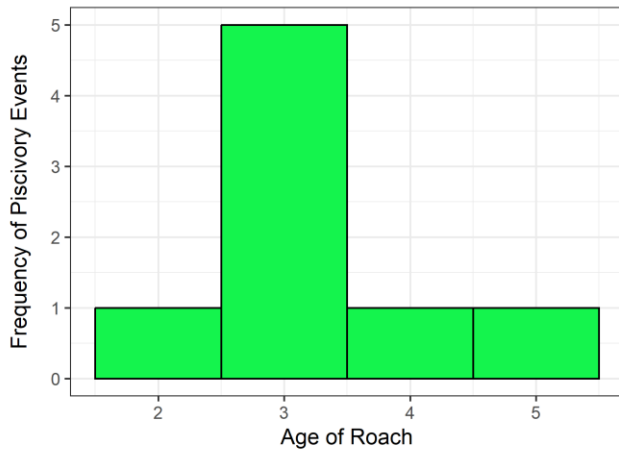
Figure B2 The histograms portray the age of individuals engaging in piscivory, based on the back calculated age data, showing frequency of piscivory events at different ages for a) perch in red and b) roach in green.

Table B1 An overview of roach larvae in the age group 0+ captured using dipnet or bongo net, with the mean larval length for every sampling date and the corresponding standard deviation (SD).

Date	N	Larval length	SD
26.5.	29	7.6	0.96
28.5.	31	9.5	0.29
30.5.	33	9.4	0.34
1.6.	32	9.1	0.47
3.6.	31	10.4	0.75
5.6.	27	11.4	0.74
8.6.	38	12.8	0.73
10.6.	30	13.3	1.16
12.6.	30	13.3	0.78
14.6.	30	12.1	1.11
27.6.	29	16.9	2.46
Total	340	-	-

Figure B3 Pictures captured at sampling days 7 and 8, when larval roach were active and swimming around the boat. Mid picture is the day with the largest catch from the Bongo net (day 7).
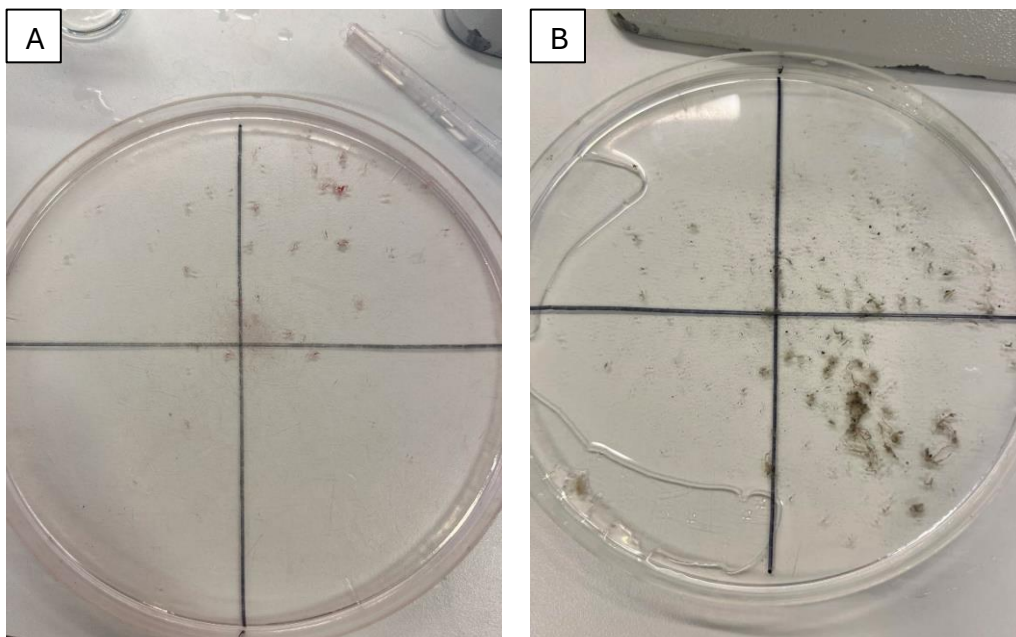
Figure B4 Gut content from roach (a) and perch (b), to show the relative size of fish larvae.
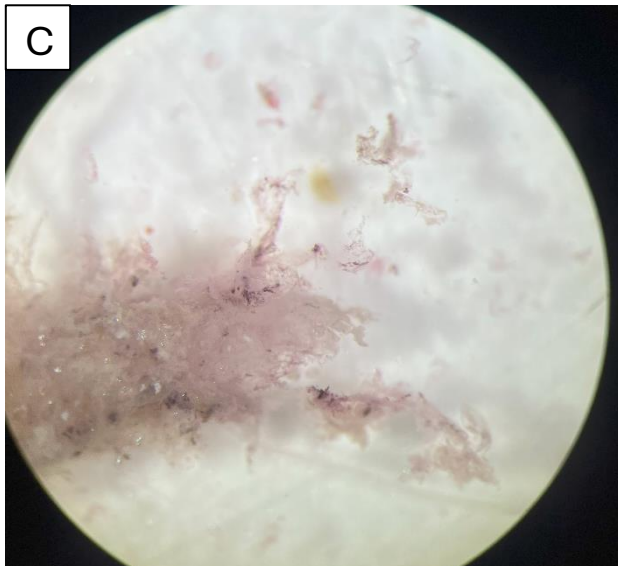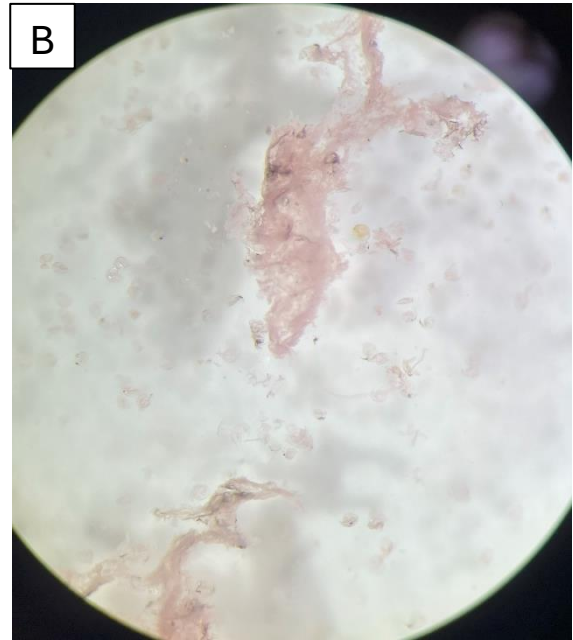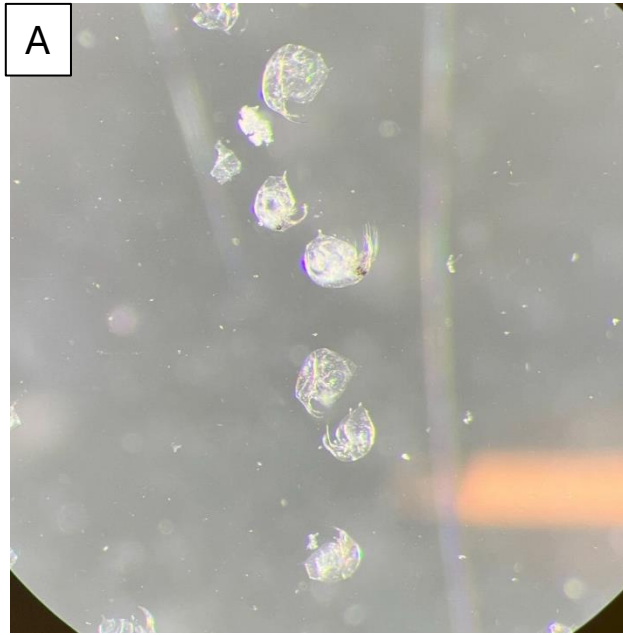
Figure B5 Gut contents of a) zooplankton Daphnia and b) 'pink pigmented remnants' from a roach individual, caught 10th June showing that the exoskeleton is almost undamaged after being eaten, as well as from two roach indviduals c) and d) caught 5th June and 10th June respectively to show pigmentation and form of the tissue clouds.
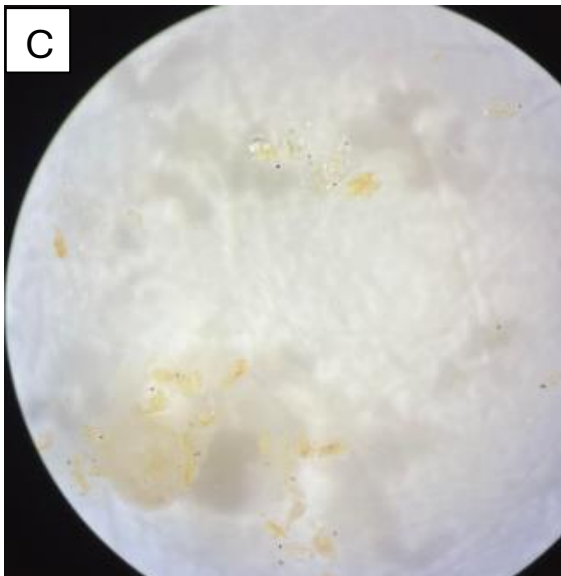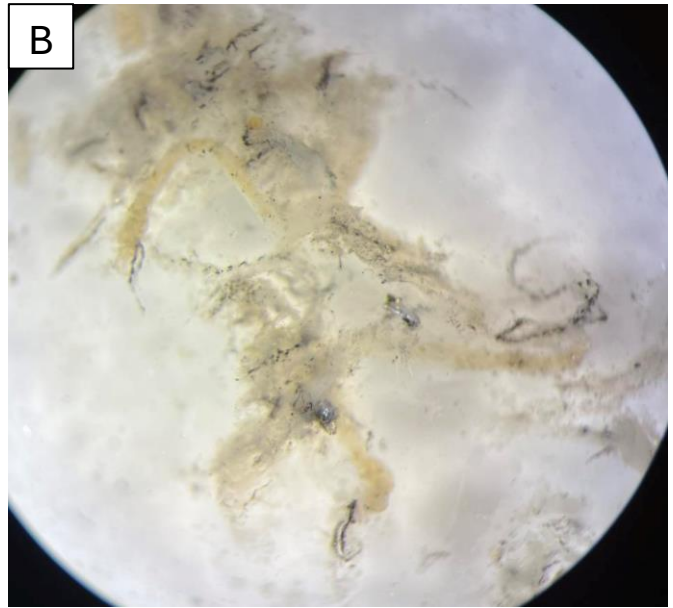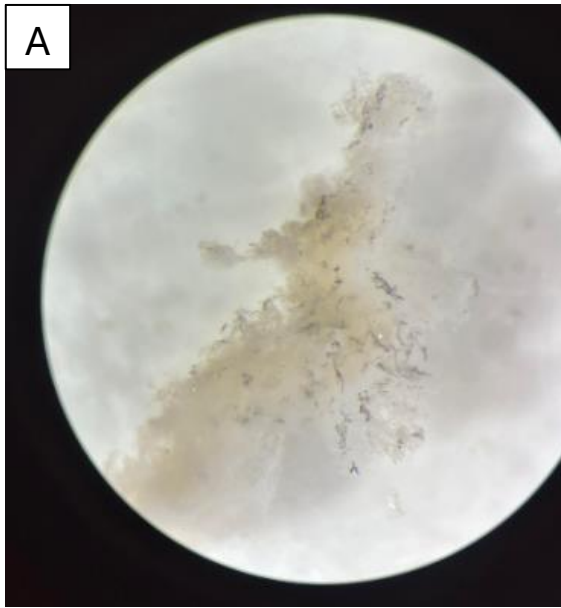
Figure B6 The gut content from perch individuals compared to the 'pink pigmented remnants' present in roach gut, have similar cloud formations with black pigmentation from fish larvae (a and b). Perch gut content that only contained zooplankton (c) had less black pigmentation.
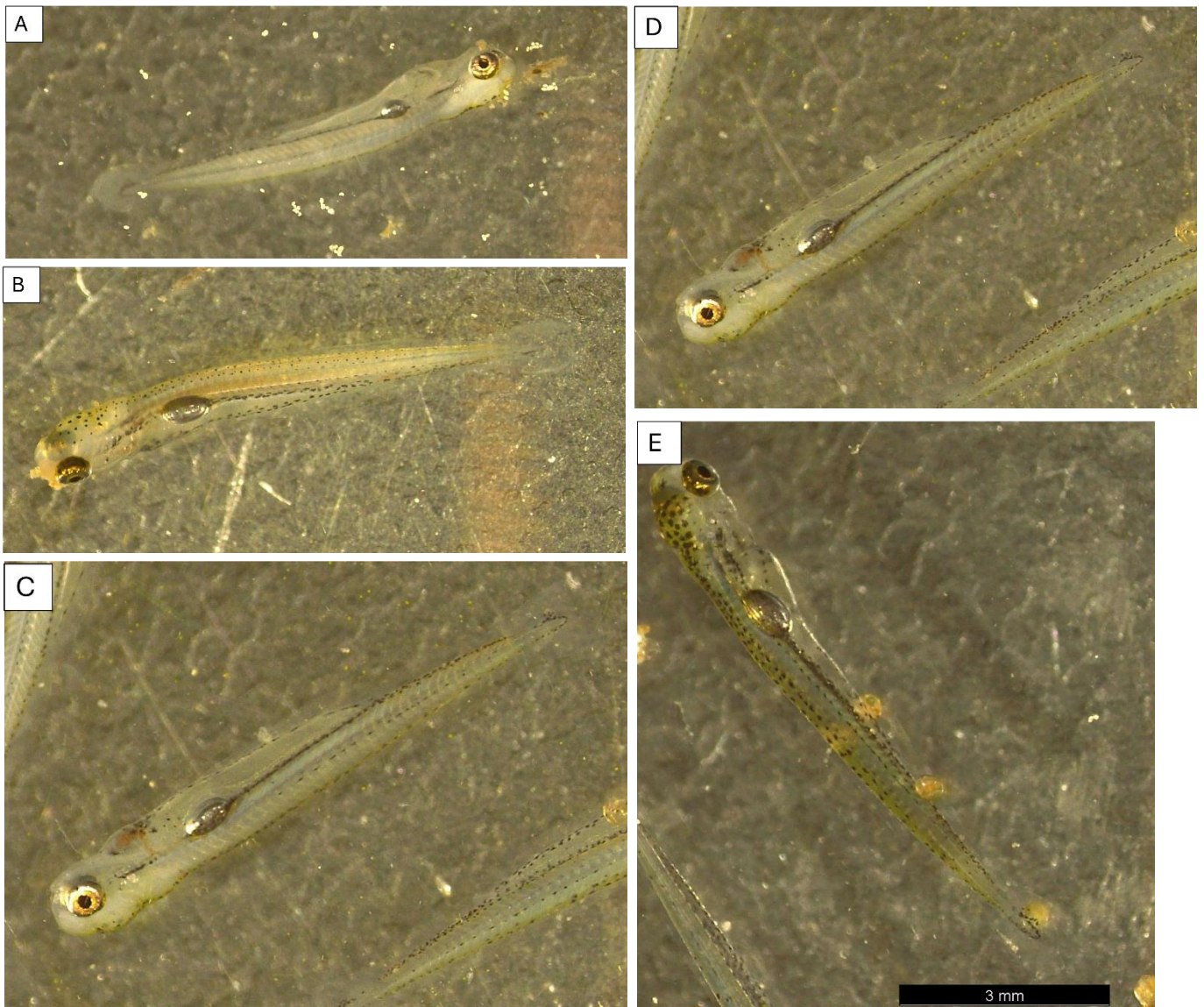
Figure B7 The development of roach from pre-larvae (free embryo phase) to larvae (Hammer, 1985) from dates 26.5 (A), 28.5 (B), 30.5 (C), 1.6 (D) and 3.6 (E).
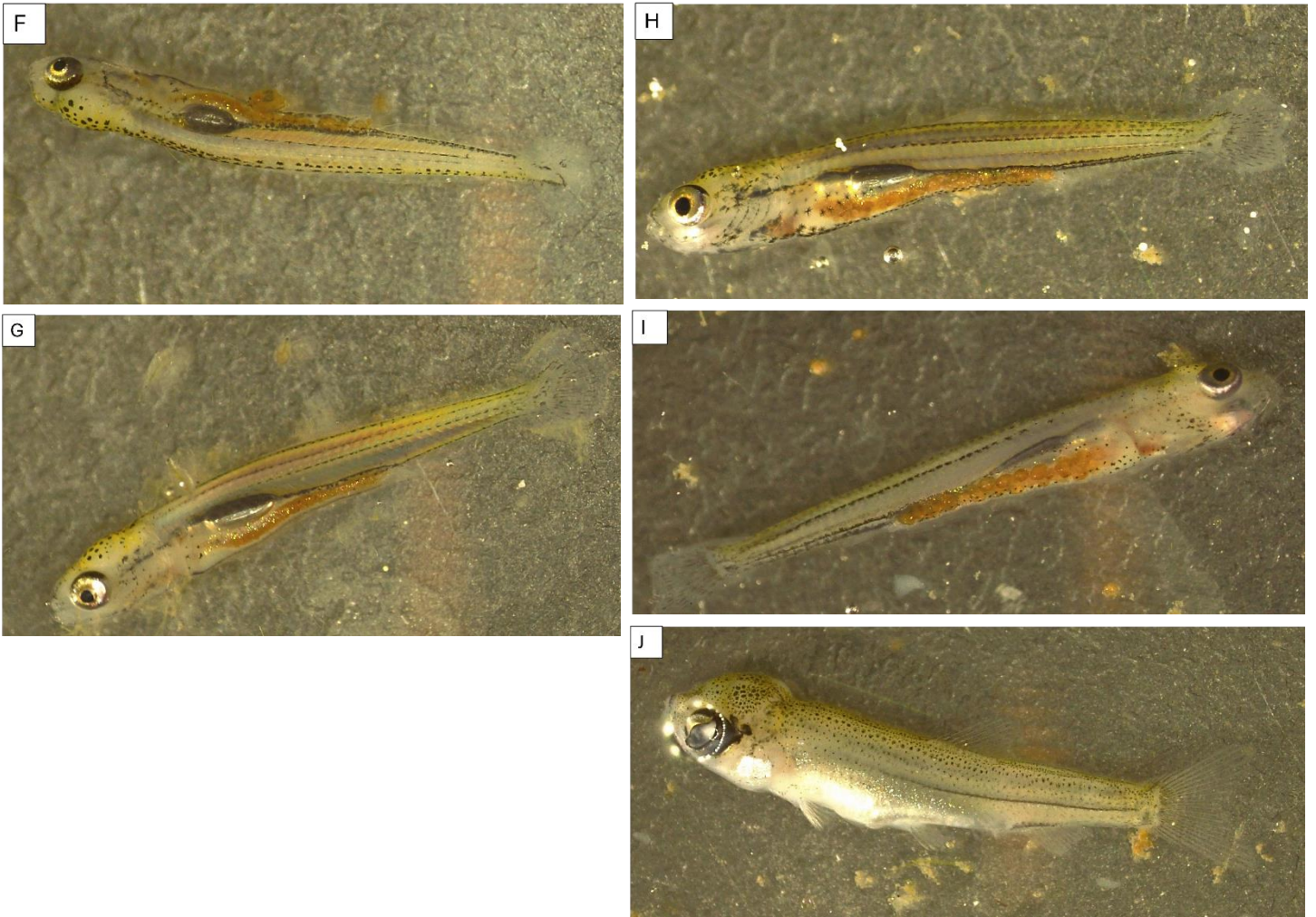
Figure B8 The development of roach larvae (Hammer, 1985) from dates 5.6 (F), 8.6 (G), 10.6 (H), 12.6 (I) and 27.6 (J).
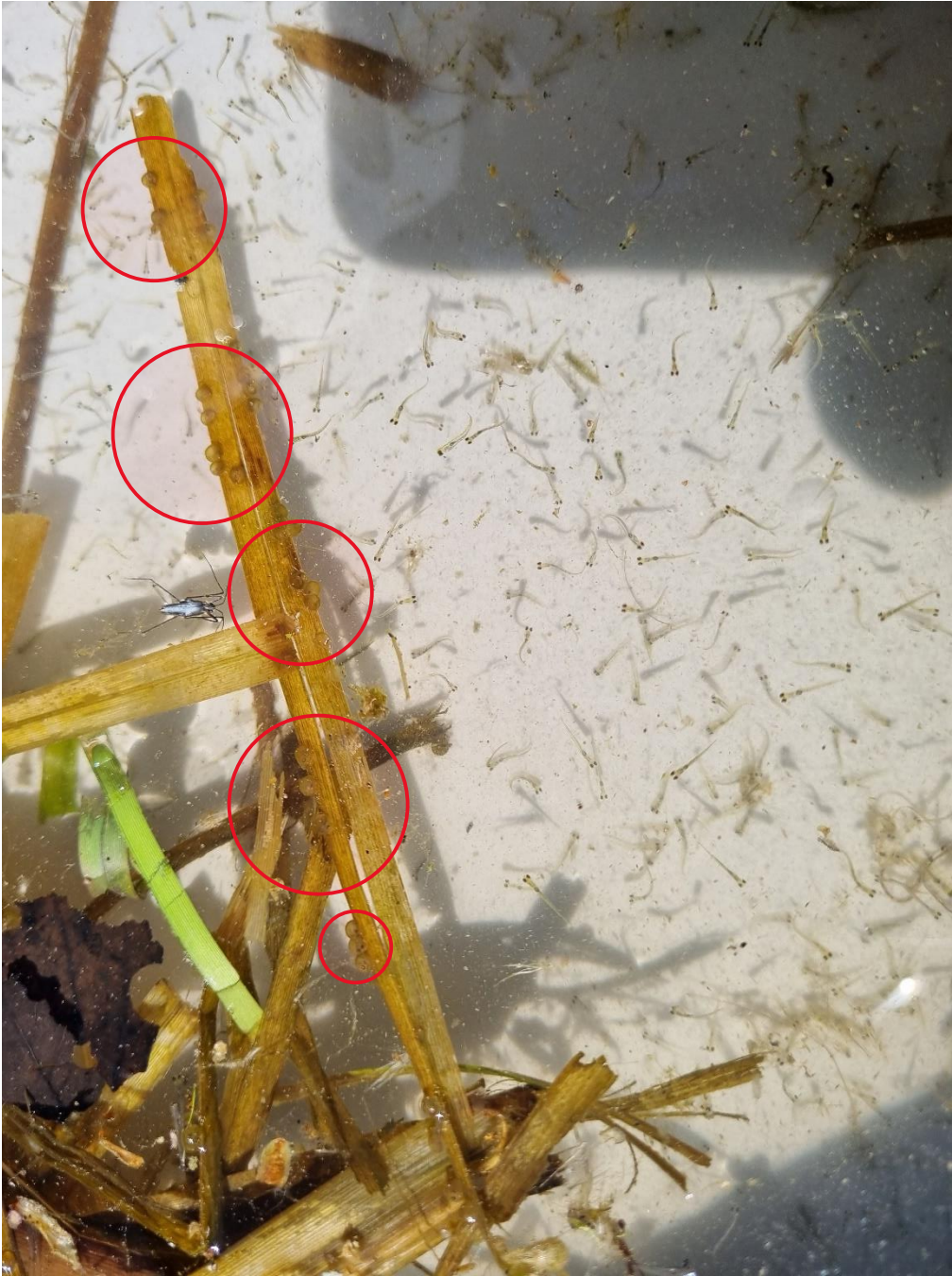
Figure B9 Picture taken from May 28th, where unhatched eggs were still attached to the reed, as one can clearly see eyes in some of them. Hatched pre-larvae are also swimming next to it, indicating that hatching had begun at this point.