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Master's thesis in MSc in Biology

Supervisor: Jan Grimsrud Davidsen

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NTNU University Museum  
Department of Natural History



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## **Sammendrag**

Individuelle forskjeller i økologiske trekk, som diett og livshistorie, er blant de viktigste driverne av artsdannelse, biologisk samfunns- og populasjonsdynamikk. I noen populasjoner er individuelle fenotyper forskjellige mellom subpopulasjoner eller «morfer». En populasjon viser ressurs-polymorfisme hvis morfene oppholder seg i ulike habitat og har ulike dietter. Her testes det om en ørretpopulasjon består av forskjellige morfer som har ulik ressursbruk, og om morfer i så tilfelle også kan separeres basert på morfologiske- (kroppsfarge, kroppslengde, kjønn) og livshistorietrekk (alder, vekst og kjønnsmodning). Det ble fisket med garn i det litorale og pelagiske habitatet, slik at lengde, kroppsfarge, kjønn, kjønnsmodning og diett kunne sammenlignes mellom habitatene. Diettanalysene baserte seg på mageinnhold og stabile isotoper, og skjell ble brukt til estimering av vekst og alder. Til tross for overlappende diett- og isotopnisjer var det forskjeller i lengde, alder, relativ vekst og diettkomposisjon mellom habitatene. Det ble vist at fargemorfene i Storvatnet skiller seg fra hverandre i noen grad, basert på økologi og ressursbruk. Resultatene indikerte en mulig ressurs-polymorfisme og to potensielle morfer; én bestående av brunfargede, litorale, generalist-spisere som var eldre og større, og én bestående av sølvfargede, pelagiske, spesialiserte planktonspisere som var yngre og mindre. Dette fenomenet er sjeldent rapportert hos ørret. Denne studien er derfor et nyttig bidrag i arbeidet med å forstå populasjonssatbarhet og tilpasningsevne.

## **Abstract**

Individual differences in ecological traits, such as diet and life history, are among the major drivers of population and community dynamics as well as of species' evolution. In some populations, individual phenotypes differ between subpopulations or 'morphs'. A population show resource polymorphism if the morphs differ in habitat and prey utilization. Here, I tested if a population of brown trout had separate morphs differing in resource use, and if the groups additionally differed in morphological (skin color, length, sex) and/or life history traits (age, maturation, growth). The sampling was done in the littoral and the pelagic habitat using gillnets enabling habitat comparisons of length, skin color, sex, maturation stage and diet. Dietary analyses were based on stomach content and stable isotopes, and scales were used for estimation of growth and age. Despite overlapping dietary and isotopic niches, there were habitat differences in length, age, relative growth and diet composition. The results suggest that the color morphs of trout in Storvatnet differ in ecology and resource use to some extent. There was therefore some indication of resource polymorphism and divergence into at least two potential morphs with one brown-colored generalistic littoral feeder that were larger and older, and one silver-colored specialized zooplanktivorous pelagic feeder which were smaller and younger. This phenomenon is seldom reported for brown trout. This study therefore provides valuable information which may be important for understanding population stability and adaptability.

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## **Introduction**

Individuals within populations often exhibit phenotypic variation (Hegrenes, 2001; Svanbäck & Schluter, 2012; Skúlason et al., 2019). In some populations, the phenotypes do not only differ between individuals, but also between subpopulation groups consisting of individuals with similar phenotypes. The term ‘morph’ is used to describe different phenotypic variants within a population that differ in morphology and ecological niches (Meyer, 1989; Bell et al., 2004; Skúlason et al., 2019). A polymorphic population refers to a population in which there are more than one morph. When morphs use different habitats and prey resources, the population show resource polymorphism (Skúlason & Smith, 1995; Komiya et al., 2011; Thomas et al., 2019). This phenomenon often arises in heterogenous ecosystems with high intraspecific competition (Ruzzante et al., 2003; Skúlason et al., 2019). Resource polymorphism may promote speciation, resource partitioning and population stability through lowered intraspecific competition and spatial separation and is therefore a topic of interest in evolutionary biology and ecology (Skúlason & Smith, 1995; Wennersten & Forsman, 2012; Dall et al., 2012).

Polymorphism has been reported for several vertebrate species, and freshwater fish taxa have been of particular interest (Kusche, 2013; Thomas et al., 2019; Skúlason et al., 2019). One example is the salmonid Arctic charr (*Salvelinus alpinus*) for which differences in morphology (e.g. body shape or color) and resource utilization (e.g. habitat and prey) have repeatedly been identified for two, three or four coexisting resident morphs in several lakes (Jonsson & Jonsson, 2001; Johnston et al., 2004; Skoglund et al., 2015). In addition, Arctic charr can exhibit an anadromous morph in lakes connected to the sea (Jonsson & Jonsson, 2001). In contrast, for another salmonid brown trout (*Salmo trutta*), studies seldom use the term ‘morph’ to describe groups within a population that differ in morphology and ecology (Ferguson & Taggart, 1991; Piggott et al., 2018). Like Arctic charr, some brown trout populations are anadromous and express a wide range of phenotypes (Jonsson & Jonsson, 2006; Westley et al., 2013). However, little is known about the patterns of phenotypic variation within resident brown trout populations (Klemetsen et al., 2003; Jonsson & Jonsson, 2006).

The phenotypic variation displayed by brown trout has been found to reflect both genetic variation and environmentally induced plasticity (Hegrenes, 2001; Hutchings, 2011; Piggott et

al., 2018). Brown trout can occupy different habitats depending on sex, age, size and dietary preferences, and most often polymorphism involves divergence of morphs between the littoral and pelagic habitats (Knudsen et al., 2006). Jonsson (1989) found that females were more likely to inhabit the pelagic zone than males of the same age. Both in lakes with and without interspecific competition, young and small equal-aged brown trout often inhabit streams and the littoral zone, while older, large trout utilize the pelagic zone of lakes, something that may be linked to different dietary preferences, reproductive ecology and predation risk (Haraldstad & Jonsson, 1983; Jonsson, 1989; Saksgård & Hesthagen, 2004).

Different age-groups of brown trout have been found to have different dietary preferences. However, few differences in diet have been found for different age groups living in the same habitat, suggesting that the effect of age on diet disappears within habitat (Jonsson, 1989). Brown trout from the littoral zone may feed on zoobenthos (e.g. snails, insect larvae and amphipods), while the pelagic fish feed on zooplankton and surface insects (Jonsson, 1985; Jansen et al., 2002). To enhance energy intake and increase growth rates, brown trout can express a size related change to a piscivorous diet (Kara & Alp, 2005; Sánchez-Hernández et al., 2019). In some lakes, piscivorous brown trout are most abundant in the littoral zone (Næsje et al., 1998), while in other lakes they mainly feed in the pelagic zone (Jensen et al., 2004), depending on the distribution of the prey species and the community composition (Sánchez-Hernández et al., 2017). Brown trout typically feed on Arctic charr, European whitefish (*Coregonus lavaretus*) and sticklebacks, but they can also be cannibalistic (L'Abée-Lund et al., 1992; Næsje et al., 1998).

Morphological color change is a change in color that occurs over weeks, and not instantaneously. Skin coloration of brown trout has been recognized as a plastic trait, and color morphs (a light and dark morph) have been observed and connected to different habitats and substrates, both in the field (Westley et al. 2012) and experimentally (Westley et al. 2013). Skin color can be an adaptation towards predator avoidance, as seen for anadromous brown trout that change from brown to silver during the smoltification process (Hoar, 1988). In signalling of individual dominance or stress, coloration may also play a role, where subordinates and stressed individuals exhibit a darker skin color, but this change is instantaneous and is referred to as physiological color change (Höjesjö et al., 2002; Kaspersson et al., 2010; Westley et al. 2013). In contrast, darker skin color has been linked to

a higher production of viable offspring for males, thus indicating that dark males are a reproductive partner of high quality, producing high quality offspring (Wedekind et al., 2008).

Studying variation in niche use can be complex, as the ecology of a population is affected by spatial and temporal interactions between biotic and abiotic factors in the ecosystem. Individuals of brown trout commonly undergo ontogenetic niche shifts during their lifetime, referring to a size induced change in diet as individuals can handle larger prey and require more energy (Sánchez-Hernández et al., 2019). Seasonal changes in resource availability can also promote shifts in habitat and feeding behavior during the year. Typically, during spring and early summer, there is a peak in aquatic insect hatching, leading to more fish consuming this prey (Hindar & Jonsson, 1982). Pelagic zooplankton biomass is on the other hand low during the spring, and at its highest during late summer and autumn (Hindar & Jonsson, 1982; Jonsson & Gravem, 1985). In addition, there is a great variety of available niches for a brown trout population depending on the lake system and availability of associated marine, river and lake habitats. In some systems, brown trout do not encounter interspecific competition, while in other lakes several competing species coexist, potentially limiting the feeding opportunities of trout (Jonsson, 1989; Jensen et al., 2004; Eloranta et al., 2013). Despite being aggressive and competitive, the generalist feeding of brown trout is limited when the species coexists with competitors with similar diet and habitat preferences (Jansen et al., 2002; Eloranta et al., 2013).

Studies of brown trout focusing on phenotypic variation within a population are sparse. Between geographically close populations of brown trout, genetic and phenotypic differences have been reported a number of times (Ferguson & Taggart, 1991; Stelkens et al., 2012). In addition, niche use and life history traits of brown trout have been studied in systems where it shows interspecific competition with Arctic charr and brook trout (*Salvelinus fontinalis*); however, within-species variation has been overlooked in these studies (Öhlund et al., 2008; Gunnarsson & Steingrímsson, 2011; Eloranta et al., 2013). Although large-sized piscivorous and silver anadromous morphs are widely reported, other niche specializations are under-reported (Næsje et al., 1998; Jonsson & Jonsson, 2006; Piggott et al., 2018). Brown trout are therefore rarely reported as polymorphic (Piggott et al., 2018).

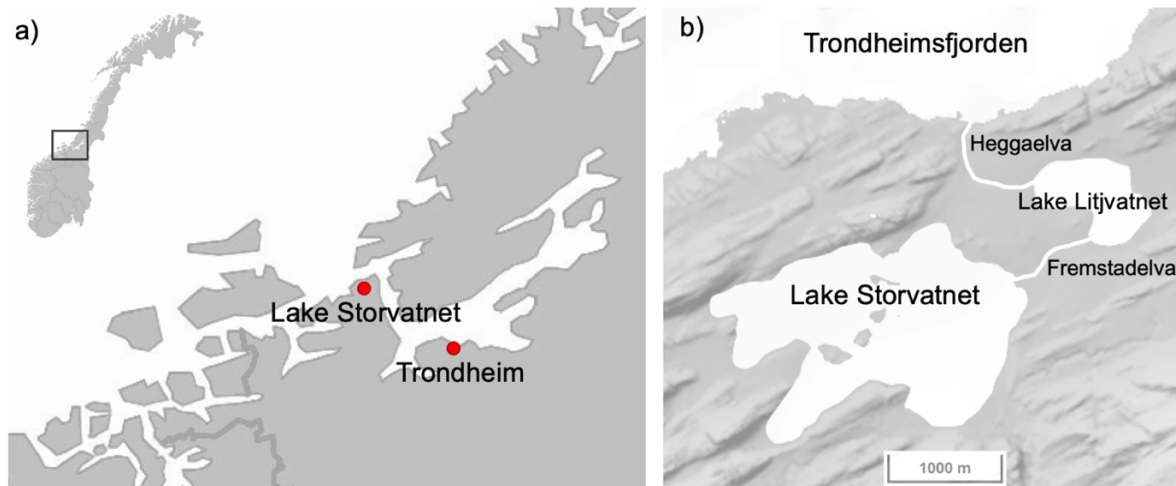
The objective of this study was to explore how individual brown trout differed in resource use. I hypothesized that the brown trout population in Lake Storvatnet express resource

polymorphism. I therefore expected brown trout individuals caught in the two habitats, littoral and pelagic, to differ in their expression of ecological traits such as body length, growth, age and diet. Secondly, I expected different expression of the aforementioned ecological traits between the three color morphs as well.

## **Methods**

### **Study system**

Storvatnet is an oligotrophic coastal lake belonging to the Fremstad catchment area ( $63^{\circ}37'N$ ,  $9^{\circ}38'E$ ) in the outer region of Trondheimsfjorden, central Norway (Figure 1). Storvatnet has a surface area of 2.92 km<sup>2</sup>, max. depth of 16 m, and mean depth of 8 m (Paterson et al., 2021; Norges vassdrag- og energidirektorat (NVE), 1998). The lake has a drainage area of 22.1 km<sup>2</sup>, is situated 6 m above the sea level, and is located on marine sediments (Ulsund, 2013; NVE, 1998). The rivers Fremstadelva (0.8 km) and Heggaelva (1.0 km) connect Storvatnet to Litjvatnet (area 0.47 km<sup>2</sup>) and Litjvatnet to Trondheimsfjord, respectively. The fish community in Storvatnet consists of anadromous and resident brown trout, anadromous Atlantic salmon (*Salmo salar*) and three-spined stickleback (*Gasterosteus aculeatus*).



**Figure 1:** Map of the study site showing a) the location of Lake Storvatnet in central Norway and b) Lake Storvatnet and the rest of the catchment including Lake Litjvatnet, the rivers Fremstadelva and Heggaelva. The maps are modified from a) Kartverket and b) Norges vassdrags- og energidirektorat.



## **Sample collection**

### **Fish sampling**

Brown trout were sampled in September 2021, using three types of multi-panel gillnets (Nordic bottom gillnets, Nordic floating gillnets and SNSF floating gillnets) and standard sized one-panel gillnets. Nordic bottom gillnets (30 x 1.5 m) with twelve mesh sizes (5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, 55 mm) were set in the littoral zone (0 – 12 m). Floating gillnets from the Nordic (30 x 6 m, mesh sizes: 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, 55 mm) and the SNSF series (52 x 6 m, mesh sizes: 10, 12.5, 16, 19.5, 24, 30, 35, 45 mm) were set in the pelagic zone (0 – 6 m). In addition, standard sized (30 x 1.5 m) gillnets were set in the littoral zone. Fish from standard nets used in this dataset were caught in nets with mesh sizes 21, 22.5, 26, and 29 mm. A total of 44 Nordic bottom gillnets, 8 Nordic floating gillnets, 4 SNSF gillnets and 15 standard gillnets were set overnight in the span of four days (06.09.21-10.09.21).

In the field lab, 297 brown trout were classified into three different color morphs: brown, intermediate and silver. Natural length (mm) (from tip of closed mouth to the end of the caudal fin, when the fish was lying in a natural position), and weight (g) were measured for the 297 trout. These trout had a natural body length ranging from 84 to 560 mm (mean±S.D. = 231±62 mm).

The further fish processing was performed on a subsample of the 297 brown trout. For these fish we determined the traits sex, age, growth, stomach content, and maturation state. Scales were sampled from the area past the dorsal fin and above the lateral line in the field lab. The subsample were selected to represent the three different morphs and the two habitat types equally, and the combination of different color morphs and habitats made up six groups (Table 1). Random selection among multi-panel gillnets was used within these groups to get a good representation of the length frequency distribution of all the fish caught. These trout had a natural body length ranging from 99 to 471 mm (mean±S.D. = 234±65 mm), making them only 3 mm longer on average, than the 297 brown trout that we caught. Thus the subsample represents the sampled population in this measured trait. As the goal was equal representation, we initially wanted 30 brown trout from each morph-habitat combination (total n=180). However, one of the 30 silver fish from the pelagic habitat was damaged, and no individual of the same size was available to replace it. Additionally, only 10 individuals of the brown

morph were available from the pelagic habitat. To obtain 30 silver fish from the littoral zone, five randomly selected fish from the standard gillnets were also included. This resulted in a total sample size of 159 brown trout (Table 1). For some fish, we could not determine the sex or maturation state because they were missing gonads or were too young.

The scales of some fish had poor quality precluding the age and growth determination. For the stable isotope analysis (SIA) a subsample of the 159 brown consisting of 49 individuals was used (Table 1). These fish were selected to represent individuals of different lengths from the three different color morph groups. These fish had a natural body length ranging from 99 to 471 mm (mean±S.D. = 241±92 mm), making them 10 mm longer than the 297 brown trout that we caught, and 7 mm longer than trout that had sex, age, growth, stomach content, and maturation state measured and determined. Dorsal muscle tissue samples were collected from each brown trout individual in the field lab and stored frozen for later stable isotope analysis ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ).

**Table 1:** Overview of the six different group combinations of habitat and color morph, and the number of individual brown trout within each group. The first number represent trout that had data the traits sex, age, growth, stomach content and maturation. The number in parenthesis represent trout used in stable isotope analysis.

<b>Habitat</b>	<b>Color morph</b>		
	Brown	Intermediate	Silver
Littoral zone	30 (10)	30 (9)	30 (5)
Pelagic zone	10 (5)	30 (6)	29 (14)

## **Dietary analyses**

### **Stomach content analysis**

The relative fullness method was used to analyze the stomach content (Amundsen & Sánchez-Hernández, 2019; Hyslop, 1980). In the NINA laboratory, stomachs were opened and the percentage degree of fullness was visually determined (0-100%). A stereoscopic microscope was used to identify the prey items to the lowest practical taxonomic level. Relative contribution of each prey category to the estimated stomach fullness value was estimated as prey volume of total stomach content volume (%). The fullness contribution of each prey

category was decided summing up to the total stomach fullness. Parasites within the stomach content were removed and were not included in stomach fullness assessments. The identified prey taxa were further divided into the five prey groups; fish, zoobenthos, zooplankton, pupae and surface insects. A prey group were characterized as most abundant when it made up a larger volume of the stomach content, compared to the other prey groups. The most abundant prey group was the information used from each trout individual in the analyses.

### Stable isotope analysis (SIA)

Qualitative samples of zoobenthos, zooplankton and sticklebacks were also collected in September 2021 to obtain isotope data of potential food sources for brown trout. Zoobenthos were collected from the littoral zone with a kick net (mesh size: 500  $\mu\text{m}$ ) and by hand from the shallowest areas (depth < 1 m) and with a benthic sledge (mesh size: 248 $\mu\text{m}$ ) from deeper areas (depth 1–4 m). Pelagic zooplankton were collected with several replicate hauls ( $n = 3\text{--}5$ ) through the uppermost (0–10 m) water column using a plankton net (mesh size: 90 $\mu\text{m}$ ). Sticklebacks were caught using traps and gillnets. All frozen SIA samples were later freeze-dried for 48 h at NTNU prior to transportation to the University of Jyväskylä, Finland. Finally, the samples were homogenized into fine powder using a metallic pestle and weighed (1.900–2.100 mg) into tin cups for final analysis at the University of Jyväskylä conducted using an Isoprime 100 CF-SIRMS (Isoprime Ltd, Stockport, U.K.) coupled with Elementar vario PYRO cube elemental analyzer (ElementarAnalysensysteme GmbH, Hanau, Germany). Stable nitrogen and carbon isotope ratios are expressed as delta values ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , respectively) relative to the international standards for nitrogen (atmospheric nitrogen) and carbon (Vienna Pee Dee Belemnite).

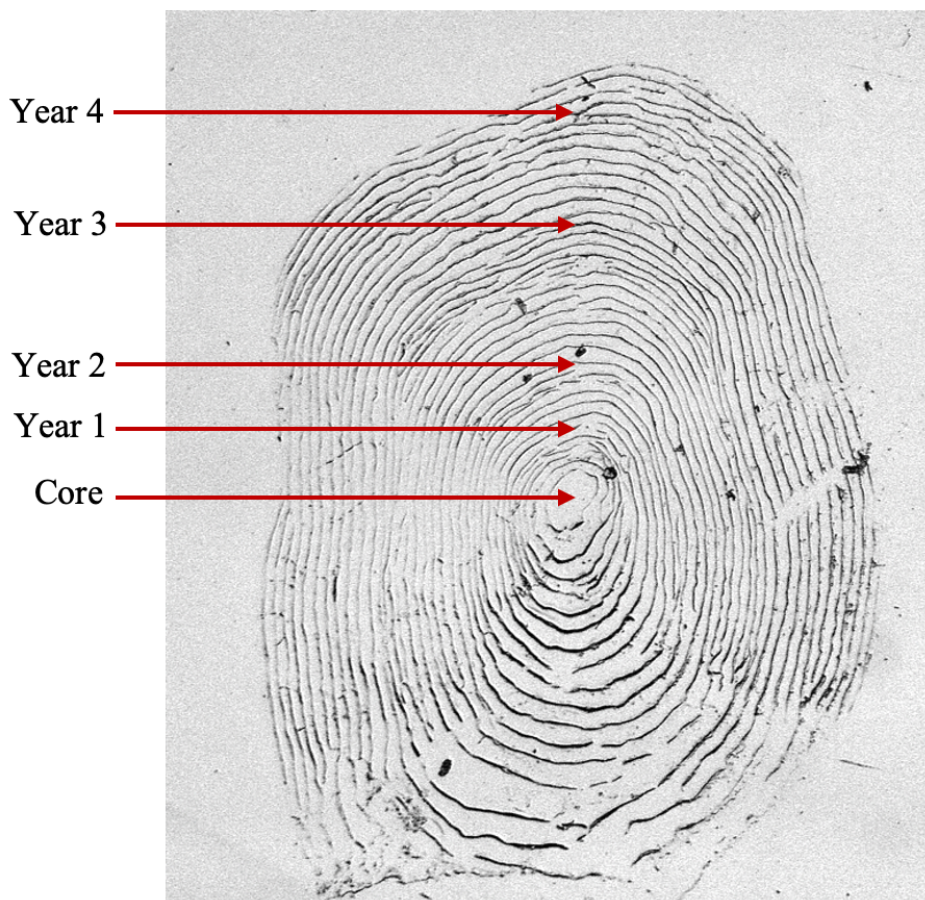
### **Estimation of growth and age**

A light microscope was used to select the best 6-8 scales with clear circuli rings all the way into the center of the scale. These scales were pressed, making imprints of the scales on Lexan plates. The imprints were analyzed using a computer stereoscope equipped with a camera (Leica M165C, camera: Leica MC170 HD). Photos were taken and uploaded in a software (LAS V4.5, Leica systems, Sankt Gallen, Switzerland; Figure 2). Widely and closely spaced circuli rings of the scales indicate periods of rapid growth during the summer and slow growth during the winter, respectively. The fish age was determined by counting the annulus (Elliott

& Chambers, 1996; Figure 2). Back calculation of growth was done using the Dahl-Lea equation, which assumes that body length increases linearly with scale radius:

$$L_i = L_c \frac{S_i}{S_c} ,$$

where  $L_i$  is the length of the fish at a certain age (at the  $i^{\text{th}}$  annulus),  $L_c$  is the length at capture,  $S_i$  is the length from the center of the scale to the  $i^{\text{th}}$  annulus, while  $S_c$  is the radius of the scale (Francis, 1990). These measurements were performed in the software LAS V4.5. Estimation of age and back-calculation of growth were done two times independently for each scale. For fish whose scales were hard to read, otoliths were used to estimate age. Due to replacement scales, age determination was not possible for all individuals. Quality check of scales that were hard to read was performed by a technician, to ensure reliable results. For the analyses relative growth was used as a measure of growth. The relative growth was measured as last year growth (in mm) divided on the length of the trout (in mm), the year before capture. By doing this, relative growth represent growth as a proportion/percentage of body length.



**Figure 2:** Scale of a four-year-old trout showing widely and closely spaced circuli rings that represent rapid and slow growth periods (annulus), respectively.

## **Statistical analyses**

Statistical analyses were performed in R 4.2.2 (R Core Team 2022), with  $p < 0.05$  as the chosen level for statistical significance. All figures were made with the `ggplot()` function from the `ggplot2` package (Wickham & Chang, 2016), or the `ggbarstats()` function from the `ggstatsplot` package (Patil, 2021).

## **Habitat use**

To examine if the probability of capture of brown trout in the littoral and pelagic habitats varied with color morphs and length, a binomial generalized mixed effects model (GLMM; logit link function) with habitat (0/1) as the response variable was used. Color morph and body length were included as predictor variables, and the `glmer()` function from the `lme4` package (Bates et al., 2014), was used to run the model with a binomial error distribution. Sampler was included as a random effect, as the color morph was subjectively determined, potentially causing a non-independence of color morph observations. Length may vary between the color morphs and thus the model also included a two-way interaction term between the brown trout length and color morph. Model selection was conducted using Akaike's information criterion (AIC) with the `AIC()` function from the `stats` package, as the sample size ( $n$ ) was large compared to estimated parameters ( $K$ ):  $n/K > 40$ . The dispersion parameter of the generalized mixed effects model was 1.1, indicating that the dispersion of data was accounted for by the model.

The potential variation in age, length, growth and sex between the littoral and pelagic habitats were examined with a binomial GLM (logit link function), that modeled the probabilities of being caught in the littoral habitat related to versions of these traits. Habitat (0/1) was therefore included as the response variable. The model was run with the `glm()` function from the `stats` package (R Core Team) with a binomial error distribution. Because of the stratified sampling based on habitat and color morph, color morph could not be included as an explanatory variable in the model. Strong correlations between predictor variables can lead to collinearity issues in a model. Thus, the Pearson product-moment correlation coefficients were obtained for 1) age and relative growth, 2) age and body length, and 3) relative growth and body length with the `cor.test()` function from the `stats` package. The correlation coefficients are displayed in a correlation matrix (Table 2). Each of the correlated predictors; age, length and relative growth, were evaluated in separate preliminary models, to avoid

problems with model selection and parameter estimation. Model selection was conducted using the second order Akaike's Information Criteria (AICc), as the sample size ( $n$ ) was small compared to estimated parameters ( $K$ ):  $n/K < 40$ . The `aictab()` function from the `AICcmodavg` package (Mazerolle, 2023) was used to produce tables with AICc-values (Appendix, Table A1).

Age was found to be the best predictor explaining the variation in the data the best, therefore model selection was performed for a global model including age and sex as predictors ( $n=111$ ). Gillnet number was not included as a random factor, as the nets were of different sizes between the littoral and pelagic zone and within the pelagic zone. Additionally, unequal numbers of nets were used in the different habitats. The best model was selected based on AICc-value. The dispersion parameter of 1.35, indicating that the dispersion of data was accounted for by the model.

**Table 2:** Pairwise correlations between the four traits relative growth, body length, age and last year growth. The correlation coefficients with associated  $p$ -values are displayed.

	Body length	Age
Relative growth	$r=-0.56$ $p<0.001$	$r=-0.67$ $p<0.001$
Body length		$r=0.78$ $p<0.001$

### Length, age, growth

To quantify how the continuous variables relative growth, length and age differed between habitats, color morphs, sexes and sexual maturation state (mature/immature), a set of linear models (ANOVA) were run with the `lm()` function from the `stats` package. Relative growth ( $n=128$ ), length ( $n=153$ ) and age ( $n=114$ ) were analyzed as response variables in three different models. When there were several candidate models derived from a global model ( $\Delta AICc < 2$ ), the `MuMIn` package (Barton & Barton, 2019) was used for model selection with the `dredge()` function and model averaging with the `model.avg()` function. All the three different models with relative growth, length and age as response variables had more than one candidate model. In the relative growth model an interaction between growth and maturation state was included, as one would expect mature females to have grown less than mature

males, because of how energetically costly it is for females to develop mature gonads. However, based on the AICc-value, the model without the interaction was the best model. The fit of the linear models were evaluated using the plot() function from the base package. The variable relative growth was log transformed due to non-normality in the linear model.

### Diet

To investigate whether or not the proportions of prey groups differed between and within (a) the two habitats, and (b) the three color morphs, Pearson's chi-square test for categorical variables was performed, using the chisq.test() function from the native stats package.

A linear model with length as a covariate (ANCOVA) was run to test the effect of length, habitat and color morph on the  $\delta^{15}\text{N}$  values of muscle tissue, indicating trout trophic position in the lake food web (Post, 2002). The response variable of the model was  $\delta^{15}\text{N}$ , while habitat and color morph was included as predictors in addition to length. The effect of length could differ between the habitats or the color morphs and therefore two-way interactions between length and the two other predictors were included. Model selection was conducted using AICc. The fit of the linear models were evaluated using the plot() function from the base package. The Kruskal-Wallis test and the Mann-Whitney U test were performed with the kruskal.test() and wilcox.test() function from the stats package when normality assumptions were violated. This approach was used to compare isotopic composition of the trout to examine habitat and color morph differences. The Kruskal-Wallis test were also used to test if prey sources were separated by  $\delta^{13}\text{C}$  values.

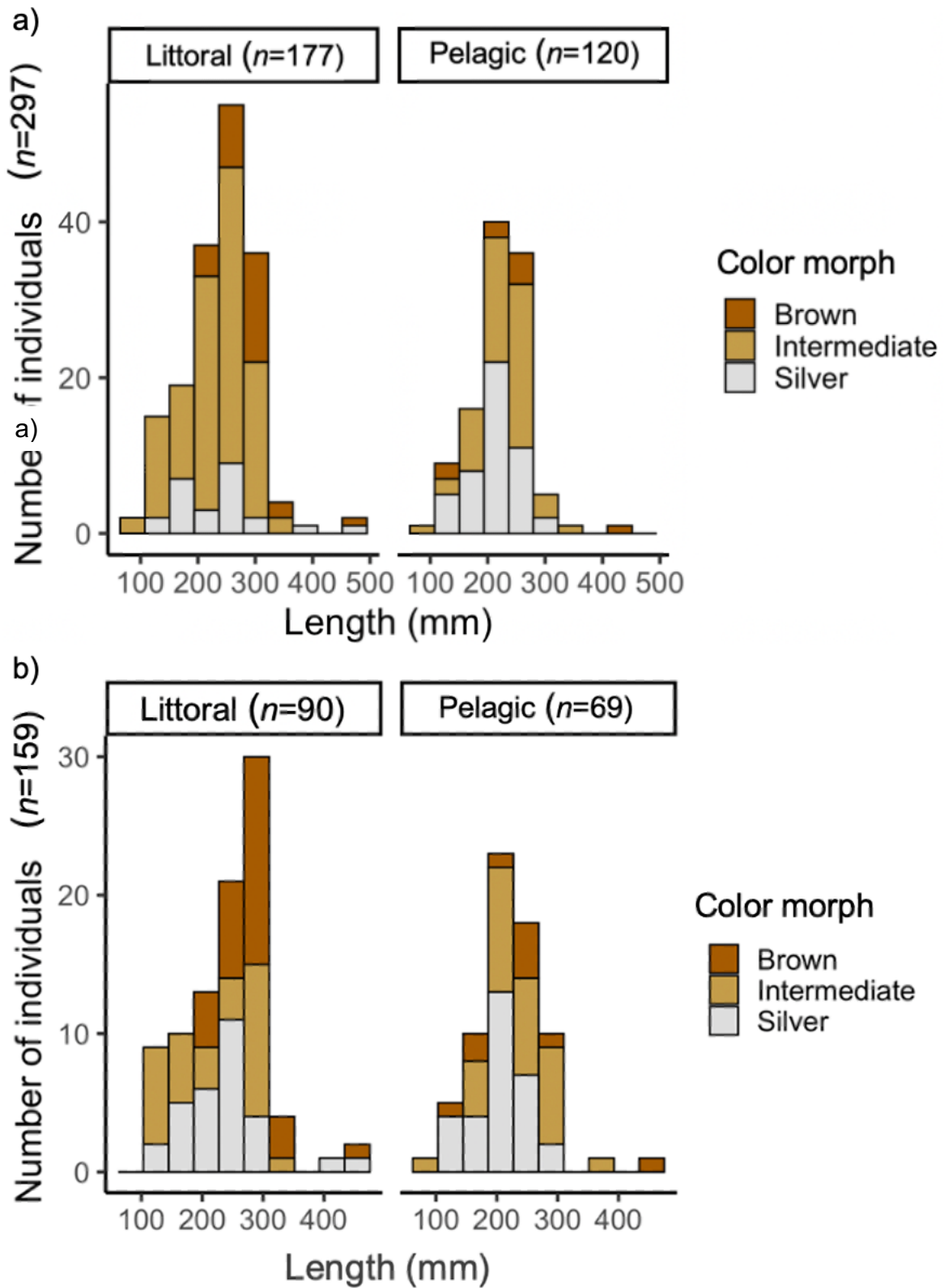
MixSIAR isotopic mixing model was conducted with the run\_model() function from the MixSIAR package (Stock et al., 2018), to estimate dietary contributions from consumers, prey groups and trophic fractionation factors, in addition to consider uncertainties related to isotopic variation. Two separate models with run="long" were run with 1) habitat and 2) color morph as factors. Trophic fractionation factors used were in figures and in the isotopic mixing model ( $3.4 \pm 1.0\%$  for  $\delta^{15}\text{N}$  and  $0.4 \pm 1.3\%$  for  $\delta^{13}\text{C}$ ) to account for the change in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values when the isotopes from the prey source are assimilated to the body tissues of the consumer (Post, 2002). The three food sources included in the MixSIAR model differed significantly by their  $\delta^{15}\text{N}$  and/or  $\delta^{13}\text{C}$  values (Kruskal-Wallis tests;  $p < 0.01$ ; pairwise Mann-Whitney U-tests;  $p < 0.01$  for all comparisons).

## **Results**

### Characteristics

Of the 297 brown trout caught in lake Storvatnet, 43 were considered brown, 178 intermediate and 76 silver. More fish were captured from the littoral zone ( $n=177$ ) than the pelagic zone ( $n=120$ ). Littoral-caught trout (mean $\pm$ S.D. =  $238\pm 68$  mm,  $n=177$ ) were on average longer than pelagic-caught trout (mean $\pm$ S.D. =  $221\pm 50$  mm,  $n=120$ ; Figure 3a). Trout that had their sex, age, growth, stomach content, and maturation state measured and determined, had age ranging from 1 to 7 years (mean $\pm$ S.D. =  $3.6\pm 1.1$  years). In the subsample littoral-caught trout (mean $\pm$ S.D. =  $247\pm 67$  mm,  $n=90$ ) were on average longer than pelagic-caught trout (mean $\pm$ S.D. =  $221\pm 56$  mm,  $n=69$ ; Figure 3b).





**Figure 3:** Length distributions of the brown, intermediate and silver color morphs of brown trout caught from the littoral and pelagic habitats for all 297 trout captured (panel a) and the 159 fish that had data the traits sex, age, growth, stomach content and maturation (panel b).

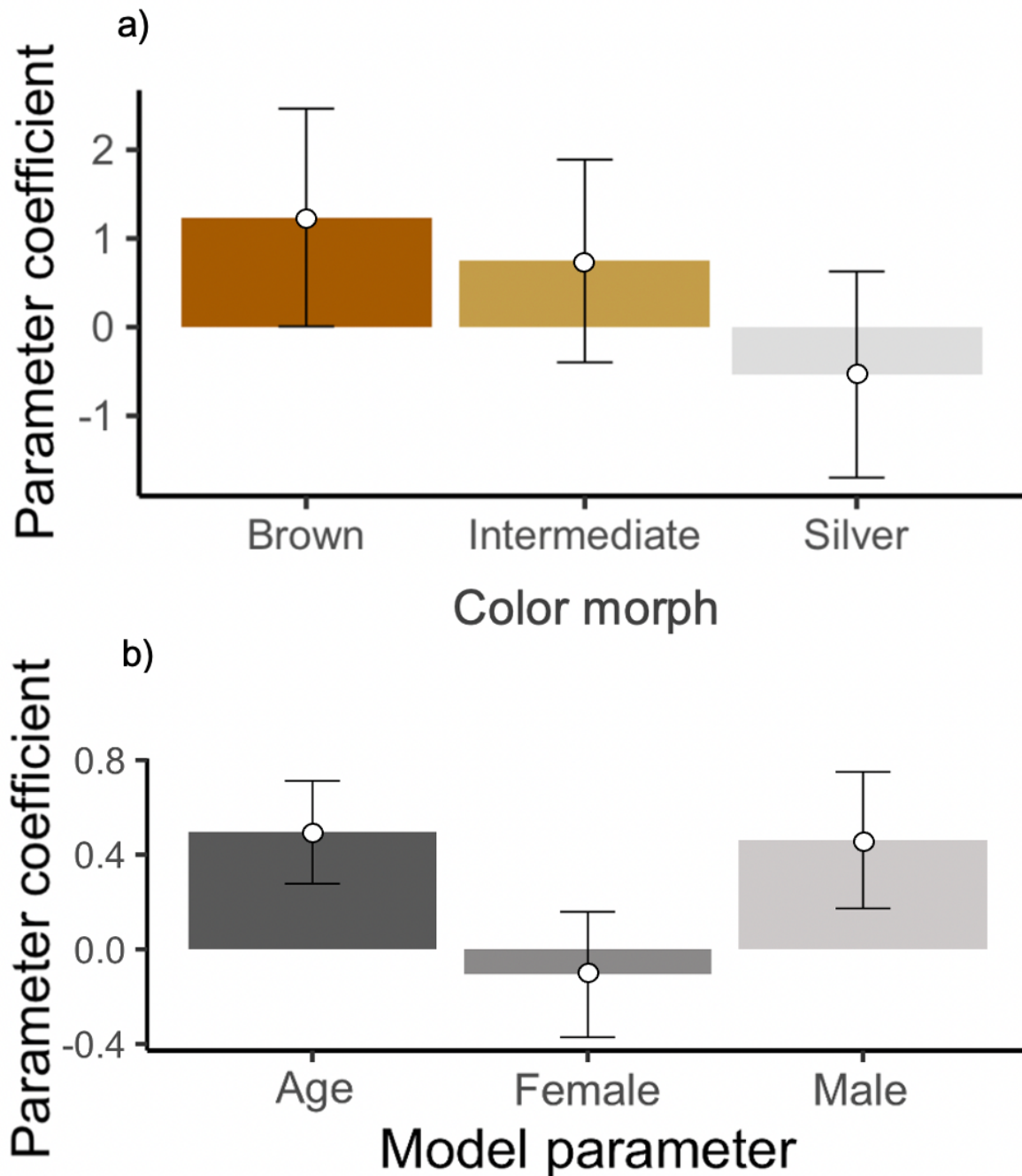
### Habitat use

Brown individuals were 40% more likely to be caught in the littoral habitat than silver individuals (GLM,  $p < 0.001$ ,  $n = 177$ ; Figure 4a), while intermediate individuals were 31% more likely to be caught in the littoral habitat than silver individuals ( $p < 0.001$ ). The probability of being caught in littoral habitat vs pelagic habitat was not different from 50% for any of the three color morphs, but the estimated probabilities for presence in the littoral habitat was highest for the brown color morph (78%), followed by the intermediate morph (68%) and the silver morph (37%; Figure 4a). Additionally, there was no difference in probability of littoral habitat use between the brown morph and the intermediate morph ( $p = 0.28$ ).

Model selection suggested that the best model to explain the variation in probability of catching trout in the littoral or pelagic habitat was the model including age and sex as predictors, without an interaction between the predictors (Table 3). The probability of catching trout in the littoral zone increased with age for the fish (GLM,  $p < 0.05$ ,  $n = 111$ ; Figure 4b). The probability of catch in the littoral zone did not differ between the sexes ( $p = 0.11$ ; Figure 4b).

**Table 3:** Model selection of binomial generalized models predicting littoral habitat use of brown trout with age and sex as predictors. The models are ranked by increasing  $\Delta AICc$ . AICc weight are also displayed.

Model	AICc	$\Delta AICc$	AIC weight
Habitat ~ Age + Sex	156.33	0.00	0.72
Habitat ~ Age + Sex + Sex*Age	158.42	2.09	0.25
Habitat ~ Age	162.68	6.36	0.03
Habitat ~ Sex	210.98	54.7	0.00



**Figure 4:** Estimated parameter coefficients (dots) for littoral habitat use by brown trout (log-it scale). Panel **a** shows the estimated parameters of the three color morphs brown, intermediate and silver. Panel **b** shows the estimated parameters for age and sex. A positive parameter coefficient indicates an increased probability of littoral habitat use. A negative parameter coefficient indicates a *reduced* probability of littoral habitat use, which translates to an increased probability of pelagic habitat use. A parameter coefficient of 0 indicates that there is a 50% probability of being caught in either of the habitats. A parameter coefficient of 1 represents a 70% probability of being caught in the littoral zone, while a parameter coefficient of -1 represents a 70% probability of being caught in the pelagic zone. The whiskers show the standard error of the estimates.

## Age

There were two equally good models explaining the variation in age ( $\Delta\text{AICc} < 2$ , Table 4). The first model included habitat and maturation as predictors, while the second also included sex as a predictor. On average, littoral trout were  $0.4 \pm 0.2$  years older than pelagic trout (ANOVA,  $p < 0.05$ ,  $n = 114$ , Table 5, Figure 5a). Mature fish were  $0.8 \pm 0.2$  years older than immature individuals, on average ( $p < 0.001$ , Table 5, Figure 5a). There were no differences between the sexes ( $p = 0.27$ ). Color morph were excluded from the model (Table 4).

**Table 4:** The table shows the candidate models included in the model averaging ( $\Delta\text{AICc} < 2$ ), based on model selection of linear models (ANOVA) predicting brown trout age as a function of habitat, sexual maturation and sex. The models are ranked by increasing  $\Delta\text{AICc}$  and the degrees of freedom (df) and AIC weights are shown.

Response	Parameters	df	AICc	$\Delta\text{AICc}$	AIC weight
Age	Habitat + Maturation	4	314.4	0.00	0.45
Age	Habitat + Maturation + Sex	5	315.3	0.90	0.28

**Table 5:** Model estimates of the predictors (habitat, maturation and sex) for age after conditional model averaging with the two best models (Table 4). Associated standard errors, z-values and p-values are also given.

Predictor	Estimate	Standard error	z-value	p-value
Intercept (Littoral habitat, mature, female)	4.50	0.19	23.6	<0.001
Pelagic habitat	-0.42	0.18	2.34	0.019
Immature	-0.82	0.19	4.27	<0.001
Male	-0.20	0.18	1.11	0.270

## Relative growth

There were four equally good models explaining the variation in relative growth ( $\Delta\text{AICc} < 2$ , Table 6). The first model included habitat and maturation as predictors, while the second also included sex as predictor. In the pelagic habitat the trout had on average a  $13.9 \pm 6.0\%$  higher relative growth, compared to in the littoral habitat (ANOVA,  $p < 0.05$ ,  $n = 128$ , Table 7, Figure 5b). The silver morph had on average  $14.6 \pm 8.2\%$  higher growth than the brown morph ( $p < 0.05$ ). Immature fish had on average  $17.6 \pm 6.8\%$  higher relative growth than mature fish ( $p < 0.001$ ). There were no significant differences between silver and intermediate individuals ( $p = 0.10$ ), between brown and intermediate individuals ( $p = 0.49$ ) or between the two sexes ( $p = 0.26$ ).

**Table 6:** The table shows the candidate models included in the model averaging ( $\Delta AICc < 2$ ), based on model selection of linear models (ANOVA) predicting relative growth of brown trout as a function of habitat, sexual maturation, sex and color morph. The models are ranked by increasing  $\Delta AICc$  and the degrees of freedom (df) and AIC weights are shown.

Response	Parameters	df	AICc	$\Delta AICc$	AIC weight
Relative growth	Maturation + Habitat + Color morph	6	82.2	0.00	0.22
Relative growth	Maturation + Habitat	4	82.4	0.20	0.22
Relative growth	Maturation + Habitat + Color morph + Sex	7	82.6	0.39	0.21
Relative growth	Maturation + Habitat + Sex	5	83.9	1.65	0.15

**Table 7:** Model estimates of the predictors (habitat, maturation, color morph and sex) for log-transformed relative growth back transformed estimates after conditional model averaging with the four best models (Table 6). Associated standard errors, z-values and p-values are also given.

Predictor	Log (Estimate)	Back transformed estimate (inv(log))	Standard error	z-value	p-value
Intercept (Littoral habitat, mature, brown, female)	-1.23	0.06	0.08	16.0	<0.001
Pelagic habitat	0.13	0.14	0.06	2.14	0.032
Immature	0.29	0.18	0.07	4.27	<0.001
Silver color morph	0.17	0.15	0.08	2.02	0.044
Intermediate color morph	0.06	0.13	0.08	0.70	0.490
Male	0.07	0.13	0.06	1.12	0.265

### Body length

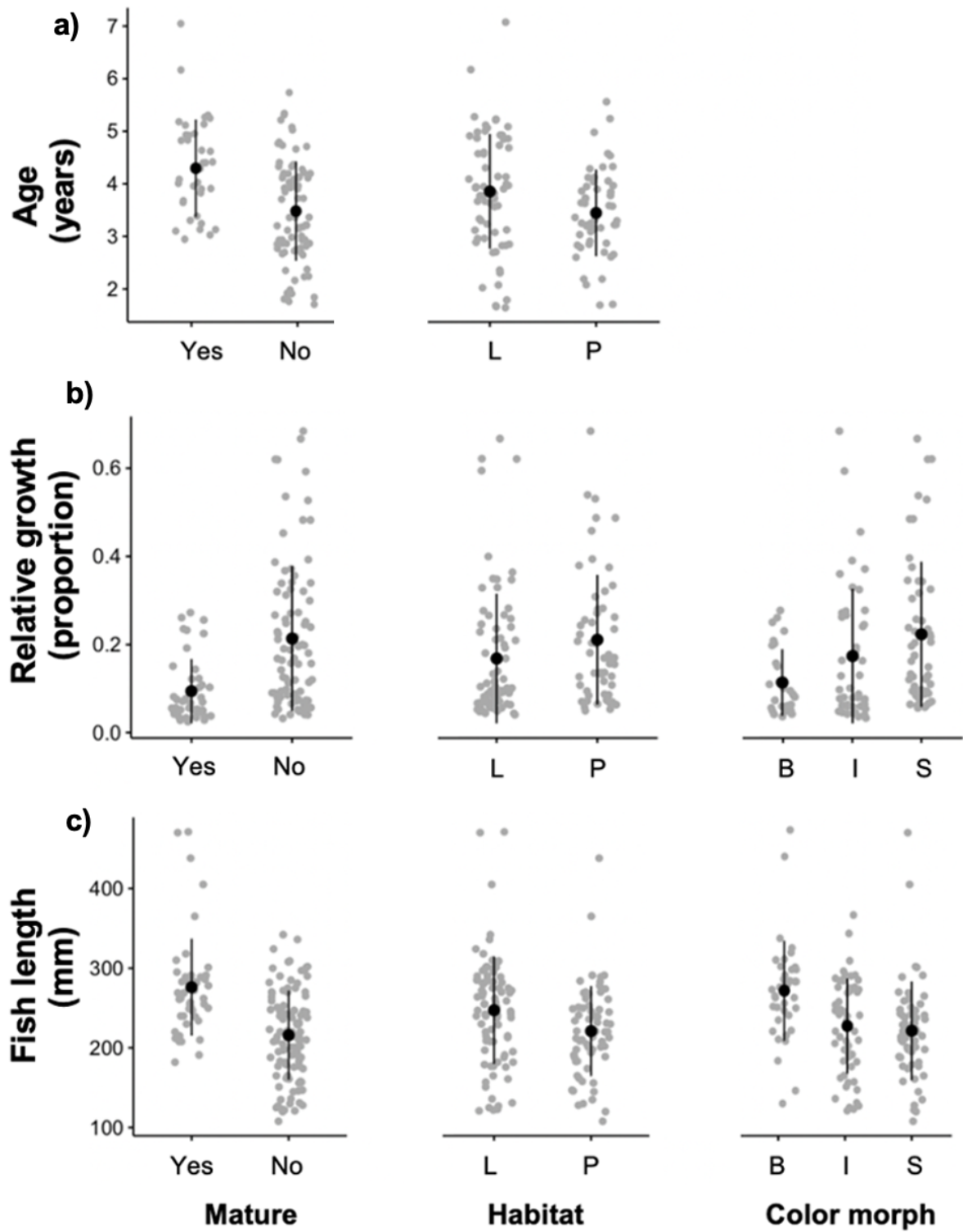
There were two equally good models explaining the variation in body length ( $\Delta AICc < 2$ , Table 8). The first model included habitat, maturation and color morph as predictors, while the second also included sex as predictor. Trout from the littoral habitat were on average  $19 \pm 9$  mm longer than pelagic trout (ANOVA,  $p < 0.05$ ,  $n = 153$ , Table 9, Figure 5c). Mature fish were on average  $55 \pm 10$  mm longer than immature fish ( $p < 0.001$ ). The silver color morph was on average  $25 \pm 12$  mm shorter than the brown morph ( $p < 0.05$ ), while the intermediate morph was on average  $33 \pm 12$  mm shorter than brown fish ( $p < 0.01$ ). There were no significant differences between the sexes ( $p = 0.62$ ), and between silver and intermediate morphs ( $p = 0.50$ ).

**Table 8:** The table shows the candidate models included in the model averaging ( $\Delta\text{AICc} < 2$ ), based on model selection of linear models (ANOVA) predicting brown trout length as a function of habitat, sexual maturation, sex and color morph. The models are ranked by increasing  $\Delta\text{AICc}$  and the degrees of freedom (df) and AIC weights are shown.

Response	Parameters	df	AICc	$\Delta\text{AICc}$	AIC weight
Body length	Habitat + Maturation + Color morph	6	1670.1	0.00	0.49
Body length	Habitat + Maturation + Color morph + Sex	7	1672.0	1.94	0.19

**Table 9:** Model estimates of the predictors (habitat, maturation, color morph and sex) for body length after conditional model averaging with the two best models (Table 8). Associated standard errors, z-values and p-values are also given.

Predictor	Estimate	Standard error	z-value	p-value
Intercept (Littoral habitat, mature, brown, female)	303.4	11	27.1	<0.001
Pelagic habitat	-19.6	9.3	2.10	0.036
Immature	-55.0	10	5.46	<0.001
Silver color morph	-25.4	13	2.03	0.042
Intermediate color morph	-32.7	12	2.73	0.006
Male	-4.70	9.5	0.50	0.620



**Figure 5:** Differences in age (panel a), relative growth (panel b) and length (panel c) between mature (Yes) and immature (No), littoral- (L) and pelagic-caught (P), as well as brown (B), intermediate (I) and silver (S) color morphs of brown trout, with the grey dots presenting individual values and the black dots and whiskers showing the mean and SD values.

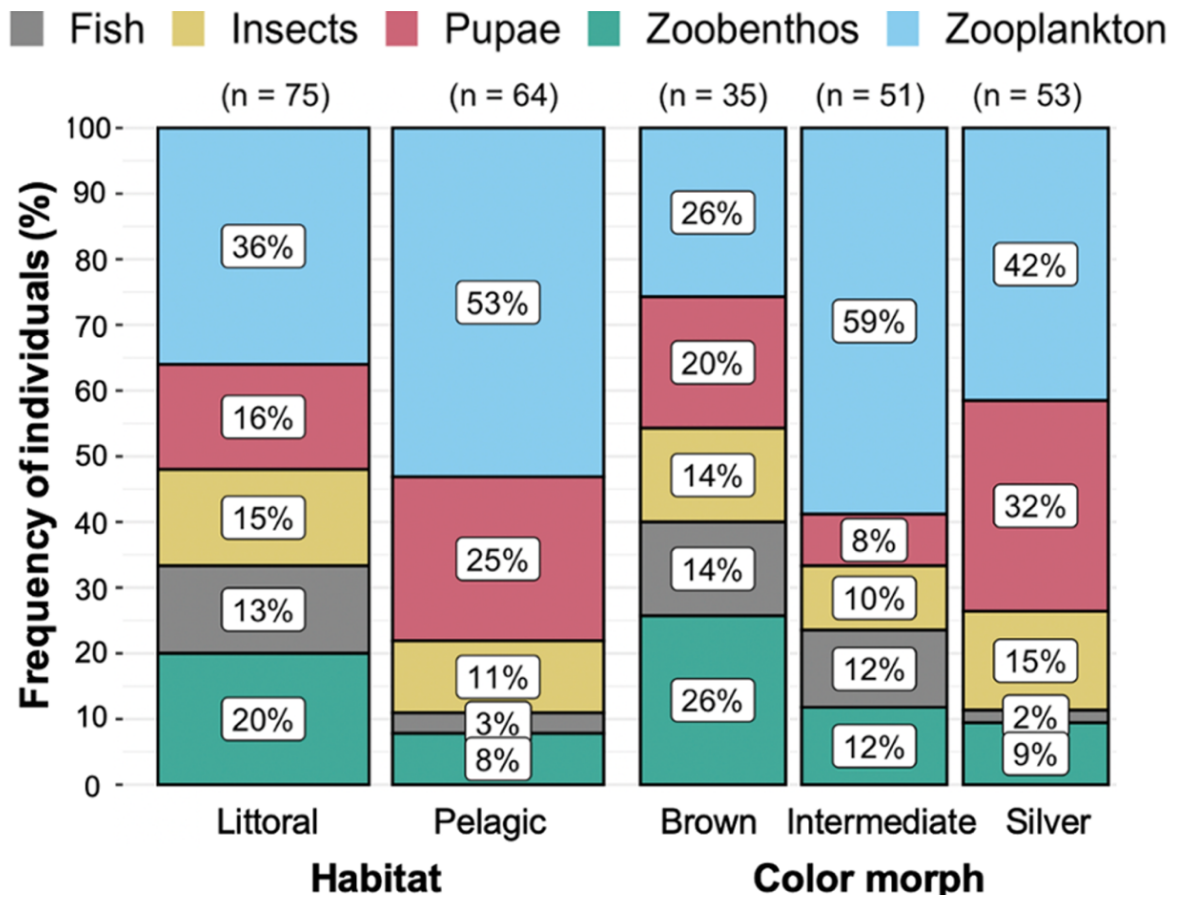
## Diet

A total of 140 trout stomachs contained prey, while 19 (14%) were empty. The average percentage degree of fullness was 37% for stomachs containing prey. Based on stomach contents data, there were significant between-habitat ( $\chi^2 = 11.8$ , d.f. = 4,  $p < 0.05$ ,  $n = 140$ ) and between-morph ( $\chi^2 = 22.4$ , d.f. = 8,  $p < 0.01$ ,  $n = 140$ ) differences in the brown trout diets. Littoral caught trout ate more fish ( $\chi^2 = 5.3$ , d.f. = 1,  $p < 0.05$ ,  $n = 12$ ) and zoobenthos ( $\chi^2 = 5.0$ , d.f. = 1,  $p < 0.05$ ,  $n = 20$ ) than pelagic trout. Zooplankton dominated the diets of both littoral- and pelagic-caught trout, but the littoral-caught trout showed more variable diets (Figure 6). The silver morph ate more pupae ( $\chi^2 = 4.2$ , d.f. = 1,  $p < 0.05$ ,  $n = 28$ ) and zooplankton ( $\chi^2 = 5.5$ , d.f. = 1,  $p < 0.05$ ,  $n = 61$ ) than the brown morph. The intermediate morph also ate more zooplankton than the brown morph ( $\chi^2 = 11.3$ , d.f. = 1,  $p < 0.001$ ,  $n = 61$ ), while the silver morph ate more pupae than intermediate ( $\chi^2 = 8.0$ , d.f. = 1,  $p < 0.01$ ,  $n = 28$ ). Zooplankton contributed most to the diets from in the littoral and pelagic habitats and for the silver and intermediate morphs. For the brown morph, zooplankton and zoobenthos made up an equally large contribution to the diet (Figure 6).

Model selection suggested that the best model to explain the variation in  $\delta^{15}\text{N}$  was the model including length, color morph and the interaction length x color morph (Table 10). The brown color morph had higher  $\delta^{15}\text{N}$  values than the intermediate color morph, on average (ANCOVA,  $p < 0.05$ ,  $n = 49$ , Figure 7). The  $\delta^{15}\text{N}$  values increased with length for the intermediate and the brown color morphs ( $p < 0.001$ ,  $n = 49$ ), but faster for the former morph ( $p < 0.05$ ,  $n = 49$ ). There were no significant differences in the  $\delta^{13}\text{C}$  values of littoral- and pelagic-caught brown trout (Kruskal-Wallis tests,  $\chi^2 = 0.048$ ,  $df = 1$ ,  $p = 0.83$ ) or between the three color morphs ( $\chi^2 = 3.05$ ,  $df = 2$ ,  $p = 0.22$ , Figure 7).

The MixSIAR model indicated some between-habitat and between-morph differences in the long-term assimilated diets of brown trout (Table 11). Based on the isotope data, pelagic-caught trout seemed to occupy a slightly lower trophic position (low  $\delta^{15}\text{N}$ ; Figure 7a) and to feed more on zooplankton and less on sticklebacks as compared to littoral-caught trout (Table 11). Although the 95% Bayesian credibility intervals for prey proportions overlapped between the trout color morphs (Table 11), the brown color morph tended to feed more on sticklebacks than the others, with the high trophic position indicated by the high  $\delta^{15}\text{N}$  values of the brown morph caught from the littoral habitat (Figure 7b).





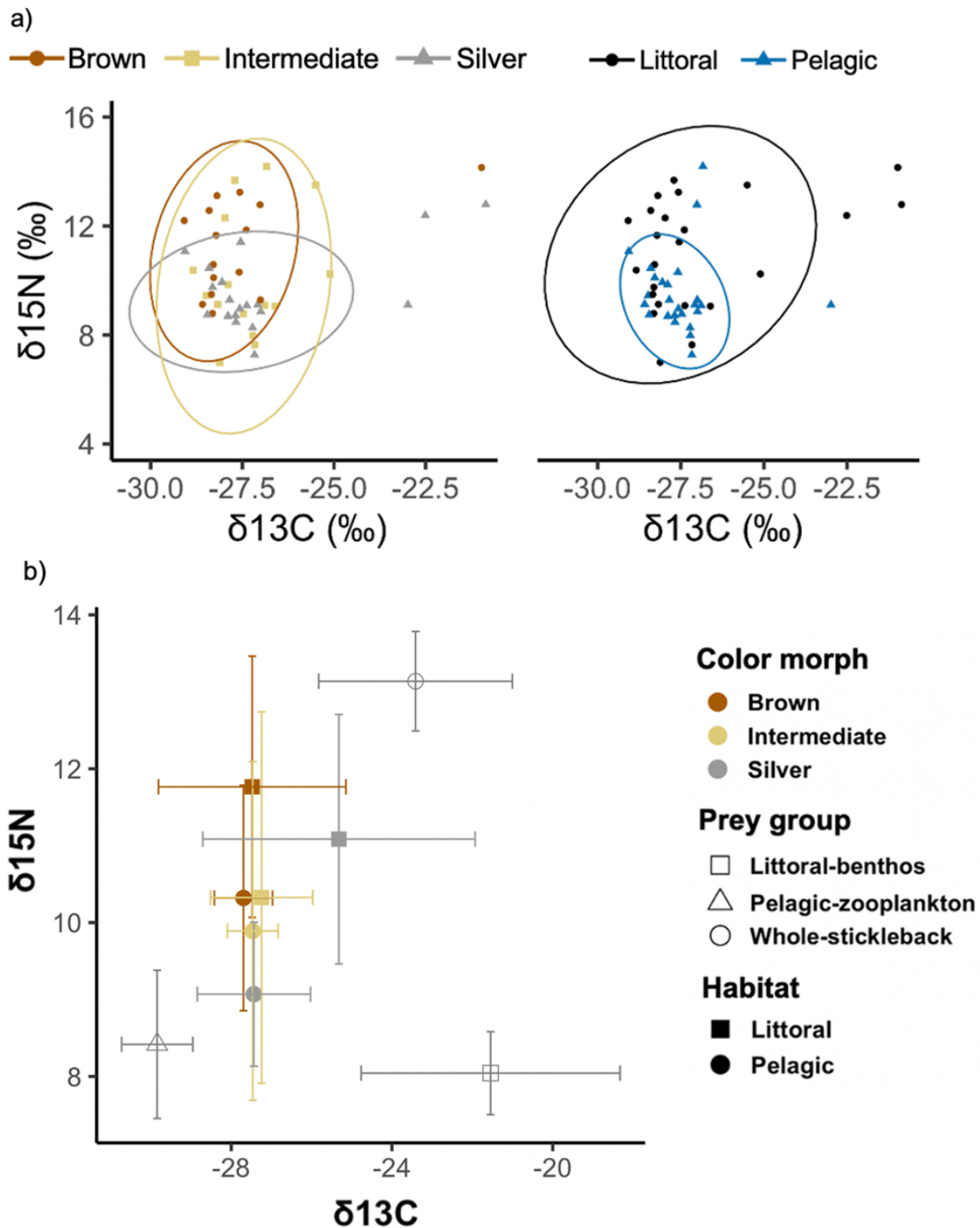
**Figure 6:** The relative proportions of different prey categories observed in the stomach contents of brown trout caught from the littoral and pelagic habitats and showing different colour morphs. The sample sizes are provided in parentheses above the bars. The blue color represent zooplankton, red pupae, yellow insects, grey fish and green zoobenthos.

**Table 10:** Model selection of linear models for  $\delta^{15}\text{N}$  showing the models where  $\Delta\text{AICc} < 2$ . The models are ranked by decreasing  $\Delta\text{AICc}$ . In addition the degrees of freedom (df) and AICc weight are displayed. The best ranked model have the parameters color morph, length and the interaction length x color morph.

Response	Parameters	df	AICc	$\Delta\text{AICc}$	AICc weight
$\delta^{15}\text{N}$	Color morph + Length + Length*Color morph	7	141.5	0.0	0.37
$\delta^{15}\text{N}$	Habitat + Color morph + Length + Length*Color morph	8	142.5	1.0	0.22
$\delta^{15}\text{N}$	Color morph	5	143.4	1.9	0.15

**Table 11:** The results of the MixSIAR isotope mixing model estimating the relative proportions of zoobenthos, zooplankton and sticklebacks in the long-term diets of brown trout caught from the littoral and pelagic habitats and representing the three different color morphs. The means and SDs of diet proportions are provided along with the 95% Bayesian credibility intervals.

	<b>Proportion of diet (%)</b>	<b>SD (%)</b>	<b>95% CI</b>
Littoral trout			
Zoobenthos	6.0	4.4	0.5-17
Zooplankton	40	9.3	20-57
Sticklebacks	55	8.7	38-72
Pelagic trout			
Zoobenthos	11	6.6	0.3-25
Zooplankton	62	6.4	49-74
Sticklebacks	27	7.3	12-41
Brown color morph			
Zoobenthos	7.2	4.7	0.6-18
Zooplankton	51	10	30-72
Sticklebacks	46	10	24-62
Intermediate color morph			
Zoobenthos	7.4	5.8	0.3-21
Zooplankton	61	8.3	45-78
Sticklebacks	30	9.0	13-49
Silver color morph			
Zoobenthos	17	11	0.4-40
Zooplankton	53	9.0	34-70
Sticklebacks	29	10	10-50



**Figure 7:** Panel **a** shows the stable isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ), and ellipses showing the 95% confidence interval, for the brown, intermediate and silver color morphs (shown in different colors), and for the littoral and pelagic habitats (shown in different colors). Each point represent one trout individual. Higher  $\delta^{13}\text{C}$  values indicate a more littoral diet, while lower values indicate a more pelagic diet. Higher  $\delta^{15}\text{N}$  indicate a higher trophic position in the food web. Panel **b** shows the mean stable isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ), and error bars showing the standard deviations. Color morphs are separated by colors, while habitats and prey groups are separated by shapes.

## **Discussion**

This study investigated potential resource polymorphism of a brown trout population by examining between-habitat and between-morph differences in ecological traits. Despite overlapping dietary and isotopic niches, there were habitat differences in length, age, relative growth and diet composition. The data suggests that the color morphs of trout in Storvatnet differ in ecology and resource use to some extent. There was therefore some indication of divergence into at least two potential morphs based on morphological- and life history traits, and to a lesser extent based on diet. Brown morph individuals were more likely to be caught from the littoral habitat. They were also longer, older and showed lower relative growth and more variable diets than silver morph individuals that used mainly the pelagic habitat and had more specialized diets. A possible third morph was characterized by intermediate skin color, age and growth and a broad isotopic niche, but a narrower zooplanktivorous diet based on stomach content data.

In this study brown trout were prevalent in the littoral and the pelagic zone. Several studies report that brown trout are most abundant in, and partly restricted to, the littoral zone, but that applies to lakes in which trout is exposed to interspecific competition (Saksgård & Hesthagen, 2004; Eloranta et al., 2013). In lake Storvatnet trout coexist with sticklebacks, however the latter function as a food resource and not as a competitor. Jonsson (1989) observed the similar habitat distribution as in this study in two lakes where interspecific competition was absent. In this study, the stomach content and stable isotope data indicated only minor differences in the short- and long-term diets of littoral- and pelagic-caught trout. Interestingly, zooplankton contributed heavily to the diet for fish from both habitats. Even though the pelagic trout seemed to occupy a lower trophic position, the trophic niches of littoral and pelagic fish overlapped. The observed zooplankton contribution to the diet of pelagic fish was similar to other observations of pelagic trout and charr (Eloranta et al., 2013; Piggot et al., 2018). For the littoral trout, the literature shows inconsistent results. Surface insects, insect larvae- and pupae, and zoobenthos have all been found to be the dominating food source for littoral caught trout in different lakes (Jonsson, 1985; Eloranta et al., 2013; Jensen et al., 2017). Considering that this study was conducted in the autumn, it is not surprising that zooplankton contributed abundantly to the diets, as the biomass is at its highest around that time (Hindar & Jonsson, 1982; Jonsson & Gravem, 1985). This indicates a possibility for seasonal changes in niche divergence between the morphs due to the changes in prey availability, that may alter

the diet of littoral-caught trout to consist of more zooplankton. Whilst this has not been previously documented for brown trout, Hindar & Jonsson's (1982) study of a polymorphic charr population detected no resource segregation between two morphs in the autumn, only when the prey availability was low in the spring did the morphs differ in habitat and diet.

Polymorphism can be induced by high intraspecific competition (Skúlason et al., 2019), and this competition will necessarily increase when the feeding opportunity and prey availability are low. Even though fish and zoobenthos are more energy rich prey than zooplankton (Næsje et al., 1998; Cochran-Biederman & Vondracek, 2017), there are trade-offs involved in maximising feeding efficiency, minimizing energy use and predation risk. The littoral trout can be territorial feeders (Eloranta et al., 2013), which is an energy efficient strategy, but it requires large size, physical dominance and hiding from avian predators. Littoral-caught subordinates in this study could be forced to be opportunistic feeders utilizing all resources, or the intraspecific competition could be low due to great abundance of prey, thus the need for a specialized diet is limited. The most interesting finding in terms of resource use is the seemingly importance of zooplankton, that could indicate bottom-up control of the zooplankton on the trout population, in both habitats. If this major food source would change, like it has been suggested to due to climate change (Braun et al., 2021), it may alter the dynamics of resident pelagic and littoral trout, as well as the anadromous trout. More individuals might end up with the latter strategy. Studies observing resource use is important, because we need information about different systems to know how to manage the functioning of different lakes to sustain salmonid fish populations.

Whilst resource polymorphism in salmonids often refers to morphs differing between habitats (Knudsen et al., 2006), the three different skin colors of brown trout in Storvatnet are referred to as color morphs which can be easily recognized. This is common among tropical freshwater fish species such as zebrafish and cichlids (Spence & Smith, 2007; Kusche, 2013). Color morphs could partially be linked to habitat, as the brown and intermediate color morph was more likely to be caught in the littoral zone than the silver morph. This observation was expected, because skin color likely functions as a camouflage in the different environments, both to be less visible when feeding, and to avoid predation from large trout and birds (Hoar, 1988; Kusche, 2013). Brown colored littoral fish and silver coloured pelagic fish have also been reported in previous findings in salmonids, supporting the predictions further (Woods et al., 2012; Skoglund et al., 2015; Arostegui & Quinn, 2019). In contrast, Piggott et al. (2018)

observed dark pelagic trout and littoral trout that were paler than the pelagic, indicating that camouflage is not the driver of this coloration. One possible explanation could be a low predation pressure on trout. These color morphs also differed genetically (Piggott et al., 2018), therefore it is possible that the coloration reflects genetically determined differences, and not only morphological color change.

Westley et al. (2013) found skin color to be a plastic response to substrate lightness/darkness for individuals from different brown trout populations. All fish reared on dark substrate exhibited darker skin colors on average than the fish on light substrate (Westley et al., 2013). For the intermediate color morph, one can therefore think of two scenarios that would promote this color. The intermediate color could be an adaptation to a lighter substrate in parts of the littoral zone. In this way, the intermediate morph could be one of two littoral morphs together with the brown morph, using different micro-habitats. The other, more likely explanation could be that the intermediate morph are the most opportunistic generalist feeders that are semi-adapted to both habitats. In lake Storvatnet, since anadromous trout are present, the silver individuals could both be pelagic zooplanktivores, but also out-migrating smolts or returned sea trout. Mature fish could also skew the color data in the littoral habitat by overrepresenting the brown color morph in the autumn before spawning in the streams connected to the littoral habitat (Wedekind et al., 2008). It is not known if the observed skin color is a plastic trait like Westley et al. (2013) suggest, or if there is a genetic difference between the morphs (Wedekind et al., 2008; Piggott et al., 2018), but the observation of differing color morphs is a useful finding, given that there is a link between color and associated traits (e.g. high  $\delta^{15}\text{N}$  for the brown morph). The proportions of the color morphs could shift over short time periods if it is a plastic trait responding to the environment, or over generations if the optimum color morph ratio changes as a result of natural selection (e.g. in response to food availability). If the intraspecific competition were to decrease, the morphs could become be less distinguishable, or oppositely, if competition increase the differences could increase. The individual variation in skin color would nonetheless have been important in the efficient use of all available habitats, something that is not always the case for brown trout (Eloranta et al., 2013).



The littoral-caught trout and the brown morph individuals were of similar lengths, and had similar growths and diets. Pelagic-caught trout and the silver morph individuals were also of similar lengths, and had similar growths and diets. In this study, the former were older, had lower relative growth and a longer body length than the latter. Interestingly, the literature shows the opposite relationship between size and habitat, both for trout and charr (Jonsson, 1989; Jonsson & Gravem, 1985; Sandlund et al., 1987). Since the literature span systems with and without interspecific competition, it is reasonable to think that competition is not the dominant factor affecting this difference (Haraldstad & Jonsson, 1983; Jonsson, 1989). Some factors possible affecting this unexpected observation could be the variation in depth of the littoral zone or the prey availability. If the littoral zone is very shallow, then the large fish could be exposed to avian predation, whereas if the littoral zone has deeper, heavily vegetated areas, then the large fish would be less exposed. A piscivorous diet is very energy rich, and the littoral habitat has a presence of sticklebacks. Thus, the littoral habitat could provide the most favorable prey for the large dominating individuals, leaving small, young trout to be exposed to cannibalistic predation, making them utilize the pelagic habitat (Næsje et al., 1998; Jensen et al., 2004).

Jonsson (1989) found that females were more likely to inhabit the pelagic habitat than males of the same age, but no evidence of a sex-difference was observed in this study. Again, the time of the year might influence the results, as the trout are about to spawn. Thus, mature females could have entered the littoral habitat, before entering the streams, resulting in an equal sex ratio between habitats. The differences in length, age and growth indicate that habitat could be the mechanism that previously have led to and currently maintain differences in morphology between the color morphs. This further supports the theory of polymorphism in this trout population with individuals that show a great individual variation. The observed characteristics of the trout population in lake Storvatnet could further be used to explain variation between populations. When comparing lake systems with and without polymorphism, drivers of resource polymorphism in brown trout can be identified. In a conservation perspective it would then be interesting to use models for predicting if a polymorphic trout population would be more resistant to climate change, pollution and disease than monomorphic populations, due to higher plastic adaptive potential or more genetic diversity (Forsman & Wennersten, 2016).

In the process of choosing a subsample for obtaining age, growth, sex, maturation and diet data, fish were selected to represent morphs and habitats. This limited the analysis, in that color morph could not be included as a predictor for probability of habitat use together with age and sex data. The sampling effort of multi-meshed gillnets should have been the same in both habitats, then a random selection of fish should represent the population, in size, color morph and habitat use. The color morph data can be weakened by the absence of standardized procedures. Even though different samplers were accounted for in the model, there is no guarantee that the same sampler was consistent in the color determination. In addition, the trout first caught in the gillnet turned pale before the nets were taken up, making it hard to distinguish between the brown and intermediate morph. The results of dietary analyses should be considered with caution as 1) diet data based on the stomach content only gives a snapshot of the recently consumed prey, 2) the individual data of one stomach reflected only the most abundant prey group, and did not separate between stomachs containing 100% or 50% of the prey group, and 3) the sample size in the isotope analysis might have been too small to detect the differences.

This study largely functioned as a pilot study in exploring how individual brown trout differed and provided an example of resource polymorphism. My results suggest that further research exploring polymorphism in trout should consider: 1) conducting the sampling in the spring when the zooplankton are less dominant in the ecosystem, potentially revealing niche divergences between the morphs; 2) comparing body shape measurements between morphs, as shape is commonly found to differ between morphs of Arctic charr (Skoglund et al., 2015); 3) include genetic analysis that could deny or confirm genetically differences between the morphs, revealing the ultimate mechanisms behind the observed divergence; 4) following the potential phenotypic changes of individuals to examine if the individuals show habitat residency to the littoral or pelagic habitat; 5) standardizing and quantifying the different colors into a spectrum going from a lightest to darkest skin color similar to Westley et al. (2013), providing more options for the data analyses; and 6) experimentally testing of consistent differences in behavior (e.g. aggressiveness, boldness) between the morphs that could be related to different strategies in resource utilisation.

In conclusion, this study indicates polymorphism in a brown trout population, even though the isotope analysis revealed overlapping trophic niches between the possible morphs. The two



potential morphs included one brown-colored generalistic littoral feeder that were larger and older, and one silver-colored, specialized, zooplanktivorous, pelagic feeder which were smaller and younger. Resource polymorphism often arises in systems with high intraspecific competition, and Lake Storvatnet is an example of such a system. Thus, resource polymorphism might have been facilitated, but the high resource availability before and during the field sampling could make the divergence between morphs even clearer during another season. This study provides valuable information which may be important for understanding the lake ecosystem and population adaptability of brown trout.

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## Appendix

The probability of catch in the littoral and pelagic zone may differ between females and males of the same length, age, and/or relative growth. Interactions between sex and (1) age, (2) body length, and (3) relative growth was therefore included in the preliminary models. For each of the separate preliminary models, the two models with the best AICc score are shown in Table A1. Age was found to be the best predictor to include in the global model explaining the variation in the data the best (Table A1).

Each of the correlated predictors; age, length and relative growth, were evaluated in separate preliminary models, to avoid problems with model selection and parameter estimation (Table A1). The probability of catching torut in the littoral and pelagic habitat may differ between females and males of the same length, age, and/or relative growth. Interactions between sex and (1) age, (2) body length, and (3) relative growth was therefore included in the preliminary models. For each of the separate preliminary models, the two models with the best AICc score are shown in Table A1. Age was found to be the best predictor to include in the global model explaining the variation in the data the best (Table A1).

**Table 4:** Preliminary model selection of binomial generalized models for three separate predictor variables (growth, length and age), on probability of littoral habitat use. The models are ranked by decreasing  $\Delta AICc$ . The two models with the lowest  $\Delta AICc$  is displayed for each of the three versions.

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Rank	Model	AICc	$\Delta AICc$
1	Habitat ~ age + sex	156.33	0.00
2	Habitat ~ age * sex	158.42	2.09
4	Habitat ~ relative growth*sex	176.21	19.9
5	Habitat ~ relative growth + sex	176.52	20.2
7	Habitat ~ length + sex	206.67	50.3
8	Habitat ~ length * sex	208.75	52.4

