UiT The Arctic University of Norway

Faculty of Biosciences, Fisheries and Economics
Department of Arctic and Marine Biology

The intraspecific diversity of Norwegian Arctic charr (*Salvelinus alpinus* (L.)):

An examination of repeatability and life history

Gabrielle Grenier

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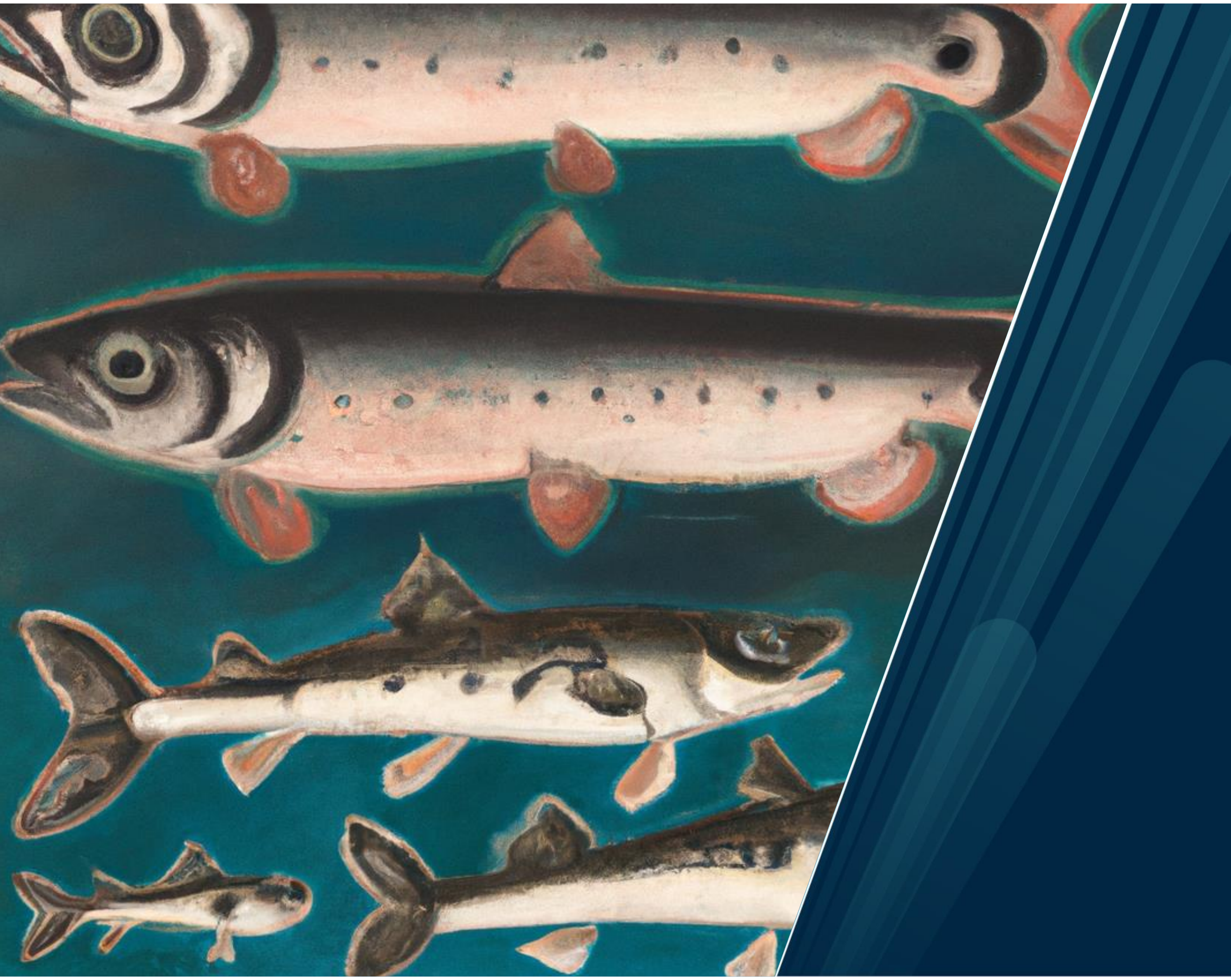

Cover Image

Currently artificial intelligence (AI) is a hot topic in the media. As AI uses pattern recognitions in the data it is provided with, I thought it would be interesting if it could find patterns in Arctic charr to produce images of ecotypes. The cover image was generated with the assistance of DALL·E 2 and the text prompt used was:

> *A painting in the style of the Group of Seven with three Arctic charr ecotypes as the subject where one is normal, one dwarf with paedomorphic morphology blunt snout and large eyes, one is piscivorous with a long head, large teeth and, a long and slender body*

I asked for a painting in the style of the Group of Seven to honour my Canadian roots. The Group of Seven was a group of Canadian painters that painted landscapes representing Canada in the early 20th century.

Images on the first page of each section are also images that were generated with DALL·E 2 using the same prompt as the cover image but in the style of Emily Carr. Emily Carr was also a famous Canadian painter active in the 20th century. She had strong links to the Canadian Group of Seven, but was never an official member.

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Acknowledgements

“*Science is a social endeavour.*”
UiT Freshwater Ecology Group motto

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Summary

Within the salmonids a high degree of variation is displayed in life history strategies (e.g., anadromy vs. freshwater residence) and life history traits (e.g., early vs. late maturation). This variation exists at both the inter- and intra-specific levels of diversity. Among anadromous salmonids, many species have a life cycle where the return to freshwater occurs following an extensive period (i.e., years) foraging in the marine environment once individuals have reached maturity. In contrast, other salmonids deviate from this life cycle and perform shorter (i.e., weeks to months) annual migrations to the marine environment, thus individuals of these species return to freshwater as juveniles and adults. At the intraspecific level in salmonids, many species show divergence of ecotypes specializing their ecological niche to the various lacustrine (i.e., littoral, benthic, pelagic) habitats. The diversity in salmonids therefore makes this group an interesting model to study life history traits and strategies, in association with the trophic niche in which they evolved, and broader evolutionary questions both at the inter- and intra-species level.

Arctic charr (*Salvelinus alpinus*, (L.)) is a species that exhibits a high intraspecific diversity in life history strategies and traits, morphology, and trophic ecology. Populations of Arctic charr exist as both anadromous and lifelong freshwater residents (i.e., lacustrine populations). We see further diversity with the repeated sympatric occurrence of more than one ecotype within both anadromous and lacustrine populations. Among the lacustrine Arctic charr, co-occurring ecotypes show repeatable patterns of diversification within the species' Holarctic distribution where an omnivorous ecotype is often found in sympatry with one or two benthivorous ecotypes. A third piscivorous ecotype can also occur with the other ecotypes. Arctic charr ecotypes are known to differ in trophic ecology, habitat preferences, morphology, and life history traits with a seemingly repeatable pattern across populations. The level of intraspecific diversity displayed within populations is also variable as two to four different ecotypes have been identified living in sympatry among Arctic charr populations.

In this study, I demonstrate that Arctic charr ecotypes show repeatable patterns in life history traits even at differing levels of intraspecific diversity. The Piscivorous ecotype shows more variation in its parameters of life history relative to the other ecotypes. Studying the variation in and correlations among functional traits of habitat, diet, morphology, and life history parameters in various ecotypes at differing levels of intraspecific diversity demonstrated that there is evidence for trait correlations as an important factor modulating the life history strategies of Arctic charr ecotypes. I refer to this as an adaptive trait syndrome in Arctic charr. The adaptive trait syndromes differed in alike ecotypes at differing levels of intraspecific diversity implying that the relationships among ecotypes are central to the co-existence of ecotypes within a population. To study traits of the anadromous life history strategy in Arctic charr, a non-lethal method using fin tissue signatures of sulfur stable isotopes was developed to quantify the number of marine migrations and relate it to diet, condition, and maturation. With increasing marine experience, a gradual shift toward higher specialisation in the trophic niche was found for anadromous Arctic charr. Males and females benefit differently from each additional migration as females require more migrations to reach maturity.

The results of this thesis show that studies of species with high intraspecific diversity require more than an exclusively single trait-based approach. The covariation of traits is important in the Arctic charr species complex at differing levels of intraspecific diversity. Furthermore, this thesis highlights how methodological advancements can help in monitoring and conserving the anadromous life history strategy in Arctic charr by providing new knowledge on the ecological shifts that occur with increasing marine experience.

List of papers

Paper I:

Grenier, G., Smalås, A., Kjær, R., and Knudsen, R. 2021. Environmentally modulated repeat evolution of polymorphic Arctic charr life history traits. Frontiers in Ecology and Evolution. 9:771309. doi: 10.3389/fevo.2021.771309

Paper II:

Grenier, G., Knudsen, R., Chavarie, L. Extent of repeatability of life history and related functional traits in polymorphic Arctic charr. (advanced manuscript)

Paper III:

Grenier, G., Knudsen, R., Jensen, H., Power, M. Marine experience is related to trophic niche shifts, condition, and maturity in anadromous Arctic charr. (advanced manuscript)

Author contributions

	Paper I	**Paper II**	**Paper III**
Concept and idea	GG, RKn, RKj	GG, LC, RKn	GG, RKn, MP, HJ
Study design and methods	GG, RKn, RKj, AS	GG, LC	GG, MP, HJ
Data gathering and interpretation	GG, RKj	GG, LC	GG, MP
Manuscript preparation	GG, RKn, RKj, AS	GG, LC	GG, MP

Abbreviations for authors (in alphabetical order): Louise Chavarie (LC), Gabrielle Grenier (GG), Hallvard Jensen (HJ), Runar Kjær (RKj), Rune Knudsen (RKn), Michael Power (MP), Aslak Smalås (AS)

Supervision

Main supervisors

Professor Rune Knudsen

Department of Arctic and Marine Biology

Faculty of Biosciences, Fisheries and Economics

UiT The Arctic University of Norway

9037 Tromsø, Norway

Associate Professor Christian Selbach

Department of Arctic and Marine Biology

Faculty of Biosciences, Fisheries and Economics

UiT The Arctic University of Norway

9037 Tromsø, Norway

Co-supervisor

Associate Professor Jarad P. Mellard

Department of Arctic and Marine Biology

Faculty of Biosciences, Fisheries and Economics

UiT The Arctic University of Norway

9037 Tromsø, Norway

1 Introduction

If we only stop for a moment and watch the world around us, we quickly start understanding the fascination naturalists had and continue to have with the apparently inexhaustible diversity in the natural world. In this moment we may start pondering why, for example, the bumblebee forages on a specific flower and not another one. Our observation indirectly poses the question of what makes the bumblebee suited to foraging on specific flowers. Furthering this line of questioning, we may start wondering if this bumblebee has certain traits related to its specific resource utilization that differ from those of other bee species and which of these traits might be involved in the speciation processes that have led to the multiple bee species we observe today.

Understanding the why and the how of species are questions that date back centuries (e.g., Darwin 1859). Although groundbreaking progress has been made in our understanding of the evolution of species and their interspecific and intraspecific diversity, especially since the coining of the biological species concept (Mayr 1969; Via 2001), many questions remain around the ecological processes that drive diversity and speciation (Langerhans and DeWitt 2004; Hendry et al. 2009; Seehausen 2009). Such questions include the causes of speciation (Hendry et al. 2009), the mechanisms which are at play to promote speciation (Seehausen 2009), and the relative importance of environment vs. genetic history (Langerhans and DeWitt 2004) in the development of species. We see multiple examples of adaptive radiation, where multiple descendants radiate from a common ancestor in response to environmental conditions through natural selection (Schluter and Grant 1984; Schluter and Rambaut 1996; Turner et al. 2001). However, a question remains, whether similar environments result in similar adaptations (Langerhans and DeWitt 2004). Put simply, is evolution repeatable?

1.1 Adaptive traits, syndromes, and landscapes

Through natural selection, only the fittest survive to reproduce and pass on their genes to future generations. An individual's fitness comes down to their growth, survival, and reproduction (Hutchings 2021). Adaptive traits are therefore those that influence an individual's fitness through effects on growth, survival, or reproduction (Dobzhansky 1956). However, various traits may synergistically act to influence an organism's fitness (Laughlin and Messier 2015). The adaptive value of a trait is therefore not only related to the trait's direct effects on growth, survival, or reproduction but also to the correlations that exist among all traits that result in an individual's phenotype. The adaptive value of a phenotype is revealed through the fitness this phenotype conveys to individuals within their environment (Dobzhansky 1956; Hutchings 2021).

Biological fitness is a measure of an individual's contribution to future generations (Smith et al. 2012). Ultimately, this is a result of successful reproduction by growing and surviving to maturity (Dobzhansky 1956; Smith et al. 2012; Hutchings 2021). However, achieving reproduction is complex and is influenced by multiple parameters which together are encompassed under the umbrella of life history theory (Dobzhansky 1956; Stearns 1992; Hutchings 2021). Within life history theory, a life history strategy describes the combination and coordination of parameters influencing an individual's fitness (Stearns 1992; Hutchings 2021). Furthermore, fitness is relative to the environment, therefore multiple life history strategies may confer similar fitness in varying contexts (Schluter 2000; Hutchings 2021).

Classically, life history in animals has been visualized as a dichotomy with r-selected (approaching r, the intrinsic rate of population growth) species and K-selected (approaching K, the carrying capacity or maximum sustainable population size) species (Mac Arthur and Wilson 1967; Smith et al. 2012; Hutchings 2021). Typically, r-selected species will have a short generation time, therefore high growth and low age at maturity, and produce many small offspring (Mac Arthur and Wilson 1967; Hutchings 2021). On the other hand, K-selected organisms have an older age and larger size at maturity related to their relatively lower growth rate and produce fewer but larger offspring (Mac Arthur and Wilson 1967; Hutchings 2021). Although this r-K model is useful to explain life history, it is imperfect. Comparisons of life history strategies across taxa with the r-K model are of low value. For example, the large range of body size among organisms of varied taxa, which is highly correlated to metabolic rates and longevity, limits the use of the r-K model to closely related taxa (Smith et al. 2012). The r-K model has nonetheless contributed to the thinking of life history strategies not as an assemblage of singular traits, but rather as a complex set of correlated traits (Hutchings 2021).

An extension to the r-K model has led to the presentation of the *fast-slow continuum hypothesis*, where organisms are placed along the continuum based on mortality (i.e., longevity) which correlates with growth, age of maturity, generation times, and fecundity (Smith et al. 2012), while also attempting to remove the effect of body size on the traits (Oli 2004). Further traits, such as metabolism and personality, were hypothesized to covary within the framework of the fast-slow continuum hypothesis, referred to as the *Pace of Life* syndrome (Ricklefs and Wikelski 2002; Réale et al. 2010; Mathot and Frankenhuis 2018). The repeated occurrence of specific trait correlations among individuals of a population has therefore been termed a syndrome (Dobzhansky 1956; Ricklefs and Wikelski 2002; Réale et al. 2010). To date, multiple syndromes have been coined (e.g., "Migratory syndrome", "Behavioural syndrome", and "Dispersal syndrome"; Dingle 2006; Dingemanse et al. 2012; Raffard et al. 2022). However if the studied traits offer an adaptive value, then we may simply consider these adaptive trait syndromes (Blasini et al. 2021).

A useful model to study the relationship between fitness and adaptive traits has been the adaptive landscape model (Wright 1932; Simpson 1944; Lande 1976; Cruzan and Rhode 2004).

On the axes of the landscape we have the phenotypic traits and the height of the landscape represents fitness with peaks representing high fitness and troughs being areas of low fitness (Lande 1976; Schluter 2000). It is possible to have multiple peaks on a single fitness landscape, as no single combination of traits offers peak fitness depending on the environmental conditions (Schluter 2000; Nosil 2012). Populations occupying valleys of adaptive landscapes are pulled towards a peak through natural selection, or the population goes extinct (Nosil 2012). Furthermore, as the environment is dynamic and changes over time so do the peaks along the adaptive landscapes (Laughlin and Messier 2015). A species' ability to move in dynamic adaptive landscapes, intensified by climate change and anthropogenic influences, is therefore linked to the species' resilience (Hutchings 2021). A multidimensional understanding of species vs. the classic singular trait approach will thus be essential in conservation efforts (Laughlin and Messier 2015).

1.2 Fishes of postglacial lakes

Postglacial lakes offer excellent systems to study questions related to how and why species have come to be as they are in dynamic adaptive landscapes. As postglacial lakes have only been recolonized following the retreat of the glaciers after the last glacial maximum approximately 10 000 to 15 000 years ago (Schluter 1996; Brunner et al. 2001), the organisms that occur within this range have had a relatively short evolutionary history within that habitat (Brunner et al. 2001). Due to their history of recolonization, postglacial lakes act as biological islands and offer relatively simple systems to study evolutionary processes (Schluter 1996). Furthermore, among the species of fishes occurring in postglacial lakes, a trend is seen in their repeated radiation and high phenotypic variation (Schluter 2000; Robinson and Parsons 2002). Multiple species of postglacial fishes have been used to study species radiations and intraspecific diversity including, but not limited to, the three-spined stickleback (*Gasterosteus aculeatus*; Schluter and McPhail 1992; Schluter 2000), fishes of the genus *Salvelinus* (Skúlason et al. 1989; Chavarie et al. 2021; Blain et al. in press), and fishes of the genus Coregonus (Bernatchez et al. 1999; Kahilainen et al. 2017; Blain et al. in press).

The three-spined stickleback (hereafter stickleback) of postglacial lakes has been used as a model organism to study the process of speciation both experimentally and ecologically (Figure 1) and is therefore used here to describe the intraspecific diversity of postglacial fishes. Sticklebacks have for a long time been known to be a very diverse group of organisms (Bell 1972). Sticklebacks repeatedly occur in an anadromous form, exploiting the marine environment and returning to freshwater to reproduce, and in repeated freshwater resident form occurring across the species' distribution (Schluter 2000; Hendry et al. 2009; Østbye et al. 2016). Within freshwater stickleback populations, we see further diversity with the repeated occurrence of species pairs. Within these species pairs that have diverged along a diet preference gradient, one species forages in the benthic habitat and the other in the pelagic habitat (Schluter and McPhail 1992; Schluter 2000). The species pairs also demonstrate variation in other traits related to their divergence along feeding habitat such as morphology (Willacker et al. 2010), life history (Baker et al. 2005), and mate recognition traits (Rundle et al. 2000). Sticklebacks have been critical in the development of our understanding of speciation as various populations fall in different stages of the speciation continuum (Hendry et al. 2009). Furthermore, as sticklebacks are well studied, they lend themselves to being a good organism to study trait covariations and have been used to further our understanding of the migratory syndrome (Dingemanse et al. 2007).

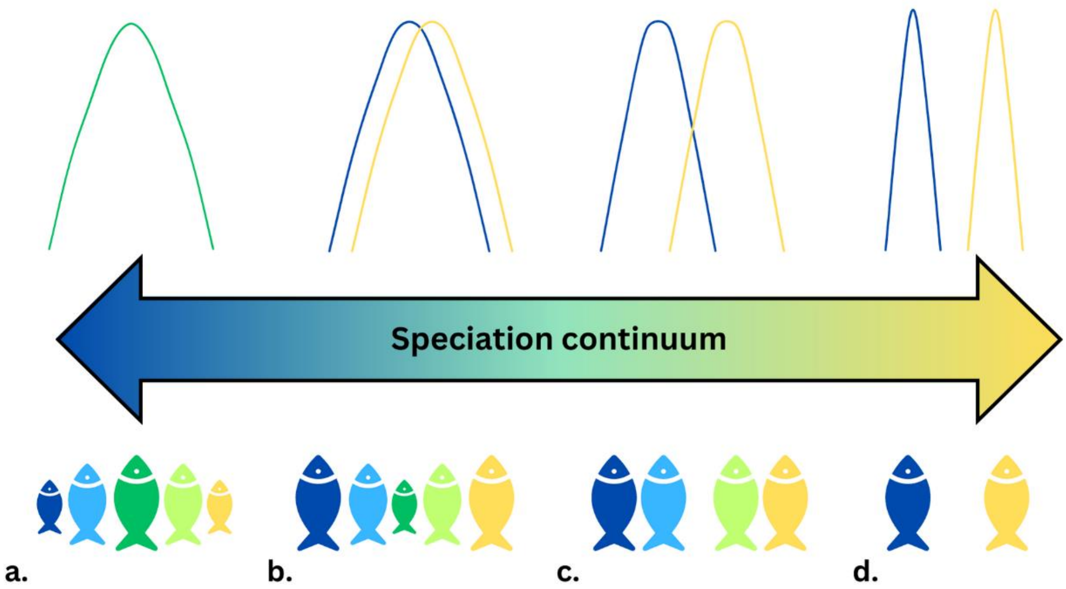

Figure 1. Representation of the species continuum with the four steps to complete speciation. a) panmictic population with a monomodal trait distribution where most individuals have an intermediate phenotype. b) start of divergence in the trait distribution where the median phenotype is no longer the most common, c) two distinct trait distributions are present in the population where individuals of alternative phenotypes can hybridize, reversal to previous stages is still possible at this step, d) there is complete reproductive isolation between the individuals of divergent trait distributions thus two separate species.

1.3 Why study Arctic charr

Similar patterns of divergence along the benthic-pelagic axis as described in the sticklebacks are seen in other fishes of postglacial lakes (whitefishes, subfamily Corigoninae and salmonids, subfamily Salmoninae; reviewed in Skúlason and Smith 1995; Schluter 2000). Fishes of the genus *Salvelinus*, the charrs, have a repeated pattern where multiple ecotypes occur within a single waterbody that is so widespread it has led to the coining of the phrase “the charr problem” concerning the Arctic charr (Nordeng 1983; Klemetsen 2010). These ecotypes refer to the different phenotypes within a population through phenotypic plasticity, therefore, the interaction of the genotype with the environment (Turesson 1922; Clemens and Schreck 2021). In Arctic charr, phenotypic plasticity is what allows for the occurrence of multiple ecotypes (Adams 1999; Adams et al. 2003). The influence phenotypic plasticity has at the individual level, however, varies among populations. For example, individuals of some populations breed true to the parental ecotype even in experimental conditions (Skúlason et al. 1989; Adams and

Huntingford 2002; Knudsen et al. 2015), while individuals of other populations may express alternative phenotypes depending on the conditions experienced (Adams et al. 2003; Moore et al. 2014). Although there are repeated occurrences of multiple Arctic charr ecotypes within a single waterbody, we still see a high degree of variability in the species among populations with some populations having only two ecotypes and others up to four (e.g., Snorrason et al. 1994; Moccetti et al. 2019; Østbye et al. 2020).

Furthering the possible diversity of Arctic charr, both lacustrine and anadromous forms exist throughout the species' Holarctic range (Johnson 1980; Klemetsen et al. 2003). Anadromous Arctic charr populations may be facultatively anadromous with some individuals adopting an alternative life history strategy to anadromy and remaining in the freshwater as lifelong residents (Nordeng 1961; Tallman et al. 1996; Klemetsen et al. 2003). The anadromous individuals have a higher age at maturity, longevity, and size at age than their lifelong freshwater resident counterparts (Tallman et al. 1996; Loewen et al. 2010). Anadromous Arctic charr may occur in sympatry with separate lacustrine Arctic charr populations (Johnson 1980; Klemetsen et al. 2003). In lacustrine Arctic charr populations, we repeatedly see sympatric ecotypes segregated along a benthic-pelagic axis (Klemetsen et al. 2003), as seen in other postglacial fishes, including sticklebacks (Schluter 2000) and coregonids (Siwertsson et al. 2013; Blain et al. in press). Moreover, Arctic charr may occur in complexes beyond two ecotypes with specialists exploiting the profundal area of the lake (Knudsen et al. 2006; Østbye et al. 2020) or with individuals becoming piscivorous (Sandlund et al. 1987; Klemetsen et al. 2003; Saltykova et al. 2017; Figure 2), suggesting multiple viable fitness peaks along the species' adaptive landscape.

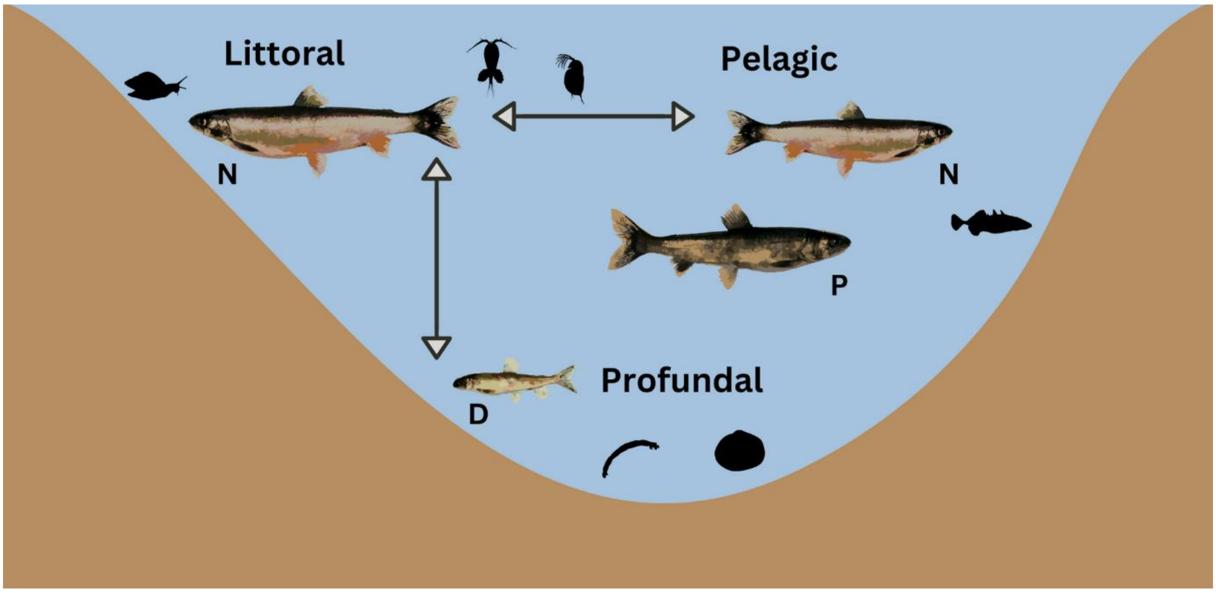

Figure 2. Axes of divergence along the horizontal (littoral-benthic) and vertical (littoral-profundal) gradient in Arctic charr. The ecotypes are approximately at scale relative to each other and represent the typical colouration and morphology of each ecotype. The Normal ecotype is identified with N, Dwarf with D, and Piscivorous with a P. Black silhouettes represent typical prey items found in each lake zone.

The Arctic charr ecotypes are known to vary in diet, habitat use, morphology, and life history parameters (Klemetsen et al. 2003). The patterns of divergence among ecotypes occur repeatably along the benthic-pelagic axis across lakes (Snorrason et al. 1994; Adams et al. 1998; Simonsen et al. 2017). Ecotypes among lakes share similarities in their morphology and life history adapted to their ecological niche (Skúlason et al. 1993; Knudsen et al. 2007), suggesting that these repeatable ecotypes are “alike”. The pelagic ecotype is often denoted anthropocentrically as the “Normal” ecotype, or a littoral spawning omnivorous ecotype based on its diet and spawning habitat (denoted as N for Normal in Figure 2, Figure 3, Box 1). The Normal ecotype has a small head relative to its body size (Smalås et al. 2013; Moccetti et al. 2019). During the spawning season, the Normal ecotype dons the typical red dress of the Arctic charr with a white leading edge on the paired fins, while immature individuals have a silverish hue and parr marks along the lateral side of the body (Klemetsen et al. 1997; Smalås et al. 2013; Moccetti et al. 2019). The Normal ecotype achieves a larger size, has a longer life span and an older age at maturity relative to the benthic ecotype of polymorphic populations (Smalås et al. 2013).

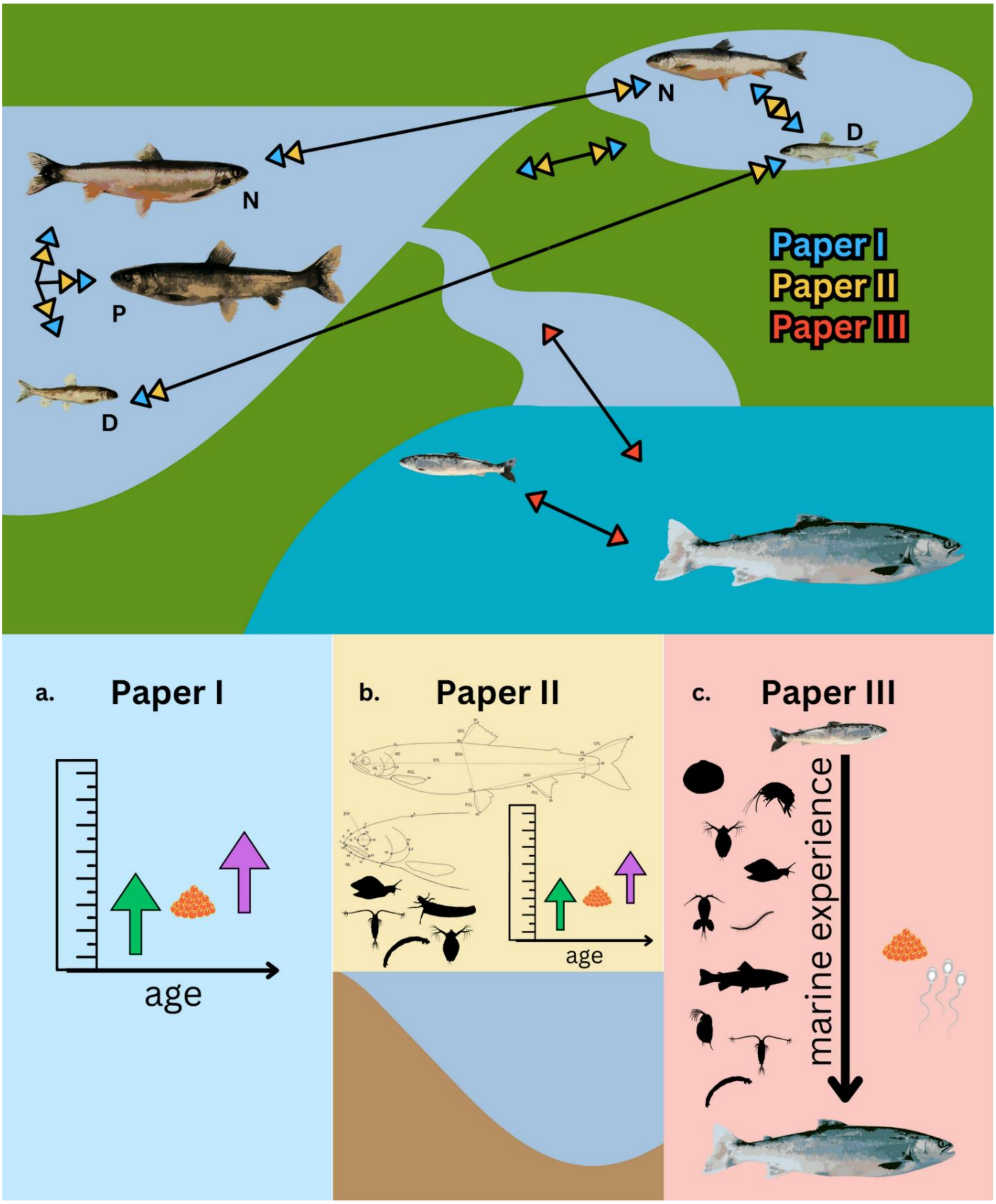

Figure 3. Graphical representation of the thesis aims. Black arrows with coloured tips represent the systems and ecotypes compared in each paper. Paper I is in blue, Paper II in yellow, and Paper III in red. Normal ecotypes are denoted with an N, Dwarfs with a D and the Piscivorous ecotype is noted with a P. The ecotypes are shown at scale relative to each other and the colourations reflect typical descriptions of the ecotypes within bi-morphic and tri-morphic lakes. Paper I compares life history parameters including length at age, growth through bi-phasic growth modelling (investment in growth (green arrow) and reproduction (purple arrow)), and length and age at maturity of Arctic charr ecotypes within and among systems. Paper II studies the relationships among four different trait spectra, habitat use, diet, morphology, and parameters of life history (bi-phasic growth modelling), of ecotypes within and among bi-morphic and tri-morphic lakes. Paper III studies how marine experience estimated from stable isotope signatures of δ^{34}S influences diet and age at maturity in males and females from a population of anadromous Arctic charr.

Box 1: Arctic charr ecotype terminology

The variable, and sometimes confusing, terminology used in the literature on intraspecifically diverse Arctic charr reflects the incredible diversity of the Arctic charr species complex. Already in the wording used to describe different individuals within an Arctic charr assemblage, we see inconsistencies. These inconsistencies are not specific to Arctic charr and reviews on the use of the terms have recently been published (Clemens and Schreck 2021; Stronen et al. 2022). The grouping of individuals within an assemblage has been referred to as ecotypes (Knudsen et al. 2008; Moore et al. 2014), morphs (Skúlason et al. 1989; Jonsson and Jonsson 2001; Amundsen et al. 2008), ecomorphs (Malmquist et al. 1992; Parsons et al. 2010), and even life history types (Tallman et al. 1996; Swanson and Kidd 2010). Adding to the complexity, some also use a combination of these terms seemingly interchangeably (Knudsen et al. 2007; May-McNally et al. 2015).

The terminology used in this thesis reflects growth throughout the PhD programme. The term morph was used in the early parts of this work (Paper I) while ecotype was preferred in the work performed later in the PhD programme. Ecotype was first defined as an "ecological unit to cover the product arising as a result of the genotypical response of an ecospecies to a particular habitat" (Turesson 1922). This definition reflects appropriately the phenotypic plasticity seen in the Arctic charr species complexes and is therefore preferred to the term morph. The term morph holds a connotation related to alternative phenotypes from genetic polymorphism, which is currently unknown in the case of the studied populations.

The terminology used to refer to the specific Arctic charr ecotypes from an assemblage is also variable in the literature. In systems with two ecotypes, the smaller ecotype is called Dwarf while the larger ecotype is referred to as the Normal ecotype (Adams 1999). Some have argued that these terms should be avoided as they place anthropocentric judgements on the ecotypes (Adams 1999; Klemetsen et al. 2003). The solution to these anthropocentric terms has been to describe ecotypes by their ecology to reflect their habitat use and dietary preferences (e.g., littoral omnivorous, profundal benthivorous) as reflected in Paper I. This system works well when studying Arctic charr assemblages within a single waterbody.

Box 1: Arctic charr ecotype terminology (continued)

However, using the ecotype's ecology presented challenges when including multiple waterbodies and comparing alike ecotypes as some differences are known even within the alike ecotypes (e.g., profundal benthivorous vs. profundal zooplanktivorous in Paper I). The terms Normal, Dwarf, and Piscivorous were preferred for Paper II and the thesis in general for multiple reasons. First, they offer a more simplistic terminology to maintain ease of reading and avoid confusion related to alike ecotypes, that have different names. Secondly, as much of the underlying theory for the analyses of Paper II comes from work done on plants, the terms used for the ecotypes therein make the research more accessible to broader fields of research. Finally, as life history constitutes a central concept of the work presented in the thesis, I felt that using the terms Normal, Dwarf, and Piscivorous to refer to the ecotypes conveyed a connotation related to life history. Table 1 outlines the equivalent terms used throughout the thesis to refer to ecotypes.

Table 1 Equivalency of ecotype terms used to refer to ecotypes throughout the introductory section of the thesis, Paper I and Paper II.

	Introduction	Paper I	Paper II
Ecotypes	Normal	Littoral Omnivorous	Normal
	Dwarf	Profundal Benthivorous/Zooplanktivorous	Dwarf
	Piscivorous	Profundal Piscivorous	Piscivorous

The benthic ecotype is typically called the "Dwarf" ecotype as it maintains its paedomorphic morphology throughout its life cycle (Klemetsen et al. 1997; Smalås et al. 2017; denoted as D for Dwarf in

Figure 2, Figure 3). The head shape is generally blunt with large eyes (Skoglund et al. 2015; Smalås et al. 2017; Moccetti et al. 2019). Mature Dwarfs do not develop the usual red colouration of the Arctic charr during the spawning season and have a brassy yellow colouration (Klemetsen et al. 1997). Dwarf individuals may have no parr marks throughout their life (Klemetsen et al. 1997) or may maintain parr marks into adulthood (Smalås et al. 2013; Moccetti et al. 2019). The Dwarf ecotype is often found exploiting the profundal areas of the lake (>15 m depth) leading to its description as a profundal spawning benthivorous ecotype.

There are however some inconsistencies reported in the diet of the profundal spawning ecotype among populations (Moccetti et al. 2019), therefore the term Dwarf is used preferentially within this work. The Dwarf ecotype consistently has shorter lengths and earlier age of maturity relative to the Normal ecotype (Klemetsen et al. 1997; Smalås et al. 2013). With increasing intraspecific diversity in Arctic charr populations, a Piscivorous ecotype (denoted as P for Piscivorous in

Figure 2, Figure 3) repeatedly occurs in tri-morphic populations (Smalås et al. 2013; Knudsen et al. 2019; Moccetti et al. 2019). Piscivorous individuals are predominantly captured from the profundal areas of the lake (Knudsen et al. 2019; Moccetti et al. 2019). Piscivorous Arctic charr individuals are slower growing than the individuals of other ecotypes, however, they achieve the greatest lengths and often delay maturation until older ages (Smalås et al. 2013). Its morphology reflects that of a piscivorous diet with a long head, large teeth, and a long and slender body (Skoglund et al. 2015; Knudsen et al. 2019; Moccetti et al. 2019).

These descriptions of Arctic charr ecotypes occurring along the benthic-pelagic axis of divergence and along a depth gradient show that there are phenotypic similarities that relate to an ecotype's ecological niche. The extent of the consistency in the phenotypes expressed among bi-morphic and tri-morphic Arctic charr populations, i.e., the repeatability of ecotypes, remains unknown as most studies on polymorphic Arctic charr examine few populations, few traits, and seldom relate traits to the life history. This limits our ability to fully understand how multiple traits act in unison to shape the intraspecific diversity seen in Arctic charr and how this extends to influence each ecotype's fitness in the environment.

1.4 Thesis objectives

This thesis aims at closing the gap in our understanding of the extent of repeatability in Arctic charr. This is done by studying the life history of the Arctic charr at different levels of intraspecific diversity by contrasting the classic ecological approaches with newer multivariate approaches and developing a new method to study the anadromous life history (Figure 3). Two different presentations of Arctic charr diversity are studied here by comparing diversified resident populations and an anadromous population, the ancestral state of resident populations. The first two papers examine the repeatability in Arctic charr intraspecific diversity in two bi-morphic and three tri-morphic resident Arctic charr populations by comparing life history (Paper I) and related functional traits under the concept of adaptive trait syndromes (Paper II). The third paper of this thesis examines the specialization occurring in the trophic ecology of anadromous Arctic charr as they gain experience in the marine environment (i.e., number of marine migrations) and links this to life history through condition and age at maturity (Paper III). The specific objectives of each paper (I, II, and III) included in the thesis and their respective research questions (a-c/d) were as follows:

I) Study the repeatability in population level parameters of life history in bi-morphic and tri-morphic Arctic charr
   a) Are there repeatable patterns in life history trait divergence among ecotypes within lakes?
   b) Are life history parameters of alike ecotypes repeatable across populations?
   c) Is there a difference in trait variation between bi-morphic and tri-morphic lakes?

II) Examine the repeatability in functional mean trait values and variation, and their correlations across varying levels of intraspecific diversity in Arctic charr
   a) Do we see repeatability in mean trait values and variation among alike ecotypes across populations?
   b) Do we see evidence for an adaptive trait syndrome in Arctic charr ecotypes?
   c) Does the number of ecotypes influence the repeatability in mean trait values, variation, or syndromes in polymorphic Arctic charr?

III) Study the influence of marine experience on diet, condition, and maturation in anadromous Arctic charr

   a) Can we quantify the number of marine migrations using stable isotopes of sulfur?
   b) How is the trophic niche influenced by marine experience?
   c) Does the condition increase with successive marine migrations?
   d) How does the marine phase influence age at maturity?

Together, these three studies provide novel insights into Arctic charr diversity by investigating life history at differing levels of diversification and relating it with trophic ecology, morphology, and/or habitat. Furthermore, as the Arctic is showing larger biodiversity loss related to climate change than previously predicted (IPCC 2023), studying Arctic species is important in terms of their conservation through the Anthropocene. Using multivariate approaches that allow us to study functional traits in unison better reflects the complexity of the natural world and will be critical to our success in predicting species' responses to environmental changes in the future (Laughlin and Messier 2015).

2 Methods

In this thesis, the intraspecific diversity in Arctic charr, sometimes denoted in the literature as "the charr problem", is examined at various levels with a unique approach being used in each paper. The thesis consists of three papers each with its methodological approach to study the repeatability in life history parameters of Arctic charr ecotypes at differing levels of intraspecific diversity (Paper I), the repeatability in functional traits and their correlations between and among Arctic charr ecotypes from populations with differing levels of intraspecific diversity (Paper II), and anadromy as a life history strategy in Arctic charr and changes in trophic niche with increasing marine experience (Paper III). In all instances, the methods used allow for relating the findings to Arctic charr life history. The following descriptions of the methods are broad to avoid redundancies with the individual papers; further details and specifications can be found in each paper appended to this work.

A total of six lakes were studied in this work with each lake having its unique presentation of intraspecific diversity within an Arctic charr population. To study these cases of intraspecific diversity in Arctic charr traditional ecological methods were used to describe the presentation of these populations from a life history perspective. Multivariate modelling was applied to combine multiple aspects of intraspecific diversity into an adaptive trait syndrome framework. Additionally, a new methodology using stable isotopes of sulfur to quantify the number of marine migrations in anadromous Arctic charr was developed and applied to life history-related traits including trophic niche.

2.1 Study systems

Arctic charr populations studied in this thesis were all located within Norway. Of the six populations five were located in northern Norway in Troms and Finnmark county, and one was located further south in central Norway in Trøndelag county (Figure 4).

The first two papers use four of the Northern lakes and the one from central Norway which have exclusively or primarily resident Arctic charr populations. These lakes have varying degrees of intraspecific diversity in their Arctic charr populations with either bi-morphic or tri-morphic presentations of the species. Genetic analyses performed on the ecotypes in most of the lakes have revealed that the ecotypes have likely evolved in sympatry and are reproductively isolated (Præbel et al. 2016; Simonsen et al. 2017; Moccetti et al. 2019). Hybridization between ecotypes is possible, however, genetic analyses have revealed that the amount of gene flow among ecotypes is low (Præbel et al. 2016; Simonsen et al. 2017; Moccetti et al. 2019). Although Arctic charr demonstrate a relatively high degree of phenotypic plasticity in relation to the environment, ecotype-specific responses occur when exposed to similar experimental conditions (Knudsen et al. 2015). This suggests a certain level of functional genetic differentiation between ecotypes. The selection of these lakes allows for comparing and contrasting ecotypes within lakes, alike ecotypes among the lakes, and testing for the effect of increasing intraspecific diversity.

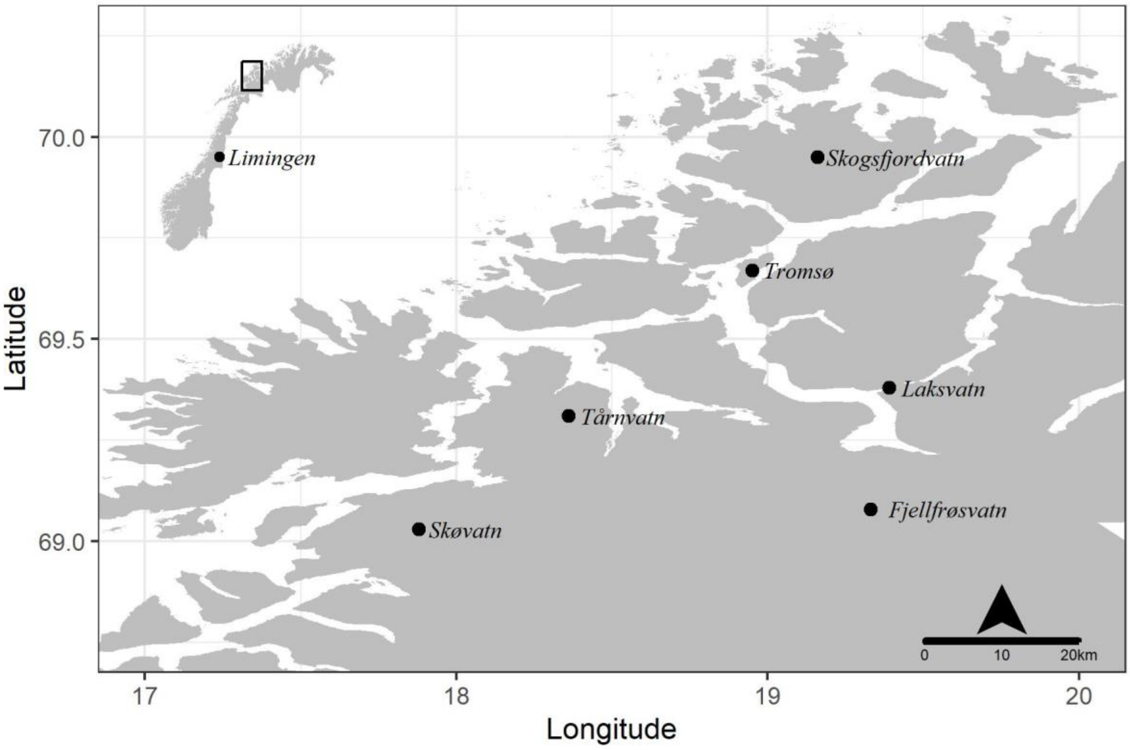

Figure 4. Location of the studied lakes within Norway with the location of Tromsø, the city where UiT is located.

The third paper uses a lake from northern Norway which is connected to the marine environment by a short river and has an anadromous Arctic charr population. This lake was selected for the study due to its accessibility and location close to Tromsø allowing daily monitoring of the field site during the extensive field season (May-September). Additionally, marine aquaculture is prohibited in the surrounding areas (Grenier et al. 2023), therefore making this a relatively pristine population to study the anadromous life history strategy in Arctic charr.

All lakes selected for the papers of this thesis have relatively low productivity as is typical for sub-Arctic lakes and are described as being dimictic and oligotrophic (Klemetsen et al. 1997; Smalås et al. 2013; Sandlund et al. 2017; Knudsen et al. 2019; Moccetti et al. 2019). Following is a short description of each lake starting with those studied in Paper I and Paper II examining Arctic charr ecotypes and intraspecific diversity and finishing with the anadromous population studied in Paper III.

- Fjellfrøsvatn (69°05'08"N, 19°20'04"E; the suffix “vatn” means lake) is not directly connected to the marine environment but is part of the Målselv river system which eventually drains in the Malangen fjord (Klemetsen et al. 1997). This lake is among the mid-sized lakes in this study with an area of 6.5 km^2 and a maximum depth of 88 m (Klemetsen et al. 1997). Fjellfrøsvatn contains two Arctic charr ecotypes (Normal and Dwarf) and brown trout (*Salmo trutta*) which complete their life cycle in freshwater as there is a steep waterfall downstream from the lake preventing migration (Klemetsen et al. 1997).
- Skøvatn (69°01'50"N, 17°52'25"E) has a comparable size to Fjellfrøsvatn with a maximum depth of 119 m and area of 6.2 km^2 (Moccetti et al. 2019). Skøvatn is connected to the marine environment and has anadromous populations of Atlantic

salmon (*S. salar*) and some anadromous Arctic charr and brown trout (Moccetti et al. 2019). The Arctic charr population in Skøvatn is bi-morphic (Normal and Dwarf; Moccetti et al. 2019).

- The smallest lake in the study, Tårnvatn (69°18'43"N, 18°21'29"E), has an area of 3.2 km^2 and is 53 m at its deepest point (Schartau et al. 2017). Tårnvatn has a population of brown trout and a tri-morphic presentation of lacustrine Arctic charr (Normal, Dwarf, and Piscivorous; Schartau 2017; Moccetti et al. 2019).
- Skogsfjordvatn (69°55'48"N, 19°9'36"E) is the largest northern lake in the study with a maximum depth of approximately 100 m and an area of 13.6 km^2 (Smalås et al. 2013). This is the most diverse lake with a total of five fish species present: European eel (*Anguilla anguilla*), three-spined stickleback (*Gasterosteus aculeatus*), Atlantic salmon, brown trout, and Arctic charr (Smalås et al. 2013). As this lake is connected to the marine environment, the Arctic charr population has some anadromous individuals in addition to three freshwater ecotypes (Normal, Dwarf, and Piscivorous; Smalås et al. 2013).
- The largest lake in the study, Lake Limingen (64°42'13"N, 13°32'40"E), is in central Norway, in Trøndelag county, and has an area of 95.7 km^2 with a depth reaching 192 m (Sandlund et al. 2017). This lake is regulated for the production of hydropower and has a maximum annual fluctuation in water level of an amplitude of 8.7 m (Sandlund et al. 2017). To compensate for the reduction in available food resources to the fish community related to the disturbance of the littoral area of the lake, *Mysis relicta*¸ a small crustacean, was introduced in 1969 (Sandlund et al. 2017). The fish community in Lake Limingen is composed of tri-morphic Arctic charr (Normal, Dwarf, and Piscivorous), brown trout, three-spined stickleback, and minnow (*Phoxinus phoxinus*) which was introduced in the 1980s (Knudsen et al. 2019).

- Laksvatn (69°22'35"N, 19°22'00"E) is located in Balsfjord and is connected to the marine environment by the river Buktelva (600 m long; Grenier et al. 2023). This lake is relatively small and has an area of 0.8 km^2 while being 15 m at its deepest point. The fish species occurring in this lake are three-spined stickleback, brown trout, a few Atlantic salmon, and anadromous Arctic charr.

2.2 Sampling methods

Most of the fish used in this thesis (Papers I and II) were selected from the archived data series from previous research endeavours in the Freshwater Ecology Group at UiT sampled between the years of 1992 and 2016. Archived data were selected for the studies examining intraspecific diversity in Arctic charr as extensive datasets were needed to support the research questions. However, the study about anadromy as a life history strategy (Paper III) in Arctic charr used data collected throughout the PhD programme in 2020 and 2021. All samples from the archived data (Paper I and II) were collected after obtaining permissions and following the appropriate ethical guidelines, while data for Paper III was collected under the permit 2020/14374 granted by the County Governor of Troms and Finnmark.

A combination of nets was used to sample the fish from the various habitats in the lakes. Multi-mesh gillnets were used to ensure a random sample and to allow for the calculation of catch per unit effort. Over the years multi-mesh gillnets have consisted of both survey nets and Nordic nets. The survey nets had 1.5 × 40 m dimensions and were made of eight 5 m panels with the following mesh sizes: 10, 12.5, 15, 18, 22, 26, 35, and 45 mm. Nordic gillnets consisted of 12 randomly ordered 2.5 m panels with mesh sizes from 5 to 55 mm. These multi-mesh gillnets were placed in the profundal (>15 m depth), littoral (0-10 m depth) and pelagic (<15 m depth) areas of the lake to ensure a representative sampling of the populations. In addition to multi-mesh gillnets, standard nets were placed strategically in the profundal and littoral habitat to specifically target Arctic charr ecotypes. These standard nets of 1.5 × 30 m dimensions had mesh sizes of 8, 10, or 12.5 mm. Nets were typically set overnight and retrieved first thing in the morning to have a comparable soak time. Anadromous individuals for Paper III were sampled during their migration returning to Laksvatn in the Buktelva River in 2020 with a fish trap (Box 2).

Box 2: Fish trap sampling methods

A fish trap (Figure 5) was installed in a narrow part of the river with a fence built to funnel the fish towards the entrance of the trap. The trap entrance did not allow for exit. Fish were removed from the trap daily and anaesthetized prior to being weighed and measured and given a unique Floy-tag (t-bar anchor). The fish were then placed past the fence and fish trap to allow them to complete their migration. In 2021, a fish trap was used again while Arctic charr were migrating downstream to the marine environment. The same sampling procedures as in 2020 were adopted with the fish collected in the fish trap, however the fish were returned downstream of the trap to allow for their migration to the marine environment. Later in the season, the fish trap was flipped to collect the fish migrating back to the freshwater. Collected individuals were once again weighed and measured and tagged if not previously tagged. From a subsample of the collected Arctic charr a fin sample was taken by clipping the adipose fin and freezing for later stable isotope analyses (Paper III). A further subsample of Arctic charr was euthanized by benzocaine overdose and frozen for later laboratory dissections.

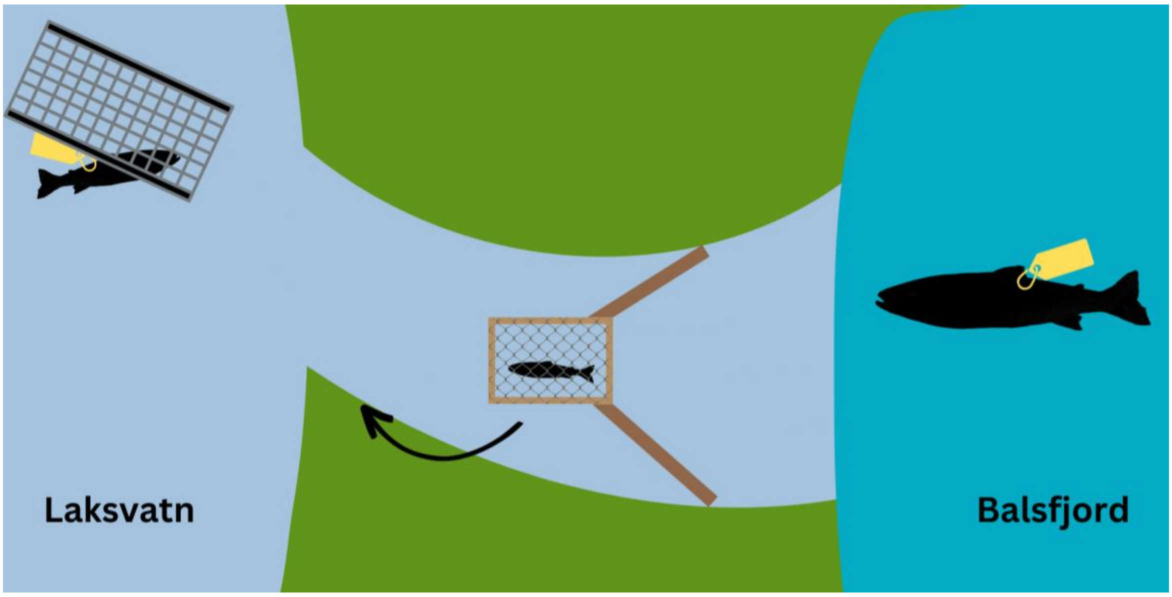

Figure 5. Schematic representation of the sampling design in Laksvatn. Note that this is a representation of the trap placement for the return migration and that the orientation of the trap is the opposite during the downstream migration. Tagging was done in both the downstream and upstream migrations in 2020 and 2021. The gillnetting within Laksvatn occurred in October after the trap had been taken down following the end of the return migration.

2.3 Sample processing

The standard methodology is to dissect the fish immediately in the field, or if required due to logistical reasons, to freeze the fish for later laboratory dissections. Before dissection, all fish were assigned an ecotype based on their morphology, colouration, and maturity (Box 3). Depending on the current research needs of each field season, pictures of the fish were taken in a standardized manner before being dissected or frozen for later dissections (Skoglund et al. 2015). For both frozen and non-frozen fish, the dissections were performed in the same manner and the same samples were collected. Arctic charr were weighed (g) and measured (fork length, mm) as a standard first step (Klemetsen et al. 1997; Smalås et al. 2013; Knudsen et al. 2019; Moccetti et al. 2019). The sagittal otoliths were removed and preserved in alcohol for age determination. The stomachs were removed and assessed to assign a degree of fullness (0 to 100%) before being preserved in ethanol for stomach content analysis (Amundsen et al. 2008). Preserved stomachs were dissected in the lab and contents were identified to estimate their contribution to the fullness estimate (Amundsen 1994). Gonads were examined for sex determination and assigned a stage of maturity (Sømme 1944; Klemetsen et al. 1997; Smalås et al. 2013). A muscle sample was excised from the muscle tissue above the lateral line, in between the dorsal fin and caudal peduncle, and frozen (Moccetti et al. 2019).

For the aging of the fish (Paper I and III), whole otoliths were submerged in glycerol and read whole under reflected light with a stereomicroscope (Kristoffersen and Klemetsen 1991). As there have been multiple different readers ageing the otoliths through the years, the group has a standard practice of regular quality checks on the aging, especially age estimates performed by inexperienced readers such as students (Smalås et al. 2013).

Box 3: Arctic charr ecotype classification

Individual Arctic charr are assigned to ecotype based on visual assessment with criteria developed and verified in previous studies (Smalås et al. 2013; Skoglund et al. 2015; Simonsen et al. 2017). Characteristics that are assessed include the fish colouration, presence of parr marks, head shape, head size relative to body size, body shape, colouration of the mouth. Maturity status may also be informative of ecotype membership (Skoglund et al. 2015; Knudsen et al. 2019).

- Normal Arctic charr ecotypes typically have a silver colouration. Juveniles of the Normal ecotype have parr marks over the silvery hued colouration. When mature, Normal ecotypes will take on a red colouration with a bright white leading edge on their paired fins. The head, mouth, and eyes of the Normal ecotype are relatively small in comparison with their body.
- Dwarf ecotypes maintain parr marks into adulthood in most populations. The colouration of the Dwarf ecotype's body typically has a brassy or yellow to brown undertone which contrasts the silver of the Normal ecotype. The head of the Dwarf ecotype is relatively large compared with its body and has a characteristic blunt snout. The Dwarf ecotype's eyes are relatively big.
- Piscivorous ecotypes are typically darker in colour with grey and black shades over parts of their body. The head of the Piscivorous ecotype is large, long, and robust. Large sharp teeth are found on the jaws, palate, and tongue. The Piscivorous ecotype's body is elongate and slender.

It is also possible to classify juvenile Arctic charr based on the size and shape of their head relative to their body and their colouration. Juvenile Normal Arctic charr have the expected relationship between head and body shape/size with silver undertones. Juvenile Dwarf ecotypes have a blunt snout and relatively large eye with brassy undertones. Juveniles of the Piscivorous ecotype have a relatively slender body, long jaw, and the inside of the mouth and the tongue is often darker in colour.

Genetic analyses have been performed in multiple lakes to verify the classification of ecotypes based on visual assessment. It was determined that ecotype membership based on phenotype effectively discriminates the different ecotypes. In lake Skogsfjordvatn the consensus between phenotypic and genetic classification was reported as 96% for the Normal and Dwarf ecotypes and 100% for the Piscivorous ecotype (Simonsen et al. 2017). Similar results have been reported for the classification of ecotypes in Fjellfrøsvatn, Skøvatn, and Tårnvatn (Præbel et al. 2016; Moccetti et al. 2019).

A subsample of the archived otoliths was photographed with a camera mounted to a stereomicroscope to allow for back-calculation of length at age for each full year of life before capture (Paper II). This allowed to increase the resolution of growth modelling, especially at younger ages, as often standardized fishing methods do not capture sufficient samples of young and small individuals. Otolith-based back calculation methods provided us with an increased sample of length estimates which were especially critical for the resolution of growth patterns in young individuals.

To compile the multiple datasets into a single useable file, some data cleaning was required to end with a final useable dataset. There were some differences in the staging of individuals through the dataset from different staging keys being used over time. Some protocols used a dichotomous scale (mature vs. immature) where individuals were assessed as being mature if they were expected to spawn this year or if they had already spawned before sampling (Smalås et al. 2013; Kjær 2018; Knudsen et al. 2019; Moccetti et al. 2019). Other protocols used a seven-stage scale specifying the extent of gonad development (Sømme 1944; Klemetsen et al. 1997). The dataset that was compiled for this work converted all the various maturity scales used to a dichotomous mature or immature scale (Paper I and II). Individuals were considered mature for this work if they had previously been assigned a status of maturing (stage III before August), mature (stages IV, V, VI), spent (stage VII), or resting (has spawned in a previous season, but is skipping spawning in the year of sampling, stage VII/II).

The tissues analyzed for stable isotopes (Paper III) were prepared for analysis by freeze-drying the samples and grinding them into fine powder (muscle tissue) or finely cutting them with dissection scissors (fin tissue). Samples were weighed and placed in small tin capsules before being analyzed for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ at the Environmental Isotope Laboratory at the University of Waterloo in Canada.

2.4 Analytical approaches

2.4.1 Paper I

Paper I used some classic ecological methods to describe at the population level the life history variation in polymorphic Arctic charr of Norwegian lakes (Figure 3a). Archived data on five different Arctic charr populations collected between the years 1992 to 2016 were re-analyzed to compare parameters of life history among five different waterbodies. This paper provides us with a snapshot of these populations and how the polymorphic Arctic charr populations compare in traits of life history relative to each other.

Using the available archived data on age, length and maturity of polymorphic Arctic charr populations, life history parameters were estimated with linear and logistic modelling techniques using R (R Core Team 2021). These included length at age, age and length at maturity (A_{50} and L_{50} respectively), and parameters of the bi-phasic growth model (Quince et al. 2008a). The use of a bi-phasic growth model allows us to better link growth as a trait of life history directly to the environment experienced by the individual (Quince et al. 2008b; Boukal et al. 2014). This is made possible through the incorporation of a term for the energy extracted from the environment and converted to growth (denoted c in this work) and a term to describe the energy diverted into reproduction (denoted as r in this work; Quince et al. 2008a). The bi-phasic growth models for each ecotype in each lake were then compared using an analysis of the residual sum of square (Chen et al. 1992; Haddon 2011; Ogle 2016) and likelihood ratio tests (Kimura 1980; Haddon 2011; Ogle 2016) to compare parameters when the curves were found to differ.

2.4.2 Paper II

Paper II uses multivariate modelling techniques to examine if an adaptive trait syndrome is present within polymorphic Arctic charr using a suit of functional traits within four trait spectra (habitat, diet, morphology, and life history; Figure 3b). The multivariate modelling, using

Markov chain Monte Carlo techniques with the MCMCglmm package (Hadfield 2010) in R, allows for the examination of multiple traits as multivariate trait spectra instead of the traditional approach of studying each trait individually. The typical pattern in research studying intraspecific diversity in Arctic charr is to examine the direct effect of singular functional traits and make inferences on the relationships between the traits studied within a manuscript. The methods used here allow for the examination of multiple functional traits simultaneously to further our understanding of the relationships between and among various trait spectra and how these relationships relate to the intraspecific diversity in Arctic charr.

The morphometric analyses of Arctic charr ecotypes were carried out by digitizing in tpsDig 2.32 (Rohlf 2021) a series of standardized landmarks on scaled photographs of individuals from all ecotypes in each lake (Skoglund et al. 2015). This allowed for the extraction of inter-landmark distances for the analysis of fin lengths and head characteristics. Head shape analysis was performed by first standardizing and scaling the landmarks with a Procrustes fit performed in MorphoJ v 1.07a.

The trait spectra included in the analysis of ecological syndromes in Arctic charr ecotypes habitat (littoral reliance), diet (trophic position, proportion of zooplankton, littoral benthos, profundal benthos preys in the diet), morphology (head shape, head and fin linear measurements), and life history (bi-phasic growth model parameters; age at maturity, c, r). Such a multivariate method has not been done in Arctic charr with respect to evaluating the repeatability of these trait spectra at differing levels of intraspecific diversity.

2.4.3 Paper III

Paper III used the analysis of stable isotopes from tissues to examine life history parameters in anadromous Arctic charr (Figure 3c). The elements that make up all materials on earth exist in the environment with various molecular weights or stable isotopes of an element. The ratio of elemental stable isotopes integrated into an organism's tissue reflects an organism's diet, therefore different food sources may result in different stable isotope signatures of tissues. Relative to international standards, a sample is either enriched or depleted in a certain isotope (Fry 2006). In an aquatic system, the ratio of carbon isotopes ($\delta^{13}C$) is higher in the benthic and lower in the pelagic areas whereas nitrogen isotopes ($\delta^{15}N$) are found in increasing proportions with increasing trophic levels (Peterson and Fry 1987; Fry 2006). For sulfur isotope ratios ($\delta^{34}S$), the gradient is low in freshwater and high in marine water (Peterson and Fry 1987; Fry 2006).

As both fin and muscle tissues were used, the first step was to ensure that these tissues were comparable as different tissues have different turnovers thus stable isotope incorporation rates (Heady and Moore 2013). Muscle stable isotope values were corrected to reflect the equivalent fin stable isotope values.

With stable isotopes of sulfur, a marker of freshwater vs. marine dietary influences, a methodology to estimate the number of marine migrations was developed. Otolith samples were available for a subset of Arctic charr and thus visual examination of these allowed us to estimate the age of the first migration at sea by identifying the first opaque band with a relatively large growth. The age of first migration in combination with the age of each individual we could estimate the number of marine migrations. By relating this number of migrations to the $\delta^{34}S$ signatures we were able to estimate the number of migrations in Arctic charr who had no otolith sample (i.e., not euthanized for sampling) by using only fin $\delta^{34}S$ values. Using this estimate of the number of marine migrations, we calculated the number of migrations performed by male and female anadromous Arctic charr to reach sexual maturity by adopting a logistic regression approach similar to A_{50}.

With the stable isotopes of $\delta^{13}C$ and $\delta^{15}N$, which are commonly used to examine trophic niches, we examined the shifts in diet with increasing marine experience in anadromous Arctic charr. We used a combination of Layman metrics and standard ellipse area calculations to determine if there was a change in diet and trophic niche breadth with the number of migrations to the marine environment.

3 Results

3.1 Paper I

Arctic charr populations with differing levels of intraspecific diversity showed repeatability among alike ecotypes in length at age, growth modelling, and age and length at maturity (Figure 6). Alike ecotypes had similar length at age relationships but interestingly the variation from the mean differed across ecotypes (Figure 2 in Paper I). Dwarf ecotypes had little variation while the Piscivorous ecotype had the highest variance in length at age. These results are furthered by the analysis of growth with bi-phasic models where a different model was estimated for each ecotype in each lake. Although the overall model for alike ecotypes differed (Figure 3 & Table 3 in Paper I), the individual model terms c (investment in somatic growth), and r (investment in reproduction), showed some consistencies. The Normal ecotype had a similar investment in reproduction in 3 out of 10 pairwise comparisons while this was true for 6 out of 10 comparisons in the Dwarf ecotype (Table 4 in Paper I). No similarities were found in the parameter for growth (c) in the Normal ecotype. Dwarfs from bi-morphic lakes shared a common c with each other and with Lake Skogsfjordvatn. All Piscivorous ecotypes had a common investment in reproduction and 2 out of 3 pairwise comparisons did not differ in their investment in growth. Analysis of age (A_{50}) and length (L_{50}) at maturity found the general pattern that Dwarf ecotypes mature at the youngest age and shortest lengths, Piscivorous individuals at the oldest age and longest lengths and Normal ecotypes at an intermediate age and length (Figure 4 in Paper I). This general pattern however is apt to local influences likely stemming from genetic diversification or in response to differing environmental gradients.

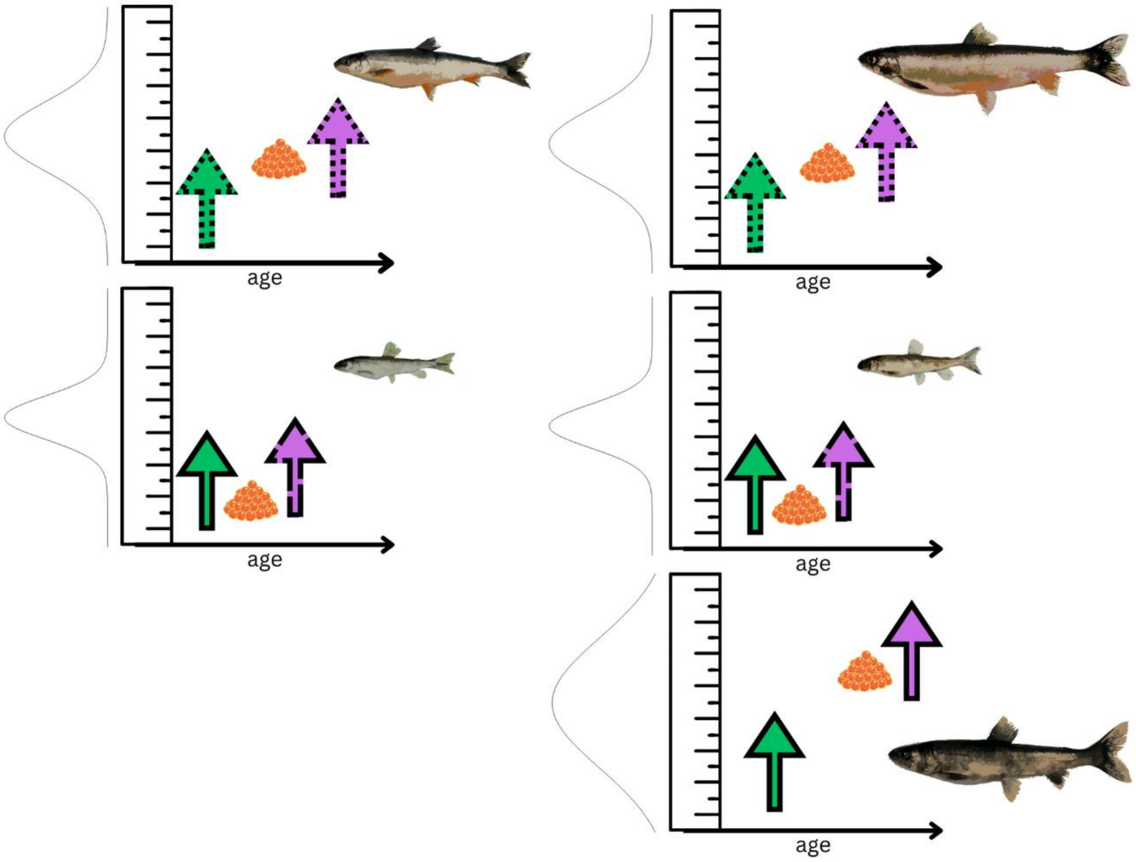

Figure 6. Graphical abstract depicting core results from Paper I where differences in life history parameters among ecotypes in bi-morphic and tri-morphic systems and among alike ecotypes across all systems were tested. The ecotypes had differences in the amount of variation in their length at age depicted by the distribution along the length (y) axis. Age at maturity differed among the ecotypes and is represented by the eggs in the length at age plot for each ecotype. Estimates of growth were obtained with the use of a bi-phasic model. The green arrow demonstrates the estimated parameter for investment in somatic growth, the purple arrow the investment in reproduction, and the border of the arrows represents the variation in the estimated terms with low (dotted), intermediate (dashed) and high (solid) variation represented.

3.2 Paper II

Measured traits of morphology, diet, habitat use, and life history in Arctic charr ecotypes across five lakes show high repeatability in mean trait values among individuals of alike ecotype (Figure 7). No trait showed patterns in the extent of trait variation (coefficient of variation or variance) related to the level of intraspecific diversity. However, the correlations among functional traits differed among ecotypes and therefore are an important factor in the specialization of ecotypes which allows them to co-occur within an environment.

Trajectory analysis of the diet trait spectra showed that alike ecotypes have similar trophic niches across the lakes and that the ecotypes of bi-morphic lakes show the least differentiation between the Normal and Dwarf ecotypes. Analysis of morphology with trajectory analyses revealed that the magnitude of divergence is greatest between the Normal and Dwarf ecotypes of bi-morphic lakes. There is also an indication that the number of morphs influences the extent of differentiation in life history traits as the Normal and Dwarf ecotypes from bi-morphic lakes show longer trajectories relative to those from tri-morphic lakes. Furthermore, the angles of divergence between ecotype pairs for the life history trait spectra are not different (with few exceptions) implying high repeatability in the life history trait spectra.

Correlations among trait spectra were present in all ecotypes indicating the existence of an adaptive trait syndrome in Arctic charr ecotypes. Each ecotype's adaptive trait syndrome was manifested in a different manner where the significant correlations were more numerous in the Normal ecotype relative to the Dwarf and Piscivorous ecotypes. For the Normal ecotype, the adaptive trait syndrome displayed strong patterns of correlation between morphology and habitat indicating the importance of morphological specialization to the ecological niche they occupy. In the Dwarf ecotype, the syndrome was manifested through correlations among traits of morphology, habitat, and life history. The morphological adaptations related to the Dwarf's diet and habitat use came with trade-offs in life history through a reduction in the investment in reproduction. The Piscivorous ecotype's adaptive trait syndrome revealed correlations among morphology, habitat use, and trophic position indicating the important relationship between morphological adaptations that allow feeding on fish prey.

At differing levels of intraspecific diversity, the syndrome in the Normal and Dwarf ecotypes differed. For the Normal ecotype, the importance between morphology and both diet and habitat persisted but correlations with parameters of life history indicated that specializations to bi-morphic and tri-morphic populations come with trade-offs. In bi-morphic Normal ecotypes, morphological adaptations were correlated with an increased investment in growth but at a cost of delaying maturation. The syndrome in the tri-morphic Normal ecotype indicated negative correlations in morphology and littoral reliance with the investment in somatic growth and reproduction. For the Dwarf ecotype of bi-morphic lakes, there was only a weak adaptive trait syndrome with few correlations among morphology and both habitat and diet. However, in tri-morphic Dwarfs, the correlations among morphology, habitat, diet, and life history demonstrated that the adaptations required to coexist with a third ecotype come at the cost of investment in growth and reproduction. Overall, there are indications that adaptive trait syndromes are important in the specialization of sympatric Arctic charr ecotypes and that the syndromes are stronger at increasing levels of intraspecific diversity.

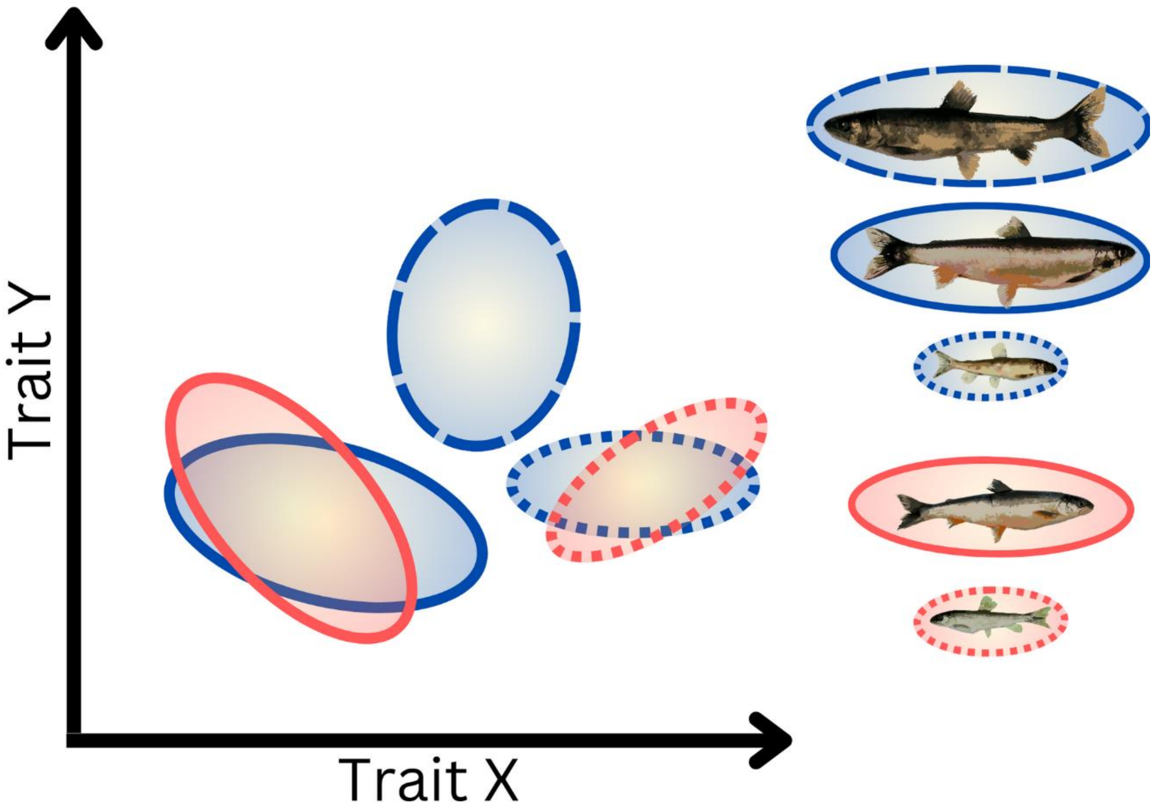

Figure 7. Graphical representation of results from Paper II. Ecotypes from bi-morphic lakes are shown in red and in blue for ecotypes from tri-morphic lakes. The Normal ecotype has a solid border, the Dwarf ecotype is shown with a dotted border and the dashed border represents the Piscivorous ecotype. Different ecotypes show different mean trait values, while alike ecotypes show similar means at different levels of intraspecific diversity. Variation in trait value is not related to the number of ecotypes in the lake. Adaptive trait syndrome is suggested in Arctic charr as traits are correlated among trait spectra and these correlations vary among ecotypes.

3.3 Paper III

Stable isotopes of sulfur are an appropriate marker to estimate the number of marine migrations and marine experience is related to the life history strategy in anadromous Arctic charr (Figure 8). The number of marine migrations estimated from otolith growth patterns is related to the $\delta^{34}S$ signature of tissues in anadromous Artic charr (Figure 2 in Paper III). With this relationship, it is possible to estimate the number of summer marine migrations in fish using an analysis of sulfur stable isotopes from a non-lethally sampled adipose fin tissue. The estimates of marine experience are further validated with a two-year mark-recapture effort confirming the observed pattern in individuals with zero, one, or two (+) migrations to the marine environment.

The number of marine migrations influences condition factor and maturity in male and female Arctic charr differently. Females mature later than the males, with an average of three additional marine migrations required to achieve sexual maturity relative to the males (Figures 4 & 5 in Paper III). Marine experience also influences trophic niches in anadromous Arctic charr. There is a gradual increase in trophic level (increase in $\delta^{15}N$) with marine experience and an increasing increase in $\delta^{13}C$ as Arctic charr migrate to the marine environment repeatedly (Figure 4 in Paper III). First-time migrants have a completely different trophic niche than the most experienced veteran migrants (6 or more migrations). Additionally, the dietary specialization increases with marine experience as the trophic niche decreases in size with additional marine migrations until a full dependency on marine prey resources is reached.

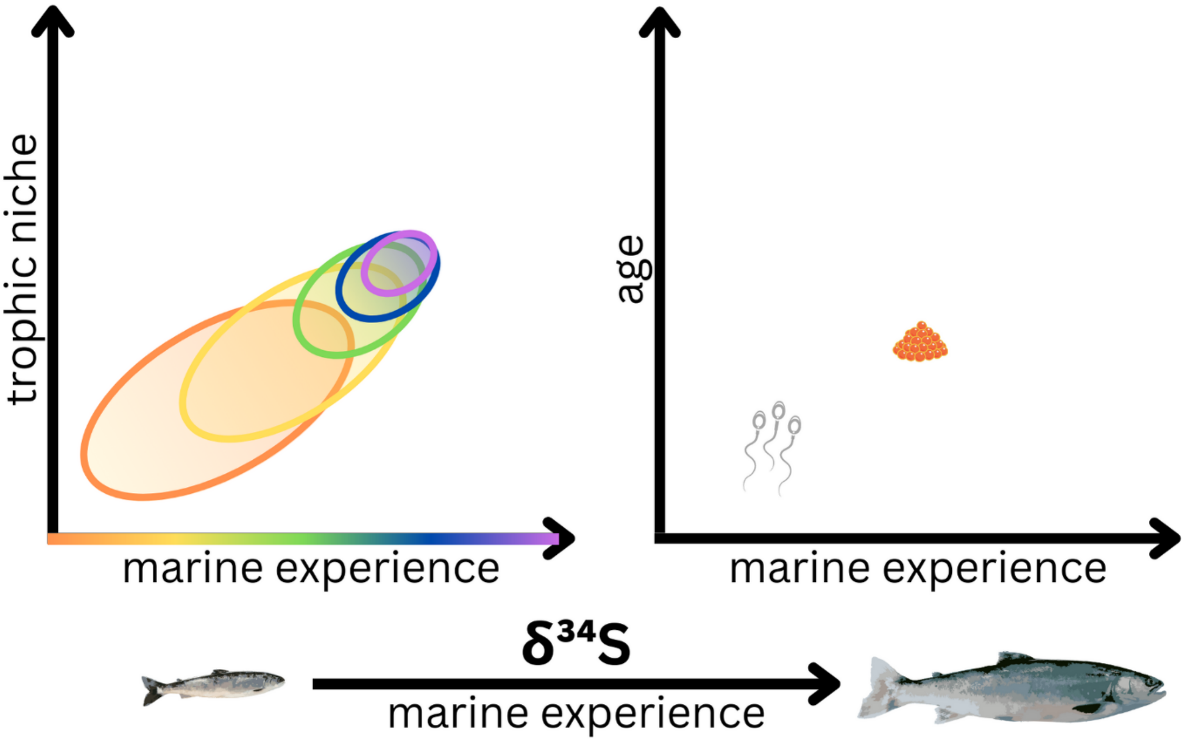

Figure 8. Graphical abstract of results from Paper III studying marine experience estimated from stable isotope signatures of sulfur and the relationship to trophic niche and maturation in anadromous Arctic charr. The successive rainbow colours on the left side plot represent the number of migrations from few (orange) to many (purple) and coloured ellipses represent the trophic niche. The number of migrations to maturity for males (sperm) and females (eggs) is represented on the right side plot.

4 Discussion

4.1 A multivariate functional trait approach to life history

Many ecological studies have taken the approach of isolating traits (e.g., trophic niche or morphology) within a single trait spectra to study how these traits might vary across different levels of biodiversity. However, we know that it is the entirety of the phenotype, or the combined effect of several traits across trait spectra, that impacts an organism's fitness through influences on survival, growth, and reproduction in a given environment or ecological niche (Hutchings 2021). In fishes of postglacial lakes, we see repeated patterns of species diverging into multiple ecotypes based on the ecological niche occupied by the ecotypes (Snorrason et al. 1994; Adams et al. 1998; Schluter 2000). Across lakes, ecotypes occupying a similar ecological niche also show similarities in morphology and life history (Skúlason et al. 1993; Knudsen et al. 2007; Loewen et al. 2009). In this thesis, I build upon the often-used method in ecology of isolating traits by also considering trait variation (Paper I) and by linking functional traits of multiple trait spectra to the life history strategies and traits of diverse Arctic charr ecotypes (Papers II & III). My results show that functional traits and the links among them are an important component of life history strategies in a highly intraspecifically diverse group of fish. The results also provide us with a more holistic understanding of anadromy as a life history strategy and the Arctic charr species complex, a key species in northern freshwater systems.

4.2 Variation in life history

Life history theory encompasses the parameters that connect an organism's characteristics to its fitness (Stearns 1976; Hutchings 2021), thus also influencing the intra- and interspecies dynamics at higher levels of biological organization (Laughlin and Messier 2015). The study of life history traits in Arctic charr ecotypes from lakes with varying levels of intraspecific diversity (Paper II) has revealed that although there are repeatable trends in the average length at age, modelled growth parameter, and age and length at maturity, the variation within these traits may also have adaptive value (Paper I).

Variation within traits is important at multiple levels (Bolnick et al. 2011). For instance, variation in traits among individuals of a population will shape an individual's ability to exploit the resources in the environment (Bolnick et al. 2011). Thus, trait variation also influences the exploited ecological niche of individuals and provides adaptive value, for example by reducing niche overlap among conspecifics (Bolnick et al. 2011; Laughlin and Messier 2015). In addition to providing individual advantages, variation is one of the requirements for natural selection, and by extension evolution and speciation (Darwin 1859; Schluter 2000). A further requirement for speciation to occur, however, is irreversible reproductive isolation between alternative phenotypes (Figure 1; Rice and Hostert 1993; Skúlason and Smith 1995; Hendry et al. 2009).

Among the studied populations there is evidence that reproductive isolation is achieved to some extent among the ecotypes (Præbel et al. 2016; Simonsen et al. 2017; Moccetti et al. 2019). There is strong evidence for reproductive isolation between the Normal and Dwarf ecotypes in most lakes, as they are known to spawn in different areas and different seasons (Klemetsen et al. 1997; Smalås et al. 2013). Therefore, ecotypes are genetically distinct (Præbel et al. 2016; Simonsen et al. 2017; Moccetti et al. 2019) and even show divergence true to their parents' phenotype even when raised in aquaria (Knudsen et al. 2015). Although ecotypes form distinct genetic clusters in most of the systems included in this work, one lake, Tårnvatn, stands out where there is lower genetic differentiation between two of the co-occurring ecotypes (i.e., Dwarf and Piscivorous ecotypes; Moccetti et al. 2019). Phenotypic plasticity may therefore influence individual phenotype (i.e., ecotype membership) differently among populations (Adams 1999). In cases of hybridization between ecotypes the external characteristics, life history traits, and diet, are sufficient to assign ecotype membership as these reflect the ecological niche exploited by the individual (Simonsen et al. 2017; Moccetti et al. 2019; Horta-

Lacueva et al. 2021). This implies that reproductive isolation among ecotypes may not be complete (Hendry et al. 2009) or that the time since divergence differs among lakes (Præbel et al. 2016). Furthermore, the extent of the role played by phenotypic plasticity in the maintenance of the ecotypes under the present conditions may differ among populations (Adams 1999; Kristjánsson et al. 2018).

Our findings suggest that, although the process of speciation in Arctic charr ecotypes may not be complete, each ecotype presents an evolutionarily stable life history strategy (i.e., ESS; Parker et al. 2001). The high variability seen in some of the life history traits of ecotypes (Paper I) suggests that variation in and the correlations among life history traits (Paper II) may be an important component in maintaining the divergence among ecotypes while also being an essential aspect of the specific life history strategies, including anadromy (Paper III). As life history strategy is a result of the interactions between phenotypes and the environment (Hutchings 2021), integrating multiple functional traits and their variation is an integral step to further understanding how intraspecific variation leads to evolutionarily stable strategies, and ultimately to new species.

4.3 Adaptive trait covariations

A further examination of variation in trait expression demonstrated that variation in functional traits of habitat, trophic ecology, and morphology, in addition to life history traits have a significance in explaining the sympatric evolution of Arctic charr ecotypes (Paper II). Examining trait correlations and covariations is a relatively new approach in ecology with reviews proposing the need for studies on the topic being published in the 2010s (Bolnick et al. 2011; Albert 2015). However, most of the published work studying trait covariations at a level above individuals has been done in terrestrial plant systems (e.g., Rueda et al. 2018; Guisan et al. 2019). The work presented in this thesis begins to fill the gap for such studies in vertebrate models and aquatic systems.

An individual’s survival is driven by how their phenotype interacts with the specific environment to grant benefits and disadvantages within that environment (Laughlin and Messier 2015; Hutchings 2021). The repeatability of phenotypes that evolved to occupy similar ecological niches demonstrates that phenotypes may be convergent (Bolnick et al. 2018). What makes up an individual’s phenotype is the entirety of traits it expresses, therefore also incorporating how these traits vary relative to each other. Trait covariations within a phenotype, therefore, have an adaptive value if they provide advantages to an individual’s fitness (i.e., survival, growth, reproduction; Rueda et al. 2018; Blasini et al. 2021).

We can better understand the adaptive value of covariation in functional and life history traits if we incorporate these results into an adaptive landscape framework (Laughlin and Messier 2015). Fitness peaks in the environment are defined by the synergistic effects of all traits (i.e., the phenotype) of an organism within an environment (Laughlin and Messier 2015). The repeatability of the average phenotype suggests that the alike ecotypes among lakes occupy fitness peaks that are in relatively similar areas of an adaptive landscape (Laughlin and Messier 2015). Some would describe this as a case of parallel evolution, however without genetic information, it is more appropriate to call this a case of convergent evolution (Bolnick et al. 2018).

With different levels of intraspecific diversity, alike ecotypes displayed differences in their observed trait covariations. Differences in trait covariations are therefore also of importance in shaping evolutionarily stable strategies at varying levels of diversity. The variation in traits and correlations among them therefore allow for specific adaptations in response to the environment for each ecotype (Laughlin and Messier 2015). It is these adaptations that shape the evolutionary stable strategies of each ecotype within a species. Trait covariations and the adaptations they confer to individuals conforming to the ecological niche they exploit have an importance in the maintenance of the evolutionary stable strategies in hybrids (Horta-Lacueva et al. 2021) and may also differ among populations (Polverino et al. 2018).

4.4 Anadromous life history strategy

Anadromy increases fitness through improved growth from the relatively better feeding conditions of the marine environment at higher latitudes (Gross et al. 1988). In salmonids, there is variation in the anadromous life history strategy where some species return to the freshwater only once mature, while others perform annual migrations and return to the freshwater even as juveniles (Klemetsen et al. 2003). In these annually migrating species, each migration to the marine environment comes with costs, especially in the first year (i.e., post-smolts) where mortality is high (Jensen et al. 2018, 2019; Kristensen et al. 2018). Thus the fitness benefits of anadromy are only conferred to individuals that survive and reproduce (Hutchings 2021). Although mortality in anadromous individuals decreases with higher growth and larger sizes (Jensen et al. 2018, 2019), there are still significant costs to additional migrations, such as the physiological costs associated with changes in osmoregulation (Aas-Hansen et al. 2005). Some theories have been proposed to explain why certain species perform annual migrations between the freshwater and marine environments. These include hypotheses such as escaping the colder winter marine temperature (Dempson and Kristofferson 1987) and reduced growth potential in the marine environment over time (Rikardsen and Elliott 2000). At the time of writing, no confirmation or rejection of these hypotheses exists, highlighting the lack of conclusive data for these central evolutionary questions. The development of new methods and approaches is warranted to improve our understanding of the variations displayed among the anadromous life history strategies in salmonid.

Until now, no non-lethally obtained estimate for the number of migrations performed by an anadromous individual existed. As set out in the aims, it was determined that stable isotopes of sulfur allows for quantification of the number of marine migrations performed by individuals of species that perform regular migrations between the freshwater and marine environment (Paper III). By extension, this method allows us to also measure and monitor other life history (i.e., migrations to maturity) and ecological (i.e., trophic niche) traits in relation to marine experience. This novel approach therefore offers a valuable non-invasive tool for an improved understanding of anadromy as a life history strategy.

Relating the number of migrations to the trophic niche provides new knowledge to the field of anadromy. Previously, changes in the trophic niche of anadromous individuals have been linked to changes in size where larger individuals typically change to a piscivorous diet (Dempson et al. 2002; Rikardsen et al. 2007). Recently, length was also linked to the proportion of reliance on marine prey in the diet and to feeding at higher trophic levels in anadromous salmonids (Davidsen et al. 2020, 2023). By relating parameters of trophic niche only to length we miss the potential effect of individual behaviour, where individuals may learn over successive migrations what prey offers the best nutrition or where to find productive patches in the marine environment (Knudsen et al. 2011). Although there is evidence that veteran migrants may learn to adopt different feeding strategies than first-time migrants (Jensen et al. 2014, 2019; Atencio et al. 2021), an estimate for the number of marine migrations allows for direct testing of more complex processes, such as a learning hypothesis in feeding behaviours of anadromous salmonids.

Multiple fish species have been documented to be expanding their range into the Arctic marine and freshwater environments (Dunmall et al. 2013; Fossheim et al. 2015; Ulrich and Tallman 2021), which creates new environmental conditions for species inhabiting the Arctic. As the benefits of anadromy are relative to remaining in freshwater (Finstad and Hein 2012), a changing Arctic ecosystem may influence the migratory patterns of anadromous salmonids. Warming freshwater systems may become more productive, thus reducing the need to migrate to the marine environment (Svenning et al. 2022). Changing lake dynamics in relation to warmer climates are also expected to have negative consequences (e.g., growth, egg viability) for lacustrine populations (Murdoch and Power 2013; Kelly et al. 2020) and may modify the existing ecological niches (Woelders et al. 2018; Sivarajah et al. 2021) required to maintain several sympatric ecotypes. For example, ecotypes exploiting the profundal areas of the lake may be relatively unaffected due to the stability of the habitat (Murdoch and Power 2013). However, the Normal ecotype may use the profundal habitat as refugia from warmer temperatures and new invading species (Morrissey-McCaffrey et al. 2019), thus influencing the dynamics of the profundal habitat for the cooccurring ecotypes. Furthermore, anadromy is important for the maintenance of genetic diversity in populations through straying (Moore et al. 2013; Santaquiteria et al. 2016) and for colonizing of newly formed lakes from deglaciation.

Similarly to the lacustrine populations, changes in the Arctic environment related to climate and anthropogenic impacts are potentially threatening the anadromous life history strategy of salmonids (Svenning and Gullestad 2002; Reist et al. 2006). Shifts in the diet of anadromous salmonids in northern Norway have been noted between the 1990s and 2000s related to changes in the relative availability of marine prey species (Rikardsen et al. 2007). Furthermore, the expansion of salmon aquaculture in the marine environment has increassed the parasite load (e.g., salmon lice) during the marine phase for anadromous salmonids (Costello 2009). High parasite loads have been found to influence the anadromous life history strategy of wild salmonids and infected individuals tend to return to the freshwater earlier than uninfected individuals (Serra-Llinares et al. 2020; Strøm et al. 2022). A method to reliably estimate the number of migrations performed by anadromous salmonids allows for monitoring of potential changes in the anadromous life history strategies of salmonids in response to anthropogenic and climate changes.

Having a baseline knowledge of the number of marine migrations required to reach sexual maturity in a population adds new information on salmonid life history strategies. This baseline also allows for monitoring of the delicate anadromous life history of salmonids in the coming ecosystem changes. Females required more marine migrations to achieve sexual maturity relative to males which is consistent with sexual maturation being less energy-demanding in males than females (Adams and Huntingford 1997; Jørgensen et al. 1997). The incidence of small maturing males demonstrates that the freshwater environment is productive enough only for precocious maturation in males. It has been suggested that males who reproduce before migrating to the marine environment will later adopt anadromy (Klemetsen et al. 2003). However, if the freshwater environment becomes more productive, or if the costs of anadromy increase it is possible we may see a reduction in the need for anadromy in salmonid populations. Climate change-related modifications to life history have been reported for other salmonids (Marschall 2019) highlighting the importance of non-lethal methods, such as the one developed in this thesis, of monitoring life history in anadromous Arctic charr in a changing environment.

5 Conclusion

This thesis demonstrates the importance of performing across-system studies that extend beyond the often-used isolated trait-based approaches. Although there is value in a trait-based approach, examinations of trait variation and correlations at the intraspecific level provide us with a better understanding of the broader trade-offs occurring at the whole phenotype level of different life history strategies. Here, new knowledge is provided on the importance of trait variation and correlations in the differentiation of and maintenance of segregation among Arctic charr ecotypes at varying levels of intraspecific diversity. This approach to studying trait variations and correlations is not limited to Arctic charr or salmonids and can be applied at both the intra- and interspecific levels (Bolnick et al. 2011; Laughlin and Messier 2015). Studies of trait correlations and variations have been touted as being critical in our understanding of biodiversity in relation to the conservation of biodiversity and the implementation of solutions to mitigate the effects of climate change (Laughlin and Messier 2015; Blasini et al. 2021). For example, the more realistic representation of complex organisms provided by such studies allows for better predictions of organisms' responses to environmental change and offers an improved capacity to match organisms to habitats in the case of restoration work (Blasini et al. 2021). Furthermore, improved baseline information on the anadromous life history strategy, the ancestral state of resident populations, of salmonids allows for better monitoring and management of the threatened life history strategy in climate change scenarios.

This thesis also demonstrates that organisms are more than the sum of their parts. It further displays how applying new approaches that consider the complexity of biodiversity allows us to gain further insights on topics such as mechanisms involved in the process of speciation. When applied, this new knowledge has the potential to improve our management and conservation efforts of the seemingly inexhaustible but certainly ever-changing and fragile diversity of the natural world that surrounds us.

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Paper I

Environmentally modulated repeat evolution of polymorphic Arctic charr life history traits

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Environmentally Modulated Repeat Evolution of Polymorphic Arctic Charr Life History Traits

Gabrielle Grenier*†, Aslak Smalås†, Runar Kjær and Rune Knudsen†

Freshwater Ecology Group, Department of Arctic Marine Biology, UiT The Arctic University of Norway, Tromsø, Norway

Edited by:
Claudia Fichtel,
Deutsches Primatenzentrum,
Germany

Reviewed by:
Peter Dijkstra,
Central Michigan University,
United States
Rebecca Nagel,
Bielefeld University, Germany

***Correspondence:**
Gabrielle Grenier
gabrielle.grenier@uit.no

†ORCID:
Gabrielle Grenier
orcid.org/0000-0002-7418-0812
Aslak Smalås
orcid.org/0000-0002-6316-2811
Rune Knudsen
orcid.org/0000-0001-8579-4687

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Sympatric Arctic charr, *Salvelinus alpinus* (L. 1758), morphs have flexible but repeated life history strategies tested across five Norwegian lakes. In several Scandinavian polymorphic Arctic charr populations differentiated by their diet and habitat use, a large littoral omnivorous (LO) morph commonly cooccurs with a smaller profundal spawning (PB/PZ) morph. A third, large piscivorous (PP) morph is also known to occur within a portion of Arctic charr populations in the profundal habitat along with the PB/PZ individuals. Life history traits, such as age at maturity, growth, and diet are known to differ among coexisting morphs. Notably, the PP morph was the longest morph with the oldest age at maturity while the PB/PZ morph showed the shortest lengths overall and youngest age with LO morph being intermediate in both traits. Growth parameters differed across all the morphs. When examining growth within morph groups, the LO morph was found to have different growth across all lakes, while similar reproductive investments and different energy acquisition patterns were seen within the PB/PZ and PP morphs. These results suggest repeat evolution in several life history strategies of reproductively isolated Arctic charr sympatric morphs, notably for the first time in the PP morph, while also highlighting the importance of the local environment in modulating life history traits.

Keywords: growth, maturity, sympatric populations, ecological evolution, biphasic growth model, *Salvelinus alpinus* L, reproductive investment, size-at-age

INTRODUCTION

An organism's life history strategy combines all traits that relate to its overall lifetime fitness (Stearns, 1976). The traits influencing lifetime fitness include, but are not limited to, age and size at maturity, growth rate, and fecundity (Stearns, 1976). Size and growth influences the timing of maturity in fishes (Roff, 1984; Perkins and Jager, 2011) and fecundity increases with fish size (Sandlund et al., 1992; Smalås et al., 2017) leading to tradeoffs in the timing of maturity and fecundity (Stearns, 1976).

Evolution is a constantly occurring process that results in individual opportunities for a species to adapt its life history strategy in relation to the currently experienced environmental conditions (Barton, 2007). In fishes, growth is indeterminate and therefore life history can be highly variable and related to the environment in which each fish grows (Wootton, 1990; Barton, 2007) and the exploited resources (Skúlason and Smith, 1995). In fishes, phenotypic plasticity and variation in traits, including life history related traits, are commonly exhibited (Gross, 1985;

Ferguson et al., 1990; Wootton, 1990; Skúlason and Smith, 1995; Klemetsen, 2013; Muir et al., 2015; Chavarie et al., 2016; Meuthen et al., 2018; Rennison et al., 2019). Life history traits evolve, therefore local adaptations towards evolutionary stable strategies are seen among populations.

In general, salmonids demonstrate extreme plasticity in life history traits and extensive local adaptation (Klemetsen, 2010; Birnie-Gauvin et al., 2021). Within species variation in life history is exhibited in multiple members of the salmonid family, notably whitefish (*Coregonus laveratus* L. 1758), brown trout (*Salmo trutta* L. 1758), the Pacific salmons (*Oncorhynchus* spp.), and the charrs (*Salvelinus* spp.) (Hutchings and Morris, 1985; Crespi and Teo, 2002; Klemetsen, 2013; Muir et al., 2015; Birnie-Gauvin et al., 2021). Since their invasion of the Arctic in the late-Pleistocene, Arctic charr have demonstrated parallel evolution of a variety of traits across their entire distribution. Arctic charr demonstrate incredible diversity within the species (Klemetsen, 2010) and have even been referred to as being the most variable vertebrate on earth (Klemetsen, 2013). Within a single waterbody, up to four different Arctic charr morphs are known to co-occur (Skúlason et al., 1989a, 1996; Snorrason et al., 1994; Østbye et al., 2020). The life history strategies adopted by the various sympatric morphs are all unique with variable age at maturity, growth, timing of spawning, diet, and habitat utilization. Across the species' Holarctic distribution instances of polymorphic Arctic charr populations are common. The specific life history traits of each morph allows individuals to maximize fitness in their respective niche.

The variation in life history traits among co-occuring morphs have been described within multiple waterbodies. In Northern Scandinavia, the co-occuring morphs are commonly categorized by diet and habitat use with an increasing number of morphs often related to lake depth (Østbye et al., 2020). In the most simple case of polymorphism in Arctic charr, where two morphs are present within a system, there is a larger omnivorous feeding morph (LO) found in the littoral and pelagic zones and a second smaller benthic dwelling morph (PB/PZ) often in the deeper profundal zone within the lake (Hindar and Jonsson, 1982; Svedäng, 1990; Klemetsen et al., 1997; Moccetti et al., 2019). In general the LO morph is described as having greater lengths at age and delayed age at maturation relative to their small profundal (PB/PZ) conspecifics (Klemetsen et al., 1997; Smalås et al., 2013; Knudsen et al., 2015; Moccetti et al., 2019). Available estimates of the maximum attainable length [i.e., von Bertalanffy growth parameter for asymptotic length (L)] from the studied populations exceed 330 mm in the LO morph and are under 200 mm for the PB/PZ morph (Smalås et al., 2013; Knudsen et al., 2019). In instances where three morphs are present both the LO and PB/PZ morphs cooccur in addition to a piscivorous (PP) morph (Smalås et al., 2013; Moccetti et al., 2019). The PP morph occupies the same colder and profundal habitat as the PB/PZ morphs and is characterized as having an old age at maturity, long and slender body shape, and darker colouration (Smalås et al., 2013) typical of predatory fish. The presence of a fourth morph, often similar to the previously described PB/PZ morph, is less common and seems to be adapated to the local environmental conditions (Hindar and Jonsson, 1982, 1993; Jonsson et al., 1988; Skúlason et al., 1989b; Snorrason et al., 1994; Østbye et al., 2020).

This work aims to examine the repeatability in life history parameters of five polymorphic Arctic charr populations. Three of the studied lakes have bi-morphic Arctic charr with the presence of the LO and PB/PZ morphs while two lakes also include the third PP morph. Previous work has confirmed the parallel evolution in terms of genetic, trophic, and morphological phenotypes across some of the morph pairs included in this study (Knudsen et al., 2016; Saltykova et al., 2017; Moccetti et al., 2019). Based on the knowledge of the differing niches used by the various morphs we expect the morphs to differ in several life-history traits such as length distribution, age and size at maturity, and growth. We predict that the LO morph will show longer and older fish, greater growth, longer lengths- and greater ages at maturity relative to the profundal morphs (PB/PZ) in each lake. When the PP morph is present in the system it will show size distributions consisting of the oldest and largest individuals, with the slowest growth, the oldest ages- and longest lengths at maturity compared to the two other morphs present in the system. We predict the variation in the parameters describing life history for each morph type (LO, PB/PZ, and PP) to be greater among the morphs than the variation seen across all lakes.

MATERIALS AND METHODS

Lake Description and Fish Collection

Arctic charr used in this study were sampled from five Norwegian lakes. Lake Limingen (64°42′13″N, 13°32′40″E) is located in central Norway in Trøndelag county while the remaining four lakes are located in Troms county in Northern Norway (**Figure 1**). These lakes have been described in other work (Klemetsen et al., 1997; Smalås et al., 2013; Knudsen et al., 2019; Moccetti et al., 2019) and the following is an overview of previous descriptions. Lakes in Troms county are typically ice covered from November/December to May/June and are described as being dimictic and oligotrophic (Klemetsen et al., 1997; Smalås et al., 2013; Moccetti et al., 2019). Lake Fjellfrøsvatn (69°05′08″N, 19°20′04″E) is part of the Målselv river system and has a surface area of 6.5 km^2 and a depth of 88m (Klemetsen et al., 1997). Brown trout (*Salmo trutta*) is the only fish species other than the bimorphic Arctic charr (LO and PB) found in this lake (Klemetsen et al., 1997). The other lake containing two Arctic charr morps (LO and PZ) is Skøvatn (69°01′50″N, 17°52′25″E). This lake is connected to the marine environment and supports populations of partially anadromous Arctic charr and brown trout, and Atlantic salmon (*S. salar* L. 1758) (Moccetti et al., 2019). Skøvatn is 119 m deep at its deepest point and has an area of 6.2 km^2 (Moccetti et al., 2019). Skogsfjordvatn (69°55′48″N, 19°9′36″E) is the largest of the northern lakes in the study with an area of 13.6 km^2 and a maximum depth of approximately 100 m. It contains, in addition to the trimorphic Arctic charr (LO, PB, and PP) with few anadromous individuals, brown trout, Atlantic salmon, three-spined stickleback (*Gasterosteus aculeatus* L. 1758) and some European eel (*Anguilla anguilla* L. 1758) (Smalås et al., 2013). Tårnvatn (69°18′43″N, 18°21′29″E) has a population of

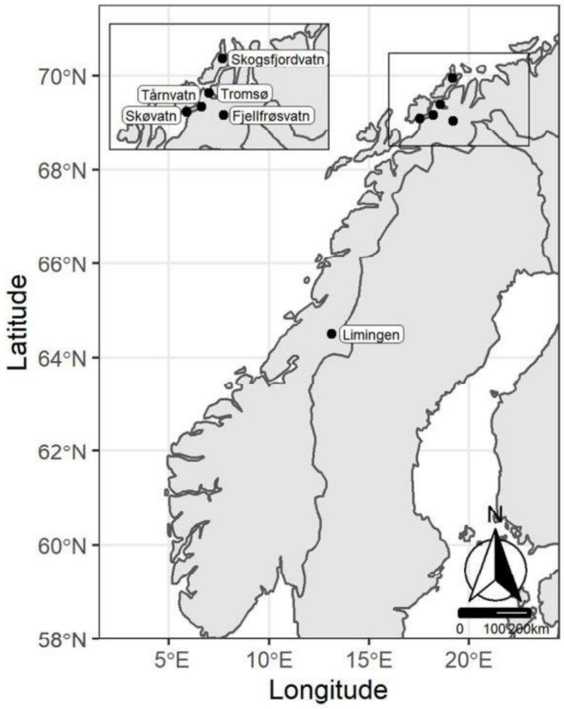

FIGURE 1 | Map of five Norwegian lakes with polymorphic Arctic charr populations used in the present study. Map prepared using the packages ggplot2 (Wickham, 2016), sf (Pebesma, 2018), ggsn (Santos Baquero, 2019), and ggspatial (Dunnington, 2021) in R (R Development Core Team, 2018) using the RStudio (RStudio Team, 2020) interface with map queried from the package rnaturalearth (South, 2017) using the ne_countries function.

trimorphic Arctic charr (LO, PB, and PP) and brown trout and is 53 m deep and 3.21 km^2 (Moccetti et al., 2019). Lake Limingen has a surface area of 95.7 km^2 and a maximum depth of 192 m. It is described as being dimictic and oligotrophic and contains in addition to the trimorphic Arctic charr (LO, PB, and PP), brown trout, minnow (*Phoxinus phoxinus* L. 1758; introduced in 1980s), and three-spined stickleback (Knudsen et al., 2019).

Fish were sampled using survey gillnets of 1.5 × 40 m dimensions which were made up of eight 5 m panels with mesh sizes of 10, 12.5, 15, 18, 22, 26, 35, and 45 mm and Nordic multi-mesh gill-nets of 12 2.5 m panels with mesh sizes from 5 to 55 mm. Additionally, a series of standard nets of 1.5 × 30 m dimensions with mesh sizes of 8, 10, or 12.5 mm were used in profundal and littoral habitats. Gillnets were placed at varying depths in the littoral (<15 m) and the profundal (>20 m) habitats. Additional survey nets placed in the pelagic habitat measured 6 × 40 m with mesh sizes of 8, 10, or 12.5 mm [further details in Klemetsen et al. (1997), Smalås et al. (2013), Smalås et al. (2017), Knudsen et al. (2019), and Moccetti et al. (2019)]. A pelagic pair trawl was used additionally to nets in lake Limingen which caught 63 LO Arctic charr [see details in Sandlund et al. (2017)].

Fish processing consisted of obtaining length (mm, fork length) and weight (g) measurements. Gonads were assessed for sex and maturity status. The key used for maturity status varied among datasets compiled for this study where some used a seven-stage scale and others a 3 stage-scale. Maturity status was re-coded using a 2 stage-scale for comparability as 1 for immature individual, where there is no indication of reproductive maturity in the year of sampling, or 2 for mature individuals. Mature individuals include those where gonads are either developed enough for spawning in the coming reproductive season and individuals with evidence of having already spawned in the sampling year or previous years. Sagittal otoliths were extracted and preserved in ethanol for later surface otolith readings in glycerol for age estimates of each individual fish. Each fish was assigned to their respective morph based on visual inspection of head and body morphology, maturation status, and colouration (Smalås et al., 2013; Skoglund et al., 2015). Genetic analyses on a subsample of the data demonstrated reproductive isolation between morphs and that visual classification of morph type is effective (Præbel et al., 2016; Simonsen et al., 2017; Moccetti et al., 2019).

Data Analyses

In all modeling, data exploration to assess the suitability of data to the statistical tests and to ensure no assumptions were violated was performed using a protocol heavily relying on data visualization using graphical plotting methods (Zuur et al., 2010). All analyses were conducted in R-4.1.0 (R Development Core Team, 2018) using the R studio (RStudio Team, 2020) interface and various packages. All figures were plotted with the use of the ggplot2 package (Wickham, 2016).

Length at Age

Data exploration using coplots prior to modeling fish length at age provided evidence for a morph-age and lake-age interaction. An ANCOVA was an unwise statistical choice as it would assume an equal effect of age for all morphs and in all lakes. Boxplots showed that the PB/PZ morph had a lower variance relative to the two other morphs. A generalized least squares [gls function nlme package version 3.1-152 (Pinheiro et al., 2019)] approach was selected for model building as it permitted the incorporation of the heterogeneity of variance within the final model. Data exploration using coplots suggested that variance should increase with age and could also potentially be variable among morphs or lakes. Age was included in the model as a continuous variable while lake and morph were included as categorical variables. Akaike's information criterion (anova function, stats package (R Development Core Team, 2018)) was used to evaluate potential models and the one with the lowest AIC value was retained as final model.

Growth Modeling

Although the von Bertalanffy growth model is often used in growth modeling of fishes, including Arctic charr, one of the main critiques of the model is that it has very little biological significance (Quince et al., 2008; Boukal et al., 2014). The biphasic model is built upon theory relating to metabolism and energetics; therefore the estimated terms relate to energy taken up from the environment and the organisms' conversion of that energy into growth and/or reproduction. The biphasic model used here assumes that immature individuals invest the entirety of their energy towards growth, however, the proportional investment in growth is reduced once an individual reaches sexual maturity. We assume here that the investment in reproduction is constant in the adult stage. The equation for the biphasic growth model is as follows:

$$L_t = \sqrt[(1-\beta)\alpha]{R^{t-t_{mat}}\left(L_0^{(1-\beta)\alpha} H t_{mat}\right) + \frac{RH}{1-R}(1 - R^{t-t_{mat}})}$$

where, $H = c(1-\beta)b^{-(1-\beta)}$ and $R = (1q^{-1}(1-\beta)r)^{-1}$ (Boukal et al., 2014). In the model: $\beta = 0.7$ (Jobling, 1983) and is the scaling exponent for the relationship between food consumption and growth in weight; α is a scaling exponent describing the relationship between length and weight calculated for each population; L is the length (in mm); $q = 1$, this term is the correction for the difference in energy requirement for production of gonadal tissue vs somatic tissues which was assumed to be equal in the present study; t represents the age of the fish with t_{mat} being the age at maturity for the population; c is estimated and informs us about the environment through representing the energy available to the organism for growth; r is estimated and informs us on the energy consumed which is diverted to reproduction.

Age at maturity was calculated using a cumulative distribution function (i.e., ogive) where the point of 50% maturity was used. All individuals with an age lower than the age at maturity were assessed with a model using $r = 0$. Length at age zero (i.e., model intercept) is unknown for our populations and was estimated to be 45mm for LO and PP morphs and 42mm for PB/PZ morphs (Frost, 1965). Model parameters c and r were estimated for each morph within each lake using a non-linear least-squares estimation with the nls function from base R. Models were evaluated using an analysis of residual sum of squares (AoRSS; also called extra sum-of-squares; Chen et al., 1992; Haddon, 2011; Ogle, 2016) to determine if the modeled curves differed among morphs within lake and within morph among lakes. If curves were determined to differ, further analyses of pairwise comparisons using likelihood ratio tests (Kimura, 1980; Haddon, 2011; Ogle, 2016) were performed to determine which of the parameters, r or c, differed in the comparison in question. This test compares whether the difference in the terms is significant between pooled and unpooled samples. Significance was corrected by dividing 0.05 by the number of comparisons, 20 in the case of LO and PB/PZ morphs (α 0.0025), and 6 in the case of the PP morph (α 0.0083).

A50 and L50

Age (A_{50}) and Length (L_{50}) where 50% of the population have reached maturity were calculated using a logistic regression (glm function, stats package base R (R Development Core Team, 2018)). Sexes were pooled for the analysis as sample size of groups (morph within lake) were small (e.g., only 7 mature individuals of the PP morph in Limingen). Data exploration with coplots suggested interactions between lake, age, and morph. Model selection was performed with the drop1 (stats package base R (R Development Core Team, 2018) command, starting from the most complex model, to evaluate if removing terms resulted in a statistically similar fit (Zuur et al., 2009). Once the model was fit, the estimate of age or length where 50% of the population reached maturity was calculated by dividing the intercept by the slope for each morph within each lake (Collett, 1991).

RESULTS

Of the five lakes included in this study two lakes contained two Arctic charr morphs and three lakes were composed of three morphs. In the LO (N = 2741) morph age ranged from 1 to 16 years, length from 64 to 494 mm, and weight from 2.2 to 1220 g (**Table 1**). The PB/PZ morph (N = 353) varied in age from 1 to 13 years, length from 72 to 272 mm, and weight from 3.4 to 231.1 g (**Table 1**). Age, weight, and length in the PP morph (N = 233) ranged from 2 to 17 years, 99 to 517 mm, and 8.2 and 1668 g, respectively (**Table 1**).

Length at Age

The analysis for fish length at age included individuals (N = 3327) across the five lakes and of the three possible morphs that had complete information on age and length. The AIC indicated that the model with a variance structure that allowed for different variances for each morph, with the PB/PZ morph having the lowest variance and the PP morph the highest variance (σ LO = 1.00, PB/PZ = 0.56, and PP = 1.11), while also allowing for an increase in variance with increasing ages (δ = 0.14) best described the data (**Supplementary Table 1**). The final model did not use sex as a predictor ($\chi^2(1) = 2.50, p = 0.1135$) therefore males and females had similar length at age. The final model was as follows:

$$\begin{aligned} Length &= intercept + Morph \times Age + Lake \times Age + \varepsilon \\ V(\varepsilon_i) &= \sigma^2_{Morph} \times e^{2\delta \times Age} \end{aligned}$$

TABLE 1 | Metadata and sample size of Arctic charr samples from five Norwegian lakes used in the research.

Lake	Morph	Number of fish	Length (mm)	Weight (g)	Age
Fjellfrøsvatn	LO	1843	177 ± 3	73 ± 4	4.1 ± 0.1
	PB	113	98 ± 2	8 ± 1	4.5 ± 0.3
Limingen	LO	72	258 ± 24	219 ± 50	5.4 ± 0.7
	PB	81	150 ± 8	29 ± 5	4.6 ± 0.6
	PP	18	274 ± 32	200 ± 82	8.4 ± 1.7
Skogsfjordvatn	LO	538	207 ± 6	120 ± 10	4.9 ± 0.2
	PB	73	107 ± 4	12 ± 1	4.1 ± 0.3
	PP	184	248 ± 9	170 ± 25	7.7 ± 0.4
Skøvatn	LO	130	191 ± 13	114 ± 28	5.3 ± 0.5
	PZ	51	95 ± 5	8 ± 1	4.8 ± 0.5
Tårnvatn	LO	158	193 ± 10	101 ± 14	5.9 ± 0.5
	PB	35	126 ± 15	28 ± 15	5.7 ± 1.0
	PP	31	278 ± 38	281 ± 99	10.8 ± 1.2

Length, weight, and age are shown as the mean ± standard error.

The estimated coefficients and standard errors of the fixed components of the model are shown in **Supplementary Table 2**. The residual standard error of the model is 14.09545.

Fish length increased with age (estimate 27.50, $p < 0.001$) for all groups, and the PB/PZ (estimate 7.20, $p = 0.005$) and PP (estimate 28.58, $p < 0.001$) morphs had larger intercepts relative to the LO morph. The effect of age on length, however, differed across morphs (**Figure 2** and **Supplementary Table 2**). The positive effect of age on length was lower in morphs PB/PZ (estimate −20.31, $p < 0.001$) and PP (−8.78 $p < 0.001$) relative to LO which relates to growth patterns presented further in the results section. Within all morph groups, charr from Tårnvatn (estimate −1.87, $p < 0.001$) had the shortest lengths at age while Limingen had the highest lengths at age (estimate 7.55, $p < 0.001$; **Figure 2**).

Growth Modeling

The biphasic growth model, unlike the Von Bertalanffy growth model, incorporates biologically significant parameters. Estimated model parameters r, relating to reproductive investment, and c, related to energy acquisition, for each population along with the reference equation parameters used for the likelihood ratio tests are found in **Table 2**. The initial tests of curve coincidence, with AoRSS, informed us that there are differences in parameter estimates within each comparable morph (**Figure 3**), and within each lake (**Table 3**). Further pairwise comparisons using a likelihood ratio approach informed us which parameters, r and/or c, differed and between which lake/morph. The estimates for c in the LO morph ranged from 1.28 to 2.04 and for the parameter r the range was from 0.13 to 0.41. In the LO morph, c was unique between each lake, whereas r did not differ between LO individuals from the following lake pairs: Skogsfjordvatn and Tårnvatn, Skogsfjordvatn and Limingen, Skogsfjordvatn and Skøvatn, and Skøvatn and Limingen (**Tables 2**, **4**). For the PB/PZ morph in Skogsfjordvatn, Skøvatn, and Fjellfrøsvatn no differences were found in the parameter c which ranged from 0.57 to 2.30 across all lakes (**Tables 2**, **4**). In the PB/PZ morph the parameter r, relating to reproductive investment, ranged from 0.01 to 0.98 and was similar across most pairs while only differing between Limingen and Skogsfjordvatn, Limingen and Skøvatn, and Limingen and Tårnvatn (**Tables 2**, **4**). Finally, the only difference in parameters in the PP morph was between Tårnvatn and Limingen for the parameter c which ranged from 0.92 to 1.43 (**Tables 2**, **4**). The

TABLE 2 | Estimated coefficients and their standard error for parameters r and c of the biphasic growth model along with the L_0 value used the estimating of each curve for Arctic charr morphs (LO, PB/PZ, and PP) from five Norwegian lakes.

Lake	Morph	*r*	SE	*p*-value	c	SE	*p*-value	L0 (mm)	Linf (mm)
Skg	LO	0.13	0.02	0.0000*	1.28	0.02	<0.0001*	45	892
	PB/PZ	0.98	0.17	0.0000*	2.30	0.27	<0.0001*	42	148
	PP	0.26	0.03	0.0000*	1.43	0.03	<0.0001*	45	439
Tar	LO	0.37	0.04	<0.0001*	1.54	0.03	<0.0001*	45	294
	PB/PZ	0.01	0.03	0.8180	0.84	0.04	<0.0001*	42	13619
	PP	−0.05	0.06	0.4630	0.92	0.13	<0.0001*	45	Inf
Lim	LO	0.41	0.06	0.0000*	2.04	0.04	<0.0001*	45	407
	PB/PZ	0.53	0.04	<0.0001*	1.81	0.06	<0.0001*	42	255
	PP	0.31	0.08	0.0009*	1.72	0.13	<0.0001*	45	446
Skv	LO	0.24	0.04	0.0000*	1.50	0.04	<0.0001*	45	496
	PB/PZ	0.13	0.04	0.0031*	0.57	0.02	<0.0001*	42	416
Fje	LO	0.24	0.01	<0.0001*	1.77	0.01	<0.0001*	45	599
	PB/PZ	0.42	0.03	<0.0001*	0.90	0.02	<0.0001*	42	132
All	LO	0.36	0.01	<0.0001*	1.71	0.01	<0.0001*	45	361
	PB/PZ	0.19	0.03	0.0000*	0.95	0.03	<0.0001*	42	387
	PP	0.20	0.02	0.0000*	1.37	0.03	<0.0001*	45	604

Significance is shown with (*).

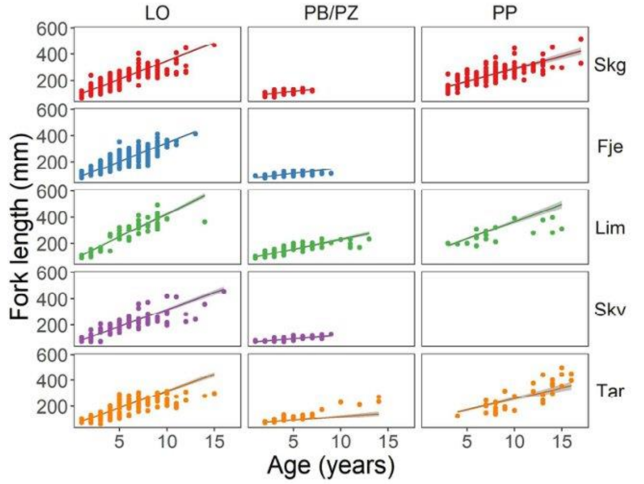

FIGURE 2 | Scatter plot of Arctic charr fork length (mm) at age for each morph type within each lake included in the study. The model is represented by a line with shading representing the 95% confidence interval. Skg, Skogsfjordvatn; Fje, Fjellfrøsvatn; Lim, Limingen; Skv, Skøvatn; and Tar, Tårnvatn.

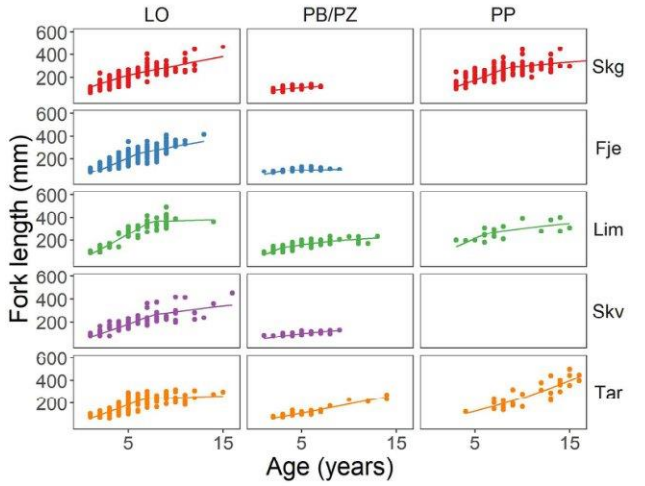

FIGURE 3 | Biphasic growth model-based length at age estimates of three Arctic charr morphs in the studied lakes. The point of inflection in the model indicates the age where energy is diverted from somatic growth to reproductive investment. Skg, Skogsfjordvatn; Fje, Fjellfrøsvatn; Lim, Limingen; Skv, Skøvatn; and Tar, Tårnvatn.

TABLE 3 | Analysis of residual sum of squares comparing the overall incidence of curves modeled by the bi-phasic growth model within morph type across all lakes (LO, PB/PZ, and PP) and among morphs within lake.

Comparison	RSSp	RSSs	DFd	DFn	F-statistic	*p*-value
LO	2776285	2173407	2731	8	94.69	<0.0001*
PB/PZ	260943.2	66093.39	343	8	126.40	<0.0001*
PP	606360.2	512547.6	227	4	41.55	<0.0001*
Fjellfrøsvatn	2171993	1143630	1952	2	877.63	<0.0001*
Limingen	613234.5	177358.2	165	4	101.38	<0.0001*
Skogsfjordvatn	1328744	891649.6	789	4	96.69	<0.0001*
Skøvatn	552320.9	232822.4	177	2	121.45	<0.0001*
Tårnvatn	524081.2	306329.3	218	4	38.74	<0.0001*

TABLE 4 | Likelihood Ratio Test *p*-values from pairwise comparisons testing for differences when parameters r or c were kept constant in the LO morph (top), PB/PZ (mid), and PP (bottom).

RC	Skg	Tar	Lim	Skv	Fje
Skg	–	1 1 1	1 <0.0002* 1	0.003 1 –	<0.0001* 1 –
Tar	<0.0001* 0.0002* 1	–	<0.0001* <0.0001* 0.3998	<0.0001* 1 –	<0.0001* 1 –
Lim	<0.0001* <0.0001* 1	<0.0001* <0.0001* <0.0007*	–	1 0,0006* –	<0.0001* 0.1005 –
Skv	<0.0001* 1 –	<0.0001* <0.0001* –	<0.0001* <0.0001* –	–	<0.0001* 1 –
Fje	<0.0001* 1 –	<0.0001* <0.0001* –	<0.0001* <0.0001* –	<0.0001* 1 –	–

*Significantly differing terms are indicated by * at the corrected multiple pairwise comparison alpha of 0.0025 for LO and PB/PZ morphs and of 0.0083 for the PP morph.*

parameter r in the PP morph ranged from −0.05 to 0.31 and did not differ among the three lakes (**Tables 2, 4**).

A50 and L50

Age where 50% of the population has matured (hereafter age at maturity) was estimated using all individuals with complete information on age or length ($N = 3323$), and maturity. Age and length at 50% maturity were influenced by the combination of factors morph type (LO, PB/PZ, and PP) and lake. The equation for the model used was as follows where A_{50} and Age are replaced by L_{50} and Length, respectively, when determining the length at maturity:

$$A_{50} = intercept + Age \times Morph \times Lake + \varepsilon$$

The estimates of the model coefficients for A_{50} are found in **Supplementary Table 3**. The probability of being mature increased with age (estimate 1.49, $p < 0.001$). The general trend in the age at maturity across lake was that the PB/PZ morph had the lowest age at maturity, the LO an intermediate age at maturity and the PP morph the highest age at maturity (**Figure 4**, **Supplementary Table 3**, and **Supplementary Figure 1**). However, in some lakes, pairs of coexisting morphs may have very similar ages at maturity, notably in Skøvatn where the LO and PB/PZ morphs had an estimated A50 of 5.8- and 6.0 years, respectively, while in Tårnvatn which had an estimated age at maturity of 6.9 years for the LO and 7.5 years for the PP morph (**Figure 4** and **Supplementary Table 4**). Age influenced the probability of maturing differently in the various morphs. The positive effect of age on probability of reaching maturity was reduced in the PP morph relative to the LO morph (estimate −0.88, $p < 0.00$, **Supplementary Table 3**) where the PP morph (overall mean 7.3 years) reached maturity at older ages relative to LO morph (overall mean 6.3 years). Individuals in lakes Tårnvatn and Skøvatn reached sexual maturity at higher ages relative to individuals in Skogsfjordvatn (estimates −0.83, −1.11, respectively, $p < 0.01$, **Supplementary Table 3**). Of note, the age morph interaction in Tårnvatn was modified (estimate 0.71, $p < 0.02$, **Supplementary Table 3**) where individuals of the PP morph (7.5 years) reached maturity at a lower age relative to individuals of the PP morph in Skogsfjordvatn (8.3 years). The PB/PZ morphs in lake Skøvatn and Tårnvatn had a further reduction in the probability of attaining sexual maturity (estimate −5.03, −14.29, $p < 0.02$, 0,03, respectively, **Supplementary Table 3**), therefore matured at an older age (6.0- and 5.9 years, **Supplementary Table 4**) relative to the PB/PZ morph of lake Skogsfjordvatn (2.6 years, **Supplementary Table 4**).

The coefficient estimates for length where 50 percent of the population have reached sexual maturity (hereafter length at maturity) are found in **Supplementary Table 6**. Length had a positive effect on the probability of maturing where, as a fish grows longer it increased its probability of reaching sexual maturity (estimate = 0.06, $p < 0.001$, **Supplementary Table 6**). The probability of maturing was increased in the PB/PZ

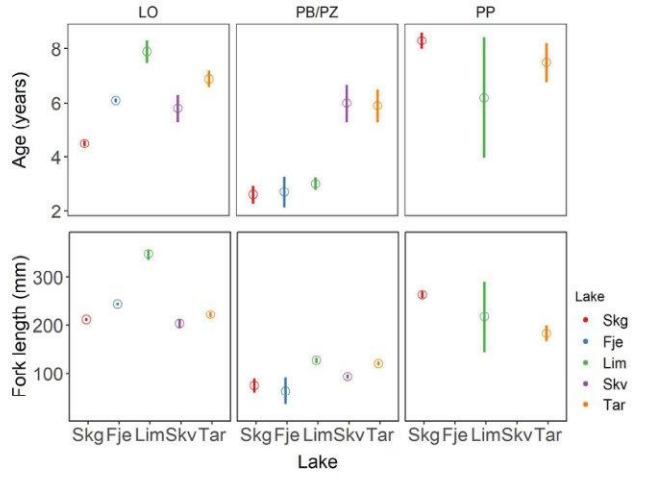

FIGURE 4 | Age and length where 50% of the population is mature in three Arctic charr morphs from the 5 studied lakes. Open circles represent the estimated obtained from logistic regression with standard error. Skg, Skogsfjordvatn; Fje, Fjellfrøsvatn; Lim, Limingen; Skv, Skøvatn; and Tar, Tårnvatn.

(estimate = 9.35, $p < 0.001$, **Supplementary Table 6**) and PP (estimate = 6.31, $p < 0.01$, **Supplementary Table 6**) morphs, therefore these morphs reached sexual maturity at shorter lengths relative to the LO morph (**Figure 4**, **Supplementary Figure 2**, and **Supplementary Table 7**). The positive effect of length on the probability of maturing was lower in the PP morph, which resulted in a greater length at maturity in the PP morph (estimate −0.04, $p < 0.001$, **Supplementary Table 6**) relative to LO.

Generally, the probability of reaching sexual maturity in all individuals from the lakes Fjellfrøsvatn, Skøvatn, and Tårnvatn was increased (i.e., maturity at shorter lengths) relative to individuals from lake Skogsfjordvatn (**Supplementary Table 6**). However, a negative interaction between lake and fish length was present in all lakes resulting in greater length at maturity relative to Skogsfjordvatn (**Supplementary Table 6**). In general, individuals from Limingen were longer at sexual maturity compared to those from Skogsfjordvatn (estimate −0.02, $p < 0.04$, **Supplementary Table 6**). Individuals of the PB/PZ morph in Tårnvatn (L50 = 104 mm) Skøvatn (L50 = 102 mm) were longer at maturity than those of Skogsfjordvatn (L50 = 75 mm) through interactions between morph and lake (estimate = −15.78, −13.52, repectively, $p < 0.01$, **Supplementary Table 6**), and further in Skøvatn through an interacion among morph, lake, and length (estimate 0.08, $p = 0.02$, **Supplementary Table 6**).

DISCUSSION

This study provides evidence from Norwegian lakes supporting the repeated evolution in life history traits of the Arctic charr morph complexes. Distinct populations within each waterbody had differentiation in the analyzed life history traits and corresponding morphs among lakes demonstrated similar patterns in life history parameters. The analysis of length at age showed that the distinct morphs have different patterns and that these patterns show consistencies in the comparable morphs across lakes. Further analyses of growth patterns demonstrated that all populations adopt unique growth trajectories while also highlighting the importance of ontogenetic niche shifts and the investment in reproduction in the differentiation of the morphs. Finally patterns in age and size (length, mm) at maturity supported the results from the reproductive investment in the biphasic growth modeling with the PB/PZ morph having the youngest age at maturity and the PP morph delaying maturation to older ages.

Fish length at age followed the expected pattern with the PB/PZ morph being shortest, the LO morph being longer, and the PP morph, when present, exceeding the length of the LO morph. This study corroborates that the PB/PZ morph is often referred to as a "dwarf" (Hindar and Jonsson, 1982; Svedäng, 1990; Klemetsen et al., 1997). The PB/PZ morph is also described as being paedomorphic (Skoglund et al., 2015; Simonsen et al., 2017), which is retaining their juvenile traits into adulthood. Our results are consistent with these often used (although, rightfully so, less in more recent literature) anthropomorphic terms. When the third PP morph is present, individuals of this morph are on average the longest and oldest fish of all the morphs. This is consistent with multiple studies reporting length in polymorphic Arctic charr populations (Snorrason et al., 1994; Klemetsen et al., 1997; Smalås et al., 2013; Sandlund et al., 2017). However, we determined that at a given age, the LO morph is longer than the PP morph of the same age. Although with a relatively slower growth, the PP morph is able to outgrow their LO counterpart through a higher estimated asymptotic length and greater longevity (Smalås et al., 2013).

Examinations of somatic growth in this study demonstrated that there is high variation in growth within the various studied Arctic charr populations. The sympatric morphs had significantly different growth trajectories which is in accordance with other studies (Smalås et al., 2013; Knudsen et al., 2015, 2019). We determined that all sympatric morphs have different growth trajectories but did not further examine how the model parameters differed among the three morphs as the aim here was to examine repeatability of evolution within comparable morphs. Within similar morph groupings, we determined that the LO morph across all lakes has a very large variation in the estimated parameters for both energy acquisition and reproductive investment. The parameter c, relating to the energy acquired, ranged from 1.28 to 2.04 and was found to be different in all pairwise comparisons across lakes. When comparing the morphs while disregarding the lakes, we see that the LO strategy is a high investment in both growth and reproduction. The growth strategy adopted by the LO morph seems to be quite broad, however. This suggests heterogeneity among the environments along with local adaptation. The limnological descriptions of the studied lakes are relatively comparable, however, it is likely that the LO morphs within the different lakes focus their realized niche differently related to environmental heterogeneity as Arctic charr is known to have specialist individuals who restrict themselves to narrow realized niches (Amundsen, 1995). The lakes studied here contain differing number of species, including brown trout which is a competitor and predator of Arctic charr, therefore imposing varying pressures on Arctic charr niche (Prati et al., 2021). Of interest would be to assess the growth of the morphs in relation to environmental variables, such as lake size (Eloranta et al., 2015), latitude (Chavarie et al., 2010), temperature (Knudsen et al., 2015), and/or competition (Prati et al., 2021), to assess the contribution of the environment to the realized niche of Arctic charr morphs. Among the pairwise comparisons examining the LO morph's investment in reproduction few similarities (4 of 10) were found, highlighting the breadth in the LO morphs life history strategy.

Growth within the PB/PZ morph had more similarities than the parameters of the growth modeling of the LO morph. Three of 10 pairwise comparisons did not differ in the parameter c while only two differed for the parameter r in the PB/PZ morph. A similar pattern was seen in the PP morph where the populations in the different lakes did not differ in reproductive investment with only one pairwise comparison differing for the energy acquisition term. Similarities in the parameter accounting for energy acquired from the environment were expected as both the PB/PZ and PP morphs occupy a narrower realized diet and habitat niche relative to the LO morph. The PB/PZ morph is known to have a more specialized diet than their generalist LO counterparts (Sandlund et al., 1992; Knudsen et al., 2019; Moccetti et al., 2019) while the PP morph mostly consumes fish prey at least as adults (Amundsen, 1994; Skoglund et al., 2015; Knudsen et al., 2016, 2019). The only difference found when comparing growth parameters in the PP morph was in the term for energy taken from the environment (c) where PP individuals from Tårnvatn have a lower abundance of fish in the stomach content than the PP morph in Limingen (Knudsen et al., 2019; Moccetti et al., 2019). Tårnvatn is the only lake supporting trimorphic Arctic charr in the absence of small fish species, such as minnow and stickleback. Piscivorous fish in Tårnvatn may only prey upon smaller salmonids and must therefore supplement their diet with other food sources and potentially expanding their niche to overlap with the other morphs (Moccetti et al., 2019). Indeed, the reproductive isolation between the two profundal morphs in Tårnvatn is not complete (Moccetti et al., 2019). The narrow niches occupied by each morph leave little to no opportunities for individual specialists within the PB/PZ and PP population's niche (Amundsen, 1995) resulting in very similar energy acquisition potential among lakes. These results suggest that Arctic charr can specialize within various niches (Prati et al., 2021) even within what we consider comparable morphs. However, the constraints put on by the narrowed niche seem to influence the reproductive tradeoffs in a similar manner within the morph types.

Once an individual matures, it is assumed that the investment in somatic growth is reduced, and energy is directed towards the production of gonads. Our results corroborate this assumption as growth slowed down significantly following the onset of maturation in all populations with the exception of the PP morph in Tårnvatn. We suppose that this is related to the change in diet to a piscivorous life style as ontogenetic niche shifts influence growth rate, with a piscivorous diet being a very efficient food source (Barton, 2007), which would explain the negative value for r in the biphasic growth model. In the case of Tårnvatn, where only salmonids are present, a shift to a piscivorous diet would occur at a larger size than in the other lakes in this study which contain smaller fish species in addition to the salmonids. Ontogenetic niche shifts occur when the cost of the current preferred prey outweighs the benefits of this prey source (Forseth et al., 1994). Prey size is related to the predator's size therefore we would predict that small individuals, notably juveniles, would share more similarities in behavior (i.e., predator avoidance), and trophic position and feeding preference (Amundsen et al., 2008; Skoglund et al., 2015; Knudsen et al., 2019; Moccetti et al., 2019). These similarities would be reduced as individuals of each morph age, become larger, and shift to their "adult niche" (Moccetti et al., 2019). Individuals of the PP morph are known to have very low growth during their early years (Smalås et al., 2013) likely related to the poorer performance of their piscivorous jaw morphology (Saltykova et al., 2017) on benthos, especially in competition with the PB/PZ morph, and their use of the colder profundal habitat. Their eventual size related shift to a piscivorous diet (Amundsen, 1994; Moccetti et al., 2019) along with their relatively long life span shown here likely compensate for their slow start. For the first time, repeatability in life history traits of the PP morph across multiple lakes is substantiated here.

The expected trends in age and length at maturity were observed in the study with the PB/PZ morph having the youngest age and shortest length at maturity. There were clear indications in tradeoffs in timing of reproduction and fecundity based on the timing of the onset of maturity in the studied populations with the PB/PZ morph maturing earliest. By adopting a fast life history and reproducing early at a relatively smaller size, the PB/PZ morph can avoid predation before their first reproductive event whilst the other morphs reproducing at larger sizes increase the reproductive output of a single reproductive event (Smalås et al., 2017). The smaller PB/PZ morph is known to have a lower fecundity (Sandlund et al., 1992; Smalås et al., 2017). An early reproduction may allow for multiple reproductive seasons in the iteroparous Arctic charr as the number of reproductive events is a greater contributor to fitness than a single large reproductive event (Stearns, 1992). In addition, a lower fecundity in the PB/PZ morph might be offset by a relatively large investment in gonadal vs somatic growth (Sandlund et al., 1992) which we see evidence of here with the relatively high r for the PB/PZ morph in the biphasic growth modeling.

Maturation in the PP morph, however, seems to have a more complex relationship with age and length and is potentially related to the relatively limited sample size in this study. The PP morph matures at older ages while still being shorter than their LO counterparts (except for length in Skogsfjordvatn). The PP morph has a relatively long and slender shape body (Smalås et al., 2013) with a large head (Skoglund et al., 2015) and a lower condition factor relative to the two other sympatric morphs (unpublished G. Grenier). Condition is known to be a good predictor maturity where a minimum threshold is necessary for successful maturation (Dutil, 1986). During their juvenile years deep in the cold profundal habitat growth in the PP morph is relatively slow (Smalås et al., 2013, this study). To consume fish prey, which is relatively large in relation to other potential prey sources in freshwater environments, the gape-limited predator's size must permit the consumption of prey of such size. The combination of slow growth (in length and girth) along with a large head suggests that the PP morph concentrates its energy into developing a phenotype permissible of piscivory before initiating reproduction. Thus, the PP morph requires more time to attain a gape permissible of piscivory and obtain the required nutritional status for maturation, hence their reproduction at shorter lengths but older ages than the LO individuals.

Through Arctic charr's iteroparous nature, multiple strategies are viable options when it comes to maximize fitness through variations of age and size at maturity along with annual investment in reproductive effort and fecundity. When considering age at maturity, there is much variation within each comparable morph type among lake analyses once again suggest local adaptation. With the large variation in life history seen among comparable morphs, here length seems to be a superior predictor of maturity relative to age.

Future work could examine the point in life where an individual's life history trajectory is set to determine the extent to which genetics and environment influence individual life history. This would help elucidate the process of evolution and speciation within the Arctic charr complex along with the evolutionary history of the various morphs. In addition, studies of life history and evolution in Arctic and subarctic fish communities are warranted as salmonids are predicted to be negatively impacted within these communities in relation to climate change (Hayden et al., 2017). Further studies examining the contribution of the environment to the evolution of Arctic charr life history are necessary to protect and preserve the world's most variable vertebrate (Klemetsen, 2013).

CONCLUSION

Our results support repeatability in the evolution of life history traits between morphs in Arctic charr, while also highlighting the importance of local adaptation in the modulation of life history traits of these morphs. This is further supported by similar patterns of parallelism in other traits, such as skull morphology, diet, and parasite load, in Arctic charr inhabiting similar environments within Northern Scandinavia (Eloranta et al., 2013; Siwertsson et al., 2013, 2016; Skoglund et al., 2015). Notably, this is the first study to substantiate repeatability in life history traits of the PP morph. Within the five studied lakes, the PP morph adopts a slow life history strategy while the PB/PZ morph adopts a fast strategy and the LO morph finds itself in an intermediate strategy. The LO morph demonstrates a wide variability in possible life history traits through its generalist nature while the PB/PZ and PP morphs occupy a more specialized niche thus more restricted variation in life history parameters. The PP morph improves its growth trajectory through an ontogenetic niche shift and has an old age at maturity. The PB/PZ morph avoids the need to grow big by maturing early and at smaller sizes. The strategies seen within each morph seem to be evolutionarily stable strategies that have evolved repeatably.

DATA AVAILABILITY STATEMENT

Requests to access these datasets should be directed to GG, gabrielle.grenier@uit.no.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because this study was performed using archived samples therefore no approval was directly required.

AUTHOR CONTRIBUTIONS

GG conceived and designed the study with contributions from RKn and RKj, performed the statistical analyses with contributions from AS, and wrote the first draft of the manuscript. All authors contributed to manuscript revisions, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.771309/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Supplementary Material

1 Supplementary Figures and Tables

Supplementary Table 1. Variance structures assessed for inclusion in the modelling of length at age of Arctic charr morphs from five Norwegian lakes along with the model selection results.

Variance name	Variance structure	AIC	ΔAIC
varComb (Ident, Exp)	$\sigma^2_{Morph} \times e^{2\delta \times Age}$	31165.81	0
varComb (Ident, Exp)	$\sigma^2_{Lake} \times e^{2\delta \times Age}$	31245.03	79.22
VarExp	$\sigma^2 \times e^{2\delta \times Age_{Morph}}$	31222.9	57.09
VarExp	$\sigma^2 \times e^{2\delta \times Age_{Lake}}$	31360.55	194.74
VarIdent	σ^2_{Lake}	31781.39	615.58
VarIdent	σ^2_{Morph}	31878.43	712.62
None	No variance structure	32127.46	961.65

Supplementary Material

1 Supplementary Figures and Tables

Supplementary Table 2. Model estimates for fish length at age of Arctic charr morphs from five Norwegian lakes. The LO morph from lake Skogsfjordvatn is used as reference group. Significant terms are indicated by an asterix (*).

Coefficient	**Estimate**	**S.E.**	**t-value**	**p-value**	
Intercept	74.09	1.95	37.94	0.0000	*
Age	27.50	0.48	56.70	0.0000	*
Morph PB/PZ	7.20	2.58	2.80	0.0052	*
Morph PP	28.58	7.81	3.66	0.0003	*
Lake Fje	-15.88	2.33	-6.83	0.0000	*
Lake Lim	1.55	3.60	0.43	0.6663	
Lake Skv	-14.54	3.78	-3.85	0.0001	*
Lake Tar	-12.55	4.01	-3.13	0.0018	*
Age*Morph PB/PZ	-20.31	0.63	-32.22	0.0000	*
Age*Morph PP	-8.78	1.25	-7.03	0.0000	*
Age*Lake Fje	1.29	0.59	2.19	0.0288	*
Age*Lake Lim	7.55	0.90	8.37	0.0000	*
Age*Lake Skv	-1.58	0.92	-1.72	0.0860	
Age*Lake Tar	-1.87	0.88	-2.12	0.0338	

Supplementary Material

1 Supplementary Figures and Tables

Supplementary Table 3. Coefficient estimates for modelling of age at 50% maturity of Arctic charr morphs from five Norwegian lakes. The LO morph from lake Skogsfjordvatn is used as reference group. Significant terms are indicated by an asterix (*).

Coefficient	Estimate	S.E.	z-value	p-value	
Intercept	-6.77	0.61	-11.04	<0.0000	*
Age	1.49	0.13	11.63	<0.0000	*
Morph PB/PZ	3.14	1.66	1.89	0.0589	
Morph PP	1.72	0.98	1.75	0.0796	
Lake Fje	-1.26	0.73	-1.72	0.0854	
Lake Lim	-0.97	2.04	-0.48	0.6338	
Lake Skv	4.57	0.79	5.82	0.0000	*
Lake Tar	2.15	0.94	2.29	0.0220	*
Age*Morph PB/PZ	-0.11	0.47	-0.24	0.8115	
Age*Morph PP	-0.88	0.16	-5.50	0.0000	*
Age*Fje	-0.17	0.15	-1.17	0.2439	
Age*Lim	-0.51	0.29	-1.80	0.0713	
Age*Skv	-1.11	0.15	-7.17	0.0000	*
Age*Tar	-0.83	0.17	-5.00	0.0000	*
Morph PB/PZ*Fje	3.32	1.87	1.78	0.0760	
Morph PB/PZ*Lim	0.48	2.80	0.17	0.8630	
Morph PB/PZ*Skv	-5.03	2.11	-2.39	0.0170	*
Morph PB/PZ*Tar	-14.29	6.60	-2.17	0.0303	
Morph PP*Lim	4.46	2.59	1.72	0.0852	
Morph PP*Tar	-0.75	2.39	-0.31	0.7551	
Age*Morph PB/PZ*Fje	-0.61	0.51	-1.20	0.2298	
Age*Morph PB/PZ*Lim	0.52	0.63	0.82	0.4148	
Age*Morph PB/PZ*Skv	0.43	0.53	0.82	0.4128	
Age*Morph PB/PZ*Tar	2.26	1.21	1.86	0.0629	
Age*Morph PP*Lim	0.16	0.35	0.46	0.6483	
Age*Morph PP*Tar	0.73	0.30	2.41	0.0159	*

Supplementary Material

1 Supplementary Figures and Tables

Supplementary Table 4. Estimates of age at maturity using logistic regression where 50% of the Arctic charr population of different morphs has reached sexual maturity in five Norwegian lakes. The lower and upper values represent the 95% confidence interval.

Morph	Lake	N A50	Estimate A50	Lower	Upper	S.E.	Mean
LO	Skg	538	4.5	4.4	4.7	0.10	6.3
	Fje	1840	6.1	6.0	6.2	0.07	
	Skv	130	5.8	4.9	6.7	0.50	
	Tar	159	6.9	6.3	7.5	0.30	
	Lim	71	7.9	7.1	8.8	0.41	
PB/PZ	Skg	73	2.6	2.0	3.3	0.33	4.0
	Fje	113	2.7	1.6	3.8	0.56	
	Skv	51	6.0	4.6	7.4	0.70	
	Tar	35	5.9	4.7	7.0	0.60	
	Lim	81	3.0	2.5	3.5	0.24	
PP	Skg	184	8.3	7.7	8.9	0.31	7.3
	Tar	31	7.5	6.0	9.0	0.70	
	Lim	18	6.2	1.8	10.5	2.23	

Supplementary Material

1 Supplementary Figures and Tables

Supplementary Table 5. Estimates from logistic regression for age and length where 50% of the population has achieved sexual maturity in Arctic charr morphs from five Norwegian lakes. The lowest age and shortest length of mature fish in the raw data for each morph and population along with the estimated age at maturity (oogive) used in the biphasic modelling are included for reference.

Lake	**Morph**	**Number of fish**	**Age at first maturity (years)**	**A50 ±SE (years)**		**Length at first maturity (cm)**	**L50±SE (cm)**		**Age at maturity oogive**
Fjellfrøsvatn	LO	1840	3	6.1	±0.1	147	245	±2.4	6.9
	PB	113	3	2.7	±0.6	82	63	±27.8	4.4
Limingen	LO	71	6	7.9	±0.4	294	347	±11.8	8.2
	PB	81	2	3.0	±0.2	96	127	±5.5	3.6
	PP	18	4	6.2	±2.2	195	217	±72.4	7.2
Skogsfjordvatn	LO	538	2	4.5	±0.1	143	211	±2.7	5.3
	PB	73	3	2.6	±0.3	73	75	±14.3	1.7
	PP	184	5	8.3	±0.3	184	264	±7.3	9.5
Skøvatn	LO	130	3	5.8	±0.5	167	203	±9.4	8.4
	PZ	51	3	6.0	±0.7	89	102	±4.3	5.3
Tårnvatn	LO	161	3	6.9	±0.3	132	221	±6.3	7.4
	PB	32	5	5.9	±0.6	104	120	±4.4	6.1
	PP	31	7	7.5	±0.7	142	141	±56.7	6.3

Supplementary Material

1 Supplementary Figures and Tables

Supplementary Table 6. Coefficient estimates for modelling of Length at 50% maturity of Arctic charr morphs from five Norwegian lakes. The LO morph from lake Skogsfjordvatn is used as reference group. Significant terms are indicated by an asterix (*).

Coefficient	Estimate	S.E.	z-value	p-value	
Intercept	-12.80	1.29	-9.92	<0.0000	*
Length	0.06	0.01	10.56	<0.0000	*
Morph PB/PZ	9.35	2.59	3.61	0.0003	*
Morph PP	6.31	1.70	3.72	0.0002	*
Lake Fje	3.29	1.39	2.38	0.0175	*
Lake Lim	0.35	3.68	0.09	0.9250	
Lake Skv	8.32	1.61	5.16	0.0000	*
Lake Tar	5.00	1.82	2.76	0.0059	*
Length*Morph PB/PZ	-0.01	0.02	-0.64	0.5218	
Length*Morph PP	-0.04	0.01	-5.03	0.0000	*
Length*Fje	-0.02	0.01	-3.53	0.0004	*
Length*Lim	-0.02	0.01	-2.09	0.0366	*
Length*Skv	-0.04	0.01	-5.15	0.0000	*
Length*Tar	-0.03	0.01	-3.13	0.0017	*
Morph PB/PZ*Fje	-1.52	3.32	-0.46	0.6478	
Morph PB/PZ*Lim	-4.70	4.73	-1.00	0.3199	
Morph PB/PZ*Skv	-13.52	3.64	-3.72	0.0002	*
Morph PB/PZ*Tar	-15.78	5.97	-2.65	0.0082	
Morph PP*Lim	4.25	4.44	0.96	0.3376	
Morph PP*Tar	-0.17	2.56	-0.07	0.9460	
Length*Morph PB/PZ*Fje	0.00	0.03	0.07	0.9413	
Length*Morph PB/PZ*Lim	0.04	0.03	1.40	0.1624	
Length*Morph PB/PZ*Skv	0.08	0.03	2.32	0.0202	*
Length*Morph PB/PZ*Tar	0.10	0.05	1.95	0.0518	
Length*Morph PP*Lim	0.01	0.02	0.59	0.5563	
Length*Morph PP*Tar	0.01	0.01	1.13	0.2570	

Supplementary Material

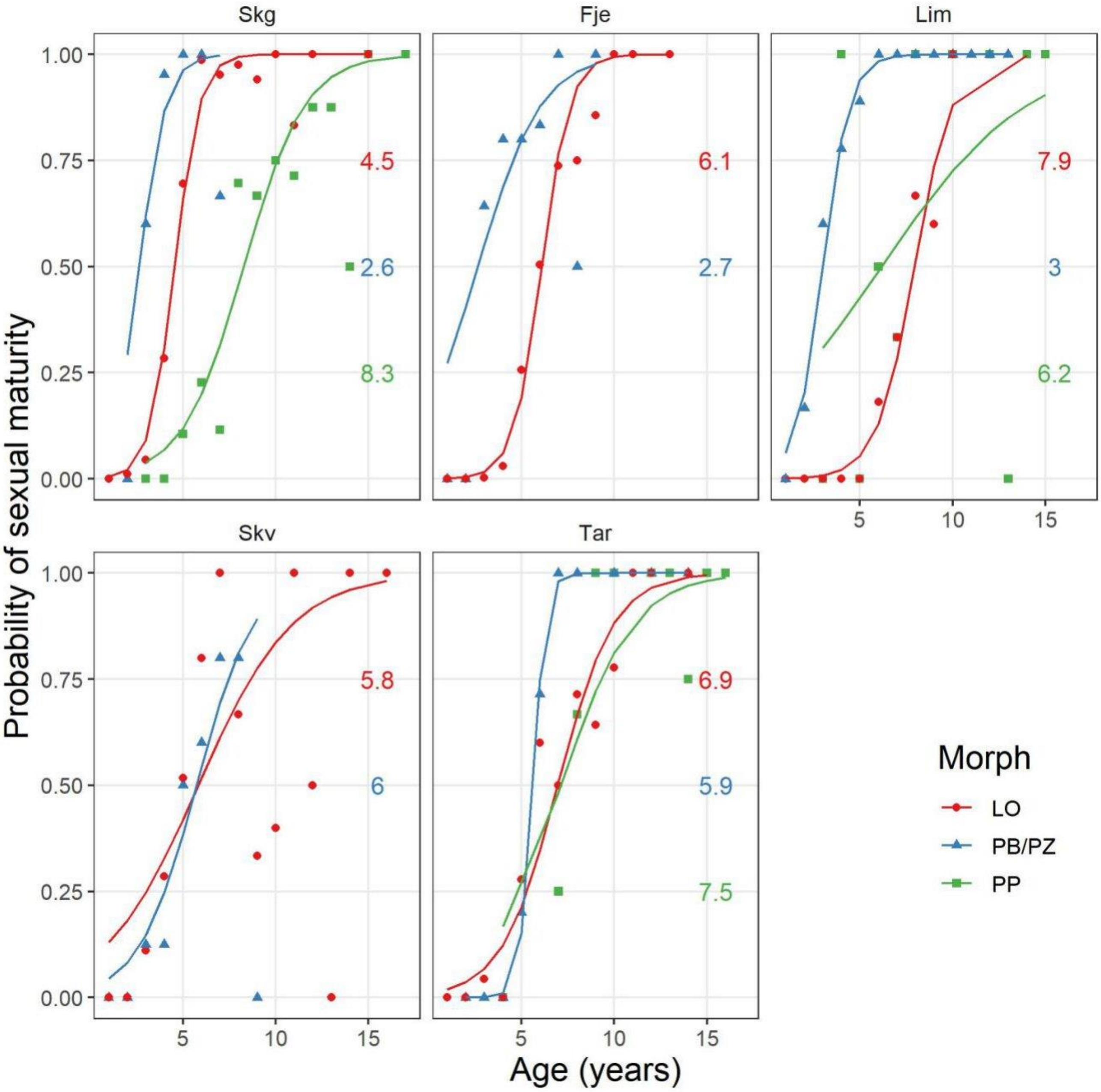
1 Supplementary Figures and Tables

Supplementary Table 7. Estimates of length at maturity using logistic regression where 50% of the Arctic charr population of different morphs has reached sexual maturity in five Norwegian lakes. The lower and upper values represent the 95% confidence interval.

Morph	Lake	N L50	Estimate L50 (mm)	Lower	Upper	S.E.	Mean
LO	Skg	538	211	206	216	2.7	245
	Fje	1840	245	240	249	2.4	
	Skv	130	203	185	222	9.4	
	Tar	162	221	208	233	6.3	
	Lim	71	347	323	370	11.8	
PB/PZ	Skg	73	75	47	103	14.3	97
	Fje	113	63	9	117	27.8	
	Skv	51	102	93	110	4.3	
	Tar	32	120	112	129	4.4	
	Lim	81	127	116	138	5.5	
PP	Skg	184	264	250	278	7.3	207
	Tar	31	141	30	252	56.7	
	Lim	18	217	76	359	72.4	

Supplementary Material

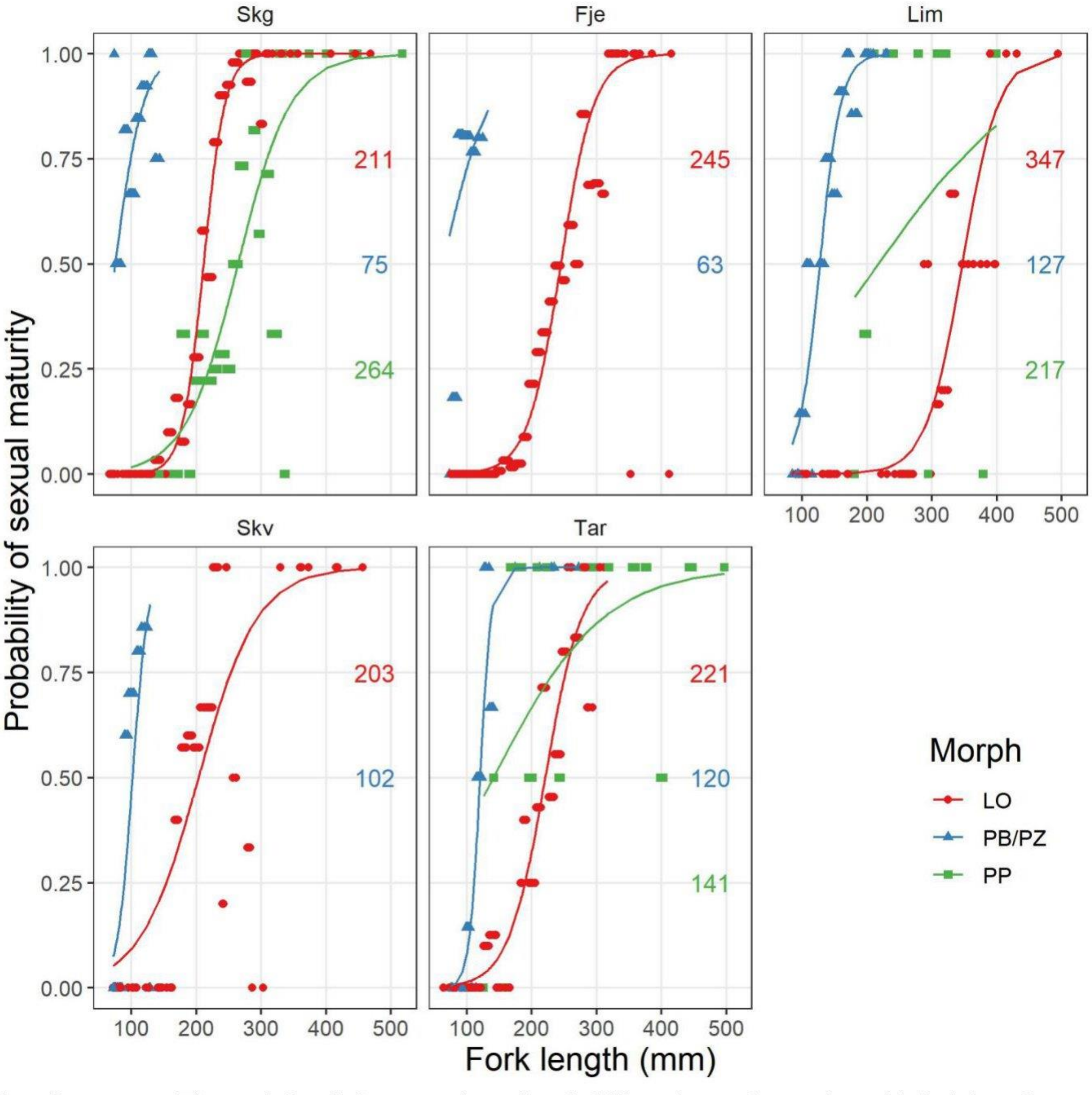
1 Supplementary Figures and Tables



Supplementary Figure 1. Logistic regression of probability of sexual maturity at age (years) of Arctic charr morphs from five Norwegian lakes. Abbreviations for lakes are as follow; Skg= Skogsfjordvatn, Fje=Fjellfrøsvatn, Lim=Limingen, Skv=Skøvatn, and Tar=Tårnvatn.

Supplementary Material

1 Supplementary Figures and Tables



Supplementary Figure 2. Logistic regression of probability of sexual maturity with fork length (mm) of Arctic charr morphs from five Norwegian lakes. Abbreviations for lakes are as follow; Skg= Skogsfjordvatn, Fje=Fjellfrøsvatn, Lim=Limingen, Skv=Skøvatn, and Tar=Tårnvatn.

Paper II

Extent of repeatability of life history and related functional traits in polymorphic Arctic charr

Extent of repeatability of life history and related functional traits in polymorphic Arctic charr

Authors

Grenier, G.[1], Knudsen, R.[1], Chavarie, L.[2]

[1] Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, Tromsø, Norway

[2] Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway

Keywords

Adaptive value, trait correlations, ecotype, intraspecific diversity, syndrome

Abstract

Across Arctic charr's circumpolar distribution, multiple examples of sympatric ecotypes with an array of functional diversity can be encountered. In Scandinavian lakes, sympatric Arctic charr ecotypes generally segregate along a depth gradient with each ecotype exploiting different niches; i.e., prey types within their preferred depth habitat. Whether each occurrence of polymorphic Arctic charr is a random event or if there is repeatability in the pattern of ecotype diversity and intraspecific trait coordination remains unknown. Here, we studied five oligotrophic subarctic Norwegian lakes with either bi-morphic or tri-morphic Arctic charr populations. All lakes contained a "Normal" ecotype and a "Dwarf" ecotype, while tri-morphic lakes had an additional "Piscivorous" ecotype. We examined 14 functional traits encompassing four trait spectra: diet, habitat use, morphology, and life history. We tested for the repeatability in mean traits by comparing trait distribution and with the application of linear modelling approaches. Repeatability in trait variation was tested by assessing the coefficient of variation or variance of each trait. We also tested the repeatability of each trait spectra as a multivariate entity with a trajectory analysis and using trait correlations. Finally, we used multivariate Bayesian modelling to explore the correlations among trait spectra of habitat use, diet, morphology, and life history to determine 1) if there is evidence of an adaptive trait syndrome (i.e., consistent individual differences in trait correlations) in polymorphic Arctic charr and 2) if the level of intraspecific diversity affects the syndrome's level. We found that morphology, diet, and life history traits were repeatable in all ecotypes and that trait variation in all trait spectra was not related to the number of ecotypes present in a lake. We determined that traits were correlated among trait spectra in all ecotypes and that correlations had greater importance in the maintenance of sympatric tri-morphic than bi-morphic ecotype assemblages. This study is among the first to find an adaptive trait syndrome in postglacial fishes and offers new avenues to study adaptive divergence in intraspecifically diverse organisms.

1 Introduction

Polymorphic species which show a high degree of variability among individuals (e.g., cichlids, sticklebacks, salmonids) have often been used to study how intraspecific variability relates to the specialization of ecotypes and speciation (Schluter 2000). Within the salmonids, the genus *Salvelinus*, commonly known as charrs, exhibits high variability in their morphology, diet, habitat use, and overall life history traits (Klemetsen et al. 2003a; Klemetsen 2013; Chavarie et al. 2021). Arctic charr, (*Salvelinus alpinus* L.), is used here as a model species to study how traits covary within a species. Notably, charrs occur in the northern hemisphere reaching the Arctic areas of the globe. Owing to the circumpolar environment's recent (<20,000 years) deglaciation the fishes' adaptations to the polar habitats are, from an evolutionary scope, of recent occurrence (Brunner et al. 2001). These fishes inhabiting postglacial lakes have proven to be important models in the research efforts allowing us to peer into the first stages of the processes of adaptation, evolution, and speciation (Klemetsen 2010; Knudsen et al. 2016b). Few studies, however, have focussed on examining the extent of repeatability in ecological and life history traits synergistically across multiple waterbodies in the Arctic charr distribution range.

Arctic charr, the world’s northernmost freshwater fish, shows extreme phenotypic diversity across its range (Klemetsen 2010). Within Scandinavian populations of Arctic charr, segregation of different ecotypes along a depth gradient and diet preferences have been repeatedly recorded (Klemetsen et al. 2002; Smalås et al. 2013; Moccetti et al. 2019). Arctic charr ecotypes are generally characterized by their mean trait values (e.g., life history parameters, morphology) that often correspond to an individual’s habitat and feeding (Sandlund et al. 1987; Adams et al. 1998; Smalås et al. 2013). From this, we gather that polymorphic Arctic charr may be occurring in a repeated manner especially when considering ecologically functional traits (Knudsen et al. 2016a; Saltykova et al. 2017; Jacobs et al. 2020).

Within the typical polymorphic Arctic charr populations found in Scandinavia, a littoral spawning omnivorous ecotype (hereafter Normal ecotype) commonly co-occurs with a profundal spawning benthic ecotype (hereafter Dwarf ecotype; Klemetsen et al. 1997; Grenier et al. 2021). The Dwarf ecotype is generally characterized by an early maturation at a small size and maintains a paedomorphic appearance relative to the Normal ecotype. Frequently, a third ecotype is also known to co-occur in the profundal zone of the lake, having a piscivorous diet and slower life history (i.e., slower growth, later age of maturation, and longer life span) relative to the normal ecotype (hereafter Piscivorous ecotype; Smalås et al. 2013). Higher intraspecific competition for food resources has regulating effects on food consumption and trophic niche breadth in Arctic charr (Amundsen et al. 2007; Prati et al. 2021). Ecotypes of polymorphic populations show stability in their discrete ecological niche utilization (Malmquist et al. 1992; Siwertsson et al. 2013; Rochat et al. 2022). Thus, specialized ecotypes may occur within a population as the level of intraspecific competition increases as a means to avoid niche overlap among individuals (Bolnick 2004; Woods et al. 2012).

Variation in a trait and its relationship to other traits can have adaptive value (Blasini et al. 2021), but in general, is seldom studied or discussed (Laughlin and Messier 2015). The introduction of the *r-K model of life history*, which classified organisms' fitness based on population growth rates (MacArthur and Wilson 1967), promoted ecologists to consider correlations among life history traits and how these correlations conferred adaptive value to organisms in an environment (Hutchings 2021). An extension of this model led to the *pace-of-life syndrome hypothesis* where metabolic rate and personality traits are correlated to trade-offs in life history (Stamps 2007; Réale et al. 2010). A syndrome in ecology can therefore be defined as consistent individual differences in trait correlations (Dobzhansky 1956; Ricklefs and Wikelski 2002; Réale et al. 2010). Multiple syndromes have now been proposed and identified in ecology (e.g., "*migratory syndrome*", "*behavioural syndrome*", and "*dispersal syndrome*"; Dingle 2006; Dingemanse et al. 2012; Raffard et al. 2022) with the adaptive trait syndrome postulating that the correlations which exist among a suite of traits have an adaptive value related to the specific environment (Rueda et al. 2018; Blasini et al. 2021). Although adaptive trait syndromes have been used to examine trait variability permissible of local adaptations in tree populations (Rueda et al. 2018; Blasini et al. 2021), this approach is not commonly applied in an adaptive sense to vertebrates. To fully understand how Arctic charr ecotypes specialize to their respective environment under the adaptive syndrome framework, it is crucial to examine both the variation within traits and the correlation among these traits. Furthermore, it is of interest to know if the variation in traits and correlations among traits differ with increasing level of intraspecific diversity (e.g., bi- vs. tri-morphic).

In this paper, we aim to determine the extent of repeatability in 14 functional traits from four trait spectra (habitat, diet, morphology, life history) of polymorphic Arctic charr populations across five Norwegian postglacial lakes. We predict that alike ecotypes will show repeatability in the mean trait value of measured functional traits among all lakes. We also hypothesize that the variation in mean trait values within an ecotype among lakes will be related to the level of intraspecific variability with ecotypes. This means that ecotypes among tri-morphic lakes will show less variation than ecotypes among bi-morphic lakes to avoid niche overlap. Similarly, when examining the repeatability of whole trait spectra (i.e., multivariate analysis of each of the four trait spectra), we predict that the trajectory between ecotype pairs from bi-morphic lakes will show larger angles of divergence and longer trajectories than tri-morphic lakes that must divide the trait space among more ecotypes (i.e., narrowed realized niche). We predict that traits within each trait spectra will show correlations and that these correlations will be stronger in tri-morphic than in bi-morphic systems. Finally, we hypothesize that correlations exist among traits of the four studied spectra and that these correlations will be influenced by the level of intraspecific diversity with ecotypes from tri-morphic lakes having stronger correlations related to the higher intraspecific competition.

2 Methods

2.1 Lake description

Five Norwegian lakes with coexisting Arctic charr (*Salvelinus alpinus*) ecotypes were selected for this study. Fjellfrøsvatn (the suffix ‘vatn means lake) and Skøvatn are both located in Troms and Finnmark County in Northern Norway and have two Arctic charr ecotypes present, the Normal and the Dwarf ecotypes. Fjellfrøsvatn (69°05'08"N, 19°20'04"E) is 88 m deep at its deepest point and has an area of 6.5 km^2. The lake has Arctic charr along with some brown trout (*Salmo trutta*) as the only other fish species inhabiting the lake. Skøvatn (69°01'50"N, 17°52'25''E) has an area of 6.2 km^2 and a maximum depth of 119 m. Arctic charr co-exist in this lake with Atlantic salmon (*S. salar*), brown trout and a small stock of anadromous Arctic charr.

Of the three tri-morphic lakes, Skogsfjordvatn and Tårnvatn are also located in Troms and Finnmark County, whereas Lake Limingen is found in central Norway in Trøndelag county. All tri-morphic lakes have a Normal, a Dwarf, and a Piscivorous Arctic charr ecotype. Skogsfjordvatn (69°55'48''N, 19°9'36''E) has an area of 13.6 km^2 and a depth of 100 m. Other fish species include brown trout, Atlantic salmon, three-spined stickleback (*Gasterosteus aculeatus*), European eel (*Anguilla anguilla*), and anadromous Arctic charr. Tårnvatn (69°18'43''N, 18°21'29''E) has a depth of 53 m and an area of 3.2 km^2 and brown trout is the only additional species to the Arctic charr. Lake Limingen (64°42'13''N, 13°32'40''E) is the largest lake of this study with a maximum depth of 192 m and an area of 95.7 km^2. In addition to Arctic charr, we find brown trout, three-spined stickleback, and minnow (*Phoxinus phoxinus*). This lake is regulated for the production of hydropower and has a maximum amplitude of 8.7 m annually (Sandlund et al. 2017). To compensate for the reduction in food resources available to the fish community related to the regulation of the waterbody, a small crustacean, *Mysis relicta*, was introduced to the lake in 1969 (Sandlund et al. 2017).

2.2 Measured traits

We measured 14 traits on the two or three ecotypes present in the five studied lakes. The traits were categorized according to the trait spectrum they best represented which included habitat use, diet, morphology, and life history. The habitat use trait spectra consisted of individual stable isotope-based littoral reliance as its only trait. Diet trait spectra included four traits: individual stable isotope-based trophic position, and the proportions of zooplankton, littoral benthos and profundal benthos prey in stomachs. For the morphology trait spectrum, we used the first and second principal components from an analysis of head shape, head linear measurements, and linear measurements of fins as traits. Finally, the life history trait spectra included three traits estimated from an otolith back calculation-based bi-phasic growth model: investment in growth, investment in reproduction, and age at maturity.

2.3 Sampling

The fish for the data in this study were collected between 1992 to 2016 (see Table S 1 for an overview of sample sizes). Fish material was collected with gillnets in all lakes, except Lake Limingen, where a trawl was used additionally to target the piscivorous ecotype (Sandlund et al. 2017). To strategically target Arctic charr ecotypes, standard gillnets with dimensions of 1.5 × 30 m and mesh sizes of 8, 10, and 12.5 mm were set on the bottom in profundal (>15 m depth) and littoral (<10 m depth) habitats. In addition, multimesh gillnets made up of eight (10, 12.5, 15, 18, 22, 26, 35, and 45 mm mesh) randomly organized 5 m panels for a net size of 1.5 × 40 m, and Nordic nets with 12 panels of 2.5 m (mesh from 5 to 55 mm) were used in the profundal, littoral, and pelagic (<15 m depth) habitats to collect different sizes of the population.

Fish processing consisted of measuring the fork length (mm) and wet weight (g). Sagittal otoliths were extracted and preserved in ethanol. A piece of muscle tissue was excised from the lateral side of the fish above the lateral line and posterior to the dorsal fin and immediately frozen for analyses of stable isotopes. The gonads were inspected for sex and maturity status (i.e., mature or immature). Individuals were considered mature if they were expected to spawn in the coming reproductive season or if they had already spawned if sampled after the reproductive season (Klemetsen et al. 1997; Smalås et al. 2013; Kjær 2018). Stomachs were dissected and stored in ethanol for analysis of stomach contents.

2.4 Back calculation and growth modelling

A sample of 5 otoliths from each age class for each ecotype in each lake was used as the otolith selection method to give more reliable estimates of growth curves (Chih 2009) giving a total of 832 analyzed otoliths (Table S 1). Otoliths were immersed in glycerol under a dark background and photographed whole under reflected light with a Leica S9i stereomicroscope at 40X magnification. Images were then measured in ImageJ (Schneider et al. 2012) using an ObjectJ plugin (Denechaud et al. 2020) constructed for otolith measurements, where images were calibrated to a 1 mm scale. Measurements of the otolith radius and the growth of the otolith within a one-year period were made following a transect extending from the nucleus to the outer ventral edge on the posterior end of the otolith (Godiksen et al. 2012). The distance from the nucleus to the edge of the hatch zone was also measured to estimate the length of the fish at hatching (Florø-Larsen et al. 2016) for use in the growth modelling.

The relationship between the otolith size (i.e., radius measurement) and the fish length at sampling varied among the ecotypes and with age. The back-calculation model to estimate fish length at previous ages incorporated an interaction term for ecotype and lake and an interaction term between age and fish length (Finstad 2003) as these will correct for any decoupling of growth with age. Fish length was estimated for each year of growth for each individual using the back-calculation model. The model resulted in negative length estimates in early ages (i.e., length at hatch, ages 1 and 2) for some individuals. To correct for these negative estimates, a weighted regression was used to increase the weight of younger samples (based on length at capture; Francis 1990) and ages with lower sample sizes. The weighted regression did not influence the estimates of older ages; however, it did increase the negative estimates of hatch size to a positive mean and resulted in positive mean estimates of length for fish of age 1 in each ecotype. As most of the fish were caught after the start of the growth season, the back calculated lengths will only represent growth until the start of the summer growth season which might result in slightly lower values than the length at capture data for individuals captured later in the summer. However, the slope of a regression model of the back calculated lengths at age did not differ from the slope for the length at capture and age ($t_{(6194)}=5.253$, $p<0.001$) therefore validating the back-calculated data. Model residuals were examined for heteroscedasticity and normality to test for model assumptions (Zuur et al. 2009).

The growth of each individual was modelled using a bi-phasic growth model (Boukal et al. 2014; Grenier et al. 2021) built with the nls function from the nlme package version 3.1-160 (Pinheiro et al. 2019) . Parameters (c, r, and age at maturity) were estimated using starting values informed from (Grenier et al. 2021) and were set to 1.43, 0.31, and 5.6 respectively. The mean of the estimated length at hatch from the back calculations was used to set the length at age zero (L_0, i.e., model intercept) for each ecotype in each lake.

2.5 Morphometric and linear measurements

Each fish was photographed on their left side in the field and sampled between the months of August to October to minimize the seasonal changes in head morphology resulting from secondary sexual characteristics. Both sexes and both juvenile and mature individuals were used to ensure a sufficient sample size (Table S 1). All pictures were imported to tpsUtil v.1.82 (Rohlf 2022) and their order was randomized therein. Each image was scaled in tpsDig 2.32 using the image edit tool to measure 1 cm on a ruler included in each photograph. A total of 30 landmarks (Figure 1) were digitized in tpsDig 2.32. To remove the effect of body size, scale, and positioning of the fish on the headshape, a Procrustes fit was performed on the landmarks using MorphoJ v 1.07a. This provided us with landmark coordinates to analyze head morphology. Measurements of linear traits from marked images were extracted with the geomorph package version 4.0.4 (Baken et al. 2021; Adams et al. 2022). All linear trait measurements were standardized with the standard length of the individual using the allometric growth formula (Reist 1985).

A principal component analysis (PCA) was performed in MorphoJ on the head shape landmark coordinates and PC1 and PC2 were retained for subsequent analyses (hereafter referred to HSPC1 and HSPC2). The head and fin linear measurements were also analyzed with a PCA performed with the package factoExtra (Kassambara and Mundt 2020). The first and second principal components were retained for the head linear measurements (hereafter HLPC1 and HLPC2) and for the fin linear measurements (hereafter FinPC1 and FinPC2) for subsequent analyses.

2.6 Littoral reliance and trophic position (stable isotopes)

Individual littoral reliance and trophic position were calculated using carbon and nitrogen stable isotopes from muscle tissue on a subsample of individuals (Table S 1). Littoral isotopic baselines were estimated for each lake from benthic macro-invertebrates (snails, amphipods, and chironomid larvae) collected from the littoral zone from each lake. Zooplankton collected from each lake was used for the pelagic baseline. No baseline samples were available for Lake Limingen, therefore the mean littoral and pelagic samples from all lakes combined was used as baseline in the calculation of mean littoral reliance. This was considered a suitable approach as estimates of trophic position are more sensitive to the trophic discrimination factors than baseline samples (Post 2002). Trophic discrimination factors used were 0.4±1.3‰ for $\delta^{13}C$ and 3.4±1.0‰ for $\delta^{15}N$ (Eloranta et al. 2015).

2.7 Stomach contents

Stomachs were assessed a degree of fullness (0 to 100%). The prey contained in the stomachs was then categorized as belonging to the broader categories of zooplankton, pleuston, littoral benthos, profundal benthos, fish, or eggs. The relative contribution of each prey category to the stomach’s degree of fullness was estimated providing a proportional contribution of each prey type to an individual diet (Amundsen 1994; Moccetti et al. 2019).

2.8 Statistical analyses

2.8.1 Repeatability in traits

All traits were assessed for differences in the mean trait value distribution with a combined Anderson-Darling k-Samples test using the ad.test function of the kSamples package (Scholz and Zhu 2019). This test informs us if the distribution of the measured trait in sympatric ecotype pairs are different within each lake and if the sympatric ecotype pairs express different trait distributions across all lakes. We also assessed the distribution of traits within the Normal and the Dwarf ecotypes with the Anderson-Darling k-samples test to determine if the mean trait value was different in alike ecotypes from bi-morphic and tri-morphic lakes. The proportion of zooplankton, littoral benthos, and profundal benthos was zero-inflated in the Piscivorous ecotype, therefore a non-parametric nested rank Mann-Whitney-Wilcoxon test was used to test for differences between these ecotypes with the nestedRanksTest function from the package nestedRanksTest (Scofield n.d.; Thompson et al. 2014).

We tested if the coefficient of variation (CV) of each trait differed in alike ecotypes from all lakes using a modified signed-likelihood ratio test with the mslr_test function from the package cvequality (Marwick and Krishnamoorthy 2019). If the coefficient of variation of alike ecotypes differed among lakes, we assessed if the level of intraspecific diversity influenced the variation by comparing the CV of the bi-morphic and tri-morphic lakes. If the bi-morphic lakes had different (lower or higher) CV relative to the tri-morphic lakes, then it would suggest an effect of intraspecific diversity level (i.e., bi- vs. tri-morphic population) on trait variation. Because means of PC1 and PC2 for head shape, head linear measurements, and fin linear measurements were close to zero, a Brown-Forsythe test was carried out on the variance using the function bf.test from the package onewaytests (Dag et al. 2023). In the case of a significant difference, we assessed for an effect of intraspecific diversity level as with the CV.

To further assess the repeatability of traits, a linear model was built with each individual trait as the response variable. The fixed effects included in the model were 'ecotype' to test for repeatability, the interaction between 'lake' and 'ecotype' to examine non-repeatability in the traits, and 'lake' to test for any unique components specific to each lake (Jacobs et al. 2020). From the linear models, we calculated the effect size of repeatable effects (ecotype) and non-repeatable effects (ecotype*lake) by calculating the partial eta squared (η^2, Wilk's partial eta) using the eta_squared function from the rstatix package (Kassambara 2023). Lower values of η^2 signify a small effect size, while larger values imply a large effect size and can be visualized by plotting each trait's repeatable by non-repeatable effects. Traits that fall above the 1:1 line have greater repeatability than non-repeatability. We then calculated the distance between partial eta squared and the 1:1 line to visually represent the extent of repeatability or non-repeatability within each trait spectra (Bolnick et al. 2018). Here positive values denote repeatability and negative values represent non-repeatability. As non-repeatability within a trait may come from differences in magnitude or direction of differentiation or both, a trajectory analysis approach was taken to better understand each trait spectra (see below for more details).

2.8.2 Repeatability in trajectories

A trajectory analysis was performed for each trait spectra between ecotype pairs in each lake using the trajectory.analysis function from the RRPP package (Collyer and Adams 2018, 2019) to examine the repeatability of three studied trait spectra. The trajectory analysis for each trait spectrum assesses the distance and angle of divergence between the centroids for ecotype pairs after an orthogonal projection of the combined traits from each trait spectrum (Elmer et al. 2014). We used 1,000 permutations (Jacobs et al. 2020) to assess the significance in magnitude (length) of differentiation and direction of differentiation (angle) in pairwise comparison of alike ecotypes pairs. Comparisons with values non-significantly different from zero were considered repeatable in either magnitude, direction, or both.

2.8.3 Correlations among traits

Multiresponse linear mixed models were used to test for trait correlations among trait spectra 1) across alike ecotypes, and 2) at differing levels of intraspecific diversity. A simulated dataset was built as the trait spectra for an ecotype were not always sampled from the same individuals. Lake Tårnvatn was excluded from the simulated dataset as the sample size for the Piscivorous ecotype was too low to use the simulation technique. For each ecotype in each lake, a simulated dataset was built from the existing data which had the same trait distribution and correlations using the function sim_df from the package faux (DeBruine et al. 2023). Traits included in the multiresponse linear mixed models were the littoral reliance for the habitat use, trophic position for the diet trait spectra, the first two principal component axes of head shape, head linear measurements, and fin measurements for morphology, and all three parameters of life history (c, r, age of investment in reproduction) from the bi-phasic modelling as response variables. All response variables were centred and scaled by their standard deviations in the model. As each sampled individual provides only one measure for each trait, we treated the ecotype as individual in the model and each sample within a lake as a repeated measure of its respective ecotype.

We calculated the correlations between traits for all of these models with the use of the model's variance-covariance matrices (Equation 1; Dingemanse and Dochtermann 2013; Horta-lacueva et al. 2021).

Equation 1

$$r_{T_xT_y} = \frac{COV_{T_xT_y}}{\sqrt{V_{T_xT_y}}}$$

Multivariate models were built under the Bayesian framework using the MCMCglmm function in the MCMCglmm package (Hadfield 2010). Weakly informative priors were specified for each model (Table S 2). The number of iterations for each model was set to 19,500,000 with a thinning interval of 15,000 and a burnin of 4,500,000 iterations. These parameters were selected as model convergence was suggested from examinations of trace plots, posterior density plots, and effective sample size. The significance of trait correlations was assessed using 95% credible intervals (Wilson et al. 2010).

3 Results

3.1 Habitat

The three ecotypes showed different reliance on the littoral environment through all pairwise comparisons (Normal-Dwarf AD = 41.90, p<0.01; Dwarf-Piscivorous AD = 45.18, p<0.01; Normal-Piscivorous AD = 74.75, p<0.01; Figure 2). The coefficient of variation for the littoral reliance did not differ among lakes for the Piscivorous ecotype (MSLR = 4.72, p = 0.09, Table S 3). The coefficient of variation for the littoral reliance varied among lakes for the Normal and the Dwarf ecotypes but changes were unrelated to the number of ecotypes (Normal MSLR = 43.69, p<0.01; Dwarf MSLR = 85.48, p<0.01; Table S 3). The linear modelling of littoral reliance had a higher effect size of repeatability than non-repeatability with lakes pooled (η_M^2 = 0.70, $\eta_{M\times L}^2$ = 0.11; Figure 3). The repeatable effect was higher in bi-morphic than in tri-morphic lakes (bi: η_M^2 = 0.25, $\eta_{M\times L}^2$ <0.01; tri: η_M^2 = 0.11, $\eta_{M\times L}^2$= 0.06; Figure 3).

3.2 Diet

Ecotypes differed in mean trophic position (Normal-Dwarf AD = 141.50, p<0.01; Dwarf-Piscivorous AD = 42.61, p<0.01; Normal-Piscivorous AD = 135.30, p<0.01; Figure 2). Only the Dwarfs had a divergence in the coefficient of variation for trophic position among lakes (Normal MSLR = 5.85, p = 0.21; Dwarf MSLR = 59.37, p<0.01; Piscivorous MSLR = 3.00, p = 0.22; Table S 3), where the Skøvatn Dwarf had the highest amount of variation relative to the Dwarf ecotype from the other lakes (Table S 3).

Normal and Dwarf ecotypes had different diets with divergent distributions for the proportion of littoral and profundal benthos and zooplankton preys (littoral benthos AD = 40.33, p<0.01; profundal benthos AD = 192.80, p<0.01; zooplankton AD = 114.10, p<0.01; Figure 2). The Normal ecotype had a diet that was mainly composed of zooplankton and littoral benthos items (Figure S 1). Profundal benthos was the preferred prey of most Dwarfs; however, individuals in Skøvatn relied heavily on zooplankton (Figure S 1). The Piscivorous ecotype had a diet mainly consisting of profundal benthos and fish preys (Figure S 1). Within alike ecotypes, one prey source did not vary in its proportional contribution to the diet (Table S 3). All Normal ecotypes showed the same amount of variance in the proportion of consumed littoral benthos (MSLR = 11.20, p = 0.02). All Dwarfs were consistent in their proportional consumption of profundal benthos (MSLR = 50.42, p<0.01). All Piscivorous ecotypes had a common coefficient of variation for a low proportion of zooplankton in their diets (MSLR = 0.39, p = 0.82).

The traits measured for diet displayed high repeatability as the effect size of the repeatable term for ecotype was typically stronger relative to the term including the interaction with the lake representing non-repeatability within linear models (Figure 3). Trophic position and the proportion of profundal benthos were highly repeatable at all the examined levels (Table S 4). With all lakes pooled, the measured diet metrics were more influenced by the repeatable ecotype effect than the non-repeatable interaction (Table S 4). The effect of ecotype, and therefore repeatability, was generally stronger in tri-morphic lakes (Figure 3) than in bi-morphic lakes, suggesting that dietary niche is a strong element of repeatability as intraspecific diversity increases.

Examination of diet in trajectory analyses revealed both repeatable and non-repeatable components in the diet. The Normal and Dwarf ecotypes in Fjellfrøsvatn, Limingen, and Tårnvatn were indistinguishable in both direction and magnitude of differentiation (Figure 4). In Skøvatn, the trajectories of the Normal and Dwarf ecotypes were the shortest and had the largest difference in direction with the other lakes. The Skøvatn Dwarf's differences in trajectories indicated different trophic niche use compared to all the other Dwarf ecotypes studied (Figure 4; Table S 5). Comparisons of the trajectory for the Normal and Piscivorous ecotypes revealed some patterns of repeatability in both direction and magnitude with two out of the three pairwise comparisons not showing differences (Figure 4; Table S 5). The Dwarf and Piscivorous ecotypes showed more repeatability in their angle of divergence than in magnitude, where Skogsfjordvatn had the longest trajectory Figure 4; Table S 5).

3.3 Morphology

Principal component 1 accounted for 27.28% of the variation in head shape and PC2 incorporated 13.79% of the variation (hereafter HSPC1 and HSPC2, respectively; Figure S 2). HSPC1 discriminated individuals with a narrower head and larger eyes (i.e., Dwarf ecotype) from those with a deeper, more rounded head and smaller eyes clustered (i.e., Normal ecotype). HSPC2 separated individuals with longer heads and longer upper maxilla (i.e., Piscivorous ecotype) from the ones with shorter heads and shorter upper maxilla (i.e., Dwarf and Normal ecotypes). The first principal component of head linear measurements accounted for 72.07% of the variation and PC2 accounted for 20.71% of the variance (hereafter HLPC1 and HLPC2;

Figure S 3). HLPC1 separated Dwarf and Normal ecotypes based on eye width, whereas HLPC2 discriminated among individuals with a longer snout and longer upper maxilla (i.e., Piscivorous ecotype) from individuals with a shorter snout and shorter upper maxilla (i.e., Normal and Dwarf ecotypes). Principal components 1 and 2 of linear measurements of fins accounted for 46.20% and 13.98% of the variation in fin lengths (hereafter FinPC1 and FinPC2, respectively; Figure S 4). FinPC1 discriminated ecotypes based on shorter fins for the Normal and Piscivorous ecotypes relative to the Dwarf ecotype on the other hand, FinPC2 discriminated ecotypes based on longer caudal fins for the Dwarf ecotype versus the Normal and Piscivorous ecotypes.

Ecotypes showed morphological differences in head shape across all lakes (HSPC1: Normal-Dwarf AD = 85.18, $p<0.01$; Dwarf-Piscivorous AD = 18.39, $p<0.01$; Normal-Piscivorous AD = 15.36, $p<0.01$; Figure 2). However, the distribution of HSPC2 did not differ between the Normal and Dwarf ecotypes across lakes (Normal-Dwarf AD = 6.84, $p = 0.13$) but differed for the Normal-Piscivorous and Dwarf-Piscivorous ecotypes (Skogsfjordvatn and Limingen only; Dwarf-Piscivorous AD = 5.57, $p = 0.01$; Normal-Piscivorous AD = 10.85, $p<0.01$). Normal ecotypes from bi-morphic and tri-morphic lakes had the same distribution in head shape for both HSPC1 (Bi-Tri AD = 1.02, $p = 0.35$) and HSPC2 (Bi-Tri AD = 1.09, $p = 0.31$), while an effect of the level of intraspecific diversity was found for the Dwarf on the mean trait expression of HSPC1 (Bi-Tri AD = 20.99, $p<0.01$) but not in HSPC2 (Bi-Tri AD = 0.81, $p = 0.48$; Figure 2, Figure S 2). The Dwarf ecotype was the only ecotype with different variance in HSPC1 among the lakes (B-F = 21.68, $p<0.01$) but it was unrelated to the number of ecotypes (Table S 3). The variance in HSPC2 differed among lakes for the Dwarf (B-F = 6.51, $p<0.01$) and the Normal (B-F = 12.91, $p<0.01$) ecotypes but patterns were unrelated to the number of ecotypes

(Table S 3). The Piscivorous ecotype had a similar variance in HSPC2 across lakes (B-F = 2.98, p = 0.09).

All sympatric ecotypes differed in linear head measurements in HLPC1 (Normal-Dwarf AD = 94.35, p<0.01; Dwarf-Piscivorous AD = 22.10, p<0.01; Normal-Piscivorous AD = 23.46, p<0.01) and HLPC2 (Normal-Dwarf AD = 18.64, p<0.01; Dwarf-Piscivorous AD = 26.10, p<0.01; Normal-Piscivorous AD = 20.14, p<0.01; Figure 2, Figure S 3). The variance of HLPC1 and HLPC2 differed among lakes for the Normal (HLPC1 B-F = 5.08, p<0.01; HLPC2 B-F = 16.54, p<0.01) and the Dwarf (HLPC1 B-F = 33.46, p<0.01; HLPC2 B-F = 12.05, p<0.01) ecotypes but patterns were unrelated to the level of intraspecific diversity. Piscivorous ecotypes had the same variance in the first and second principal components of head linear measurements across all lakes (HLPC1 B-F = 2.83, p = 0.13; HLPC2 B-F = 0.53, p = 0.62).

Dwarf ecotypes fin linear measurements differed from the other ecotypes along FinPC1 (Dwarf-Normal AD = 54.53, p<0.01; Dwarf-Piscivorous AD = 18.42, p<0.01) and FinPC2 (Dwarf-Normal AD = 20.65, p<0.01; Dwarf-Piscivorous AD = 5.11, p = 0.01). The Normal and Piscivorous ecotypes did not differ in fin linear measurements (FinPC1: Normal-Piscivorous AD = 3.06, p = 0.14; FinPC2: Normal-Piscivorous AD = 2.25, p = 0.31). The Normal ecotype had a lower variance in FinPC1 in bi-morphic lakes than in tri-morphic lakes (B-F = 11.45, p<0.01; Table S 3). Piscivorous ecotypes showed different variances in FinPC1 among lakes (B-F = 4.60, p = 0.02), while Dwarf (B-F = 1.78, p = 0.14) ecotypes had similar variances in FinPC1 across all lakes. The variance along FinPC2 differed among lakes for the Normal (B-F = 9.82, p<0.01) and Dwarf ecotypes (B-F = 19.24, p<0.01) but there were no effects from the level of intraspecific diversity. The Piscivorous ecotype did not have different variances in FinPC2 among lakes (B-F = 2.059, p = 0.196).

There are stronger patterns of repeatability than no- repeatability in all the morphological traits when examining all lakes pooled (Figure 3, Table S 6). In bi- and tri-morphic lakes, all first principal components had higher effects of repeatability than non-repeatability. However, the stronger effects of repeatability found in bi-morphic lakes than in tri-morphic lakes suggests that some aspects of morphology are more repeatable among two-ecotype assemblages (Figure 3, Table S 6).

The multivariate trajectory analysis of morphology determined that the Normal and Dwarf ecotypes had angles of divergence that did not differ in four out of seven pairwise lake comparisons ($\theta<11°$, Figure 5, Table S 7). Bi-morphic lakes had the longest trajectories of morphological divergence between the Dwarf and the Normal ecotypes. Additionally, the Normal and Dwarf trajectory in bi-morphic lakes had the largest angle of divergence between them ($\theta = 18.94°$, Figure 5, Table S 7) than with all other lakes. However, the angle of divergence between Skøvatn and Tårnvatn Normal and Dwarf ecotype trajectory was also large ($\theta = 18.13°$, Figure 5, Table S 7). The trajectory lengths did not differ among lakes for the Dwarf - Piscivorous ecotypes nor for the Normal - Piscivorous ecotypes (Table S 7). The direction of differentiation was similar for the Dwarf - Piscivorous ecotypes in two of the three lake comparisons but only for one of three comparisons of the trajectory between the Normal - Piscivorous ecotypes (Figure 5).

3.4 Growth modelling

The Normal ecotype had the highest investment in somatic growth in all lakes (Normal-Dwarf AD = 36.42, $p<0.01$; Normal-Piscivorous AD = 20.69, $p<0.01$; Figure 2) but had different coefficients of variance among lakes, but the trend was unrelated to the number of ecotypes (MSLR = 11.62, $p=0.02$; Table S 3). Dwarf and Piscivorous ecotypes had a similar investment in somatic growth (AD = 4.78, $p = 0.09$; Figure 2), which did not show variance among lakes

(Dwarf MSLR = 6.35, p = 0.17; Piscivorous MSLR = 1.52, p = 0.47). The investment in reproduction differed among all ecotype pairs (Normal-Dwarf AD = 22.59, p<0.01; Dwarf-Piscivorous AD = 10.97, p<0.01; Normal-Piscivorous AD = 11.43, p<0.01; Figure 2), with the Dwarf ecotype having higher investment than the Normal and the Piscivorous ecotypes in all lakes (Figure 2). The age at which individuals begin investing in reproduction was different between the Normal and Dwarf ecotypes (AD = 11.27, p<0.01) and the trend was unrelated to the number of sympatric ecotypes (Figure 2). The Piscivorous ecotype started to invest in reproduction at the same age as the Dwarf ecotype (AD = 2.13, p = 0.72; Figure 2) but at a later age than the Normal ecotype (AD = 11.93, p<0.01). The coefficient of variation in the age where ecotypes begin investing in reproduction remained consistent across lakes (MSLR = 2.13-4.24, p>0.13).

The parameters for investment in growth and reproduction in the life history trait spectrum showed that they are repeatable within ecotypes at all studied levels (Figure 3, Table S 8). The effect size of the ecotype term for the investment in both reproduction and growth was stronger in bi-morphic lakes than in tri-morphic lakes (Table S 9). The age at which individuals begin investing in reproduction demonstrated weak non-repeatable effects, which were slightly stronger than the repeatable term in pooled and bi-morphic lakes (Table S 9). However, in the tri-morphic lakes, the weak repeatable effect of the ecotype term for the age of maturity was slightly stronger than the non-repeatable term (Table S 9).

The direction of differentiation in the trajectory analysis of life history trait was repeatable in all ecotype pairs within all lakes, except for the Normal-Dwarf trajectory in Skøvatn vs. Fjellfrøsvatn (θ = 88.44°) and Skøvatn vs. Limingen (θ = 88.75°; Figure 6, Table S 10). Similar trajectory lengths were found with all Normal-Piscivorous and Dwarf-Piscivorous ecotype pairs demonstrating repeatability in the extent of divergence (Figure 6, Table S 10). In the magnitude of Normal-Dwarf trajectories, the bi-morphic lakes (Fjellfrøsvatn and Skøvatn) have the longest trajectories of all lakes (Figure 6, Table S 10).

3.5 Adaptive trait syndrome

Ecotypes had differences in the number and direction of correlations among measured traits of diet, habitat use, morphology, and life history (Table 11, Figure 7). For the Normal ecotype across all lakes, the littoral reliance was positively correlated to all morphological traits, while trophic position correlated only with FinPC2. The parameter for the investment in growth correlated positively with the trophic position and FinPC2 in the Normal ecotype. Negative correlations for the Normal ecotype were found between the investment in reproduction and HSPC2 and between the age of maturity and HLPC2 and FinPC2. For the Dwarf ecotype, the littoral reliance correlated positively with all measures of morphology except the second principal components of head shape (HSPC2) and fin linear measurements (FinPC2). The investment in reproduction for the Dwarf ecotype was negatively correlated with head shape traits (HSPC1, HS2PC, HLPC1). The Piscivorous ecotype had a positive correlation between littoral reliance and trophic position. Littoral reliance and trophic position were positively correlated with FinPC2 in the Piscivorous ecotype. The first principal component of linear head measurement (HLPC1) was negatively correlated with trophic position and littoral reliance and the second principal component of linear head measurement (HSPC2) was negatively correlated with trophic position.

The Normal ecotype showed both similarities and differences in the correlations among traits of diet, habitat use, morphology, and life history in bi-morphic and tri-morphic lakes (Table 2, Figure 7). In both systems, the Normal ecotype showed positive correlations between littoral reliance and morphological traits except for FinPC2 which negatively correlated in the tri-morphic systems with littoral reliance. In bi-morphic lakes, the Normal ecotype’s littoral reliance and trophic position had positive correlations with growth and negative correlations with the age of investment in reproduction. Traits of morphology, except HLPC1, for the Normal ecotype in bi-morphic lakes correlated positively with growth but were negatively correlated with the age of investment in reproduction. In tri-morphic lakes, the littoral reliance of the Normal ecotype was negatively correlated with growth and investment in reproduction. Trophic position had positive correlations with growth and investment in reproduction. The growth and investment in reproduction for the Normal ecotype of tri-morphic systems were negatively correlated with morphological traits except FinPC2.

The Dwarf ecotype had different correlations among trait spectra depending on the number of sympatric ecotypes within the lake (Table 2, Figure 7). Dwarfs from bi-morphic lakes showed positive correlations of littoral reliance with morphology (HLPC1, FinPC2) and trophic position. The trophic position of bi-morphic Dwarfs was positively correlated with traits of morphology (HLPC1, FinPC2). No correlations existed with parameters of life history in bi-morphic Dwarfs. In tri-morphic lakes, the Dwarf's littoral reliance correlated negatively with the trophic position. The trophic position of tri-morphic Dwarfs was also negatively correlated with all traits of morphology except for FinPC2. The parameter for growth of tri-morphic Dwarfs was negatively correlated with head morphology (HSPC1, HSPC2, HLPC1, HLPC2) but positively correlated with FinPC2. The investment in reproduction in Dwarfs from tri-morphic systems was negatively correlated with head morphology (HSPC1, HSPC2, HLPC1) and was positively correlated with linear measurements of fin (FinPC1, FinPC2).

4 Discussion

Our results demonstrated some evidence for an adaptive trait syndrome in Arctic charr ecotypes based on the repeatability and correlations among habitat use, traits of diet and morphology, and parameters of life history. Different levels of an adaptive trait syndrome were found among ecotypes and might be related to adaptive values for each ecotype in relation to the environment in which they develop (Rueda et al. 2018; Blasini et al. 2021). The different levels of the adaptive trait syndrome observed in relation to the number of cooccurring ecotypes suggest that intraspecific trait variations and the level of diversity are related in postglacial fishes. This is supported by recent findings from other salmonid model systems (Blain et al., in press). Patterns in trait correlations were seen in the adaptive trait syndrome of the Normal and Dwarf ecotypes related to the number of ecotypes present in the lake. There was a clear importance of correlations with life history traits in tri-morphic lakes but less in bi-morphic lakes, especially for the Dwarf ecotype. While the links between morphology and trophic niche in Arctic charr have been extensively discussed (e.g., Snorrason et al. 1994; Adams et al. 1998; Knudsen et al. 2007), our results highlight the novel aspects of the adaptive value of the relationships among morphology and ecological niche through traits of life history.

Our prediction of repeatability in mean trait values for the studied trait spectra among alike ecotypes was supported especially when comparing within lakes of the same level of intraspecific diversity (i.e., bi- or tri-morphic lakes; Figure 7). This can be explained through the common niche of alike ecotypes across lakes. Organisms, including fishes, diverging along similar gradients of habitat tend to show similar adaptations to these environments through the convergence of phenotypes (Yoder et al. 2010; McGlothlin et al. 2018; Blain et al. in press). We did not find evidence for reduced trait variation related to an increase in intraspecific diversity as hypothesized. This corroborates other findings where under higher competition, Arctic charr from a monomorphic population may increase their niche width (Prati et al. 2021).

The prominent correlations among the traits of morphology and littoral reliance in the Normal ecotype confirm that morphological adaptations to the habitat are important in the specialization of this ecotype (Kristjánsson et al. 2011; Skoglund et al. 2015; Recknagel et al. 2017). The similarity in the average littoral reliance of the Normal ecotype across all lakes can be explained by the presence of a strong competitor of Arctic charr for the resources in the littoral environment (Forseth et al. 2003; Hammar 2014; Sandlund et al. 2016), brown trout in all the studied lakes. There were indications that the age at which the Normal ecotype begins investing in reproduction may be negatively influenced by the morphological adaptations required for their specialization to the habitat. This may be related to the different morphological and developmental pathways of the ecotypes (Skúlason et al. 1996). Growth rate in fishes can influence morphology (Franklin et al. 2018; Horta-Lacueva et al. 2021). At high growth rates, there is potential for high morphological plasticity related to the available surplus energy, while at lower growth rates all the energy is diverted to basic metabolic needs and reproduction, therefore not leaving energy for plasticity through morphological changes (Olsson et al. 2006).

Morphological adaptations in the Dwarf ecotype come with the trade-off of lowered investment in reproduction. The small size of the Dwarf has been found to be related to lower fecundity and/or egg size and other related traits of reproductive success relative to other ecotypes (Klemetsen et al. 2002; Smalås et al. 2017; Beck et al. 2022). Although the Dwarf morphology was related to constraints on its reproduction, it was positively correlated with the littoral reliance implying trade-offs among morphology, life history, and adaptations to the habitat in the Dwarf ecotype. Links among habitat, life history and morphology have been inferred (Klemetsen et al. 1997; Smalås et al. 2017), but here we provide novel evidence on how these traits covary within the Dwarf ecotype. The correlations among littoral reliance and morphology in the Dwarf ecotype were fewer relative to the Normal ecotype, thus the major influences shaping the adaptive trait syndrome in Arctic charr differ between the ecotypes as is common when examining trait syndromes within species (Agrawal 2020). While habitat seemed to be the main driver in the Normal ecotype's adaptive trait syndrome, life history seemed to be the stronger element in the differentiation of the Dwarf ecotype.

Naturally, feeding on fish implies feeding at a higher trophic level in subarctic lakes (Eloranta et al. 2015), shaping the adaptive landscape of the Piscivorous ecotype. Trophic position associated with morphological traits is an important factor for the shift towards piscivory starting at lengths > 20 - 25 cm in Arctic charr (Jonsson and Jonsson 2001). Specific morphological adaptations such as a large mouth and teeth are associated with piscivore specialization (Adams et al. 1998; Skoglund et al. 2015). Interestingly, no parameters of life history were correlated with other measured traits. It has been suggested that the shift to feeding on fish would lead to an important trade-off, for instance between fecundity and egg size (Smalås et al. 2013, 2017). The results provided in this work suggest that there were no consistent trade-offs between the morphology, ecology, and life history in the Piscivorous ecotype at the among population level. However, these trade-offs may be highly population specific (Raffard et al. 2019a) and our examination at the among population level would not reveal the same adaptive trait syndrome at the within population level (Laughlin and Messier 2015; Agrawal 2020).

In this study, repeatability and correlations among traits were influenced by the number of ecotypes present within lakes, supporting our hypothesis for an effect of the level of intraspecific diversity on adaptive traits (see also Blain et al., in press). In bi-morphic lakes, the Normal and the Dwarf ecotypes demonstrated that correlations in morphology with their ecology (i.e., habitat and diet) were important in the maintenance of their separation (Power et al. 2005, 2009; Amundsen et al. 2008). We saw the highest repeatable effects in aspects of head morphology (shape and linear measurements) in bi-morphic lakes compared to any other morphological trait at all the studied levels. The pairwise comparison of ecotype trajectories of morphological divergence showed the largest magnitude in the Normal – Dwarf trajectory of bi-morphic lakes therefore suggesting that they have the largest differences in ecological niche. Discrete feeding niches and ecology are known to be important in the divergence of Arctic charr ecotypes (Hindar and Jonsson 1982; Malmquist et al. 1992; Jacobs et al. 2020).

The adaptations specific to the Normal ecotype of bi-morphic lakes displayed multiple correlations with parameters of life history. In the bi-morphic Normal ecotype, all trait spectra were related to an increase in the energy invested in somatic growth with a trade-off in delaying the age where individuals invest in reproductive tissues. The trade-off between growth and reproduction is central in life history theory (Hutchings 2021) and this trade-off is known to be especially important in fish, as female fecundity relates to size (Wootton and Smith 2014; Smalås et al. 2017; Takatsu et al. 2023). Our results demonstrated that the Normal ecotype in bi-morphic lakes adopted a strategy prioritizing investment in attaining a larger size for reproduction. Related to female size and fecundity, it was a surprising result that the Dwarf ecotype in bi-morphic lakes showed no correlations with traits of the life history trait spectra. In the description of the Dwarf ecotype of bi-morphic lakes across the literature, we found many references to its small size, lower growth, and early maturation (Jonsson and Jonsson 2001; Klemetsen et al. 2003a; Smalås et al. 2013) suggesting that we might have found correlations between life history and other examined traits. The constraints that exist for minimum requirements for egg size and quality for successful reproduction (Jonsson and Jonsson 2001; Klemetsen et al. 2003b) might be stronger drivers of life history than the correlations among the other studied traits for the bi-morphic Dwarf. Although we have not examined features of fecundity, others have reported that trade-offs in fecundity (e.g., egg size, number) are important aspects of reproduction in the Dwarf ecotype (Smalås et al. 2017) and potentially related to the expressed phenotype in Arctic charr (Beck et al. 2022). Surprisingly, the Dwarf ecotype had no correlations with the age at maturity as female age may influence the trade-offs related to fecundity (Lasne et al. 2018). A syndrome including correlations with traits of life history may therefore become evident when studying the bi-morphic Dwarf ecotype at a within population scale as the syndrome can vary across populations (Raffard et al. 2019a).

When examining the correlations among studied traits at a higher level of intraspecific diversity we once again see that habitat is critical in the adaptive trait syndrome of the Normal ecotype. Stability in the habitat preferences of the Normal ecotype for the pelagic habitat from a tri-morphic Arctic charr population has been demonstrated in laboratory experiments (Mikheev et al. 1996). The repeated correlations among traits in the Normal ecotype across studied levels implied that there was high stability in the ecology of the Normal ecotype as reported previously in tri-morphic populations (Siwertsson et al. 2016; Rochat et al. 2022). The Normal ecotype in tri-morphic lakes showed the most correlations among parameters of life history traits out of all the studied levels of intraspecific diversity, providing support for our prediction that adaptive trait syndromes would be stronger at the tri-morphic level of intraspecific diversity. In contrast to the Normal ecotype of bi-morphic lakes, the correlations among morphology and growth in the tri-morphic Normal ecotype were negative. The Normal ecotype can feed on fish (Amundsen 2016), but when occurring with a Piscivorous ecotype, fish as prey in the Normal ecotypes' diet is of low occurrence (Malmquist et al. 1992; Adams et al. 1998; Moccetti et al. 2019). With the presence of the Piscivorous ecotype, the adaptations required in the Normal ecotype to avoid niche overlap with a third ecotype come at a cost of reducing the energy available for growth similar to what has been reported for the influence of intraspecific diversity in monomorphic charr populations (Amundsen et al. 2007). In the studied populations, the juveniles of the Piscivorous ecotype are resource competitors of the Dwarf ecotype in the profundal habitat (Knudsen et al. 2019), therefore also influencing the niche of the Dwarf ecotype in tri-morphic populations. The change of energy invested in reproduction in tri-morphic lakes vs. bi-morphic for both Normal and Dwarf ecotypes when a third ecotype was maintained implies that a change of realized niches from intraspecific competition had similar cascading effects.

The extent to which genetic vs. phenotypic plasticity influences are involved in the observed trait repeatability and correlations in Arctic charr is debatable and may depend on the populations in question. Many studies of several groups of polymorphic species (e.g., fish, reptiles, birds; Bell and Aguirre 2013; McGlothlin et al. 2018; Gómez-Bahamón et al. 2020) have shown that both genetics and phenotypic plasticity may be involved in radiations (reviewed in: Pfennig et al. 2010; Levis and Pfennig 2016; Jamie and Meier 2020). Arctic charr is described as a highly phenotypically plastic species (Klemetsen 2010; Eloranta et al. 2011; Kristjánsson et al. 2018), however with specialized ecotypes, such as described in this manuscript. Typically sympatric Arctic charr ecotypes are to some extent reproductively isolated (Gordeeva et al. 2015; May-McNally et al. 2015; Guðbrandsson et al. 2019), and this is the case for the present lakes (Præbel et al. 2016; Simonsen et al. 2017; Moccetti et al. 2019). Relatively few experimental studies examining the extent of plastic vs. genetic components of the phenotypic variability in Arctic charr ecotypes exist (but see Adams 1999; Garduño-Paz and Adams 2010; Kristjánsson et al. 2018). For the lakes included in this study, there are indications that morphology and behaviour, especially related to food acquisition, and growth are to some extent under genetic control (Klemetsen et al. 2002, 2006; Knudsen et al. 2015). However, little knowledge is available for the present studied populations to allow for disentangling the influence of genetics and phenotypic plasticity in the phenotypes of the ecotypes. It is likely that both genetic and phenotypic plasticity play a role in the traits and syndrome described here for Arctic charr ecotypes therefore warranting future in-depth studies which include a genetic component.

5 Conclusion

Our study demonstrated clear repeatability in functional and life history traits of polymorphic Arctic charr populations across lakes. Altogether, the study demonstrated that Arctic charr is a promising study system for novel knowledge under the framework of adaptive trait syndromes. Results suggest the existence of a general adaptive trait syndrome as our predictions were validated in this study. Based on these general findings, the adaptive trait syndrome in the Normal Arctic charr ecotype is driven by correlations among traits of morphology and habitat use at all the studied levels. For the Dwarf ecotype, it seems that habitat plays a generally consistent role in its adaptive trait syndrome, but life history and trophic niche are especially important at increasing levels of intraspecific diversity. The Piscivorous ecotype shows important correlations with littoral reliance and trophic position highlighting that ecological niche is key in the ecotype's adaptive trait syndrome. The presence of the Piscivorous ecotype also shapes the life history of the other sympatric ecotypes through modifications of the Normal and Dwarf ecotypes' available niches.

We show that Arctic charr is an excellent model species to study questions related to adaptive trait syndromes. Patterns in syndromes are best understood when we can study trait correlations and variations at both the species and population levels (Araya-ajoy et al. 2018; Agrawal 2020). Additionally, the repeated instances of bi-morphic and tri-morphic populations of Arctic charr allow for studies examining adaptive trait syndromes along a gradient of intraspecific diversity (Knudsen et al. 2016b), which can influence the manifestation of adaptive trait syndromes through its influence on trait expression (Blain et al., in press; Raffard et al. 2019b). As Arctic charr populations show ecotypes with differing positions along the speciation continuum, the species offers an interesting model to study how adaptive trait syndromes are shaped at differing stages of evolution. By combining functional traits with parameters of life history under the adaptive trait framework, we may shed light on the causes for the high intraspecific diversity seen among charrs. Such studies examining adaptive trait syndromes in various ecotypes or genotypes of a species will be important in our conservation and management efforts with escalating climate change and other anthropogenic disturbances (Laughlin and Messier 2015; Blasini et al. 2021). Studies such as this one have the potential to greatly improve our predictive abilities of how biodiversity might change in future climate change scenarios by incorporating intraspecific variation (Laughlin and Messier 2015; Des Roches et al. 2018).

6 Tables

Table 1. Correlations among trait spectra of habitat (littoral reliance (LR) mid-grey shading), diet (trophic position (TP) dark-grey shading), morphology (PC1 and PC2 of head shape (HSPC1 and HSPC2, respectively), PC1 and PC2 of head linear measurements (HLPC1 and HLPC2, respectively), PC1 and PC2 of linear measurements of fins (FinPC1 and FinPC2, respectively, light-grey shading)) and life history (c: investment in somatic growth, r: investment in reproduction, age: age of investment in reproduction, white) trait spectra for the normal (top) the dwarf (center) and piscivorous (bottom) ecotypes. Significant correlations that had 95% credible intervals that did not cross zero are bolded (Wilson et al. 2010). The trait correlations for the Piscivorous ecotype are found on the following page.

Normal ecotype

	HSPC1	HSPC2	HLPC1	HLPC2	FinPC1	FinPC2	LR	TP
c	-0.407	-0.808	-0.759	0.415	-0.145	**0.991**	-0.426	**0.964**
r	-0.931	**-0.967**	-0.929	-0.224	-0.696	0.877	-0.897	0.788
age	-0.955	-0.497	-0.895	**-0.992**	-0.904	**-0.996**	-0.989	**-0.996**
HSPC1							**0.996**	0.896
HSPC2							**0.994**	0.294
HLPC1							**0.996**	0.707
HLPC2							**0.997**	0.947
FinPC1							**0.999**	0.884
FinPC2							**0.972**	**0.995**
LR								0.983
TP								

Dwarf ecotype

	HSPC1	HSPC2	HLPC1	HLPC2	FinPC1	FinPC2	LR	TP
c	-0.241	-0.789	-0.800	-0.209	0.929	0.033	0.038	0.203
r	**-0.913**	**-0.988**	**-0.919**	-0.800	0.966	0.607	-0.754	-0.395
age	0.992	0.985	0.968	0.967	-0.979	-0.969	0.946	-0.083
HSPC1							**0.886**	-0.181
HSPC2							0.914	0.781
HLPC1							**0.918**	0.870
HLPC2							**0.854**	-0.266
FinPC1							-0.808	-0.949
FinPC2							-0.816	0.430
LR								0.855
TP								

Piscivorous ecotype

	HSPC1	HSPC2	HLPC1	HLPC2	FinPC1	FinPC2	LR	TP
c	0.984	0.989	0.990	-0.986	0.983	-0.990	-0.990	-0.991
r	0.984	0.985	0.990	-0.986	0.983	-0.986	-0.986	-0.986
age	0.989	0.997	0.998	0.984	0.986	-0.995	-0.995	-0.996
HSPC1							-0.998	-0.996
HSPC2							-0.998	**-0.997**
HLPC1							**-0.997**	**-0.997**
HLPC2							-0.985	-0.990
FinPC1							-0.987	-0.987
FinPC2							**0.997**	**0.997**
LR								**0.997**
TP								

Table 2. Correlations among trait spectra of habitat (littoral reliance (LR) mid-grey shading), diet (trophic position (TP) dark-grey shading), morphology (PC1 and PC2 of head shape (HSPC1 and HSPC2, respectively), PC1 and PC2 of head linear measurements (HLPC1 and HLPC2, respectively), PC1 and PC2 of linear measurements of fins (FinPC1 and FinPC2, respectively, light-grey shading)) and life history (c: investment in somatic growth, r: investment in reproduction, age: age of investment in reproduction, white) trait spectra the normal (top) and dwarf (bottom) ecotypes at differing levels of intraspecific diversity. The correlations in the bi-morphic systems are located above the diagonal while the correlations for the tri-morphic systems (shaded values) are below the diagonal. Significant correlations that had a 95% credible interval that did not cross zero are bolded (Wilson et al. 2010). *The trait correlations for the Dwarf ecotype are found on the following page*

Normal Bi-morphic and Tri-morphic

	c	r	age	HSPC1	HSPC2	HLPC1	HLPC2	FinPC1	FinPC2	LR	TP
c				**0.997**	**0.997**	0.998	**0.996**	**0.996**	**0.996**	**0.997**	**0.996**
r				0.999	0.996	0.998	0.998	0.998	0.998	0.999	0.998
age				**-0.997**	**-0.997**	-0.998	**-1.000**	**-0.997**	**-0.997**	**-0.997**	**-1.000**
HSPC1	**-0.997**	**-0.997**	0.991							**0.997**	**0.996**
HSPC2	**-0.999**	**-0.999**	0.995							0.997	**0.997**
HLPC1	**-0.996**	**-0.996**	0.990							0.999	0.997
HLPC2	**-0.996**	**-0.996**	0.990							**0.996**	**0.999**
FinPC1	**-0.996**	**-0.996**	0.990							**0.996**	**0.998**
FinPC2	0.998	0.999	-0.988							**0.997**	**0.999**
LR	**-0.997**	**-0.997**	0.990	**0.997**	**0.997**	**0.997**	**0.997**	**0.997**	**-0.996**		**0.996**
TP	**0.993**	**0.993**	-0.990	-0.993	-0.993	-0.993	-0.993	-0.993	0.991	-0.993	

Dwarf Bi-morphic and Tri-morphic

	c	r	age	HSPC1	HSPC2	HLPC1	HLPC2	FinPC1	FinPC2	LR	TP
c				0.988	-0.988	-0.991	0.988	0.988	-0.991	-0.991	-0.991
r				0.988	-0.991	-0.998	0.989	0.997	-0.999	-0.999	-0.998
age				0.989	-0.988	-0.991	0.989	0.990	-0.991	-0.991	-0.991
HSPC1	**-0.996**	**-1.000**	0.997							-0.998	-0.996
HSPC2	**-0.997**	**-0.996**	0.997							0.993	0.994
HLPC1	**-0.996**	**-1.000**	0.997							**0.996**	**1.000**
HLPC2	**-0.997**	-0.996	0.997							-0.996	-0.995
FinPC1	0.998	**0.997**	-0.994							-0.998	-0.997
FinPC2	**0.996**	**0.996**	-0.997							**0.997**	**0.996**
LR	-0.997	-0.997	0.996	0.997	0.998	0.997	0.998	-0.994	-0.998		**0.996**
TP	**0.996**	**0.996**	-0.997	**-0.996**	**-0.997**	**-0.996**	**-0.997**	0.995	**0.997**	**-0.998**	

7 Figures

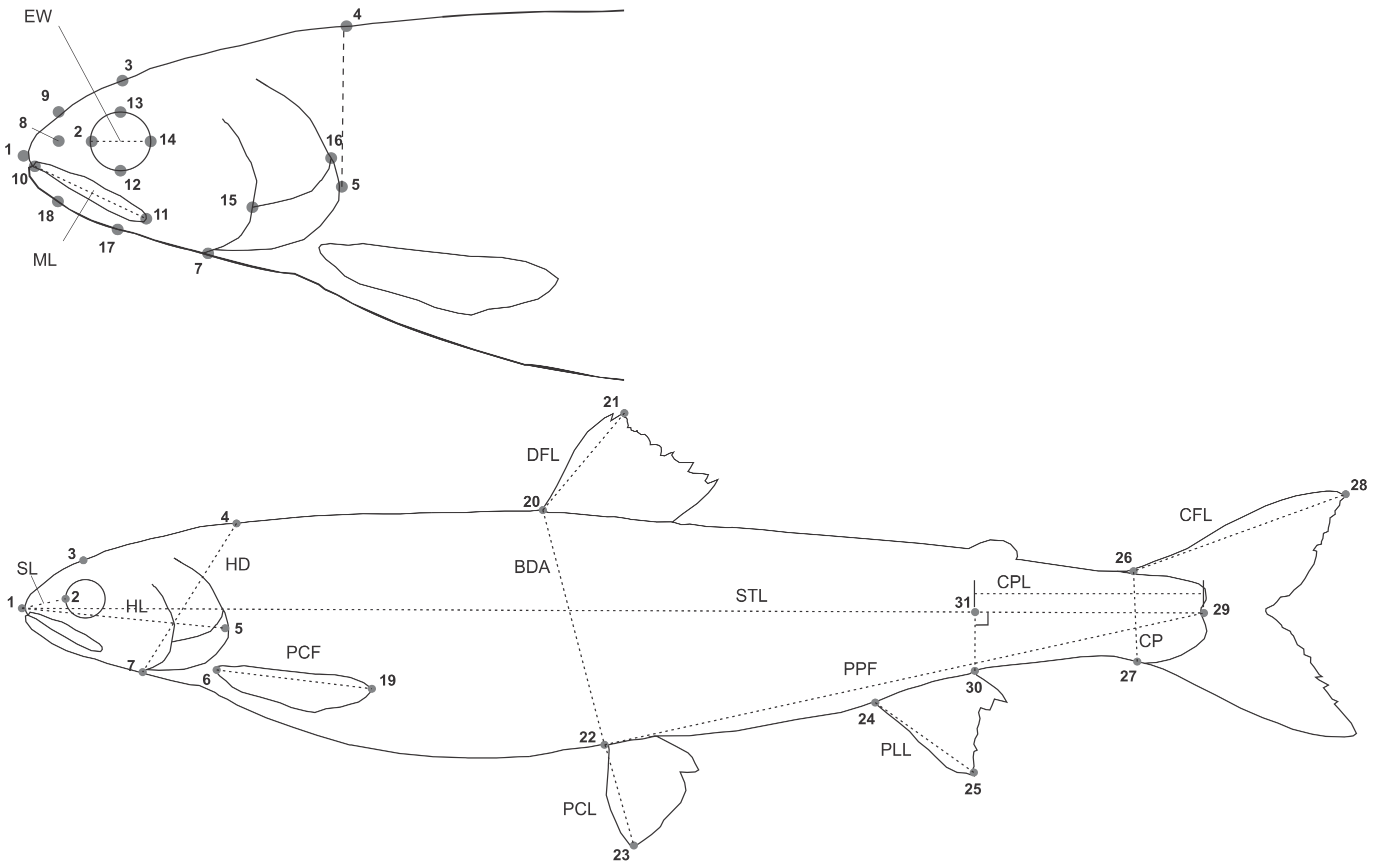


Figure 1. Landmarks used in morphometric and linear measurement traits. Landmarks used for analysis of head shape: 1: Anterior point of the snout, 2: anterior point of the bony eye orbit, 3: top of head directly over anterior point of the bony eye orbit (landmark 2), 4: top of head positioned over the extreme posterior edge of the bony opercle (landmark 5, positioning shown with a dashed line), 5:posterior point of the bony opercle, 6: insertion of the pectoral fin, 7: anterioventral point of the bony opercle, 8: center of nostril, 9: top of cranium directly over center of nostril (8), 10: anterior point of upper maxilla, 11: posterior point of upper maxilla, 12: ventral point of bony orbit of the eye, 13: dorsal point of bony orbit of the eye, 14: posterior point of bony orbit of the eye, 15: ventral point of intersection between the opercle and the preopercle bones, 16: posterior point of intersection between opercle and subopercle bones, 17: bottom of lower jaw directly under the dorsal point of the body orbit of the eye (landmark 3). 18: bottom of the lower jaw directly under the center of the nostril. Interlandmark distances of head linear trait measurements: snout length (SL): 1-2, head depth (HD): 4-7, head length (HL): 1-5, eye width (EW): 2-14,

maxilla length (ML): 10-11. Landmarks used in linear trait measurements of fins: 19: posterior tip of pectoral fin, 20: anterior insertion of the dorsal fin, 21: anterior tip of the dorsal fin, 22: anterior insertion of pectoral fin, 23: anterior tip of pectoral fin, 24: anterior insertion point of the anal fin, 25: anterior tip of the anal fin, 26: dorsal point of start of caudal fin membrane, 27: ventral point of origin of caudal fin membrane, 28: tip of the dorsal portion of the caudal fin, 29: posterior border of hypural bones at the midline, 30: posterior insertion point of the anal fin, 31: point along the horizontal axis of the body perpendicular to the posterior insertion point of the anal fin (30). Interlandmark distances of fin linear trait measurements: body depth (BDA):20-22, pectoral fin length (PCL): 6-19, dorsal fin length (DFL): 20-21, pectoral fin length (PCL): 22-23, pelvic fin length (PLL): 24-25, caudal peduncle depth (CP): 26-27, caudal fin length (CFL): 26-28, standard length (STL): 1-29, and caudal peduncle length (CPL): 31-29.

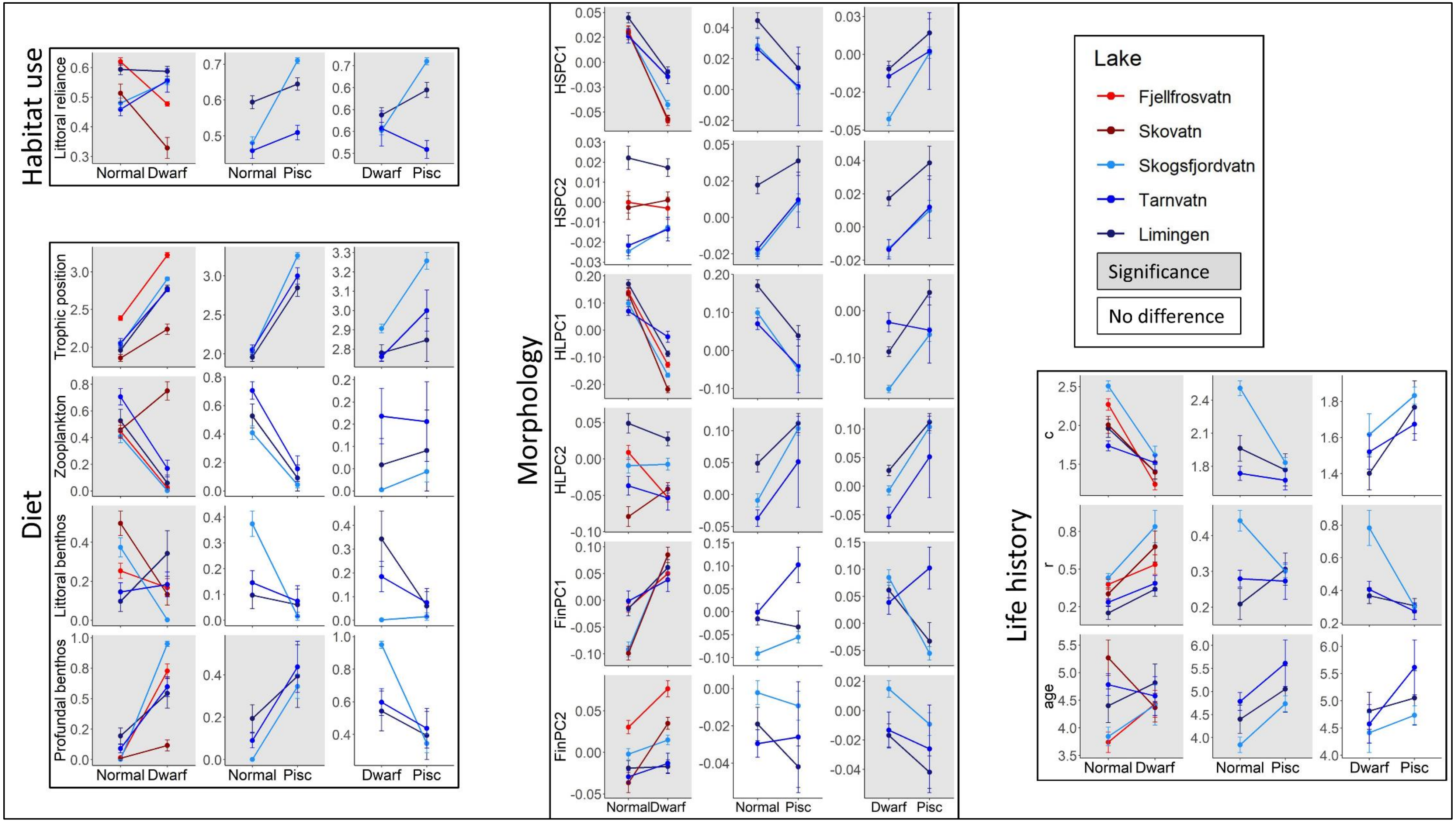

Habitat use
Littoral reliance
Diet
Trophic position
Zooplankton
Littoral benthos
Profundal benthos
Normal Dwarf
Normal Pisc
Dwarf Pisc
Morphology
HSPC1
HSPC2
HLPC1
HLPC2
FinPC1
FinPC2
NormalDwarf
Life history
c
r
age
Lake
Fjellfrosvatn
Skovatn
Skogsfjordvatn
Tarnvatn
Limingen
Significance
No difference

Figure 2. Ecotype level pairwise display of the mean trait value of all studied trait spectra of habitat use (littoral reliance), diet (trophic position and proportion of zooplankton, littoral benthos, and profundal benthos prey items in stomach contents), morphology (PC1 and PC2 of head shape (HSPC1 and HSPC2, respectively), PC1 and PC2 of head linear measurements (HLPC1 and HLPC2, respectively), PC1 and PC2 of linear measurements of fins (FinPC1 and FinPC2, respectively)), and life history (c: investment in somatic growth, r: investment in reproduction, age: age of investment in reproduction). Anderson-Darling k-samples test results of pairwise ecotype comparisons for all measured traits are indicated by the shading of each plot. Ecotype pairs that have different distributions are shaded in light grey while no shading means that the ecotype pairs share the same trait distribution. The Piscivorous ecotype is abbreviated as Pisc for the labels of the x-axis.

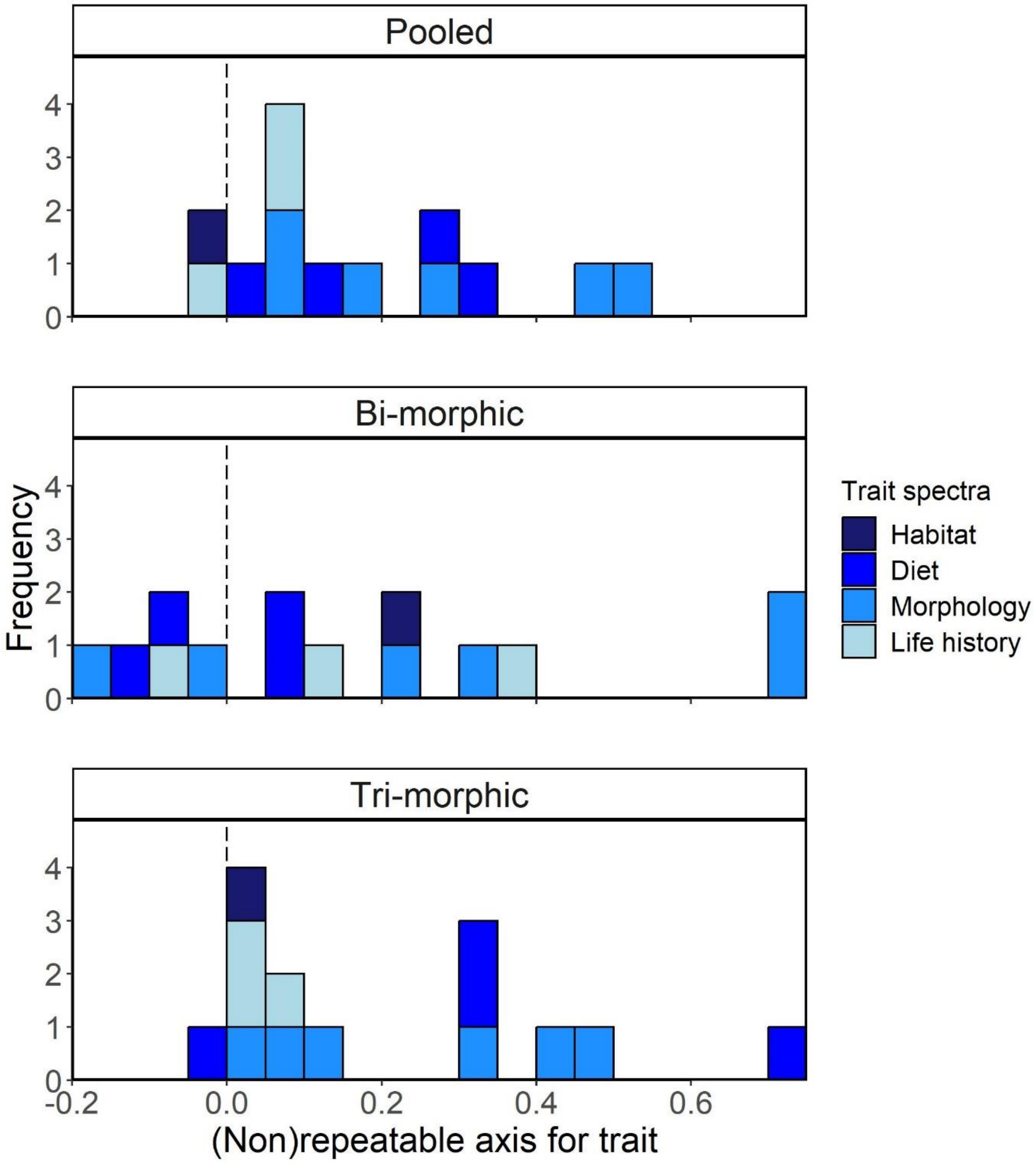


*Figure 3. Histogram of (non)repeatability in studied trait spectra by linear modelling of functional traits of habitat use, diet, morphology, and life history trait spectra for lakes pooled, bi-morphic, and tri-morphic lakes. The (non)repeatable axis represents the relative effect size of the repeatable (ecotype) vs. the non-repeatable (ecotype*lake) terms from linear modelling for each trait within its respective trait spectra. Traits located on the negative side of the axis show more non-repeatability and traits on the positive side of the axis are more repeatable within a trait spectra.*

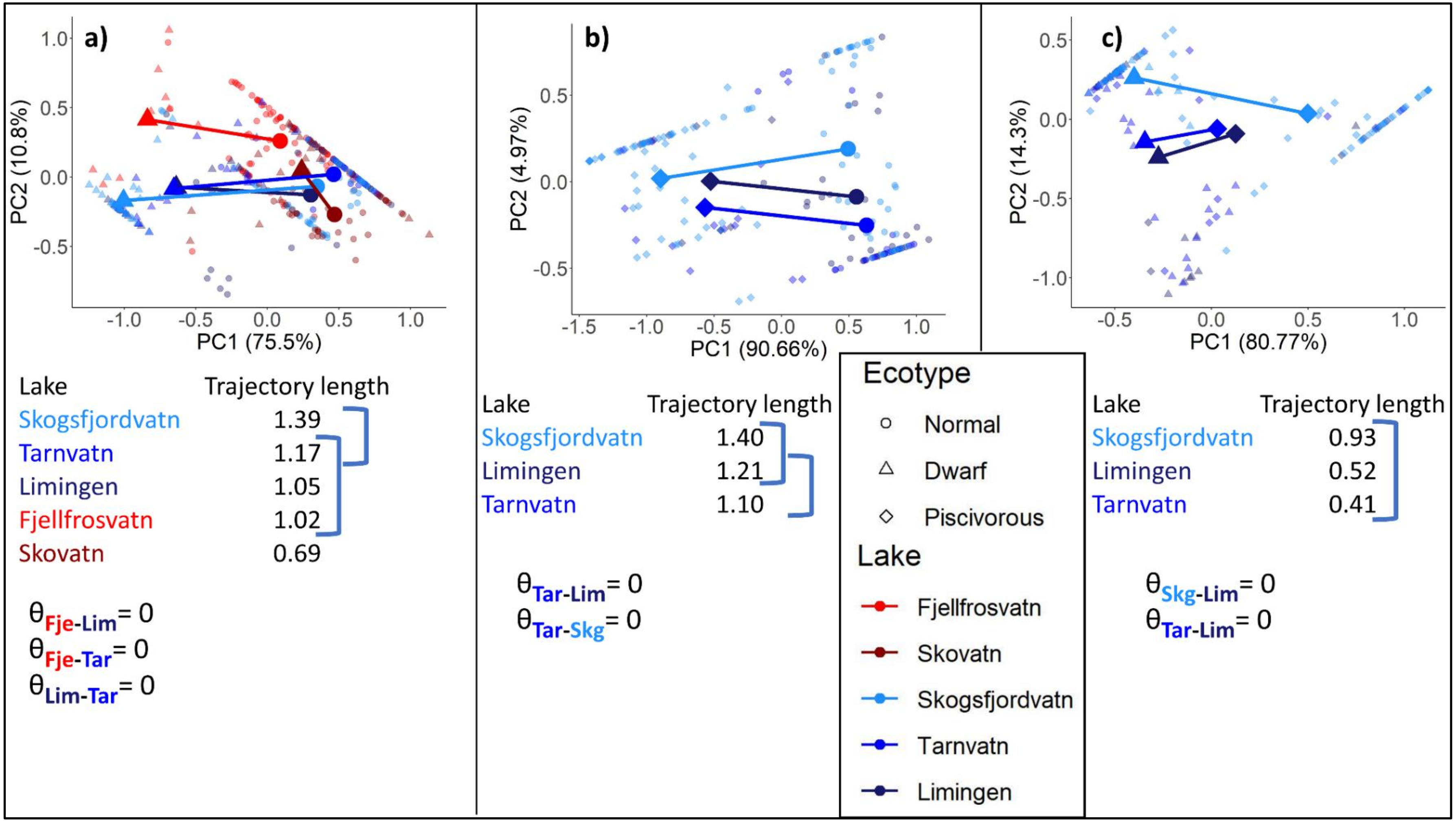


Figure 4. Trajectory analyses of magnitude (length) and direction (angle θ) in divergence in combined functional traits of diet (trophic position and proportion of zooplankton, littoral benthic, and profundal benthic preys in the diet) between ecotype pairs in bi-morphic (red) and tri-morphic (blue) lakes. Brackets represent trajectory lengths that do not differ significantly among lakes, while the angles that are not different are indicated on each plot. Ecotypes are represented as follows: Normal with circles, Dwarfs with triangles, and Piscivorous with diamonds. Each panel shows a different ecotype pair where comparisons are as follows: a) Normal and Dwarf ecotypes, b) Normal and Piscivorous ecotypes, and c) Dwarf and Piscivorous ecotypes.

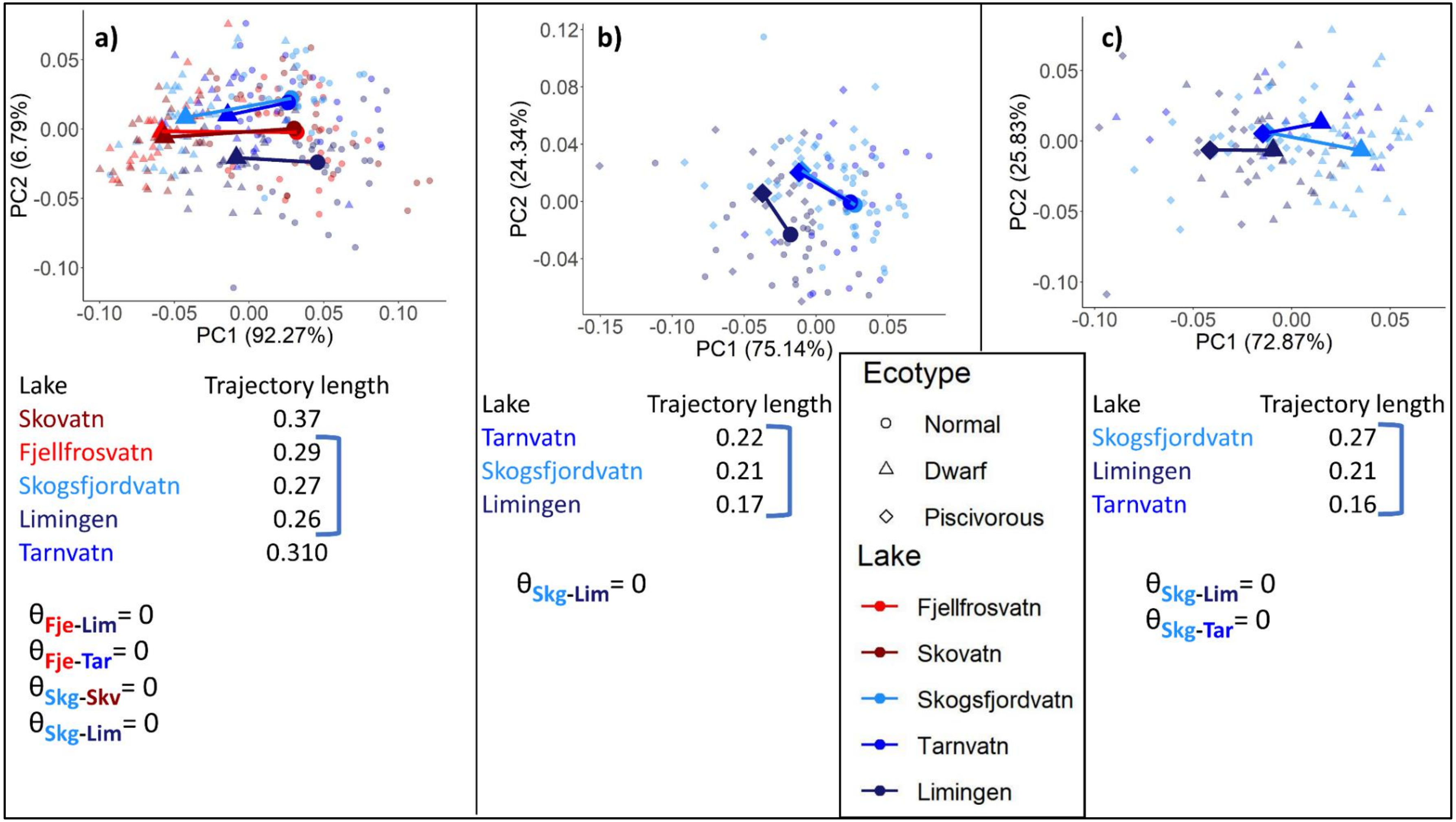
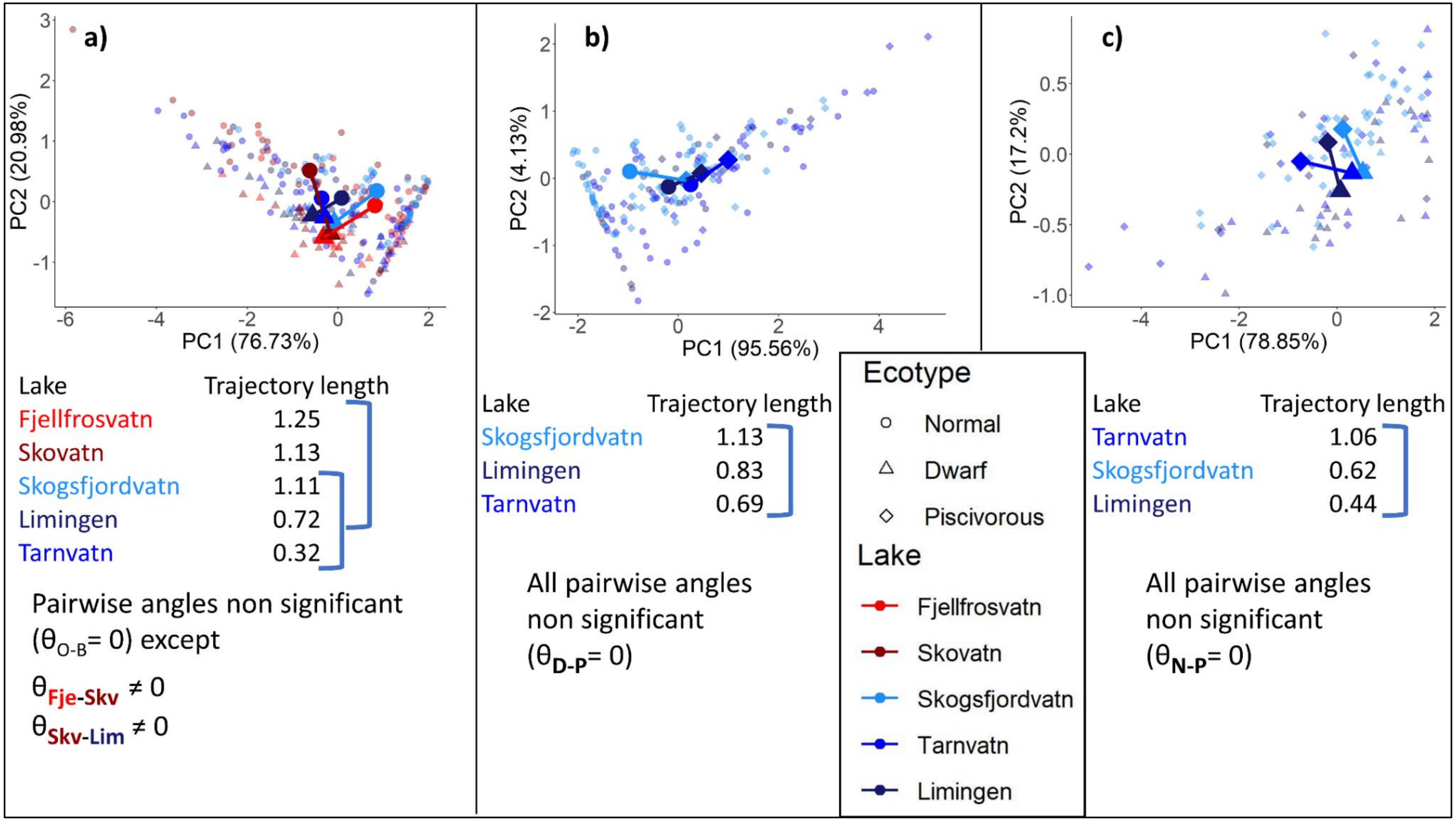


Figure 5. Trajectory analyses of magnitude (length) and direction (angle θ) in divergence in combined functional traits of morphology (PC1 and PC2 of head shape, head linear measurements, and linear measurements of fins) between ecotype pairs in bi-morphic (red) and tri-morphic (blue) lakes. Brackets represent trajectory lengths that do not differ significantly among lakes, while the angles that are not different are indicated on each plot. Ecotypes are represented as follows: Normal with circles, Dwarfs with triangles, and Piscivorous with diamonds. Each panel shows a different ecotype pair where comparisons are as follows: a) Normal and Dwarf ecotypes, b) Normal and Piscivorous ecotypes, and c) Dwarf and Piscivorous ecotypes.



a)

Lake	Trajectory length
Fjellfrosvatn	1.25
Skovatn	1.13
Skogsfjordvatn	1.11
Limingen	0.72
Tarnvatn	0.32

Pairwise angles non significant ($\theta_{O\text{-}B}$= 0) except

$\theta_{\mathbf{Fje\text{-}Skv}} \neq 0$

$\theta_{\mathbf{Skv\text{-}Lim}} \neq 0$

b)

Lake	Trajectory length
Skogsfjordvatn	1.13
Limingen	0.83
Tarnvatn	0.69

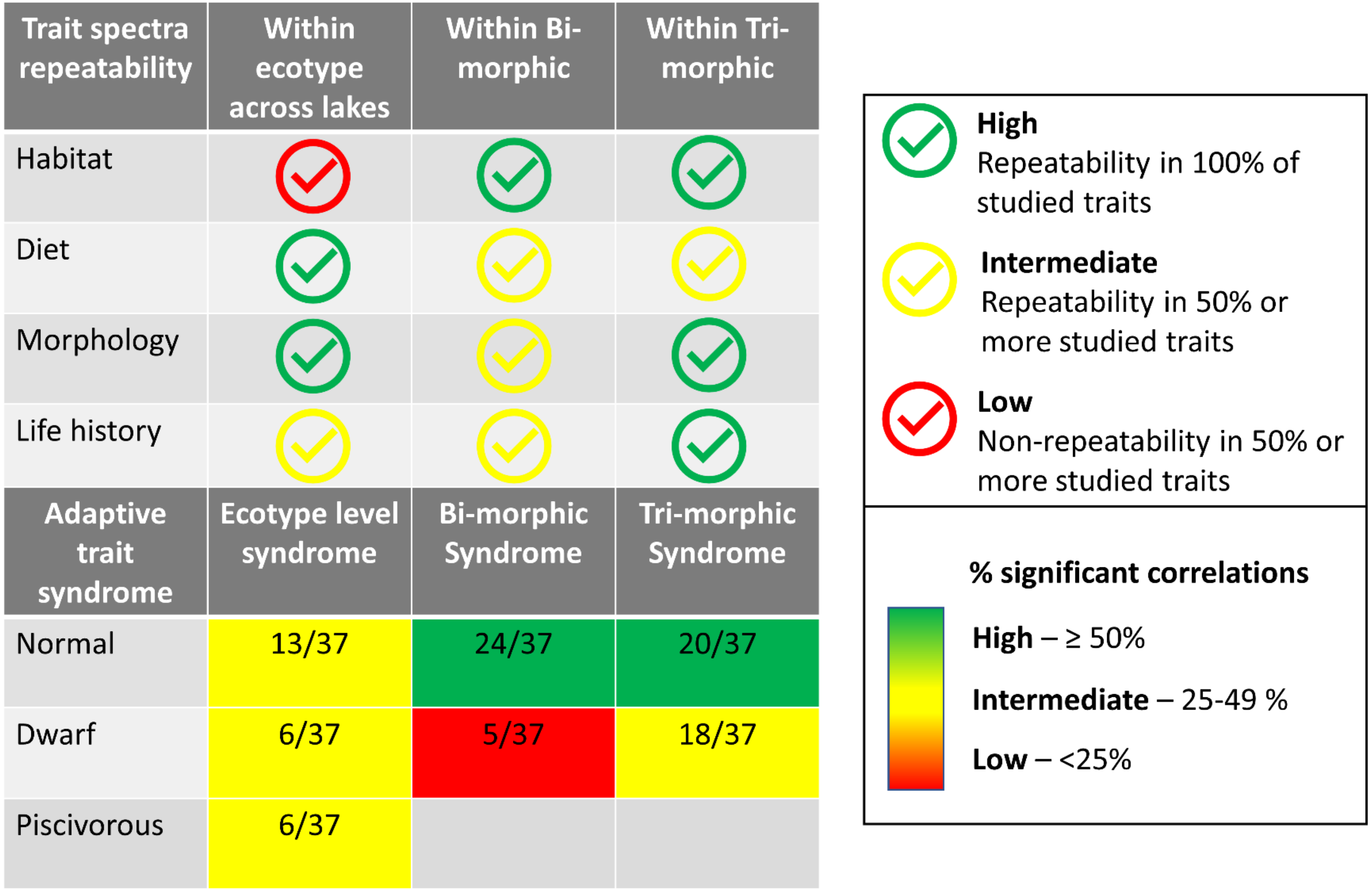
All pairwise angles non significant ($\theta_{\mathbf{D\text{-}P}}$= 0)

c)

Lake	Trajectory length
Tarnvatn	1.06
Skogsfjordvatn	0.62
Limingen	0.44

All pairwise angles non significant ($\theta_{\mathbf{N\text{-}P}}$= 0)

Figure 6. Trajectory analyses of magnitude (length) and direction (angle θ) in divergence in combined parameters of life history (c: investment in somatic growth, r: investment in reproduction, age: age of investment in reproduction between ecotype pairs in bi-morphic (red) and tri-morphic (blue) lakes. Brackets represent trajectory lengths that do not differ significantly among lakes, while the angles that are not different are indicated on each plot. Ecotypes are represented as follows: Normal with circles, Dwarfs with triangles, and Piscivorous with diamonds. Each panel shows a different ecotype pair where comparisons are as follows: a) Normal and Dwarf ecotypes, b) Normal and Piscivorous ecotypes, and c) Dwarf and Piscivorous ecotypes.



Trait spectra repeatability	Within ecotype across lakes	Within Bi-morphic	Within Tri-morphic
Habitat	🔴	🟢	🟢
Diet	🟢	🟡	🟡
Morphology	🟢	🟡	🟢
Life history	🟡	🟡	🟢
Adaptive trait syndrome	**Ecotype level syndrome**	**Bi-morphic Syndrome**	**Tri-morphic Syndrome**
Normal	🟨 13/37	🟩 24/37	🟩 20/37
Dwarf	🟨 6/37	🟥 5/37	🟨 18/37
Piscivorous	🟨 6/37		

🟢 **High**
Repeatability in 100% of studied traits

🟡 **Intermediate**
Repeatability in 50% or more studied traits

🔴 **Low**
Non-repeatability in 50% or more studied traits

% significant correlations

🟩 **High** – ≥ 50%
🟨 **Intermediate** – 25-49 %
🟥 **Low** – <25%

Figure 7. Summary of main findings examining repeatability using the effect sizes (η^2) of each studied trait spectra and the presence of an adaptive trait syndrome in Arctic charr ecotypes at varying levels of intraspecific diversity based on correlations found. In the top half of the table, symbol colour corresponds to the proportion of traits within a trait spectrum that showed stronger repeatability than non-repeatability green:100% of traits, yellow: 50-99% of traits, and red: less than 50% of traits. The lower half of the table corresponds to the adaptive trait syndrome within ecotypes of Arctic charr where green represents 50% or more correlated traits, yellow 25 to 49% of correlated traits, and red, less than 25% of traits correlated.

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9 Supplementary materials

Table S 1. Summary of sample sizes used for the measurements of habitat use, diet and morphology trait spectra and estimates of life history parameters for each lake and ecotype (N:normal, D:dwarf, P:piscivorous)

Lake	Habitat	Diet	Morphology	Life history
Fjellfrøsvatn	1992, 2010	N:79	N:29	N:133
		D:9	D:24	D:63
Skøvatn	2016	N:34	N:31	N:84
		D:23	D:30	D:39
Limingen	2016	N:32	N:31	N:47
		D:17	D:27	D:41
		P:11	P:14	P:16
Skogsfjordvatn	2011	N:53	N:31	N:115
		D:31	D:28	D:31
		P:50	P:30	P:72
Tårnvatn	2016	N:24	N:24	N:125
		D:28	D:19	D:38
		P:15	P:4	P:28

Table S 2. Priors used in the modelling of each trait spectra and of the adaptive trait syndrome.

Model	G	R
Adaptive trait syndrome	list(G1 = list(V = diag(11)*1e-6, nu = 12, alpha.mu = rep(0, 11),alpha.V = diag(11)*100))	list(V =diag(11)/2, nu = 11))

Table S 3. Coefficient of variation (or variance) of measured traits of habitat (littoral reliance, LR), diet (trophic position, TP; zooplankton, zp; littoral benthos, bl; and profundal benthos, bp), morphology (first and second principle axis of: head shape, HS; head linear measurements, HL; and linear measurements of fins, Fin), and parameters of life history from bi-phasic growth modelling (growth, c; investment in reproduction, r; and age of first investment in reproduction, age). Different ecotypes are denoted as Normal (N), Dwarf (D), and Piscivorous (P). Lakes are abbreviated as Fjellfrøsvatn (Fje), Skøvatn (Skv), Limingen (Lim), Skogsfjordvatn (Skg), and Tårnvatn (Tar).*

Ecotype	Lake	LR	TP	zp	bl	bp	HSPC1*	HSPC2*	HLPC1*	HLPC2*	FinPC1*	FinPC2*	c	r	age
N	Fje	23.981	11.667	95.006	160.479	606.570	0.001	0.001	0.005	0.003	0.002	0.002	19.463	49.403	29.382
N	Skv	38.071	14.638	112.558	76.993	237.974	0.001	0.001	0.017	0.006	0.005	0.004	31.186	65.263	35.236
N	Lim	18.306	16.338	90.951	302.789	188.539	0.002	0.001	0.007	0.006	0.006	0.003	25.859	81.823	30.260
N	Skg	50.549	14.601	102.354	126.565	0.000	0.001	0.000	0.005	0.003	0.006	0.001	16.690	40.779	27.120
N	Tar	32.650	13.919	43.222	223.864	262.866	0.001	0.001	0.006	0.004	0.009	0.001	28.156	60.482	30.850
D	Fje	5.972	3.369	0.000	77.566	119.436	0.001	0.001	0.002	0.001	0.003	0.002	21.694	45.163	20.685
D	Skv	62.355	15.022	52.782	221.694	216.971	0.001	0.001	0.005	0.002	0.006	0.002	38.944	60.429	23.108
D	Lim	10.888	6.357	412.311	140.007	92.157	0.000	0.000	0.003	0.002	0.006	0.002	26.294	50.800	28.266
D	Skg	14.284	4.331	556.776	556.776	22.128	0.001	0.001	0.002	0.002	0.006	0.001	15.813	30.796	18.452
D	Tar	39.317	4.805	217.100	181.987	69.807	0.001	0.001	0.008	0.005	0.009	0.003	27.184	52.068	32.548
P	Lim	7.961	12.966	331.662	331.662	124.463	0.000	0.001	0.010	0.003	0.017	0.002	23.463	41.540	28.084
P	Skg	13.898	9.541	386.853	707.107	170.949	0.003	0.001	0.007	0.003	0.005	0.002	16.976	39.800	23.296
P	Tar	15.454	13.681	221.857	309.549	107.080	0.001	0.001	0.020	0.020	0.006	0.004	21.897	76.895	37.001

Table S 4. Effect size (η^2) of linear model on trophic position, proportion of prey in the diet (zooplankton, littoral benthos, pleuston, and profundal benthos) for all lakes pooled, within bi-morphic lakes, and tri-morphic lakes. Effects are for ecotype (top), lake (center), and the interaction between ecotype and lake (bottom).

Diet	Pooled	Bi-morphic	Tri-morphic
trophic position	0.690	0.160	0.760
	0.350	0.520	0.070
	0.090	0.090	0.050
zooplankton	0.190	0.010	0.340
	0.070	0.010	0.080
	0.150	0.130	0.030
littoral benthos	0.070	0.010	0.070
	0.040	0.070	<0.001
	0.100	0.090	0.100
pleuston	0.060	0.040	0.040
	0.140	0.180	0.030
	0.020	0.001	0.030
profundal benthos	0.400	0.150	0.430
	0.110	0.020	0.006
	0.190	0.070	0.110

Table S 5. Pairwise comparisons of trajectories among lakes from the trajectory analysis of the diet trait spectra among Normal (N), Dwarf (D), and Piscivorous (P) ecotypes. Differences in trajectory lengths (magnitude) are above the diagonal and trajectory angles are below the diagonal. Parallel trajectories have bolded values (i.e. p>0.05). Values in red highlight pairwise comparisons of bi-morphic lakes and blue highlights comparisons between tri-morphic lakes. Lakes are abbreviated as Fjellfrøsvatn (Fje), Skøvatn (Skv), Limingen (Lim), Skogsfjordvatn (Skg), and Tårnvatn (Tar).

	FjeN-D	SkvN-D	LimN-D	SkgN-D	TarN-D	LimD-P	SkgD-P	TarD-P	LimN-P	SkgN-P	TarN-P
FjeN-D		0.330	**0.028**	0.367	**0.151**						
SkvN-D	80.008		0.359	0.697	0.481						
LimN-D	**7.170**	83.005		0.338	**0.122**						
SkgN-D	35.935	63.480	37.104		**0.216**						
TarN-D	**22.576**	86.251	**23.031**	26.441							
LimD-P							0.410	**0.112**			
SkgD-P						48.444		0.522			
TarD-P						**36.776**	**28.557**				
LimN-P										0.300	**0.106**
SkgN-P									**17.448**		**0.194**
TarN-P									**19.357**	23.669	

Table S 6. Effect size (η^2) of linear model on traits from the morphology trait spectra (first and second principal components of: head shape, HS; head linear measurements HL, and linear measurements of fins, Fin) with all lakes pooled, within bi-morphic lakes, and tri-morphic lakes. Effects are for ecotype (top), lake (center), and the interaction between ecotype and lake (bottom).

Trait	Pooled	Bi-morphic	Tri-morphic
HSPC1 – head shape	0.580	0.720	0.440
	0.140	<0.001	0.100
	0.080	0.002	0.040
HSPC2 – head shape	0.070	<0.001	0.110
	0.200	<0.001	0.280
	0.010	0.003	0.020
HLPC1 – linear measurements	0.700	0.770	0.063
	0.150	0.070	0.170
	0.180	0.060	0.160
HLPC2 – linear measurements	0.350	0.008	0.324
	0.230	0.120	0.190
	0.070	0.170	0.020
FinPC1 – Fin linear measurements	0.340	0.500	0.260
	0.040	0.050	0.040
	0.140	0.180	0.120
FinPC2 – Fin linear measurements	0.120	0.240	0.030
	0.240	0.240	0.090
	0.070	0.020	0.010

Table S 7 Pairwise comparisons of trajectories among lakes from the trajectory analysis of the morphology trait spectra among Normal (N), Dwarf (D), and Piscivorous (P) ecotypes. Differences in trajectory lengths (magnitude) are above the diagonal and trajectory angles are below the diagonal. Parallel trajectories have bolded values (i.e. p>0.05). Values in red highlight pairwise comparisons of bi-morphic lakes and blue highlights comparisons between tri-morphic lakes. Lakes are abbreviated as Fjellfrøsvatn (Fje), Skøvatn (Skv), Limingen (Lim), Skogsfjordvatn (Skg), and Tårnvatn (Tar).

	FjeN-D	SkvN-D	LimN-D	SkgN-D	TarN-D	LimD-P	SkgD-P	TarD-P	LimN-P	SkgN-P	TarN-P
FjeN-D		0.0762	**0.0253**	**0.0139**	0.1840						
SkvN-D	18.939		0.102	0.090	0.260						
LimN-D	**10.161**	10.876		**0.011**	0.159						
SkgN-D	13.578	**5.980**	**6.873**		0.170						
TarN-D	**7.532**	18.125	13.277	12.673							
LimD-P							**0.013**	**0.044**			
SkgD-P						**11.510**		**0.057**			
TarD-P						63.245	53.520				
LimN-P										**0.043**	**0.002**
SkgN-P									**12.240**		**0.044**
TarN-P									**14.217**	**3.372**	

Table S 8. Parameters estimated (mean± standard error) from the bi-phasic growth modelling based on otolith back-calculations for the Normal, Dwarf, and Piscivorous ecotypes in all lakes. The parameters are estimates of investment in growth (c), investment in reproduction (r), and age where fish first start investing in reproduction (age). The size at hatch (L_0) used in the modelling was estimated from otolith back-calculations of the hatch zone. Lakes are abbreviated as Fjellfrøsvatn (Fje), Skøvatn (Skv), Limingen (Lim), Skogsfjordvatn (Skg), and Tårnvatn (Tar).

Ecotype	Lake	c±s.e.		r±s.e.		age ±s.e.		L_0 (mm)
Normal	Fje	2.19	0.05	0.28	0.02	3.10	0.17	23.0
	Skv	2.06	0.06	0.34	0.02	4.05	0.22	15.1
	Skg	2.37	0.02	0.45	0.01	4.20	0.07	17.0
	Lim	1.74	0.03	0.33	0.03	7.23	0.2	55.8
	Tar	1.48	0.02	0.31	0.02	6.39	0.16	42.2
Dwarf	Fje	1.31	0.02	0.58	0.04	4.09	0.08	10.5
	Skv	1.52	0.06	0.65	0.05	3.06	0.12	8.2
	Skg	1.53	0.03	0.62	0.05	4.29	0.12	3.8
	Lim	1.38	0.03	0.44	0.02	5.01	0.12	31.7
	Tar	1.78	0.10	0.38	0.05	1.13	0.58	11.5
Piscivorous	Skg	1.79	0.02	0.33	0.02	5.18	0.13	26.7
	Lim	1.76	0.06	0.35	0.03	6.45	0.53	13.6
	Tar	1.68	0.08	0.20	0.03	4.25	0.81	9.3

Table S 9. Effect size (η^2) of linear model on the life history parameters (growth, c; investment in reproduction, r; and age of first investment in reproduction, age) with all lakes pooled, within bi-morphic lakes, and tri-morphic lakes. Effects are for ecotype (top), lake (center), and the interaction between ecotype and lake (bottom).

Life history	Pooled	Bi-morphic	Tri-morphic
c	0.210	0.370	0.010
	0.170	<0.001	0.040
	0.120	<0.001	0.007
r	0.120	0.150	0.070
	0.100	<0.001	0.010
	0.060	0.030	0.009
age	0.030	0.001	0.040
	0.090	0.130	0.005
	0.030	0.070	0.009

Table S 10. Pairwise comparisons of trajectories among lakes from the trajectory analysis of the life history trait spectra among Normal (N), Dwarf (D), and Piscivorous (P) ecotypes. Differences in trajectory lengths (magnitude) are above the diagonal and trajectory angles are below the diagonal. Parallel trajectories have bolded values (i.e. p>0.05). Values in red highlight pairwise comparisons of bi-morphic lakes and blue highlights comparisons between tri-morphic lakes. Lakes are abbreviated as Fjellfrøsvatn (Fje), Skøvatn (Skv), Limingen (Lim), Skogsfjordvatn (Skg), and Tårnvatn (Tar).

	FjeN-D	SkvN-D	LimN-D	SkgN-D	TarN-D	LimD-P	SkgD-P	TarD-P	LimN-P	SkgN-P	TarN-P
FjeN-D		**0.118**	**0.536**	**0.141**	0.927						
SkvN-D	88.437		**0.418**	**0.023**	0.810						
LimN-D	**7.185**	88.754		**0.395**	**0.787**						
SkgN-D	**11.944**	**83.881**	**6.229**		**0.955**						
TarN-D	**76.652**	**13.236**	**76.302**	**71.161**							
LimD-P							**0.177**	**0.615**			
SkgD-P						**47.306**		**0.438**			
TarD-P						**48.351**	**48.780**				
LimN-P										**0.441**	**0.145**
SkgN-P									**25.532**		**0.296**
TarN-P									**14.993**	**33.362**	

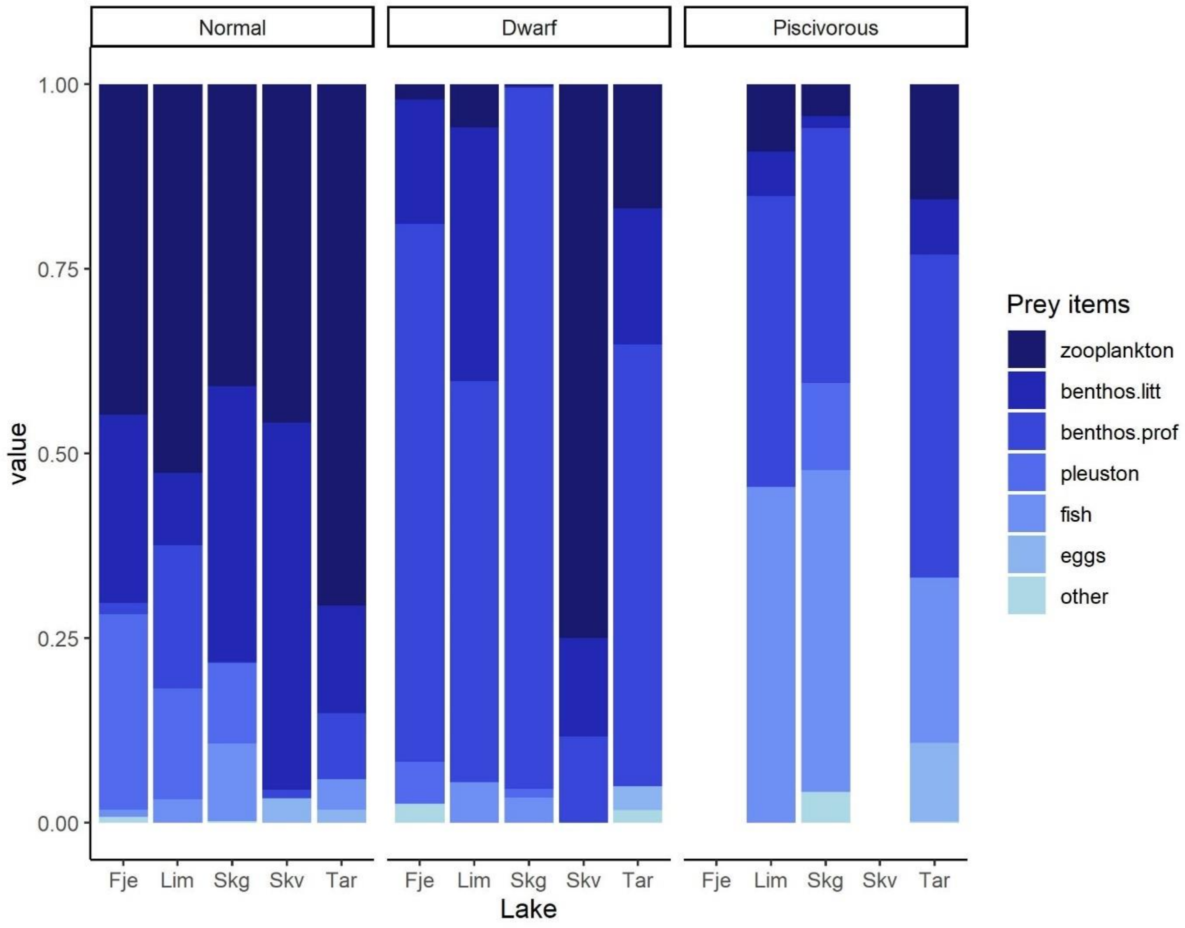

Figure S 1. Relative abundance of prey item in stomach samples of Normal, Dwarf, and Piscivorous ecotypes from all lakes. Lakes are abbreviated as Fjellfrøsvatn (Fje), Skøvatn (Skv), Limingen (Lim), Skogsfjordvatn (Skg), and Tårnvatn (Tar)

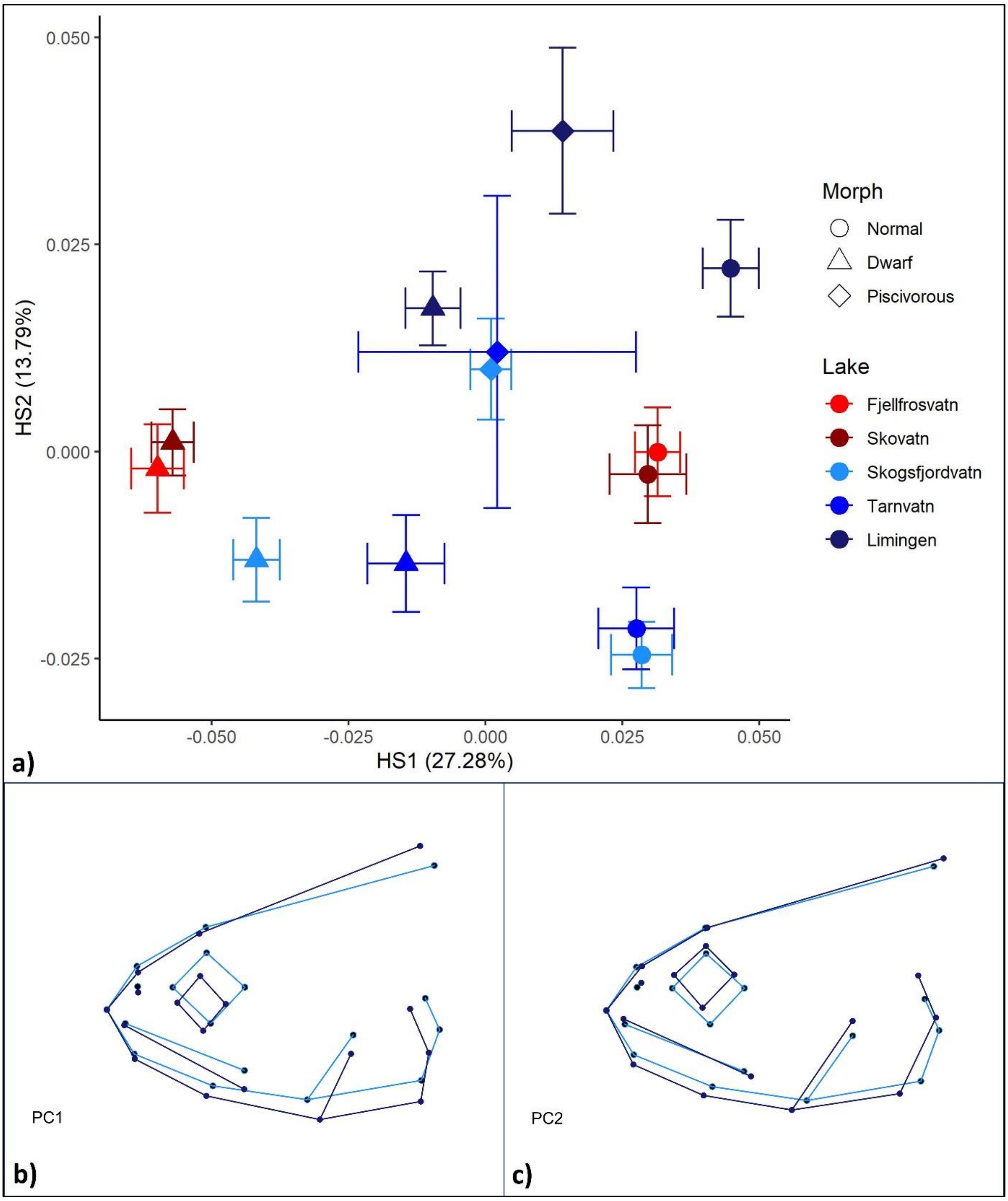

Figure S 2. a) Principal components plot based on head shape showing the mean for each ecotype from each lake. Error bars represent the standard error of the mean. Normal ecotypes are represented by circles, Dwarfs with triangles, and Piscivorous with diamonds. Bi-morphic lakes are in red and tri-morphic lakes are in blue. The third and fourth principal components (not shown) accounted for 12.14% and 9.97% of the variation respectively. The bottom panels show the wireframes of the head shape at each extreme value for b) PC1 and c) PC2. Dark blue wireframes are located at the positive end of the axis, and light blue represents the negative extreme of the axis.

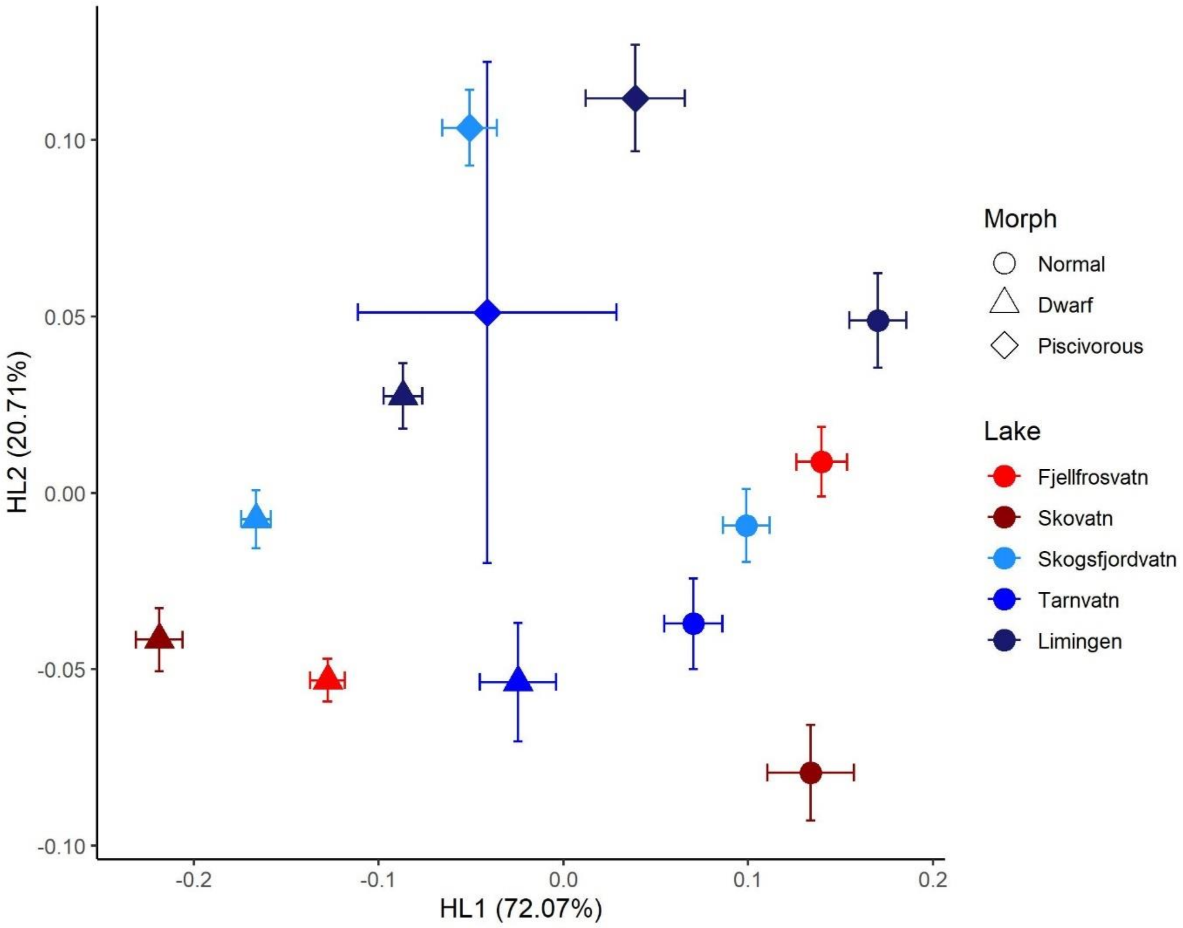

Figure S 3. Principal components plot based on head linear measurements showing the mean for each ecotype from each lake. Error bars represent the standard error of the mean. Normal ecotypes are represented by circles, Dwarfs with triangles, and Piscivorous with diamonds. Bi-morphic lakes are in red and tri-morphic lakes are in blue. The third and fourth principal components (not shown) accounted for 4.24% and 2.38% of the variation, respectively.

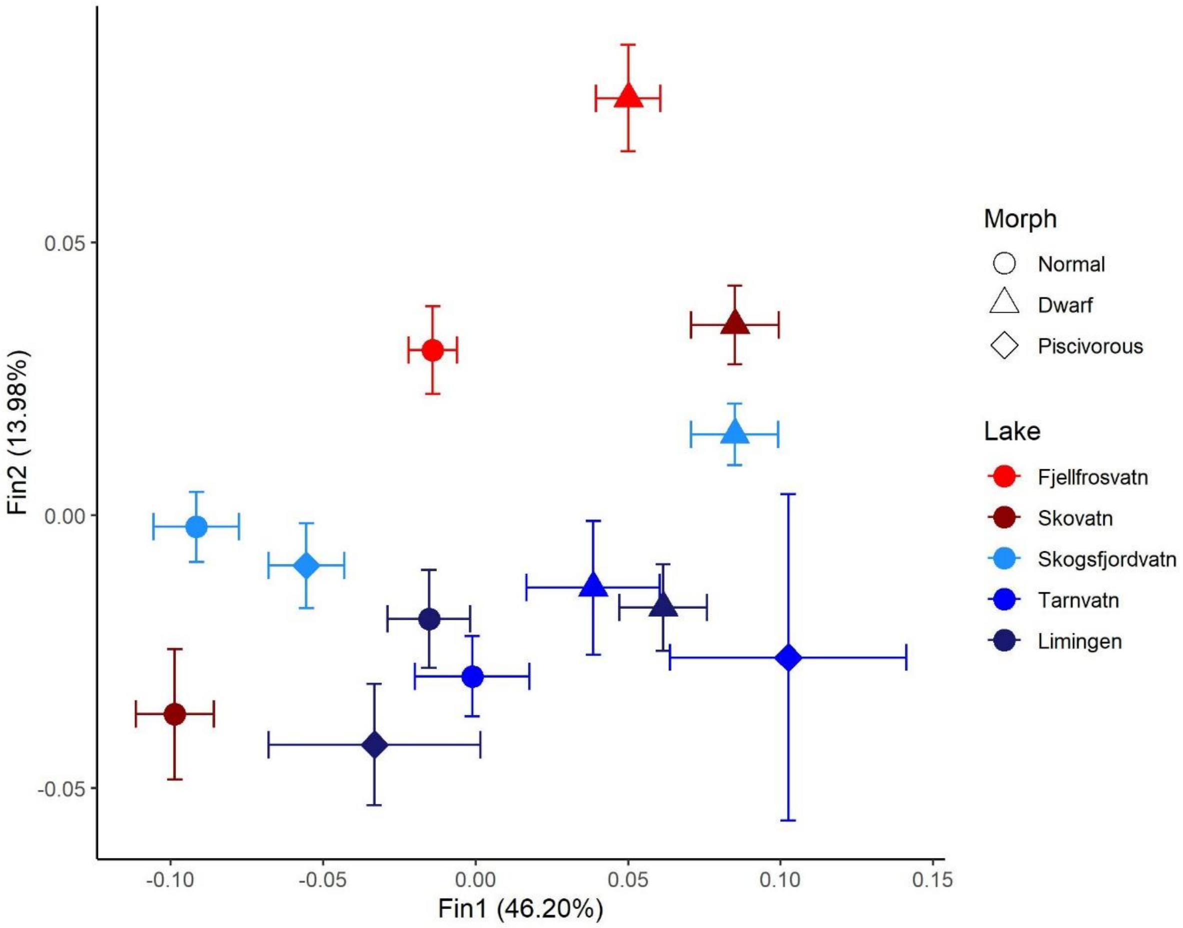

Figure S 4. Principal components plot based on head linear measurements showing the mean for each ecotype from each lake. Error bars represent the standard error of the mean. Normal ecotypes are represented by circles, Dwarfs with triangles, and Piscivorous with diamonds. Bi-morphic lakes are in red and tri-morphic lakes are in blue. The third and fourth principal components (not shown) accounted for 11.56% and 8.40% of the variation, respectively.

Paper III

Marine experience is related to trophic niche shifts, condition, and maturity in anadromous Arctic charr

Marine experience is related to trophic niche shifts, condition, and maturity in anadromous Arctic charr

Authors

Grenier, G.[1], Knudsen, R.[1], Jensen, H.[2], Power, M.[3]

[1] Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, Tromsø, Norway

[2] Norwegian Institute of Bioeconomy Research, Tromsø, Norway

[3] Department of Biology, University of Waterloo, Waterloo, ON, Canada

Keywords

Marine age, stable isotope, $\delta^{34}S$, $\delta^{13}C$, $\delta^{15}N$, life history

Abstract

Arctic charr (*Salvelinus alpinus*) are facultatively anadromous and show variation across their range in the extent of their reliance on marine migration to complete their life cycle. We assessed the number of marine migrations completed in relation to trophic niche, condition factor, and maturity status in males and females from an anadromous population of Arctic charr in Northern Norway. We determined that stable isotopes of sulfur ($\delta^{34}S$) from tissues could be used to estimate the number of marine migrations performed by individual Arctic charr. Females tend to require several marine migrations to mature while males could mature after their second migration. Both males and females showed an increase in condition factor with marine experience. The relationship between condition and marine experience was weak suggesting that other factors also influence condition. We also investigated the shift in trophic niche that occurred with an increasing number of migrations using niche size and overlap metrics based on stable isotope signatures of $\delta^{13}C$ and $\delta^{15}N$. First-time migrants have the largest niche and there is a gradual decrease in niche as individuals gain marine experience through successive marine migrations. The most experienced marine migrants' niche had no overlap with first-time migrants' niche, demonstrating a complete dietary niche shift throughout the

migration history. These results demonstrate that $\delta^{34}S$, in combination with other stable isotopes, has the potential to increase our understanding and provide new monitoring methods of the vulnerable and important anadromous life history strategy.

1 Introduction

Among the diadromous fishes, few species perform annual migrations between freshwater and marine environments (Gross 1987; McDowall 1997; Jensen and Rikardsen 2008). Most will exploit their “growth” habitat for extensive periods (up to multiple years) and return to their natal habitat for reproduction and over-wintering (Gross 1987; McDowall 1997). Diadromous fishes use the relatively richer feeding resources of their growth habitat to sustain high growth. The benefits conferred from migrating to the growth habitat must be greater than the costs of migration (e.g., high mortality, increased predation) for the diadromous life history to be evolutionarily stable (Gross 1987). Arctic charr (*Salvelinus alpinus*), however, are among those species that perform annual migrations between environments to return to freshwater after only a short feeding period, typically four to six weeks at sea (Klemetsen et al. 2003; Jensen and Rikardsen 2008). Unusually for diadromous fishes, Arctic charr that are not ready to spawn also return to the freshwater for the over-winter period (Klemetsen et al. 2003; Jensen and Rikardsen 2008).

Owing to their annual migration patterns, it can be challenging to non-lethally estimate the number of seaward migrations an individual Arctic charr has performed without the use of extensive marking, tagging, and monitoring efforts. Methods that use otoliths make it possible to estimate migration patterns (Halden et al. 1995; Swanson et al. 2010; Eldøy et al. 2020), but have the disadvantage of being lethal. The use of scales is also possible, although for Arctic charr, scales tend to be limited in reliability as a result of possible reabsorption (Sprules 1952) and/or the close spacing of circulli that make the determination of the annulus in older individuals particularly difficult (Barbour and Einarsson 1987; Campana 2001). Furthermore, using reliable, non-lethal, and cost-effective methods to study the diversity of fish life-history patterns and tactics has become increasingly important in the face of current uncertainties related to environmental changes (Reist et al. 2013), particularly climate change.

Anadromy is more common at higher latitudes and in colder climates (McDowall 1987) where the productivity difference between fresh and marine waters is typically largest, thereby providing the greatest incentive for the adoption of migratory life-history tactics (Gross 1987). One consequence of climate warming may be a reduction in the productivity differential between fresh and marine waters likely to result from changes in terrestrial vegetation affecting nutrient and carbon fluxes into freshwater ecosystems that will increase their productivity (Karlsson et al. 2005; Larson et al. 2011). For northern fishes, the reduction in the productivity differences between habitats may reduce anadromy (Campana et al. 2020). For example, Norwegian Arctic charr are predicted to reduce the prevalence of their migratory behaviour as a result of changing productivity gradients, particularly in more southerly populations (Finstad and Hein 2012). Early indications based on historical catch records show such changes may already be underway, with increased temperatures having been related to the decreasing proportions of Arctic charr reported in angling data (Svenning et al. 2022). The reduced prevalence of anadromy in southern North American populations, where differences in freshwater and marine productivity are slight (e.g., Doucett et al. 1999), further argues for a likely reduction in anadromy as climates change. Furthermore, changes in the biodiversity of the marine environment through altered marine communities (Emblemsvåg et al. 2022; Husson et al. 2022), including prey, predator, and competitor species of the anadromous species, may influence the trade-offs of an anadromous life history. With life-history adjustments to climate warming already occurring, it is important to develop and test methods for the study and reporting of anadromy within and among Arctic charr populations. Such information will be essential for the continued monitoring and understanding of the status of both Arctic charr populations and their responses to climate change. Moreover, developing reliable and non-lethal methods to study fish migration patterns could also be applied to other salmonids with similar lifehistory (e.g., sea trout).

In fisheries ecology stable isotope ratios are now commonly used to examine habitat use, trophic position and niche breadth (Guiguer et al. 2002; Eloranta et al. 2013; McNicholl et al. 2018) and have been applied to the study of habitat switching in both marine (e.g., Herzka 2005; Fry and Chumchal 2011) and freshwater environments (e.g., Hesslein et al. 1991). Whereas $\delta^{13}C$ is useful for distinguishing between littoral and pelagic food webs in lacustrine ecosystems (France 1995), $\delta^{34}S$ is more useful for distinguishing between freshwater, estuarine and marine habitat use (e.g., Hesslein et al. 1993; Deegan and Garritt 1997; Leakey et al. 2008), including in Arctic charr (Doucett et al. 1999; Davidsen et al. 2020). This is because $\delta^{34}S$ values are low in freshwater and high in marine water (Peterson and Fry 1987; Fry 2006). In the marine environment, marine sulfates are known to vary little in both space (i.e., place and depth) and time (Rees et al. 1978; Fry 2006), with the mean sulfate content of marine water being enriched by 20.99 ‰ relative to the international standard for sulfur (Rees et al. 1978; Fry 2006). As stable isotope values provide a dynamic window into food assimilation rates (DeNiro and Epstein 1981; Carleton and Martinez del Rio 2010), they may be used as biological clocks to estimate the relative lengths of time an organism has depended on a given isotopically distinct resource pool. Thus, Davidsen et al. (2020) used sulfur stable isotopes to characterize the degree of dependency on marine prey by migrating Arctic charr in southern Greenland and showed a consistent rise in $\delta^{34}S$ as a function of size (length).

Here, we further develop and test an isotopic-based approach using $\delta^{34}S$ stable isotopes to estimate the number of marine migrations completed by an individual fish by correlating $\delta^{34}S$ in sample tissues to otolith-based estimates of migration frequency. The resulting relationship is then used to assign an estimated number of marine migrations for individuals not used in the estimation dataset to test the accuracy of the migration predictions. Using the combined actual and estimated number of migrations we assess migration-dependent feeding strategies with increasing marine experience by comparing estimated trophic niches in terms of both overlap and specialization to test the hypothesis that trophic niche decreases as the number of migrations increases. With the degree of niche overlap we test the hypothesis that niche overlap decreases as the difference between migration increases. Finally, we assess how the number of migrations completed influences fish condition and the proportion of sexually mature individuals, hypothesizing that both would increase as the number of completed migrations increased. Altogether, our study provides a baseline for migration patterns in Arctic charr and how these relate to anadromous life history strategy as a whole, providing us with an improved understanding of anadromy and new monitoring and management tools.

2 Methods

2.1 Location and sampling

Laksvatn (69°22'35''N, 19°22'00'' E) is an oligotrophic lake situated in the Balsfjord Kommune in Northern Norway approximately 60 km SE from the city of Tromsø (Figure 1). The lake has a surface area of 0.8 km^2, a mean depth of 6 m and a maximum depth of 15 m (https://www.vann-nett.no/portal/#/waterbody/198-51539-L). The lake contains a fish community consisting of brown trout (*Salmo trutta*), Arctic charr, and three-spined stickleback (*Gasterosteus aculeatus*). Atlantic salmon (*Salmo salar*) have been reported but are considered low in numbers. Based on sampling and local reports, pink salmon (*Oncorhynchus gorbuscha*) were observed in the watercourse in 2021 but have not yet established within the lake.

Arctic charr were sampled over two years (2020-21) from the outlet river and within Laksvatn after the ice break-up (May) to the onset of reproductive maturation in the fall (October). A fish trap built from a wooden frame (L×W×H 147×104×90 cm) and plastic-coated metal mesh (23×23 mm) with an opening allowing passage into the trap, but no exit, was set in the river ~180 m upstream of the head of tide. Two fences built of rebar spikes and the same plastic-coated metal mesh were installed from the riverbank to the opening of the trap to direct the fish into the trap. The trap was equipped with a removable lid to facilitate the removal of the fish by dip net. The fish trap was checked twice daily and if fish were present, they were removed, sampled, and returned to the river to complete their migration. In the spring the trap was configured to collect fish migrating to the marine environment and in early to mid-June, when outward migration ceased, the trap was flipped to sample returning fish. The care and use of experimental animals complied with the Norwegian animal welfare laws, guidelines and policies as approved by the County Governor of Troms and Finnmark, permit reference number 2020/14374.

Fish were removed from the trap a few individuals at a time. Netted individuals were placed in an anaesthetic solution of benzocaine and allowed to reach a state of total anaesthesia where no response was observed when touched. Anaesthetized fish were measured (total length, mm) weighed (g), and tagged with a floy-tag (Floy T-bar anchor FD-94, Floy Tag Inc., Seattle, Wa.) inserted near the posterior base of the dorsal fin. Adipose fin clips were randomly collected from a subset of individuals and immediately frozen for later analyses. After sampling, all fish were allowed to recover in a tub of oxygenated freshwater before being returned to the river.

A second random sample of individuals from the trap in both years was euthanized and frozen for later processing in the laboratory to collect otoliths and information on sex and maturity status. In October of both years, test fishing was performed in the lake to obtain a representative sample of the population. Multimesh gillnets made up of 12 randomly distributed panels measuring 2.5 m in width and 1.5 m in height (5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm) were used and set overnight. Nets were set in the littoral area (n=6, 0-10 m depth), profundal area (n=4, 10-16 m depth), and pelagic area (n=2, 6 m floating net set near the surface in the deepest area of the lake). Fish caught in the nets were frozen for later laboratory dissections.

Fish collected and preserved from the trap and the gillnet fishing were thawed and measured (fork length, mm) and weighed (g). We extracted the sagittal otoliths and preserved them in ethanol for later age analysis following protocols described in Kristoffersen and Klemetsen (1991). A muscle sample was excised from the posterior dorsal area between the dorsal and caudal fins and above the lateral line and immediately re-frozen (Guiguer et al. 2002). If the adipose fin was present, it was removed and frozen.

Frozen muscle and fin clip samples were freeze-dried (48h, -55°C, 120 µbar) for preparation for stable isotope analyses. Muscle samples were homogenized to a fine powder with a mortar and pestle, while fin tissue was cut into small pieces using laboratory dissecting scissors before being weighed.

Stable isotope values (δ^{13}C, δ^{15}N) for muscle and fin clip samples were determined from ground material (0.293-0.365 mg for δ^{13}C and δ^{15}N) at the Environmental Isotope Laboratory, University of Waterloo, Waterloo, Canada, using a CNSO elemental analyzer (Costech Analytical Technologies Inc., Valencia, USA) connected to a Delta Plus XL Continuous Flow

Stable Isotope Ration Mass Spectrometer (ThermoFinnigan, Bremen, Germany). Reported $\delta^{13}C$ and $\delta^{15}N$ data, respectively, consisted of corrected per mil (‰) values reported against the primary reference scale of Vienna Pee Dee Belemnite for $\delta^{13}C$ (Craig 1957) and atmospheric nitrogen for $\delta^{15}N$ (Mariotti 1983). Data quality control was monitored and maintained using an array of international reference materials and in-house standards calibrated using certified international references, including the International Atomic Energy Agency (IAEA) standards IAEA-N1 + N2, IAEA-CH3 + CH6, with international materials analyzed in each run. Acquired data were considered reportable with an error of 0.2‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$ based on the use of the above-described protocols.

Sulphur stable isotope values (1.896-2.136 mg for $\delta^{34}S$) were similarly determined at the Environmental Isotope Laboratory, using an Isochrom Continuous Flow Stable Isotope Ratio Mass Spectrometer (GV Instruments, Micromass, Manchester, UK) connected to a Costech Elemental Analyzer (CNSO 4010, Costech Analytical Technologies Inc., Valencia, USA). All results were reported in per mil (‰) notation expressed against the relevant international Vienna-Canyon Diablo Troilite meteorite standard (Rees et al. 1978). Analytical precision (±0.5 ‰) was maintained with monitoring and corrections made using international references and in-house standards calibrated against certified international reference materials including: IAEA-SO-5, IAEA-SO-6, NBS-127, NBS-123, and IAEA-S1 to-S3. With the use of these quality control and assurance checks, data were considered reportable with an error of 0.3‰.

2.2 Fin and muscle correction

As tissue samples were taken from both fin and muscle tissues to allow for non-lethal and repeat sampling of individuals, only certain individuals had a matched set of both sample tissues. This subsample of individuals was used to determine the linear relationship between the fin stable isotope ratio on the x-axis and the muscle isotope ratio on the y-axis for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$.

From the subsample of individuals with matched tissue samples, one individual was removed from all analyses as it was deemed to have a high influence (Cook's D >0.5) on the estimated fin-muscle relationships. A second individual was removed in the correction for nitrogen as the fin nitrogen value similarly exerted a high influence (Cook's D >1) on the estimated fin-muscle relationship.

To assemble the final dataset each fish was assigned only one value for each of the three stable isotopes ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$), measured fin values were preferentially used, with the data being supplemented with a corrected muscle value when a fin sample was unavailable. The muscle tissues were corrected to reflect the estimated fin stable isotope value with the use of the estimated linear relationships described above. If the slope of the relationship describing the correlation between the tissue types was significant, we then tested to determine if the confidence interval of the equations' slope included 1 and, therefore, suggested a direct relationship between the tested tissues (Larocque et al. 2021). If the slope was not significant, or significant and different from 1, we tested to determine if the mean difference between the tissue types was significantly different from zero using a one sample T-test. If the difference was significant, we added the mean difference to the muscle value to produce an equivalent fin value.

2.3 Otoliths and sulfur

Ages were estimated by counting pairs of annuli (translucent and opaque) on whole sagittal otoliths immersed in glycerol and then examined under reflected light with a stereomicroscope. Otolith ages were estimated independently by multiple readers. When discrepancies occurred in the age estimates, readers worked together to examine an otolith to achieve a consensus fish age. The age at which each individual undertook their first seaward migration was estimated by identifying the first band with increased growth, i.e. first large opaque annulus (Dahl 1926;

Jonsson and L’Abée-Lund 1993; Halden et al. 1995). The number of marine migrations was estimated by subtracting the age of the first migration from the estimated total age, as anadromous Arctic charr typically perform annual migrations to the marine environment following their first smoltification (Radtke et al. 1996, 1998; Mainguy et al. 2023), and adding one to account for the year of sampling.

With individuals having both an otolith-based estimate of number of migrations and an δ^{34}S value we built and tested a model for estimating the number of marine migrations based on δ^{34}S values. To predict the number of migrations performed based on individual δ^{34}S signatures we built and tested the model by splitting our dataset (n=83) of the known number of migrations (0 to 11) into model training (n= 66) and prediction testing (n=17) sets using an 80-20 split. Models tested for suitability predicting the number of migrations from the δ^{34}S included a logistic model, a logarithmic function, and an asymptotic linear regression built with the nls function in R (R Core Team 2021). Self-starting models were built using the *SSasymp* and *SSlogis* which estimated an asymptote from the training data. We also tested models where we fixed the asymptote to the maximum marine sulfate value of 20.99‰ (Rees et al. 1978). We could not estimate the number of migrations for individuals with a δ^{34}S signature greater than the estimated or fixed asymptote, therefore we estimated them as having one additional migration than the maximum estimated number of migrations. We then assessed the predictive ability of the models using the prediction testing data to select the model with minimum bias and the "best" predictive abilities as determined using prediction testing protocols described in Power (1993). The "best" model was then used to predict the number of migrations for individuals with no available otolith data (n=79).

2.4 Trophic niche

Layman trophic niche metrics, including the C and N range (Layman et al. 2008), were calculated alongside the Bayesian standard ellipse area, $\mathrm{SEA_B}$, to quantify isotopic niche breadth and overlap using the *SIBER* package (Jackson et al. 2011) in R. For the calculation of $\mathrm{SEA_B}$ a minimum of five observations are required per group, therefore individuals with more than five migrations (6 to 11) were pooled as a 6+ migration group (n=19) to be of a comparable sample size to the other groups. The $\mathrm{SEA_B}$ for each migration group was estimated with 10,000 iterations and a burn-in of 1,000 iterations. The posterior was thinned by 10, and 2 chains were run. Layman metrics for each group were calculated using the *laymanMetrics* function. We calculated the probability that niche width decreased with increasing migration by determining the percentage of all iterations where group n+1 had a smaller niche than group n, where n is the number of migrations. The niche overlap (A_O) was calculated for $\mathrm{SEA_B}$ using the function *bayesianOverlap* using all model draws (n=4,000). The percentage of the entire niche isospace shared between successive numbers of migrations ($A_n,\ A_{n+1}$) was calculated using the following formula: $\%\ overlap = \frac{A_O}{A_n + A_{n+1} - A_O} \times 100$ (Ogloff et al. 2019).

2.5 Life history

To calculate condition, we first assessed whether the relationship between length and weight was isometric and allowed the use of Fulton's condition factor (K) to characterize condition (e.g., Froese 2006). The linear model built to assess if an increase in condition was correlated with an increasing number of migrations included terms for sex and the number of migrations and an interaction term. We assessed if the model could be simplified using an F-test with the *drop1* command from the base *stats* package (Zuur et al. 2007; R Core Team 2021).

Logistic regression modelling was used to assess the probability of sexual maturity, with number of migrations or age used as the independent variable. The mean number of migrations for sexual maturity (M_{50}) and mean age at maturity (A_{50}) were calculated from the point with 50% maturity for both sexes combined and separated. Males with precocious maturity were excluded from this analysis. To assess our estimate of M_{50} we added it to the mean age of first migration (±se), as this should represent the mean age-of-maturity and compared it with our estimate of A_{50} (±se).

3 Results

3.1 Relationship between tissues

The slope of the fin and muscle tissue $\delta^{34}S$ relationship was not significant (slope=0.237, p=0.555), implying a need for a correction between these tissues (Figure 2). The mean difference between the tissues was significantly different from zero ($t_{(27)}=9.95$, $p<0.001$). Therefore, the mean difference (1.79) was added to muscle tissue $\delta^{34}S$ values. Carbon stable isotope values of fins and muscle had a significant slope (0.644, $p<0.001$; Figure 2). However, the confidence interval for the slope did not include 1 (slope 95% CI: 0.461-0.827; $R^2=0.677$), implying an indirect relationship between tissues and the need for a correction. The mean difference in $\delta^{13}C$ between the tissue types was significant ($t_{(26)}=7.71$, $p<0.001$) and we therefore added the mean difference (0.78) between tissues to make the muscle values comparable to fins. The slope (0.93, $p<0.001$) of the equation relating muscle nitrogen values with fin nitrogen values did not differ from 1 (slope 95CI: 0.633-1.231; $R^2=0.617$; Figure 2) implying a direct comparison between tissues.

3.2 $\delta^{34}S$ and migrations

The mean age at first migration of Laksvatn Arctic charr was three years (range 1 to 6), based on otolith growth patterns. Assuming repeated annual seaward migrations following the initial migration, our sample included fish having completed between one and 11 migrations. Individuals who showed no signs of a marine migration as assessed from otolith patterns, a lack of marine parasites, or who were untagged at capture in the lake, had an average δ^{34}S of 11.02±0.67‰ while individuals with one migration had a significantly higher mean δ^{34}S of 16.17±2.47‰ (Welch's $t_{(14)} = 7.649$, $p<0.0001$; Figure 3).

Sulfur isotopes increased with the number of migrations and were best predicted by an asymptotic linear regression model (Table 1). The asymptotic linear regression model with a fixed asymptote had the lowest mean error (0.250) and mean square error (1.000), although the mean absolute error was comparable between the models with an estimated (0.824) and fixed asymptote (0.647). Of the two asymptotic linear models, the one with the estimated asymptote (Equation 1) had the best predictive ability as estimated by Thiel's U^2 statistic (0.000; Table 1). This model was also the only model where the relationship between the estimated and actual number of migrations did not differ from a 1:1 relationship (Table 1). The model parameters of the asymptotic linear regression model estimated a δ^{34}S value of 11.28‰ for individuals which had never migrated to sea. Sulfur isotopes increased with each additional migration at a proportional rate of 0.59 (i.e., $e^{(-0.53)}$) which is relative to the asymptote of 19.80‰ therefore the rate of increase is largest at lower values of δ^{34}S and slowest when approaching the asymptote.

Equation 1

$$N_{mig} = 19.80 + (11.28 - 19.80) * e^{(-e^{(-0.53)\times\delta34S})}$$

By applying the estimated asymptotic linear regression model to the sample with no otolith-based migration patterns estimates (n=79), 22 individuals were determined to never have migrated to the marine environment. From these 22 individuals, only a single individual was captured from the trap (δ^{34}S=11.20) returning from the sea while the remaining were fished within the lake. The remaining individuals (n=57) had model-based migration estimates ranging from 1 to 7 summer migrations to the marine environment. Of all the fish where the model was applied, only 1 individual ($\delta^{34}S$= 19.88) had a $\delta^{34}S$ value greater than the estimated asymptote of 19.80 and was therefore assigned the largest estimated number of migrations.

3.3 Trophic niche and migrations

The standard ellipse area of the dietary niche decreased with increasing marine experience (Figure 4; Table 2). There was a trend in the SEA_B showing a decrease with additional marine migrations, i.e. SEA_B = 4.34‰^{2} at the first marine migration and was reduced to 0.38‰^{2} in individuals having completed more than five migrations (Table 2). The only exception to this trend was between the third and fourth migration where the niche size increased slightly with the SEA_B estimates (3: 1.53, 4: 1.65). The isotopic range in $\delta^{13}C$ and $\delta^{15}N$ decreased with each successive marine migration (Table 3) except for $\delta^{15}N$ from the third to the fourth migration (3: 2.14, 4: 2.94).

The trophic niche of migrating Arctic charr also changed with increasing migrations as there was little overlap between individuals performing their first migration to sea and experienced individuals with > 5 migrations. There was limited (SEA_B = 29.5%) overlap between individuals with exclusively freshwater feeding and those with a single migration. There was a trend where the dietary niche overlap between successive migratory cohorts decreased as a function of the mean number of migrations. Individuals with the most experience (i.e., 6+ migrations) had limited overlap with the niche of 5-time migrants (Table 3). There was a relative reduction in the overlap in trophic niche from the second to the third migration. From the third to fifth migrations, we again saw strong evidence for niche overlap. Finally, the most experienced individuals with > 5 migrations had little overlap with those who had an estimated 5 migrations (SEA_B = 33.6%) and no overlap (SEA_B = 0%), with those who had only one migration.

3.4 Migrations and life history

Fulton's condition factor was positively but weakly correlated (R^2=0.107) with the number of migrations (estimate 0.01, p=0.0088; Figure 5). Males had a lower condition than females (estimate -0.05, p=0.0371) and this was consistent throughout all number of migrations as an interaction between sex and number of migrations did not improve the model ($F_{(1)}$=0.0065, p=0.94). The probability of maturity increased with an increasing number of marine migrations with males achieving maturity earlier than females (Figure 6).

After two migrations the probability of maturity exceeded 50% in males (M_{50} =1.97) while among females mean number of migrations to reach maturity was estimated at 5.37 (Figure 6). The mean age at maturity (A_{50}) for males, excluding precocious individuals, was 4.6 years while females on average matured at the age of 7.38 years. Males first migrated at the age of 3 and females had a mean age of 3.48 at first migration. The intervals (mean ± s.e.) of the age-of-maturity (A_{50}) for males, females, and sexes combined all overlapped with the interval of the sum of the age of first migration and migrations to maturity (Figure 7). The youngest mature male in the dataset was 3 years old and had undertaken one known migration to the sea. This was consistent with the lower end of the range of the sum of the mean age at first migration and the mean number of migrations to maturity (3.97 years). For females however, the lower end of the range of the sum of the mean age at first migration and the mean number of migrations to maturity (7.71 years) did not include the youngest mature female from the dataset which was 5 years old and had been recorded in the return migration in both 2020 and 2021. All the mature females in the dataset had evidence of more than one migration before maturity including the youngest three mature females (ages 5, 6, and 6) which had undertaken 2 to 3 migrations before their sampling in 2021. The dataset also included mature males with no recorded migrations to the sea or a $\delta^{34}S$ signature indicative of exclusively feeding in the freshwater ($\delta^{34}S < 11.93$, n=

9) implying a precocious maturation and these individuals were not included in the analyses of age at first migration or migrations to maturity.

4 Discussion

Our otolith-based estimates for the number of marine migrations were correlated to $\delta^{34}S$ tissue signature. Therefore, $\delta^{34}S$ can be used to estimate the number of marine migrations completed as an alternative non-lethal method to otolith-based estimates. As individuals gain marine experience their trophic niche decreases in both area and isotopic range. With increasing marine experience, the trophic niche also shifts to niche spaces with higher $\delta^{15}N$ and $\delta^{13}C$ centroids that evidence decreasing overlap with first-time migrants. The trend suggests a gradual increase in specialization on higher-quality prey. Both condition and the proportion of mature individuals increase as a function of the number of marine migrations, with the relationship being stronger for maturation than for condition. Males mature with a mean of 1.97 marine migrations while females require 5.73 migrations to achieve maturity.

One of the findings of this study determined that a correction factor to convert muscle stable isotope values to the equivalent stable isotope values in adipose fin tissue is required for some stable isotopes. Unlike research conducted for other salmonid species (Larocque et al. 2021), our results suggested that sulfur needed a correction factor when comparing fin and muscle tissues in Arctic charr. Whereas Larocque et al. (2021) exclusively used samples from the freshwater environment that varied over a limited range of $\delta^{34}S$ values (~3‰) our current work used samples from multiple environments ranging over 12‰. Replication of studies comparing tissues over large $\delta^{34}S$ ranges is required to better assess the need for and establish a tissue-specific correction factor. Similarly to our results, the carbon signature of muscle tissue was depleted relative to fin tissues in other salmonids (Larocque et al. 2021) and Arctic charr (Curry et al. 2014) while nitrogen signatures did not differ between tissues (Curry et al. 2014).

Here, we introduced a new method for quantifying the number of marine migrations in anadromous Arctic charr based on non-invasive sampling using $\delta^{34}S$ analysis of fin tissues. To quantify the number of sea migrations in anadromous Arctic charr one needs to perform extensive mark-recapture studies, long-term telemetry studies, or use lethal sampling to characterize marine migration frequency from otoliths. In some anadromous salmonid species (e.g., Atlantic salmon), one might use scales, however, Arctic charr scales are seldom used as they are relatively small and encounter the problem of resorption (Sprules 1952). The method introduced here offers an efficient alternative non-lethal method to estimate the number of marine migrations for anadromous Arctic charr once validated for the specific waterbody. However, it is likely that the relationship between the $\delta^{34}S$ and the number of marine migrations will be waterbody dependent. Validation studies will need to be performed for each lake as $\delta^{34}S$ can be highly variable among freshwater lakes (Fry 2006; Swanson et al. 2011).

We demonstrate that the $\delta^{34}S$ signature increases with an increasing number of migrations. We are the first to use sulfur isotopes to quantify the number of marine migrations in a salmonid rather than only qualify an individual as having been to the marine environment or having a reliance on marine prey (Doucett et al. 1999; Swanson et al. 2011). Our model is further validated by the estimated asymptote (19.80‰) for tissue values of $\delta^{34}S$ as it is near the theoretical maximum $\delta^{34}S$ value in fish tissues of 19.5‰ (Davidsen et al. 2020).

In combination with our estimates of the number of marine migrations, we used stable isotopes of nitrogen and carbon to show the changes in trophic niches with differing levels of marine experience. Arctic charr is often described as a generalist and opportunist feeder due to its plasticity in diet, morphology, habitat use, and behaviour (Klemetsen et al. 2003; Rikardsen and Amundsen 2005; Davidsen et al. 2023). However, some studies suggest that although the species may be generalist, at the individual level, within both lacustrine populations (Amundsen

1995; Knudsen et al. 2011b) and while feeding in the marine environment (Grønvik and Klemetsen 1987; Knudsen et al. 2011a), Arctic charr are individual specialists. Our results show that individual specialization does not occur randomly but through a gradual shift with successive migrations that is common among individuals. Such patterns have been described in relation to an increase in size (i.e., length; Davidsen et al., 2020), but this is the first report of trophic specialization using estimates for the number of individual marine migrations.

The shift in trophic niche is extensive to the point that naïve migrants have no overlap with the most experienced migrants (six or more migrations). This is consistent with other findings where smaller anadromous Arctic charr exploit different prey than larger individuals while in the marine environment (Moore and Moore 1974; Dempson et al. 2002). From telemetry studies performed on anadromous Arctic charr it has been shown that first-time migrants exploit mostly nearshore areas of the fjord and the upper layer of the water (Atencio et al. 2021; Nordli et al. 2023), and feed mostly on zooplankton (Rikardsen et al. 2000). This is consistent with our results that the first-year migrants have the lowest carbon signatures indicative of pelagic feeding while at sea. However, the high variation in $\delta^{15}N$ also suggests that some first-time migrants may be feeding at higher trophic levels. Individuals with the most migrations attain or approach the estimated asymptote in our model which is an indication of full marine reliance in feeding (Davidsen et al. 2020) while the naïve migrants may continue to exploit freshwater sources to supplement their marine feeding (Rikardsen et al. 2003). The shift in trophic niche is not only through an increased reliance on marine prey but there is also a gradual increase to higher $\delta^{15}N$ and $\delta^{13}C$ with increased marine experience. The trophic position is indicated by $\delta^{15}N$ signatures and higher $\delta^{15}N$ is related to feeding at a higher trophic level (Post 2002; Eloranta et al. 2015). As anadromous fish increase in size, they may predate upon larger prey (Moore 1975; Grønvik and Klemetsen 1987) and will shift to a diet relying more heavily on higher trophic food sources and adopt a piscivorous diet relative to their smaller counterparts (Dempson et al. 2002). Indeed, anadromous Arctic charr have been found to have low consumption of fish during their first migration to the marine environment (Rikardsen et al. 2000), while becoming virtually exclusively piscivorous at lengths greater than 400 mm (Rikardsen et al. 2007). The gradual shift in trophic niche is likely related to the increase in size, thus larger mouth gape permissible for feeding on larger prey. An alternative explanation for the gradual shift in trophic niche is the possibility that anadromous Arctic charr behaviour may change with marine experience by potentially reducing their predator avoidance behaviour which allows exploiting different feeding opportunities (L’Abée-Lund et al. 1993). It has also been proposed that naïve migrants may learn to specialize on higher-quality prey while in the marine environment (Knudsen et al. 2011a).

We find that marine migrations have a positive, although weak, influence on condition in the anadromous Arctic charr corroborating, the findings of other studies (Young et al. 2021). Body condition is related to the ability to initiate maturity in salmonids (Adams and Huntingford 1997; Tveiten et al. 1998). The commonly accepted theory for anadromy is that the increased feeding opportunities have the resulting outcome of increasing fitness (Gross 1987). Therefore, body condition is part of what links anadromy to fitness as a life history strategy. All mature females had undergone marine migrations before maturity, while males required fewer marine migrations and could even mature as precocious freshwater residents without ever exploiting marine resources. Female Arctic charr therefore seem to have more to gain from migrations to the marine environment relative to males as fecundity is more closely related to size in female fish (Wootton and Smith 2014; Takatsu et al. 2023). Interestingly, we did not find differences between the sexes in the effect of an increasing number of migrations on their condition factor. Differences between sexes in the energy stores required to produce gametes have been noted before with females mobilizing a larger proportion of their lipids for maturation (Adams and Huntingford 1997). Although females use a greater amount of resources to mature, the condition factor is similar between sexes until after spawning where females have a greater decline in condition (Tveiten et al. 1998). Variation in life history strategies is common among salmonids, especially with some males adopting a precocious maturation in the freshwater (Foote and Larkin 1988; Thorpe 1989; Rikardsen et al. 2004; Nevoux et al. 2019). In salmonids, the male condition factor is linked to their individual life history trajectory (i.e., maturation vs. migration), however, the specific trajectory is conditional to the context (Hendry et al. 2004). Typically, juvenile Arctic charr with greater growth will migrate to the marine environment (Strand and Heggberget 1994; Grenier and Tallman 2021), while slower-growing individuals with high lipid levels remain in the freshwater to mature (Rikardsen et al. 2004). A precocious maturation in Arctic charr does not however imply a lifelong freshwater residency as these individuals may migrate to the marine environment later in life (Svenning et al. 1992).

Similar to our findings for the average number of migrations required to reach maturity, a recent study examining a long-term data series has determined that Arctic charr will usually mature after two to four migrations at sea (Jensen et al. 2019). The mentioned study however did not find differences between the sexes whereas here we found that females required multiple (5) migrations at sea while males needed only two. For most males that were recorded as having been to the marine environment, they were mature from their second migration. Although we found that females required a higher number of migrations than what has been found in the Hals watershed, which is further north from Laksvatn, we determined that females typically migrated to the marine environment at the mean age of 3.48 which is earlier than the mean age of 5.04 in the Halselva population (Jensen et al. 2012) and 6.00 years in the Storvatn population (Strand and Heggberget 1994). It is known that smolt age in salmonids follows a latitudinal gradient with northern populations first migrating to the marine environment later than southern populations (Power 1981; Økland et al. 1993; Klemetsen et al. 2003). The age of first migration has a large influence on the future growth and fecundity of Arctic charr (Jensen et al. 2012) adding further complexity to the possible trade-offs of an anadromous life history. Local environmental conditions, including those in both the freshwater and the marine environment, have a large influence on parameters of life history in the highly plastic Arctic charr (Rikardsen and Elliott 2000; Michaud et al. 2010) and latitude may also influence the age of migration through the productivity gradient between fresh and marine environments (Metcalfe and Thorpe 1990).

The method introduced here is the first to quantify the number of marine migrations using stable isotopes and show changes in trophic niches in Arctic charr with increasing marine experience. The diet during the marine phase of Arctic charr is characterized, however, studies have either examined anadromous Arctic charr population as a whole (Rikardsen et al. 2007; Swanson et al. 2011; Davidsen et al. 2023), by size classifications (Dempson et al. 2002), or focused only on first-year migrants (Rikardsen et al. 2000). The method developed further allows for interesting future research studying the diet and trophic niche of anadromous Arctic charr with increasing marine experience to examine if there are appreciable changes in the marine diet of Arctic charr with the number of marine migrations. Moreover, this is the first study to examine the number of marine migrations in relation to the maturation in anadromous Arctic charr. The population studied is located in a fjord where aquaculture is not allowed (Grenier et al. 2023), thus strengthening the results of this study as a baseline for our basic understanding of the anadromous life history strategy. Our method, which permits non-lethal sampling of individuals after a population-specific validation study, offers a promising and effective method of monitoring the fragile and threatened anadromous life history. This is especially important as the anadromous life history is under increasing environmental stress coming from causes such as climate change (Svenning et al. 2022), parasites (Grenier et al. 2023), and new invading species (Lennox et al. 2023).

5 Tables

Table 1. Statistics used for assessing the predictive ability of tested models, where the asymptote is estimated from the training data or fixed to 20.99. Mean error reported in I units. Models with lower mean square and absolute error are superior. A lower Theil's U indicates superior predictive abilities. A model with good predictive ability is expected to have a relationship between the predicted and actual value represented by a linear equation where the intercept β_0= 0 and the slope β_1= 1, represented here by the estimated terms 95% confidence intervals. The "best" model judged by each statistic is underlined.

Predictive statistic	Logistic (estimated)	Logistic (fixed)	Asymptotic linear (estimated)	Asymptotic linear (fixed)	Logarithmic
Mean error	2.250	3.250	2.000	0.250	0.500
Mean square error	2.294	1.941	1.529	1.000	1.882
Mean absolute error	1.235	1.000	0.824	0.647	0.941
Theil's U^2 statistic	0.186	0.134	0.000	0.091	0.184
β_1 95% CI	0.423-0.857	0.549-0.941	0.960-1.392	0.627-0.971	0.448-0.873
β_0 95% CI	0.606-2.148	0.669-2.062	-0.712-0.823	-0.081-1.154	0.161-1.672

Table 2. Summary of standard ellipse area (SEA$_B$, mean and 95% Bayesian credibility intervals, 95CI) with the change in mean SEA$_B$ with increasing migrations and the probability that the SEA$_B$ is smaller relative to n-1 migrations. The percent overlap between successive number of migrations (mean and 95% Bayesian credibility intervals) is also provided.

Migrations	N	SEA$_B$ (‰^{2})	95CI	Δ SEA$_B$ (‰^{2})	% Change in SEA$_B$ (‰^{2})	Probability of niche reduction	Overlap (%)	95CI
0	38	5.15	(3.70-7.18)					
1	16	4.34	(2.56-7.15)	-0.81	-0.16	0.00	29.5	(20.5-40.1)
2	21	2.02	(1.29-3.17)	-2.32	-0.53	0.99	39.7	(21.7-63.7)
3	22	1.53	(0.98-2.35)	-0.49	-0.24	0.71	54.7	(34.9-74.7)
4	18	1.65	(1.03-2.76)	0.12	0.08	0.00	51.8	(33.7-70.6)
5	13	0.77	(0.42-1.32)	-0.88	-0.53	1.00	35.8	(19.3-56.4)
6+	19	0.38	(0.24-0.62)	-0.39	-0.51	0.97	33.6	(11.3-58.8)

Table 3. Layman metrics for isotopic range of nitrogen and carbon for stable isotope trophic niche by number of migrations in anadromous Arctic charr from Laksvatn.

Migrations	N range	C range
0	6.35	7.09
1	4.43	6.08
2	3.64	3.51
3	2.14	3.14
4	2.94	3.15
5	1.43	1.74
6+	1.23	1.64

6 Figures

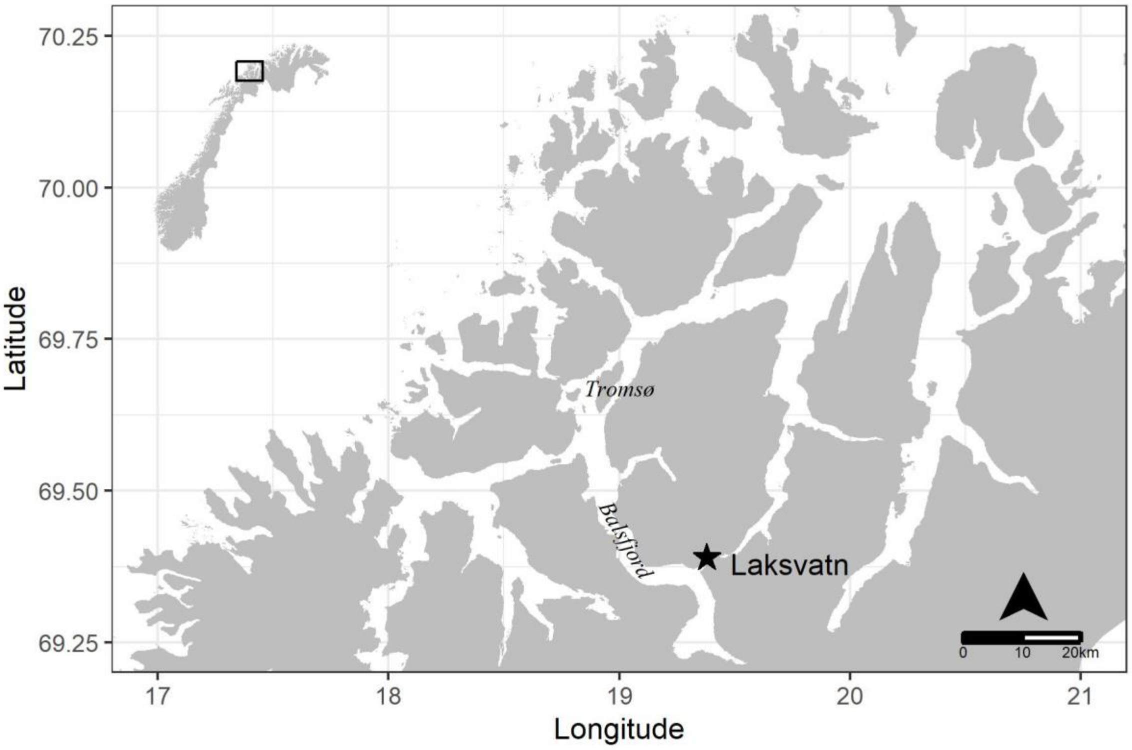

Figure 1. Map of the location of Laksvatn within Balsjfjord. The rectangle over the silhouette of Norway in the top left corner indicates the extent of the map.

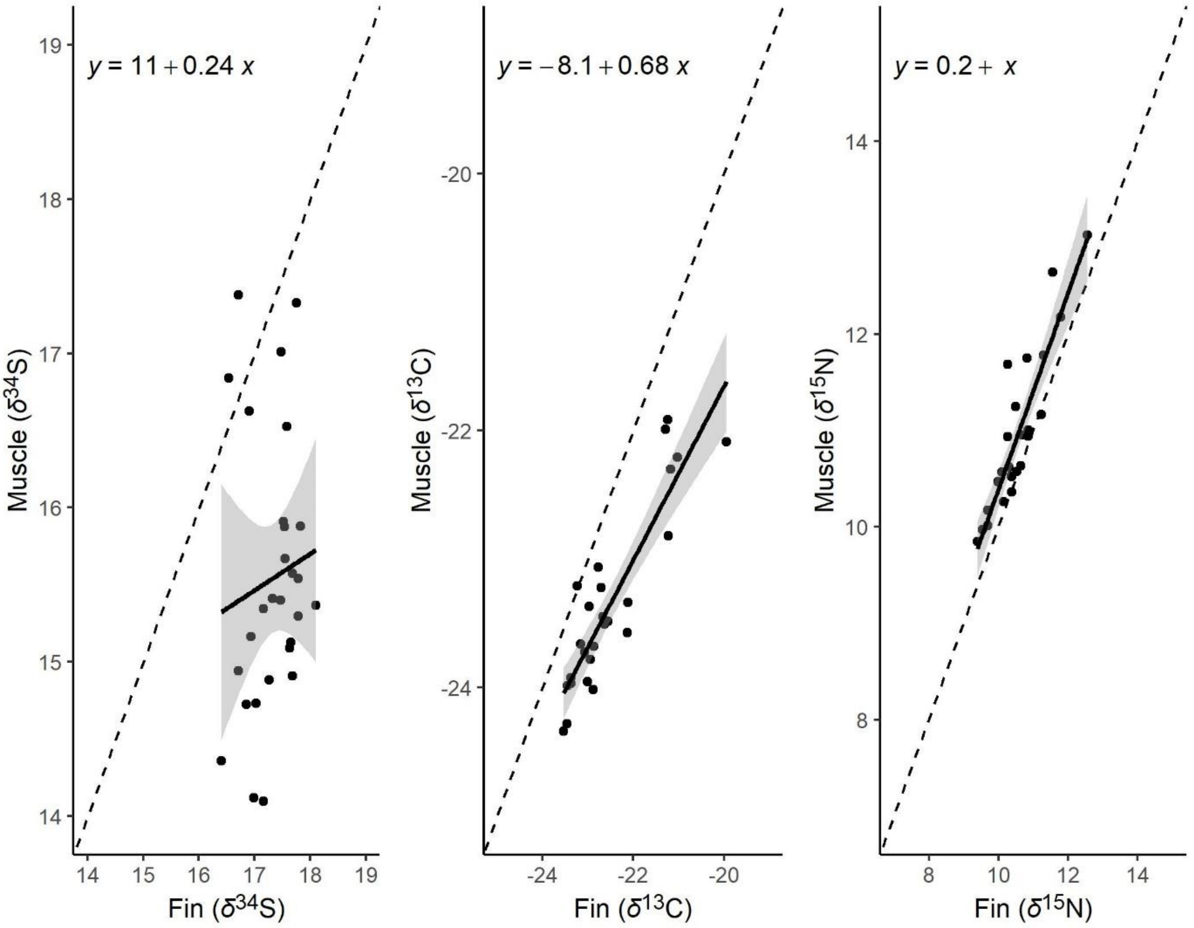

Figure 2. Relationships between δ^{34}S (left panel; n=28), δ^{13}C (center panel; n=27), and δ^{15}N (right panel; n=26) values of muscle and fin tissues in anadromous Arctic charr with paired samples. The linear equation of the relationship for each stable isotope is shown in the top lefthand corner of the panel. The dashed black line indicates the 1:1 direct relationship for reference.

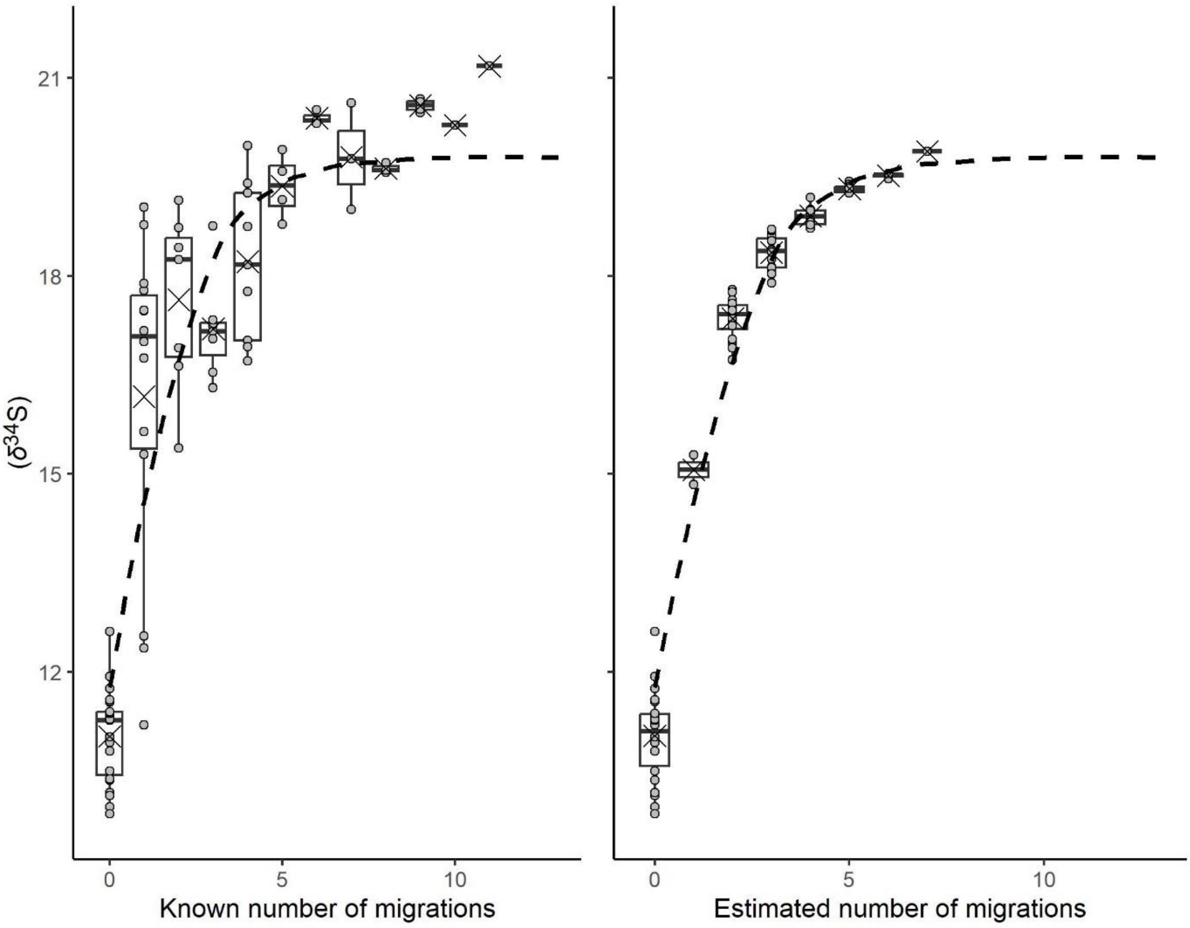

Figure 3. Increase in δ^{34}S with increasing number of known migrations for an individual and the estimated asymptotic linear equation (dashed line) used to predict the number of migrations. Boxplots represent the median (bold line) and interquartile range (box edges) with whiskers extending to encompass the range of the data. Mean is represented with an x.

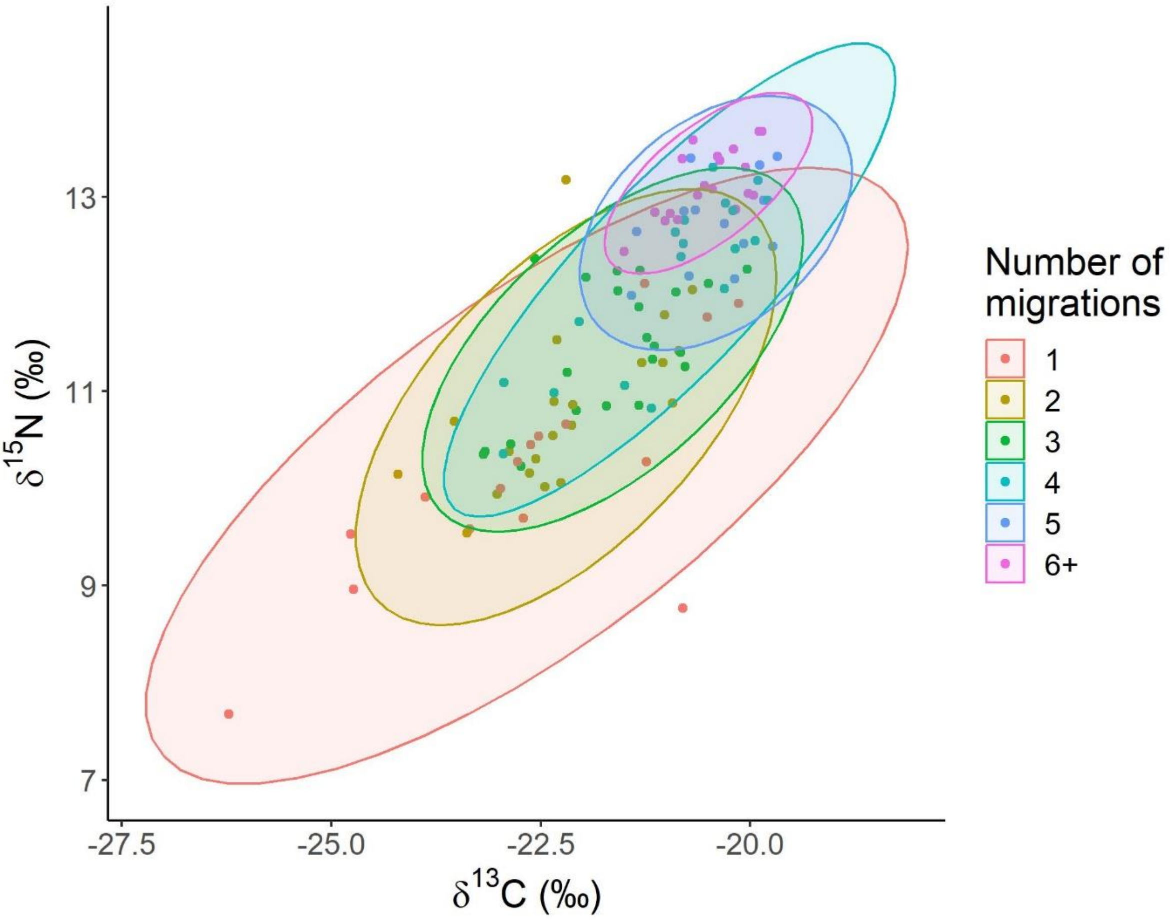

Figure 4. Standard ellipse areas (SEA_B) by number of migrations for Laksvatn Arctic charr. Fish with more than 5 migrations (6 to 11) are pooled as 6+.

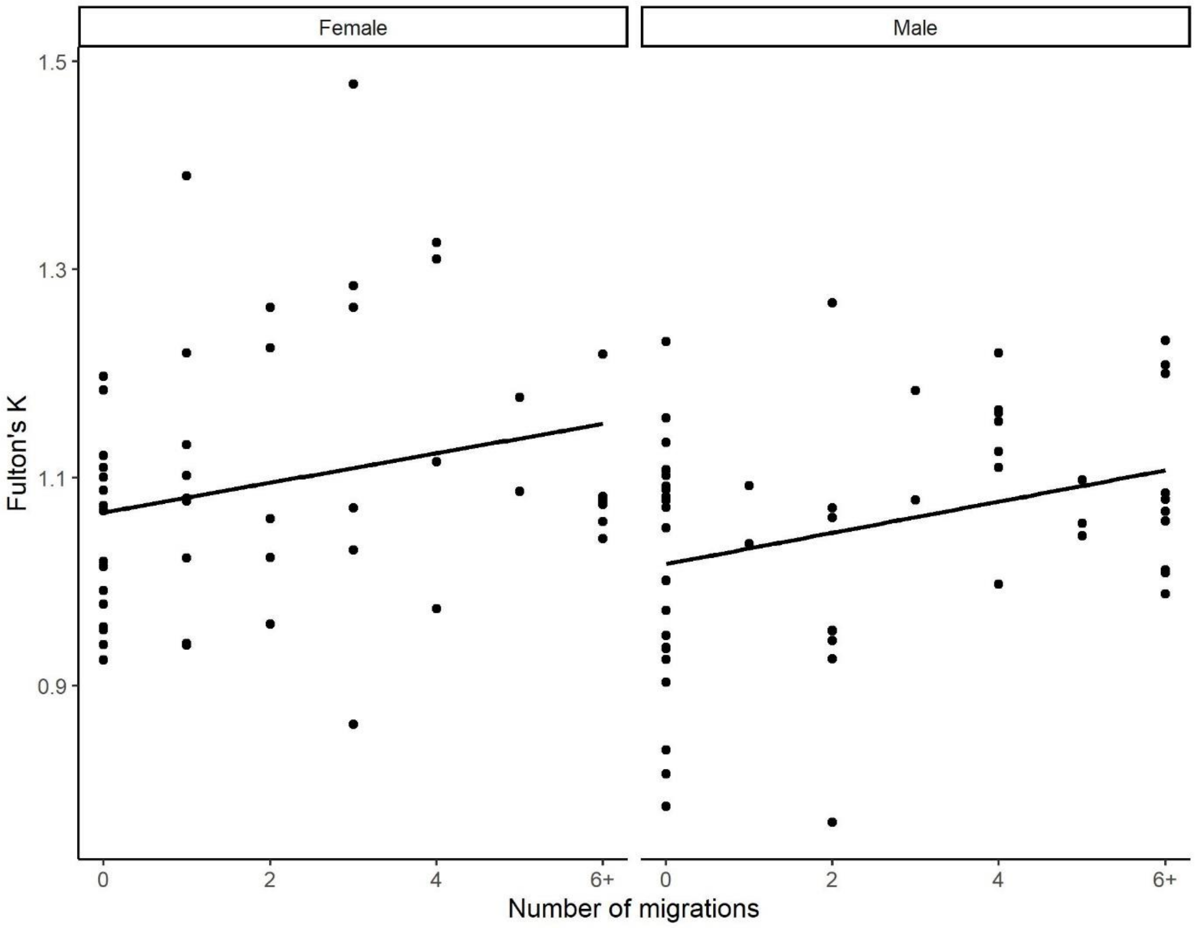

Figure 5. Condition factor (Fulton's K) with increasing number of migrations in female and male Arctic charr. Note that individuals with more than 6 migrations were pooled as 6+.

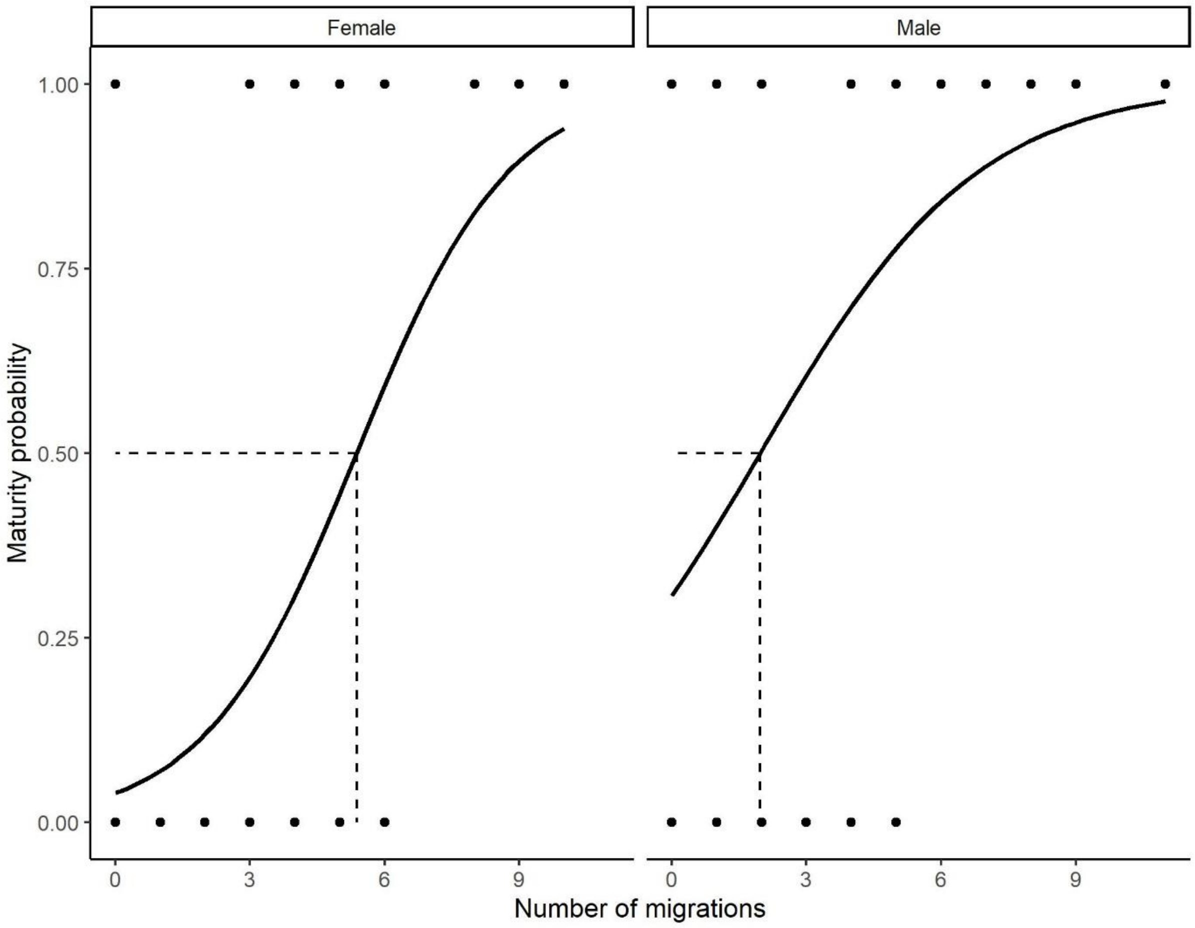

Figure 6. Logistic regression of the proportion of mature individuals by number of migrations for female and male Arctic charr. The migration where 50% of the population is mature (M_{50}) is indicated with a dashed line.

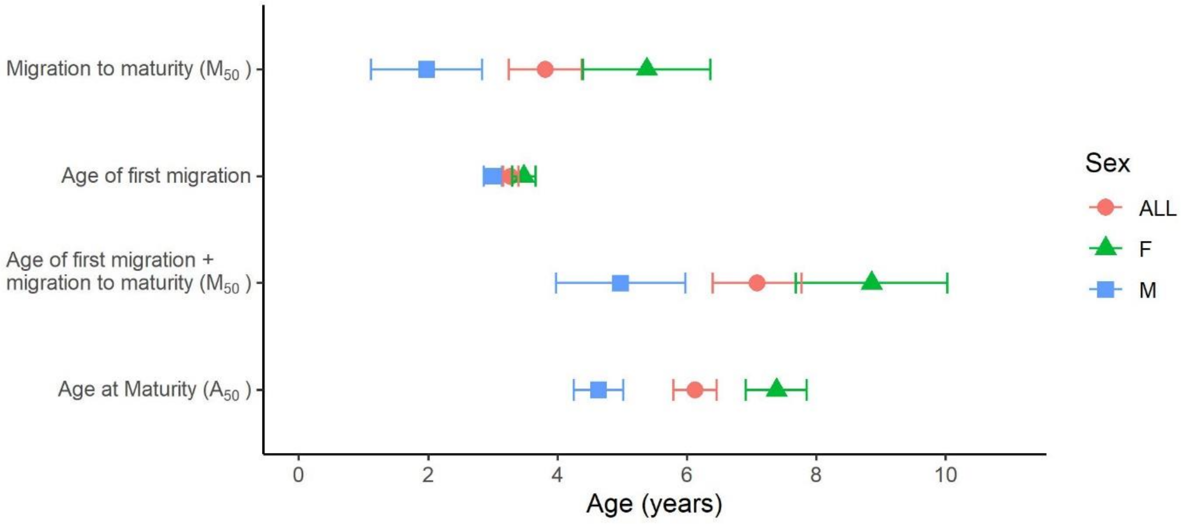

Figure 7. Age at maturity (A_{50}) and the sum of mean age of first migration and the estimated number of migrations to maturity for sexes combined (circle), females (triangles), and males (squares) in anadromous Arctic charr. The shape represents the mean and the line, the standard error of the mean.

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8 Supplementary materials

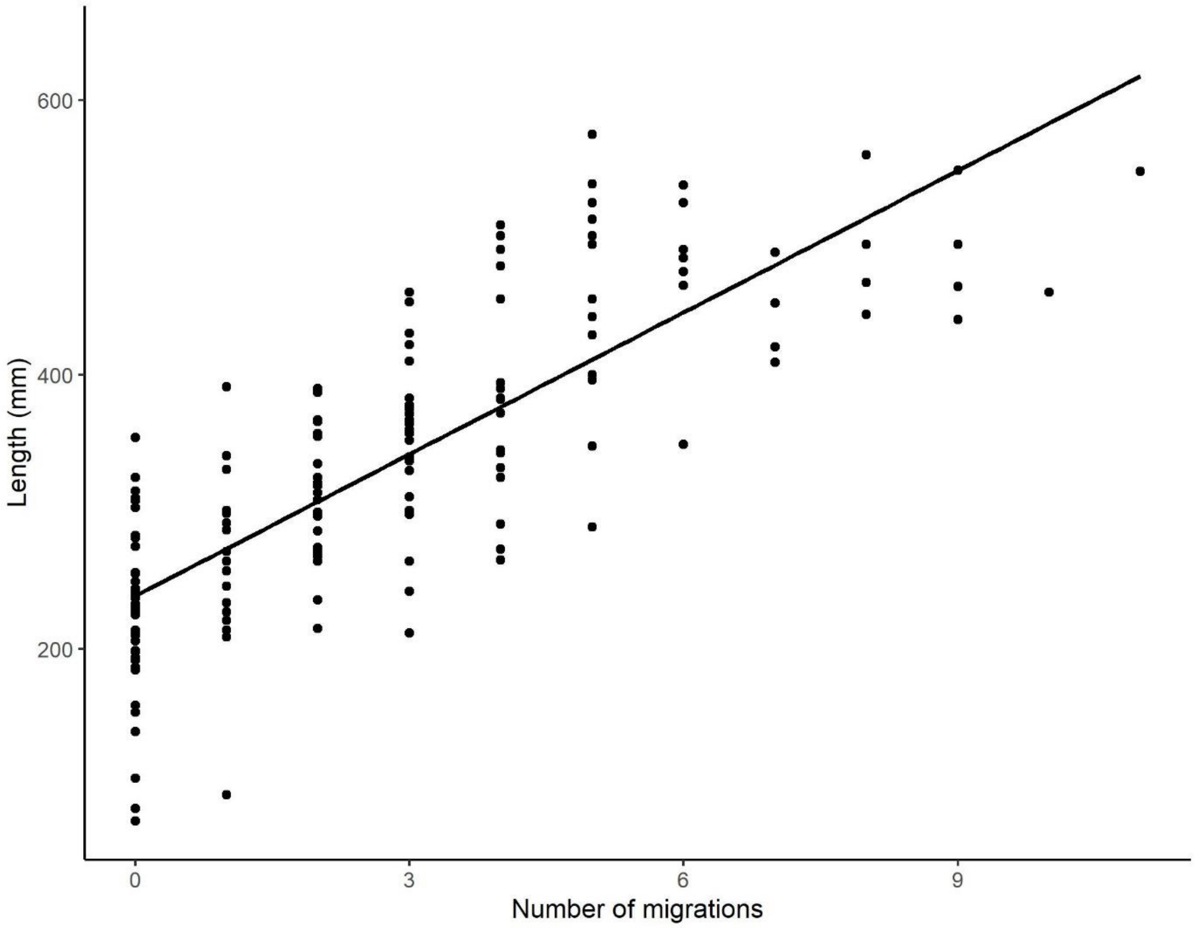

Figure S 1. Fish length as a function of the number of marine migrations completed.

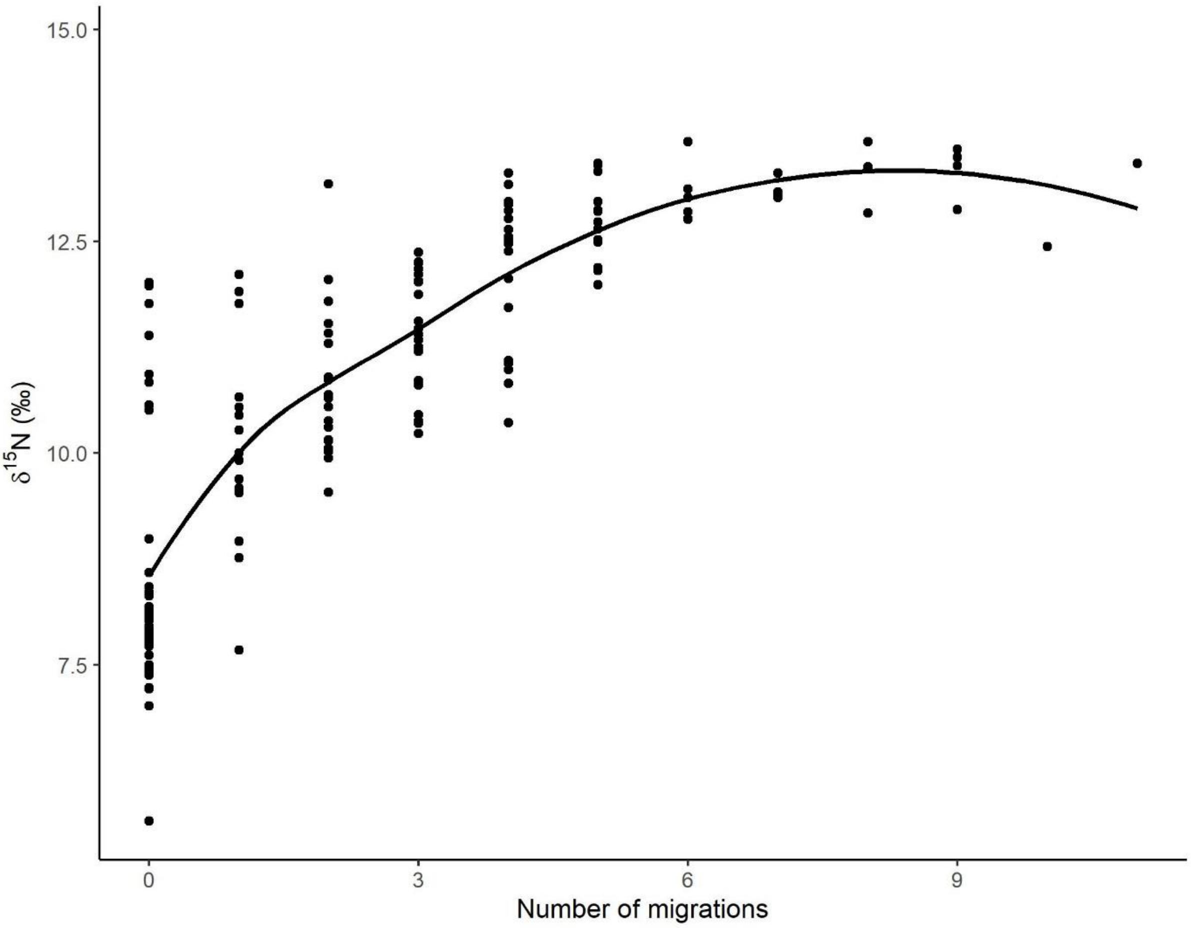

Figure S 2. Stable isotopes of nitrogen as a function of the number of marine migrations completed.