UiT The Arctic University of Norway

Faculty of Biosciences, Fisheries and Economics

Climate change impact on high latitude freshwater fish populations

Aslak Smalås

A dissertation for the degree of Philosophiae Doctor, June 2021

Supervisors

Professor Raul Primicerio
Norwegian College of Fishery Science
Faculty of Bioscience, Fisheries and Economics
UiT – The Arctic University of Norway
9037 Tromsø, Norway

Professor Per-Arne Amundsen
Department of Arctic and Marine Biology
Faculty of Bioscience, Fisheries and Economics
UiT – The Arctic University of Norway
9037 Tromsø, Norway

Acknowledgements

First of all, I want to thank my two fantastic supervisors, Raul Primicerio and Per-Arne Amundsen, for their fantastic support and guidance through the last four years. Both of you have always been positive and confident in the project and in me as a student. Thank you Raul for your inspiring enthusiasm towards science, our long hours of discussing ecology and scientific progress, and for your optimistic view on everything. Thank you Per-Arne for sharing your widespread knowledge on ecology and freshwater fish. For your everlasting care and concern for all your students, including me, and for the introduction to science as a social endeavor.

I would also like to thank the immense work that the Freshwater Ecology Group has done over the last 40 years. Their long-term data sets were fundamental for this thesis, and tons of people has been involved over the years. Especially our technicians, Laina Dalsbø, Jan Evjen, Cesilie Lien, Karin Strand Johannessen and Runar Kjær, together with the rest of the permanent staff, have been pivotal in collecting and maintaining these long-term data sets. I would also like to thank the members of the Freshwater Ecology group for their relentless focus on having a great time when working together, for all the social events and for including me as an equal member of the group. A special thanks to “god stemming gruppa” for being a vent for frustrations, for lifting spirits, for pulling the correct strings when needed and for all the laughs throughout the years. I am especially grateful for my two colleagues and dearest friends, Eirik and John, our time together at the university has been a pleasure and I am certain that without you I would have left science years ago. Thank you for making every day joyful and inspiring! It is hard to believe that Eirik and I started together as undergraduate students in 2008 and are now finishing a PhD only weeks apart. I am also grateful for the inclusion in the research group Bridge and to be involved in the ClimeFish project which I really enjoyed. A special thanks to the freshwater team within “ClimeFish” which I have learned a lot from. I am also grateful for the visits to IIASA and Ulf Dieckmann.

Finally, I would like to thank my family and friends for keeping my mind off work now and then. To my parents and my brother who sparked my interest in nature and for always being there and supporting me whenever I needed you. I am so grateful to my wife, Kristine, for your patience, endless love and support, and for always having a smile on your face when I arrive from work.

Table of contents

Summary

Climate change is one of the greatest threats to animal wildlife in high latitude freshwater ecosystems. Climate warming is rapidly increasing water temperatures in these areas, affecting biological processes of ectotherms such as growth, maturation and reproduction, which in turn trigger population responses. The magnitude of the effects of climate warming will vary depending on the thermal niche and phenotype of species. Climate change will continue to redistribute species, and fish species from warmer temperature guilds will invade and possibly take over areas where cold water fish currently dominate. Hence, it is important to establish the performance of cold vs warmer water species in a warming Arctic. The aim of this thesis is therefore to provide novel insights and predictions on population level implications of climate change for both cold- and cool water fish at high latitudes. The primary focus is on climate effects mediated by direct and indirect individual-level responses to increasing water temperatures, addressed using long-term empirical investigations and modelling in retrospective and prospective studies. In addition, the thesis addresses interactions between climate change and size-selective harvesting, a main pressure on high latitude fish populations, by modelling their cumulative effects to evaluate risks and reveal potential synergistic threats.

The thesis documents how both cold- and cool water fish at their northern range edge have increased their somatic growth rates during the last three decades of warming. However, the cool-water adapted vendace and perch displayed a higher increase in juvenile somatic growth with warming compared to cold-water Arctic charr and whitefish, stressing how the thermal niche modulates the magnitude of warming effects. The individual based models developed for this thesis predict a further increase in somatic growth towards year 2100 under warming scenarios (RCP-4.5, -8.5), with cool water fish displaying a greater increase in somatic growth rate than cold water fish. The documented and projected climate driven increase in

somatic growth rate mediates changes in survival rates and life history, including a likely increase in juvenile survival, and earlier maturation, the latter being contingent on species' maturation reaction norm. The demographic implications of these individual effects were investigated via modelling and long-term empirical studies.

The population level response to climate warming, mediated by individual effects, was evident in the cool water adapted perch, which experienced a substantial increase in density and importance relative to the cold-water adapted whitefish, which is dominant in the investigated lakes. The population response of this cool water fish was mediated by an increase in juvenile growth rate which resulted in larger size at age and earlier maturation, but also a likely increase in survival through the first critical winter. The modelled populations displayed higher biomass and yield as size at age increased with warming, but this effect was larger in the cool water specie than in the cold water species. In sum, cool water fish will benefit more from climate warming than cold water fish at high latitudes, and where they coexist, cool water fish may become the dominant player in the fish community.

The climate driven increase in size at age affects the age-specific exposure to size-selective harvesting, increasing the risk of younger individuals being caught by gillnets. The population level effect of earlier gillnet exposure is an increased age truncation, as illustrated by individual based model outcomes. Also, larger size at age increased the proportion of immature individuals being caught, with the magnitude of the effect being contingent on growth trajectories, their temperature dependence, and orientation of the maturation reaction norm. The increased juvenile mortality and more pronounced age truncation reduce recruitment, increasing the vulnerability of exploited populations to environmental stressors. Fish species with large size, slow growth, and late maturation like Arctic charr were more vulnerable to warming and harvesting than species with a faster life history, like vendace.

In conclusion, the stronger positive effects of warming on the performance of cool-water adapted species relative to cold-water salmonids, and the greater vulnerability of the latter when exposed to size-selective harvesting, warn of incipient reorganizations of Arctic fish communities, and invite climate adaptation in the management of high latitude populations.

List of papers

The thesis is based on the following manuscripts:

Paper I.

Smalås, A., Strøm, J. F., Amundsen, P.-A., Dieckmann, U., & Primicerio, R. 2020. Climate warming is predicted to enhance negative effects of harvesting on high-latitude lake fish. *Journal of Applied Ecology*, ***57***, 270-282. doi: 10.1111/1365-2664.13535.

Paper II.

Smalås, A., Primicerio, R., Dieckmann, U., Strøm, J. F., & Amundsen, P.-A. Temperature affinities and life history determine vulnerability of freshwater fish to multiple stressors in a warming Arctic. *Manuscript*.

Paper III.

Smalås, A., Primicerio, R., Kahilainen, K. K., Terentyev, P. M., Kashulin, N. A., Zubova, E. M., & Amundsen, P.-A. Increase in relative importance of cool-water fish at high latitudes emerges from individual level responses to climate warming. *Manuscript*.

Contributions

	Paper Ⅰ	**Paper Ⅱ**	**Paper Ⅲ**
Concept and idea	RP, PAA	AS, RP	AS, PAA, RP
Study design, data gathering and methods	AS, RP, PAA	AS, RP, PAA	AS, RP, PAA, KK, PT, NK, EZ
Data analyses and interpretation	AS, RP, JFS, UD	AS, RP, UD, JFS	AS, RP, PAA
Manuscript preparation	AS, JFS, PAA, UD, RP	AS, RP, UD, JFS, PAA	AS, RP, KK, PT, NK, EZ, PAA

Authors: Aslak Smalås (AS)[1], Raul Primicerio (RP)[1], Per-Arne Amundsen (PAA)[1], John Fredrik Strøm (JFS)[1,2], Ulf Dieckmann (UD)[3,6], Kimmo K. Kahilainen (KK)[4], Petr M. Terentyev (PT)[5], Nikolay A. Kashulin (NK)[5] and Elena M. Zubova (EZ)[5]

Affiliations:

[1] Faculty of Bioscience, Fisheries and Economics, UiT-The Arctic University of Norway.

[2] Institute of Marine Research, Tromsø, Norway.

[3] Evolution and Ecology Program, International Institute for Applied Systems Analysis, IIASA, Laxenburg, Austria.

[4] Lammi Biological Station, University of Helsinki, Finland.

[5] Institute of the Industrial Ecology Problems of the North (INEP) KSC RAS, Russia.

[6] Department of Evolutionary Studies of Biosystems, The Graduate University for Advanced Studies (Sokendai), Hayama, Kanagawa 240-0193, Japan.

1. Introduction

1.1. Effects of climate change in high latitude fish populations

Anthropogenic climate change is currently one of the greatest threats to both plant- and animal life, and the current speed of warming is unprecedented over the last 800 000 years (Bonan et al. 2015). The global average warming is 0.26°C per decade since 1950, and the ten warmest years since 1850 was all after 1997 (Bonan et al. 2015). There is no doubt that these changes in climate are driven by human overconsumption of natural resources, most notable the combustion of fossil fuel and deforestation (IPCC 2007, 2013). Although climate change is a global phenomenon, large regionally differences in both the rate and magnitude of warming is evident. High latitude ecosystems are experiencing a more rapid and greater warming than any other biomes on the planet, which makes these ecosystems potentially more vulnerable than others (Parmesan 2006, Wrona et al. 2016). Freshwater ecosystems hold a disproportional number of species, with 50 % of all fish species in the world residing in freshwater habitats (Hughes et al. 2021). These ecosystems are also disproportionally affected by anthropogenic stressors, with freshwater fish being five times more likely to be threatened than their marine or terrestrial counterparts (Strayer & Dudgeon 2010). In sum, high latitude freshwater ecosystems seem extremely sensitive and vulnerable to present and future anthropogenic climate change.

Similarly as air temperature, lake water temperatures are increasing globally, with lakes in northern Europe having a more rapid temperature increase than the global average (O`Reilly et al. 2015, Woolway et al. 2020). The increase in water temperature has led to changes in ice phenology, where the duration of ice cover is becoming increasingly shorter in high latitude lakes (Sharma et al. 2013, Warne et al. 2020, Woolway et al. 2020), and projected future loss of lake ice is widespread throughout the northern hemisphere (Sharma et al. 2019). A longer open season may alter the mixing regimes (Woolway & Merchant 2019), with an earlier and more stable and durable summer stratification (Woolway et al. 2020), which may increase the hypoxic conditions of the deep-water layers in high latitude dimictic lakes (Ficke et al. 2007). In addition, an increase in water temperature and subsequent shorter duration of ice cover may lead to an increase in pelagic productivity and eutrophication (Allan et al. 2005, O`Bierne et al. 2017, Maeda et al. 2019), which may fuel an increase in littoral productivity of high latitude lakes (Hayden et al. 2019). On the other hand, studies have revealed that climate warming might lead to browning of lake water from increased dissolved organic carbon mediated by increased precipitation and terrestrial greening, which might decrease lake productivity (Finstad et al. 2016, van Dorst et al. 2019). Hence, climate change will have large, complex and non-linear effects on the physical properties of high latitude lakes, which in turn may have dramatic effects on ecosystem processes and functioning (Dodds et al. 2013, Beneatau et al. 2019).

High latitude lake fish communities in Europe are chiefly dominated by cold water (opt. temp range, 6-18 °C) salmonids and to some extent also featuring cool water (opt. temp range, 15-25 °C) fishes like percids, pikes, minnows and sticklebacks (e.g. Magnuson et al. 1979, Reist et al. 2006). These ecosystems are located towards the northern distribution range of these cool water fishes, and effects of temperature appear to be greatest at the extremes of the geographic range of a species (Power & van den Heuval 1999). It is projected that fish will expand their ranges both northwards and to higher altitudes as water temperatures continue to increase (Reist et al. 2006, Comte et al. 2013, Campana et al. 2020), which may allow them to establish and potentially impose negative impacts on native species already present (Hayden et al. 2013, van Zuiden et al. 2016). Future climate warming will in addition favour cool water fish over cold water fish where they coexist (Ficke et al. 2007, Heino et al. 2009, Hein et al. 2012), and reductions in abundance and local extinctions of cold water fish in coexistence with cool water fish has already been seen across Europe and North-America (Reist et al. 2006, Jeppesen et al. 2012, Connor et al. 2019, Morrissey-McCaffrey et al. 2019). The northern border of the distribution of cool water and temperate fish are often restricted by cold summer temperatures and a long ice-covered period (McMeans et al. 2020). This affects especially the bottleneck life stages in these fishes (Dahlke et al. 2020), where a short open season with relatively cold water temperatures reduces normal development in eggs and reduces juvenile growth rate to a minimum, which substantially enhances mortality during their first winter (Heerman et al. 2009). This severely limits their survival and recruitment, but future projected water temperatures might enable establishment of cool water fish in high latitude regions.

Lakes are like isolated islands in an ocean of land, and migration between lakes are thus difficult and dependent on waterways that are possible for fish to migrate in, or they have to be translocated by humans (Crook et al. 2015). Therefore, freshwater fish species might be more vulnerable than e.g., marine fish under climate warming, because movement to colder refuges might not be possible (Woodward et al. 2010). Fish, as ectotherms, can only thermoregulate behaviourally as they have the same body temperature as the surrounding water. Hence, if migration northwards or to higher altitudes is prevented, they might select microhabitats where temperatures are closer to their optima (Ficke et al. 2007). Towards the southern range of cold water fish distribution, these fishes seek temperature refuges in the cooler hypolimnion of lakes during summer (Regier & Meisner 1990, Gerdaux 1998). However, the hypolimnion becomes increasingly hypoxic as climate warms (Gerdaux 1998), which is further restricting the available habitat of cold water fishes (Ficke et al. 2007). At the individual level, all biological rates vary as a function of body temperature, meaning that growth, reproduction, behaviour and activity are directly influenced by changes in temperature (Biro et al. 2007, Arula et al. 2017, Huss et al. 2019). Temperature-dependent growth mediates many of the organismal and population effects of climate change (Deutsch et al. 2008, Ohlberger 2013).

1.2. Temperature-dependent somatic growth mediates effects of climate change

In the simplest form, individual growth follows the principle of bioenergetics, where the energy available for growth is the difference between food consumed and the metabolic cost and waste products lost, meaning that growth is dependent on the net energy gain (Jobling 2002, Huey & Kingsolver 2019). The amount of consumed food, or the consumption rate, is dependent on the availability of food and the ambient temperature. The availability of food is dependent on the productivity of the environment, the amount of preferable prey items and number of competitors in the ecosystem (Lorenzen & Enberg 2002, Amundsen et al. 2007, Burian et al. 2020). Given excess availability of food, consumption rate increases with temperature up to an optimum temperature, before it drops precipitously (Koskela 1997, Jobling 2002) (Fig. 1, black line). The metabolic rate of fish is dependent on body temperature, where it increases exponentially with temperature (Gillooly et al. 2001, Brown et al. 2004) (Fig. 1, red line). Metabolic rate is in addition allometrically scaled with body size (Brown et al. 2004, Killen et al. 2010). Waste products could be divided into three different parts which are either proportional to the consumed (egestion) or the assimilated energy (excretion and SDA) (Jobling 1983, Deslauriers et al. 2017) (Fig. 1, grey lines). The part of the consumed energy that is not used for metabolic processes or waste products is thus available for somatic or gonadic growth, depending on the maturation status of the individual.

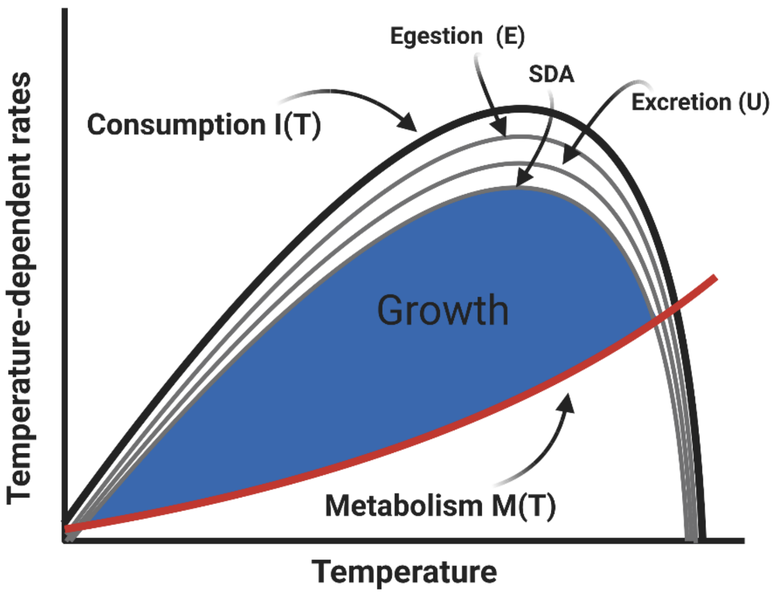


Figure 1. Temperature-dependent rates in fish. The black line (—) shows the relationship between consumption rate and temperature, the red line (—) shows the relationship between metabolic rate and temperature, the grey lines (—) depicts the relationship between consumed energy and energy lost to egestion (E), excretion (U) and standard dynamic action (SDA), and the blue area (—) shows the relationship between available energy for growth (or reproduction) and temperature.

Climate warming will increase water temperatures and therefore also body temperatures of fish inhabiting high latitude lakes. Therefore, climate warming might impact the net energy gain of individuals (Huey & Kingsolver 2019). Increase in ambient temperature will increase the body temperature and metabolic cost of ectotherms, which will lead to a higher demand of energy needed to sustain maintenance, growth and reproduction (Jobling 2002, Ficke et al. 2007, Strand et al. 2011). If this demand is not met by an increase in consumption, e.g., due to a limitation of available food resources, the optimum temperature for growth will decrease (Huey & Kingsolver 2019, see section 2.3.2). Therefore, a warmer world might lead to less energy available for growth and somatic growth rates might accordingly decrease. However, in high latitude lakes, food availability might increase with warming because productivity is likely to increase with longer ice-free season and higher summer temperatures (O`Bierne et al. 2017). Therefore, it is predicted that somatic growth rates might increase with warming in high latitude freshwater ecosystems, especially for juvenile fish (Pörtner et al. 2001, Reist et al. 2006, Deutsch et al. 2008, Huss et al. 2019). An increase in individual growth rates might have substantial effects on the population dynamics of size-structured fish species.

In fish, individual growth rates mediate other vital rates, such as mortality, maturation and reproduction (Wootton 1998, Heibo et al. 2005, Ohlberger et al. 2011). In size-structured fish populations these vital rates govern population dynamics, ecological interactions and community structures in freshwater habitats. For instance, an increase in juvenile somatic growth reduces the time in critical life stages, which might lead to higher survival and possible higher recruitment (Anderson 1988, Kjellman et al. 2003, Stawitz & Essington 2019). In addition, winter mortality of cool water fish in high latitude lakes depends often on the amount of energy acquired through somatic growth during the summer, and an increased somatic growth will therefore increase winter survival of these fishes (Johnson & Evans 1990, Heerman et al. 2009). Maturation schedules are phenotypically plastic, with the corresponding maturation reaction norms determining the age and size at maturation conditional on somatic growth (Heino et al. 2002). Therefore, an increase in growth rate will lead to larger size at age and possible a change in age and size at maturity, as individuals tend to mature at a younger age with faster growth (Dieckmann & Heino 2007). Lower age at maturation leads to a shorter generation time that might increase individual fitness (Kingsolver & Huey 2008), which might further lead to higher population fecundity depending on adult mortality and longevity. The temperature-size rule gives similar predictions, where ectotherms living in warmer conditions grow faster and mature at a younger age, but reaches a smaller final body size than conspecifics living in colder environments (Atkinson 1994, Angilletta et al. 2004, Kingsolver & Huey 2008, Verberk et al. 2021).

1.3. Size-selective harvesting

In addition to climate change, freshwater fish, are often experiencing a multitude of additional stressors, many of which are from anthropogenic sources and acting synergistically with global warming (Woodward et al. 2010, Green et al. 2015). These additional stressors might amplify or mitigate the effects of climate change (Feuchtmayer et al. 2009, Gissi et al. 2021). In high latitude freshwater ecosystem, some of the most notable anthropogenic stressors outside climate change are eutrophication, acidification, introduction of non-native species and harvesting. For instance, with wetter conditions, as projected with future climate change, run-off of nutrients from land will be higher, potentially amplifying eutrophication in high latitude lakes (Hessen et al. 1997, Jeppesen et al. 2012). Introductions of more warm tolerant species in high latitude lake systems will have greater potential for establishing when temperatures increase, which might have dramatic effects on native species and alter ecosystem functioning (Schindler 2001, Jeppesen et al. 2012, Cazelles et al. 2019).

For size-structured fish populations, selective harvesting or overharvesting are a major threat (Allan et al. 2005, Hughes 2021). The most striking example is the collapse in the cod population in the north-west Atlantic, where fisheries reduced the population to almost zero in the early 90ies, and the cod population size still remain historically low (Hutchings & Myers 1994, Olsen et al. 2004, Neuenhoff et al. 2019). Humans are important predators in high latitude lakes as well, especially in species poor ecosystems (Hughes 2021). For instance, fisheries can reduce the number of fish competitors, thereby indirectly promoting density-dependent growth (Amundsen et al. 2007, Persson et al. 2007). Harvesting of fish populations is often size-selective, targeting large and therefore also older individuals (Hansen et al. 1997, Fenberg & Roy 2008). Accordingly, a common outcome of size-selective harvesting is a truncation of size- and age-distributions as a consequence of the removal of large individuals (Conover & Munch 2002, Heino & Godø 2002). Such removals may change the character of size-structured interactions, leading to altered growth rates and changes in age and size at maturation of the fish that remain in the population (Law 2000, Olsen et al. 2005). In many populations, large fish contribute the most to recruitment and may provide a buffer against environmental perturbations (Berkeley et al. 2004, Anderson et al. 2008, Hsieh et al. 2010). Furthermore, size-selective harvesting may even cause evolutionary changes in body size and maturation schedules, and these evolutionary changes might not easily be reversed (Kuparinen et al. 2007, Enberg et al. 2009, Heino et al. 2015). Climate change will act as an additional stressor for already heavily exploited freshwater stocks and the cumulative effects of these two stressors are hard to predict.

1.4. Long-term perspective of causal ecological understanding

Climate change, as opposed to weather, are only measurable on a decadal or even longer time perspective. Therefore, ecological climate change impact studies are per definition only feasible to investigate in a similar long-term perspective (Willis & Birks 2006, Amundsen et al. 2019). The availability of continuous biological data in natural ecosystems on such a time frame is still relatively rare and recognized as highly valuable from a broad scientific community, especially in ecosystems at high latitudes (or the Arctic) (CBMP 2019). More commonly climate change impact studies either adopt experiments to artificially change climate driven variables, or use scattered sampling points over time, space-for-time approaches to mimic future conditions, scenario-based modelling or distribution modelling. However, a few multi-decadal long-term series do exist, potentially giving causal understanding on how climate warming affects ecosystems in the high north. These programs often follow what is called an adaptive monitoring framework (Lindenmayer & Likens 2009). The goal is typically to follow the development and processes as they unfold, instead of studying only start- and endpoints during a perturbation, which would be less valuable for a causal understanding of the mechanisms that led to the observed change. The adaptive monitoring framework advocates an iterative study design with well-defined scientific questions, rigorous statistical approach and a robust conceptual model for the targeted system in order to have a strong knowledge basis for adaptive management (Lindenmayer & Likens 2010, Amundsen et al. 2019). The community responses and the dynamic properties of populations from any perturbation may only be mechanistically understood when monitored over time.

1.5. Objectives

The principal aim of the thesis is to provide novel insights into how freshwater fish populations at high latitudes are affected by past and future climate warming. The thesis pursues a causal understanding of how temperature affects individual growth and life history in wild fish species, and the population level implications of these individual effects of climate warming. Further, I aim to investigate how multiple stressors, here in terms of climate warming and size-selective fisheries, jointly affect these fish populations. The explicit objectives are to:

- Investigate how climate warming has affected individual growth rates and life history in wild cold- and cool water freshwater fish populations using long-term studies in high latitude lakes (paper II & III).

- Project how climate change might affect somatic growth and life history of both cold- and cool water fish towards year 2100 using climate models and stock-specific parameterized individual based models (IBM) (paper I & II).
- Contrast the population level effects of past and future climate change between cold- and cool water freshwater fish at high latitudes, mediated by individual level responses to increased water temperatures (paper I, II & III).
- Investigate the cumulative effects of climate change and size-selective harvesting on freshwater fish species differing in both thermal preference and life history strategies (paper I & II).

Before presenting the results of the study (chapter 3), the thesis will include: a description of the method developments and challenges associated with projecting future climate, water temperature and ecological effects of climate change (chapter 2.2.-2.3). After a brief summary of the results presented in the thesis, a discussion of findings in relation to known theory and previous studies will be presented (chapter 4).

2. Methods

2.1. Study Area

In order to study how climate warming impact both past and future populations of freshwater fish, we investigated two different areas of northern Fennoscandia. Paper I addresses future climate change impacts on Arctic charr, the most cold water adapted freshwater fish in the world (Klemetsen et al. 2003), taking advantage of a 40-year long-term study in Lake Takvatn in north-western Norway (Fig. 2). Paper II compares three different cold water adapted freshwater fish in terms of vulnerability to climate change and size-selective harvesting, utilizing data from both Lake Takvatn and a 30-year long-term study conducted in the Pasvik watercourse in north-eastern Norway. Paper III investigates the effects of climate warming on a cool water adapted freshwater fish species in the Pasvik watercourse (Fig. 2).

Lake Takvatn has an area of 15 km^2, and is a dimictic lake located in the western part of northern Norway. It is situated well above the Arctic Circle at 69°N with an altitude of 214 m a.s.l and maximum depth of around 80m (Amundsen et al. 2009). The climate at Lake Takvatn is relatively cold, with maximum surface water temperatures seldom exceeding 14°C and the lake is usually ice covered from late November/early December to late May/early June (Smalås et al. 2020). The fish community consists of two salmonids, a native brown trout (*Salmo trutta*) population and Arctic charr (*Salvelinus alpinus*), which was introduced in the lake in 1930, as well as three-spined stickleback (*Gasterosteus aculeatus*), which was introduced in the 1950ies (Klemetsen et al. 1989). From the mid-80ies towards the early 90ies a large culling experiment was conducted to reduce the overcrowded Arctic charr population and to restore the almost absent brown trout population (Amundsen et al. 1993, Klemetsen et al. 2002). The experiment was successful and today there are almost equal densities of the two salmonid populations in the littoral zone of the lake (Persson et al. 2013, Amundsen et al. 2019).

In the Pasvik watercourse (Fig. 2), Lake Skrukkebukta was the main study site for this study. The watercourse is located above the Arctic Circle (69°N) in the eastern part of northern Norway, constituting the Russian-Norwegian border. Lake Skrukkebukta is dimictic, with an altitude of 21 m a.s.l. and a maximum depth of around 40 m (Sandlund et al. 2013). The climate here resembles more of a continental climate, with cold winters and relative warm summers, leading to maximum surface water temperature during summer of around 22°C, which is much higher than in Lake Takvatn. Because of cold winters, the ice duration is similar in Lake Skrukkebukta as in Lake Takvatn (Sandlund et al. 2013). The fish community consists of in total 15 species, with whitefish (*Coregonus lavaretus*), perch (*Perca fluviatilis*), northern pike (*Esox lucius*), nine-spined stickleback (*Pungitius pungitius*), grayling (*Thymallus thymallus*), burbot (*Lota lota*), brown trout (*Salmo trutta*) and the introduced vendace (*Coregonus albula*) dominating the lacustrine fish community (Amundsen et al. 2003). The vendace was introduced in Lake Inari in the 50-ies and has migrated downstream to lakes in the Pasvik watercourse, now dominating the pelagic zone of many lakes in the watercourse (Sandlund et al. 2013).

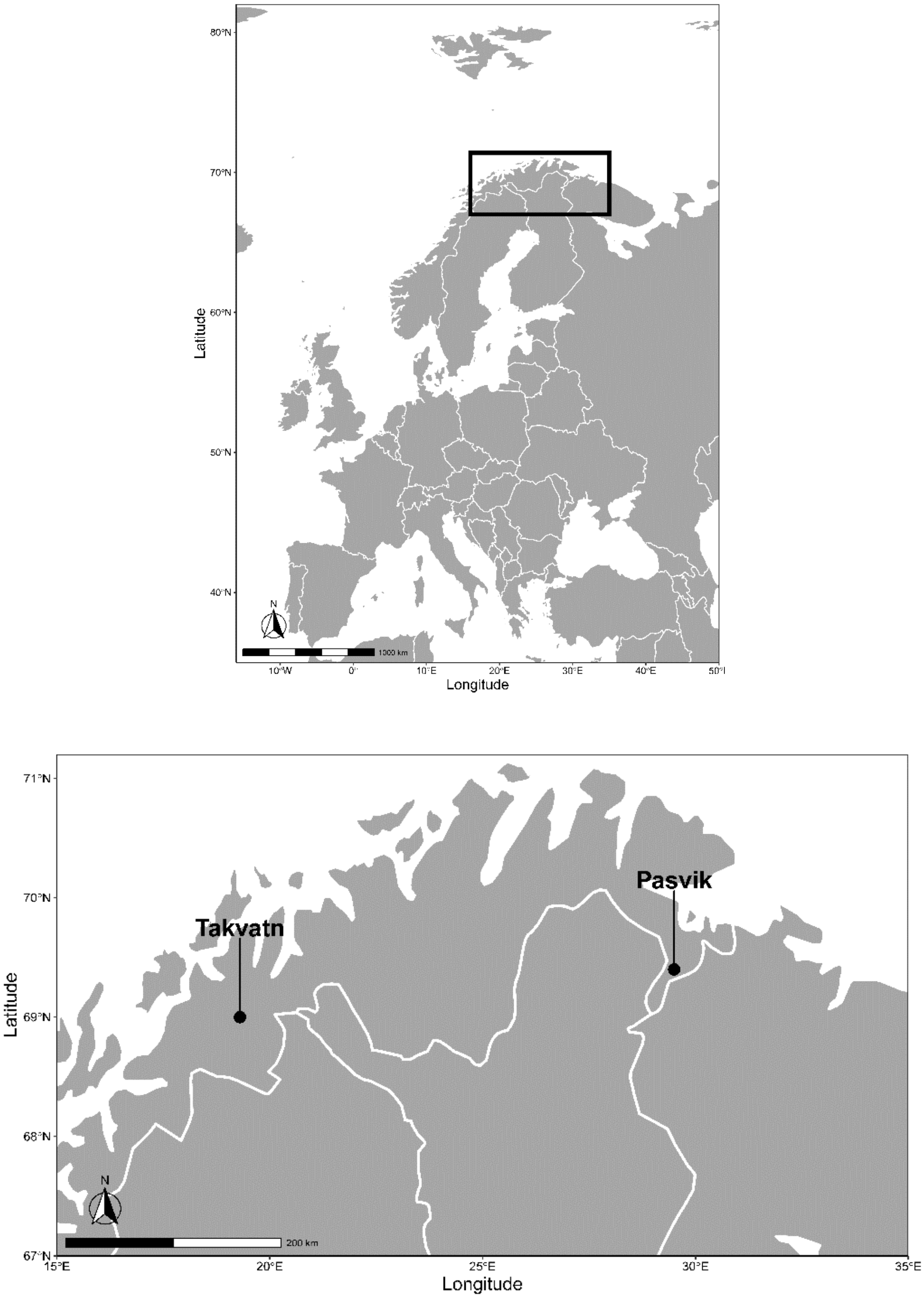


Figure 2. Top: Map of Europe with the black rectangle depicting the main study area of this thesis. Below: Northern-Fennoscandia with the location of the two main study systems (Lake Takvatn and the Pasvik watercourse).

2.2. Climate modelling

2.2.1 Climate data

Ecological studies of climate change impact incorporate research from two very different scientific fields, ecology and climate science. The lack of integration between the two fields has restricted the understanding of what is available and how to appropriately use climate models in ecological response studies (Harris et al. 2014). Ecological impact studies often address the effect of future climate change, and in order to do so, realistic scenarios about future climatic conditions are necessary. However, there exist a vast jungle of climate models and different appropriate techniques for their usage. In addition, the development in climate modelling is extremely rapid, especially with the increasingly enhanced computational power, which leaves climate model outputs rather quickly outdated (Edwards 2011). Therefore, an ecologist with limited knowledge in climate modelling might find it difficult to make well documented and knowledge-based decisions in order to separate available climate models from one another and to choose the correct way forward.

Climate models are complex computer-implemented numerical models that simulate the Earth`s climate system (Katzav & Parker 2015). The state of the art in climate modelling are Global Climate Models (GCM, or global-circulation-models) or even the more sophisticated Earth System Models (ESM). These models are extremely complex, implement extensive physical knowledge and represent a wide range of oceanic, atmospheric, biogeochemical and anthropogenic processes, coupling them together to simulate the different aspects of the observed climate (IPCC 2013, Katzav & Parker 2015). However, these models are labour intensive, expensive and need enormous computational power to operate, therefore their spatial resolution is still relatively course-grained. GCMs or ESMs currently represent climate on a spatial grid resolution of about 50 km^2 and temporal resolutions of months or years. In most ecological studies a much finer resolution in both space and time is necessary to model the effect from climate change on organisms, populations or ecosystem (Harris et al. 2014).

Today there exists many different tools to downscale the GCMs to a much finer scale, but each method has its advantageous and shortcomings. However, all are dependent on the quality of the GCM that lies underneath. Regional dynamical downscaling (also called Regionally Climate Models, RCM) is one such method, where the boundary conditions of the region of interest is driven by the GCM, but within the region a separate climate model runs on a much finer spatial and temporal resolution (Rummukainen 2010). Even though the RCM can operate on a much finer resolution, the complexity is often as comprehensive or even more so, as the GCM (Rummukainen 2010). What separates this downscaling method from others is that RCM can generate climate variable outputs that only operate at small scales, like wind-speed, humidity and evaporation. Other downscaling techniques can increase the resolution from the output of GCMs, but not generate additional data (Harris et al. 2014). Typical region sizes that are modelled in RCMs are continents, and the grid cell resolution is down to about 12 km^2. In this thesis, the climate model outputs were used to drive a one-dimensional air-to-water temperature model, which needed six different climatic input variables. Some of these input variables are only available through RCM outputs, making the choice of how to downscale the GCM rather easy.

After choosing the method of how to downscale the global climate models, came the selection of which combination of climate models were applicable for this study area. In this process, expert knowledge about climate models and their applicability from the Norwegian Meteorological Institute (NMI) were used. The chosen climate model combination of GCM and RCM that fitted our study area the best was a regionally downscaled implementation at the finest grid resolution available (0.11° or 12.5 km^2) (MPI-M-MPI-ESM-LR), forced by the global circulation model CLMcom-CCLM4-8-17 (Landgren & Haugen 2016). The model outputs used here are made available through the CORDEX project (Coordinated Regional Climate Downscaling Experiment), which was initiated by the World Climate Research Programme and aims to coordinate, gather and cooperate between different climate modelling institutions around the world (Jacob et al. 2014). A huge amount of regionally downscaled output climatic data is available through their database, which is increasingly used in climate impact studies. The data is available for both hind-casted model runs (1950-2005) and projected future model runs with different climate scenarios (2005-2100) (Jacob et al. 2014).

As earlier mentioned, climate model outputs are updated quickly as models improve and computational power increases (Edwards 2011). The data used here was part of Phase 5 of the Coupled Model Intercomparison Project (CMIP5), which was used in the Intergovernmental Panel for Climate Change (IPCC) assessment report #5 (AR5) (Jacob et al 2014). Here, the climate simulations used the Representative Concentration pathways (RCPs), defined for the IPCCs Fifth Assessment Report as future scenarios for anthropogenic emissions of greenhouse gases and future land use change (Moss et al. 2010). Four different scenarios of assumed increase in radiative forcing (W/m^2) by the end of the century relative to pre-industrial conditions were developed, the RCP-2.6, RCP-4.5, RCP-6.0 and RCP-8.5, which translates in a global mean temperature increase of about 0.7-1.0 °C, 1.8-2.3 °C, 2.2-3.7 °C and 3.7-6.5 °C, respectively (Bonan 2015). In this thesis, two of the scenarios were adopted, the RCP-4.5 and RCP-8.5. In order to translate the projected climatic conditions to water temperatures that fish would experience, the one-dimensional air-to-water temperature model called General Lake Model (GLM) was used.

2.2.2. General Lake Modelling

In the time-series data used here, continuous environmental variables were partly lacking and future prospective climatic data were available as global or regional climate models based on the IPCC climate scenarios. In the absence of long-term retrospective or prospective water temperature data, I opted to use a one-dimensional air-to-water temperature model, called General Lake Modelling (GLM) (Hipsey et al. 2014). The model requires an input of six different climatic variables (air temperature, precipitation, solar radiation, wind speed, cloud cover and relative humidity), which were available either from the different meteorological stations for the hind-casted model runs or from the climate model outputs for the projected future runs at the different lake sites. In addition, lake specific morphometries were required to translate climatic variables into water temperature. The GLM assumes no horizontal temperature variability within the water body and computes vertical temperature profiles by accounting for surface heating, surface cooling, and vertical mixing. The model also includes the effects of ice-cover formation and subsequent melting on heating and mixing processes within the lake (Hipsey et al. 2014). We calibrated and evaluated the different models using existing observed temperature profiles in the different study lakes to inspect the performance of the model and the estimated output variables from the model (Fig. 3, for an example of model performance).

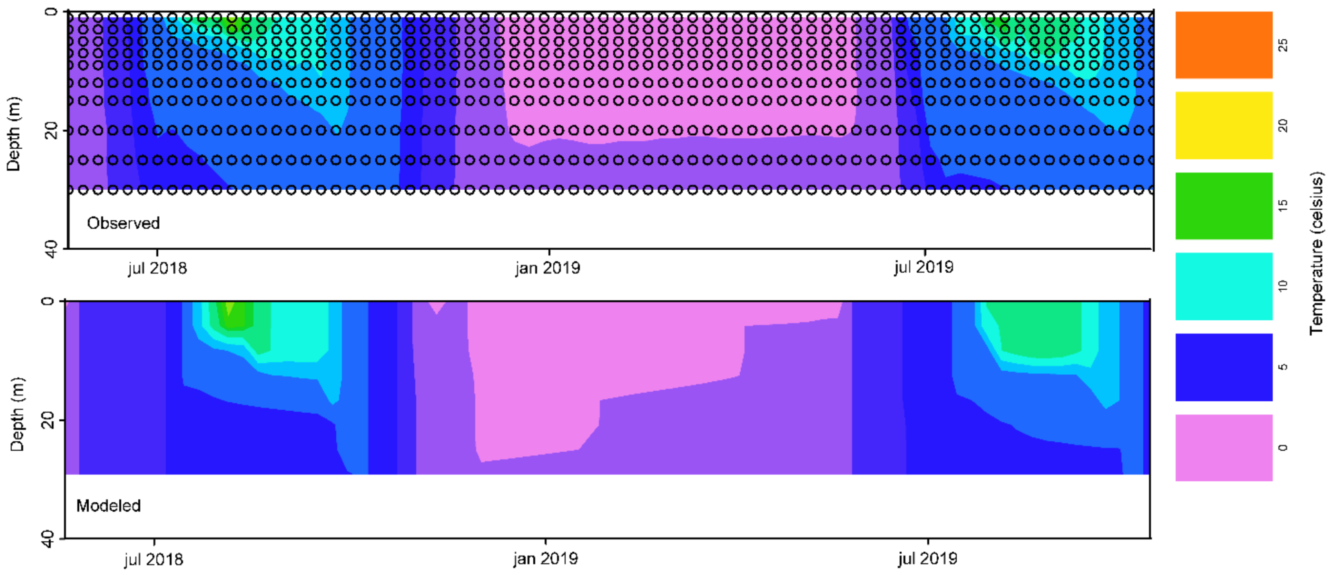


Figure 3. Comparison of observed (top panel) and modelled (bottom panel) water temperature in Lake Takvatn from May 2018 to October 2019. Open circles depict the individual measurements of water temperature by temperature loggers.

2.3. Ecological modelling

2.3.1. Development of the individual based model

Individual based models (also named agent based models (ABM)), hereafter referred to as IBMs, have a long history in biology and are widely used in ecology (Judson 1994, Grimm et al. 2006). IBMs allow studying how system level properties emerge from the adaptive behaviour of individuals (Railsback et al. 2001), and how the system or the environment affects the individuals. IBMs are important for both theoretical and managemental research, because they can handle questions analytical models usually ignore (Grimm et al. 2006). This particularly relates to individual variation, local interactions and individuals adapting to a changing internal and external environment. One such example is the recently developed IBMs that focus on increasing the causal understanding and predictive power on impacts from anthropogenic sources on adapting natural resources, which are named eco-genetic modelling (Dunlop et al. 2009). This eco-genetic modelling framework is described in Dunlop et al. (2009) (similar modelling frameworks were at the same time also developed by Wang & Höök (2009) and Okamoto et al. (2009)), and is widely used and cited in the fisheries-induced evolution literature, but also in other disciplines. The individual based model presented here, relies on the eco-genetic framework developed by Dunlop et al. (2009). Dunlop et al. (2009) and papers following this work often focus on evolutionary and ecological consequences of anthropogenic effects on fish populations. In our model, we focus strictly on ecological effects of human pressures, thus we have omitted their “Inheritance” and “Expression” steps in the annual cycle. However, our IBM routine works similar with successive events for each annual cycle, which includes mortality, maturation, growth, and reproduction (Dunlop et al. 2009) (Fig. 4, demonstrating the IBM in paper II).

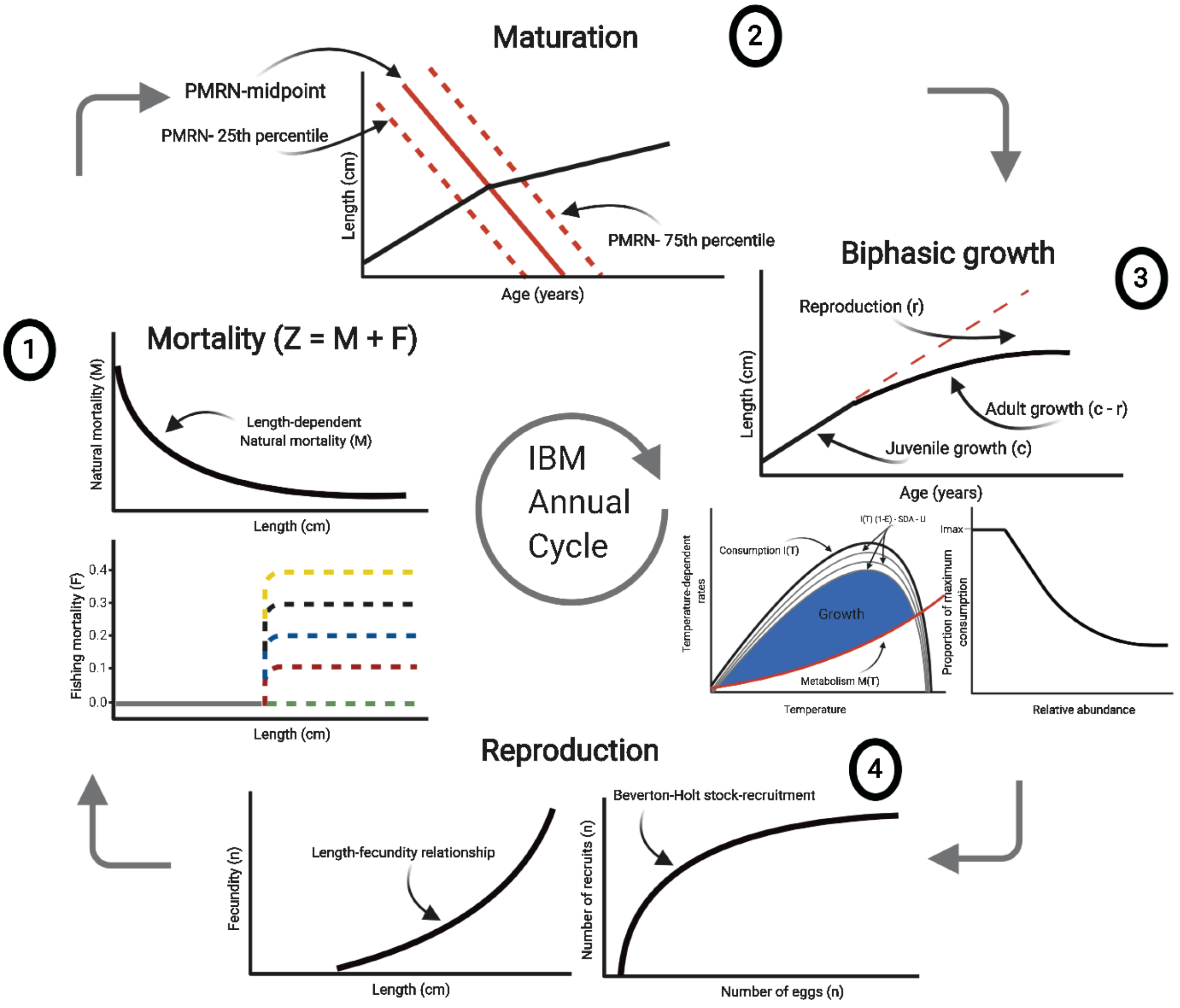


Figure 4. Schematic representation of the four successive events in the annual cycle of the individual based model. 1) Mortality, modelled as two different size-dependent components (Z = natural (M) + fishing (F)). 2) Maturation specified by a linear probabilistic maturation reaction norm (PMRN), depending on both length and age. 3) Growth, modelled as biphasic growth which is both density- and temperature-dependent. 4) Reproduction, with size dependent fecundity, and density-dependent recruitment.

2.3.2. Individual growth in the IBM

To capture how temperature affects fish individual growth in our IBM, existing knowledge on bioenergetics relationships were applied. In paper I, a phenomenological representation of the relationship between ambient temperature and somatic growth was used. Here, the von Bertalanffy growth model was implemented with a temperature-dependent growth rate for Arctic charr in Lake Takvatn:

$$L_{t+\Delta t} = L_t + (L_\infty - L_t)(1 - \exp(-K_t \Delta t)), \qquad (1a)$$

where L_t is the length of fish at age t, Δt is the time interval over which growth is considered, L_∞ is the asymptotic length at which growth is zero, and K_t is the temperature-dependent growth rate at age t (equation 1b). Equation (1a) uses the Fabens method for iteratively describing growth in the von Bertalanffy model (equation 4.1 in Fabens 1965; see also Haddon 2001, pp. 241-242). For our model, we account for daily variations in the growth rate K_t and accordingly consider daily growth increments, i.e., $\Delta t = 1\ \mathrm{day} = 365.25^{-1}\ \mathrm{yr} = 0.0027379\ \mathrm{yr}$, with a year's growth beginning on January 1st and ending on December 31st. Growth starts at age 0 from an initial length randomly drawn from a normal distribution with mean $m(L_0)$ and standard deviation $\sigma(L_0)$.

The temperature dependence of K_t follows a dome-shaped curve with a maximum of 0.35 (K_max) at the temperature optimum (T_opt) of 14.1°C (Larsson & Berglund 1998, 2005, Larsson et al. 2005, Siikavuopio et al. 2013). The maximum growth rate, K_max, is calibrated to the growth of Arctic charr in Lake Takvatn, and individual variability in growth rate is implemented by random sampling from a normal distribution centered on K_max. The temperature-dependent growth coefficient K_t in year t is set to 0 if the temperature is smaller than 1˚C (T_{min}) or larger than 20˚C (T_{max}) (Larsson & Berglund 1998, 2005, Larsson et al. 2005, Siikavuopio et al. 2009, 2010). Otherwise, K_t is calculated as follows,

$$K_t = K_{\text{max}} \frac{(T_t - T_{\text{min}})(T_t - T_{\text{max}})}{(T_t - T_{\text{min}})(T_t - T_{\text{max}}) - (T_t - T_{\text{opt}})^2}, \qquad (1b)$$

where K_{max} is the maximum growth rate parameterized for the Takvatn charr population using the average von Bertalanffy growth rate (K) and the average annual water temperature for the last ten years of the long-term data series, T_t is the average water temperature for the upper ten meters on day t, and T_{min}, T_{max}, and T_{opt} are the minimum, maximum, and optimum water temperatures for Arctic charr, respectively (see Fig. 5). Arctic charr at high latitudes predominantly utilize the shallow-water habitat, especially during the ice-free season (Hawley et al. 2017), and therefore, we use the average water temperature for the upper ten meters.

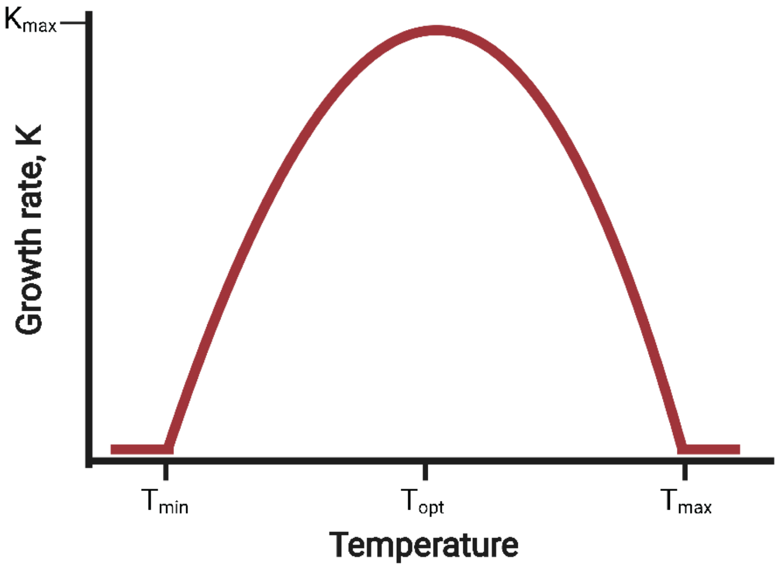


Figure 5. The von Bertalanffy's growth coefficient, K, and its relationship with water temperature in paper I. T_{min}, T_{max} and T_{opt} is the species specific minimum, maximum and

optimum temperature for growth, respectively. K_{max} is the maximum growth rate, which is obtained when temperature approaches the species specific optimum temperature (T_{opt}).

For paper II, a more mechanistic and bioenergetic approach was adopted. We assumed a biphasic growth model parameterized using standard bioenergetic assumptions, metabolic theory of ecology and density-dependence processes to capture both how temperature and density affects individual growth.

Biphasic growth model

We used the Quince-Boukal-Dieckmann (QBD) biphasic growth model (Boukal et al. 2014) to describe juvenile and adult growth trajectories,

$$L_{a+1} = \sqrt[(1-\beta)\alpha]{\frac{L_a^{(1-\beta)\alpha} + (1-\beta)cb^{-(1-\beta)}}{1+q^{-1}(1-\beta)\, r_{a+1}}}, \tag{2a}$$

where L_a is the length at age a, β is the allometric exponent relating the rate cW_a^{β} of net energy intake – measured in terms of weight gain – to the weight W_a, c scales this rate, q is the ratio between the energetic costs per unit of weight of producing gonadic versus somatic tissue, r_{a+1} is the ratio between somatic and gonadic weight at the end of the growth season at age $a + 1$, α is the allometric exponent relating the weight $W_a = bL_a^{\alpha}$ to the length L_a, and b scales this weight. For juveniles, all available energy is allocated to growth, i.e., $r_a = 0$. For adults, a fraction of the net energy intake is allocated to reproduction, i.e., $r_a > 0$. We assumed that r_a does not change with age a; therefore, we set $r_a = r$ and use the closed form of the QBD model for adult growth (Boukal et al. 2014). We used empirically derived parameters from the QBD growth model for the different species in combination with the corresponding water-temperature and density experienced by the different populations to scale c_{max} to the optimum temperature for growth for the different species (see below, paper II).

The coefficient c was jointly determined by a temperature- and density-dependent consumption rate, scaled by $I(T, D)$, and a temperature-dependent metabolic rate, scaled by $m(T)$, where T and D denote temperature and density, respectively. In other words, the consumption rate depends both on temperature and – indirectly, through the density of competitors – on food availability, while the metabolic rate depends only on temperature. This implies that the optimum temperature for growth is lower when the density of competitors is higher (Huey and Kingsolver 2019). In addition to $m(T)$, three different processes (Deslauriers et al. 2017) diminish c: egestion E is the fraction of the consumed energy that is not ingested and leaves the fish as feces, specific dynamic action SDA is the fraction of W_a^{β} used for processing the food to energy or storage (Jobling 1983), and excretion U is the fraction of W_a^{β} lost as nitrogen waste (Deslauriers et al. 2017). Therefore, c was calculated using the following bioenergetic relationship,

$$c = I(T, D)(1 - E) - SDA - U - m(T), \tag{2b}$$

For eq. 2c-2f (see below), the calculated values are given in kJ day^{-1}, but c in the QBD model have the unit of $g^{1-\beta}$ year^{-1} and we therefore first accumulated the daily energy intake over the 365 days and subsequently used a conversion factor $c = \frac{c}{z}$ to model growth on the correct scale used in QBD growth model framework. To reflect individual variation in energy acquisition, individual values of c were distributed normally around the mean value given by eq. (2b).

The temperature-dependent scaling of the consumption rate follows a Ratkowsky-type growth model (Ratkowsky et al. 1983, Larsson et al. 2005, Finstad et al. 2011), useful to describe consumption rate in salmonid fish,

$$I(T) = d(T - T_{\min})\left(1 - e^{g(T - T_{\max})}\right), \tag{2c}$$

where T is the experienced water temperature, $T_{\min}$ and $T_{\max}$ are the minimum and maximum temperatures for ingestion, respectively, and d and g are constants.

The density-dependent scaling of the consumption rate follows a negative power law described by Amundsen et al. (2007); see also Lorenzen & Enberg (2002),

$$I(D) = \delta_1 D / {d_c}^{\delta_2}, \tag{2d}$$

where D is the total density of competitors, d_c is the conversion factor from the catch-per-unit-effort scale used in Amundsen et al. 2007 to density of competitors in the model, and δ_1 and δ_2 are constants. For densities below the minimum density described in Amundsen et al. (2007) (catch-per-unit-effort (CPUE) = 4.8), $I(D)$ was set to a maximum $I_{\max}$, where $I_{\max}$= 3.35 is the maximum consumption rate seen in Amundsen et al. 2007.

To capture the combined effects of temperature and density on the consumption rate, we used the following equation,

$$I(T, D) = I(T)\left(\frac{I(D)}{I_{\max}}\right), \tag{2e}$$

where $I(T, D)$ reaches its maximum when the water temperature is optimal and the population density is lower than the minimum density described by Amundsen et al. (2007).

The temperature-dependent scaling of the metabolic rate follows the Arrhenius function (Gillooly et al. 2001, Lindmark et al. 2018),

$$m(T) = m_0 \omega e^{-\frac{E_{\mathrm{m}}(T-t_0)}{kTt_0}}, \tag{2f}$$

where m_0 is the metabolic scaling constant in terms of oxygen consumption, ω is the conversion factor from oxygen consumption to energy consumption, E_{m} is the mean activation energy of biochemical reactions in fish, k is the Boltzmann constant, T is the temperature in terms of the Kelvin scale, and t_0 is the conversion factor from Kelvin scale to Celsius scale.

Field studies of the relationship between water temperature and growth are not available for freshwater salmonids at high latitudes, while corresponding lab experiments have frequently been conducted for the most common high-latitude freshwater fish species. Therefore, we used data from lab experiments to parameterize eq. (2c): specifically, bioenergetic studies have provided estimates of the energies lost to egestion, specific dynamic action, and excretion and of the temperature-dependent metabolic rate (Deslauriers et al. 2017).

Increase in body temperature will increase the metabolic rate of ectotherms, which will lead to a higher demand of energy needed to sustain maintenance, growth and reproduction (Jobling 2002, Ficke et al. 2007, Strand et al. 2011). If this demand is not met by an increase in consumption through e.g., a limitation of food resources, optimum temperature for growth will decrease (Huey & Kingsolver 2019, Fig. 6).

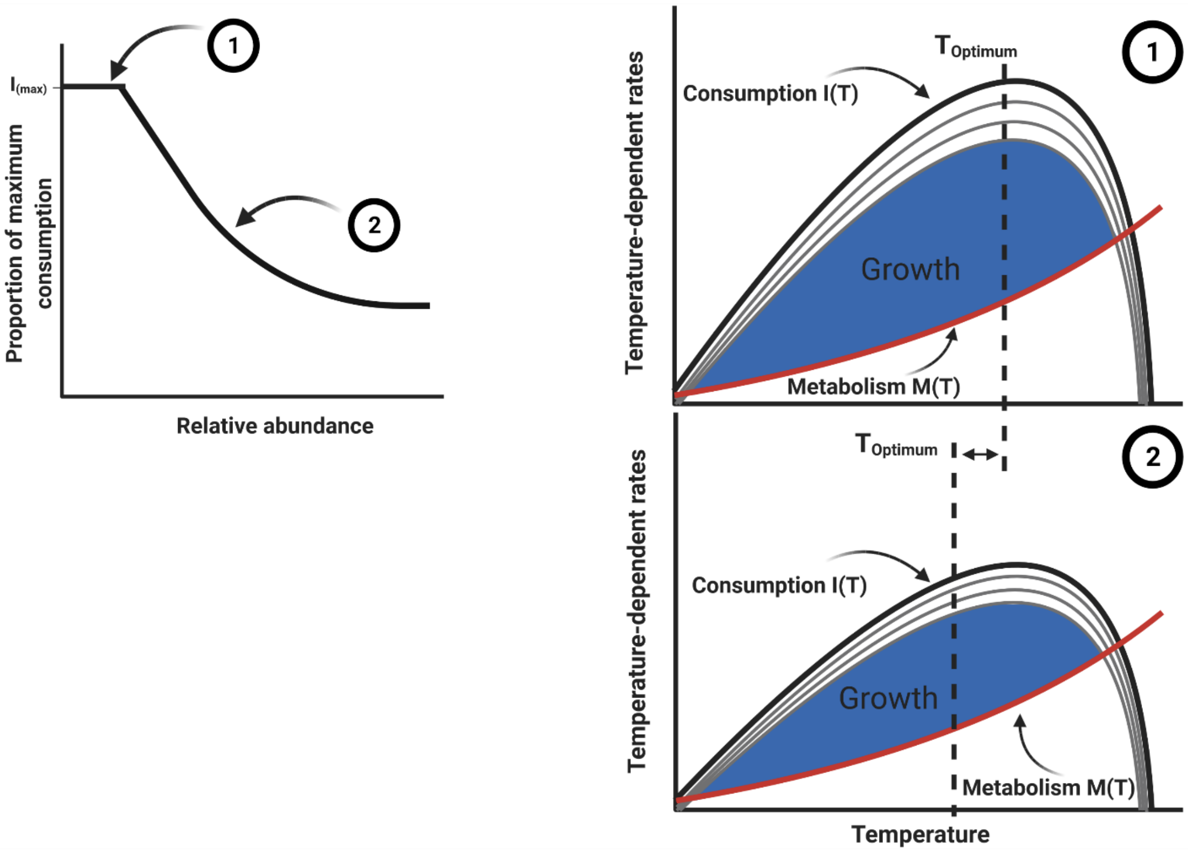


Figure 6. The relationship between relative abundance and consumption rate in the individual based model. NB: Optimum temperature decreases as food limitation increases (e.g., Huey & Kingsolver et al. 2019).

3. Summary of results

3.1 Climate warming is predicted to enhance the negative effects of harvesting on high-latitude lake fish (paper I)

The combined effects of climate warming and size-selective harvesting on somatic growth, population demography and vulnerability of Arctic charr populations in high latitude lakes were addressed. Two different climate scenarios, the RCP-4.5 and RCP-8.5 (regionally downscaled climate models from year 1950-2100 forced a one-dimensional air-to-water temperature model) with five different fishing mortality scenarios were used in an eco-genetic individual based model (IBM) to investigate synergetic effects of multiple anthropogenic stressors. The model captures successive annual life history events, including processes of size-dependent mortality, a probabilistic maturation reaction norm describing age- and size- at maturity, temperature-dependent daily growth, size-dependent reproduction and density-dependent recruitment. The model was parameterized using data from the Arctic charr population in Lake Takvatn.

The model predicts that with higher water temperature, somatic growth rate of Arctic charr will increase in high latitude lakes, leading to larger body size at age and increased stock biomass. Interestingly, the potential increase in stock biomass with future climate warming is masked by size-selective harvesting, which has a strong negative impact on biomass due to increase in mortality of large individuals. According to the model results, yield will increase substantially under climate warming only when fishing mortality is low. In addition, harvesting will target increasingly younger individuals as size-at-age increases due to climate warming, resulting in a more pronounced age truncation and a larger proportion of immature individuals in the catches. This will increase the vulnerability of the populations to additional environmental perturbations.

Conclusions

1. Climate warming might boost somatic growth in freshwater fish living towards the northern end of their distribution, increasing biomass and potential yield in low-productive Arctic areas.
2. Harvesting might mask the effects of climate warming, by removing larger fish that contribute the most to biomass which severely may increase the vulnerability of the population.
3. The multiple stressors approach used here highlights that addressing these stressors simultaneously will provide knowledge about synergetic effects that otherwise would not be possible to reveal.
4. Harvested freshwater fish populations might become less resilient and more vulnerable to climate warming than populations experiencing little or no size-selective harvesting.

3.2 Temperature affinities and life history determine vulnerability of freshwater fish to multiple stressors in a warming Arctic (paper II)

To explore the vulnerability of freshwater fish to multiple stressors in a warming Arctic, possible impacts of climate warming were analysed for different harvesting regimes in three lacustrine salmonids north of the Arctic Circle. A retrospective analysis of four decades of field data on back-calculated temperature-dependent growth was used to study the effects of past and present climate warming in Arctic charr, whitefish and vendace. An individual based model (IBM) forced by observed and modelled climate variability was used to assess how future climate warming affects the three salmonid species with differing life history strategies and temperature preferences. The IBM addressed different scenarios of climate warming (RCP-4.5

and RCP-8.5) combined with effects of density dependence and different levels of size-specific harvest mortality. The adopted model used a bioenergetic approach of temperature-dependent somatic growth, size-dependent natural and fishing mortality, maturation schedules following a probabilistic maturation reaction norm, size-dependent fecundity and density-dependent recruitment. The model was parameterized using existing long-term data from the three fish populations.

All three species increased their individual growth rates under climate warming both in the retrospective observed population and in the projected modelled populations. In the lower fishing mortality scenarios, size at age and stock biomass increased for all three modelled populations, however with a large negative effect of increasing density of competitors. Vendace, which is the least cold water adapted fish in this study, benefits substantially more in terms of somatic growth and biomass from warming than the more cold water species, Arctic charr and whitefish. Arctic charr, the species most sensitive to warming, also have the most vulnerable life history strategy under size-dependent harvesting. Effects of the multiple stressors approach used here depend on the thermal niche and life history of these study species in high latitude lakes.

Conclusions

1. In Arctic areas, climate warming increases individual growth rates of freshwater fish, an effect moderated by density (i.e., food availability).
2. The life history of the species determine their vulnerability to the cumulative impact of climate warming and fisheries, where fish species with relative slow juvenile growth and old age at maturation are less resilient and more vulnerable than species with faster somatic growth and earlier maturation.

3. Cool water fish are favoured over cold water fish in a warming Arctic because of a difference in thermal preference.

3.3. Increase in relative importance of cool water fish at high latitudes emerges from individual level responses to climate warming (paper III)

The population level responses to recent climate warming of eleven cool water fish populations were studied, and mechanisms governing the population effects were investigated at the individual level in two of these systems. Three decades of data on back-calculated juvenile length increment (mm·year^{-1}), survival through the first critical winter, and age at maturity were assessed as candidate mechanisms explaining the observed population effects. Eurasian perch (*Perca fluivitalis*), a cool water fish with optimum temperature for growth between 16 and 27 °C, was the model species, and the study systems are located towards the northern distribution edge of the species (68°N-70°N). The two lakes (Lake Vaggatem and Lake Skrukkebukta) where individual level responses to climate warming were studies, had both 30 year long-term series of population and individual level data of perch as well as continuous data on water temperature.

Ten out of the eleven perch populations have increased in relative numerical importance over the latest decades in concurrence with the ongoing climate warming. More so, in the two long-term study systems in the Pasvik watercourse the perch density significantly increased with increasing water temperatures over the last 30 years. These population effects from climate warming arose from individual level responses to increased water temperatures. Juvenile length increment (mm·year^{-1}) increased substantially with temperature, but similarly decreased with increasing perch density. Number of surviving one year old individuals showed similar response as juvenile growth, with an increase with temperature and a decrease with relative density. The observed improvement in juvenile growth, an eco-physiological process, led to earlier maturation age, which is an evolutionary plastic response. The study shows that climate warming affects population level processes via direct and indirect temperature effects on individual life history.

Conclusions

1. Water temperature increase from climate change has favoured cool water fish at high latitudes, possibly at the expense of cold water salmonids.
2. At their northern range edge, cool water fish species are becoming more abundant and may increasingly dominate fish communities at these latitudes.
3. Individual level responses to water temperature increase mediate the population effects of climate warming, with increased juvenile growth and survival, and earlier maturation all contributing to promote population growth.
4. Given the observed speed and magnitude of the perch population response to climate warming, management strategies should focus on limiting future introductions and invasions of cool water fish at these latitudes.

4. Discussion

This thesis provides new evidence and understanding on how past and future climate warming will affect high latitude fish populations, mediated by individual level responses to water temperature increase. The long-term empirical studies documented that both cold- and cool water fish experienced an improved juvenile somatic growth with warming, which affected other life-history variables, favoring cool water fish more than cold water fish at high latitudes (paper II & III). The results from the individual based models demonstrated that the projected water temperature increase towards year 2100 will accentuate the effects seen in the retrospective long-term studies (paper I & II). The population level effects were contingent on species thermal niche and life history, with cool water fish experiencing greater increase in biomass and relative importance than cold water species (paper I, II & III). This thesis also addressed the risk of cumulative effects of climate warming and size-selective harvesting, where life history and thermal preferences shape the vulnerability and resilience towards these multiple stressors (paper I & II). To my knowledge this is the first extensive study on climate change impacts on both cold- and cool water fish at their northern range edge, combining long-term field evidence and model projections of future implications of further climate warming.

4.1. Individual responses to past and future climate warming

Individuals of both the cold- and cool water adopted species displayed a positive relationship in juvenile somatic growth with increasing water temperatures (paper II & III). Even Arctic charr, the most cold water adapted freshwater fish in the world (Klemetsen et al. 2003, Klemetsen 2010), demonstrated a clear positive effect of increased water temperature on young-of-the-year somatic growth throughout the nearly 40 year long study in Lake Takvatn (paper II). Previous studies on wild Arctic charr have not been conclusive with respect to effects from temperature change on somatic growth (Power et al. 2000, Kristensen et al. 2006, Godiksen et al. 2010, Michaud et al. 2010, Murdoch & Power 2013). For the cool water fish, vendace and perch, the observed positive effect of increased water temperatures on somatic growth was as expected more pronounced, as the studied populations are situated at the northern edge of their distribution (~70°N). Several recent studies show similar results, where cool water fish experience improved growth rates with warming in populations situated in the northern reaches of their distribution (Jeppesen et al. 2012, van Dorst et al. 2019, Huss et al. 2019). The future increase in somatic growth rates projected by the IBMs under climate warming suggests that this trend will be further accentuated towards year 2100 (paper I & II).

Both the observed increase in water temperature over the last few decades and the increase predicted towards year 2100 are substantial, but not to a degree that there will be direct negative effects on somatic growth for any of the studied populations at these latitudes (paper I, II & III). This is explained by the fact that these study systems are some of the colder lakes in Europe (classified in the coldest group: Northern Frigid), and that warming to year 2100 will only increase these lakes to the second coldest classification group (Northern Cool) (Maberly et al. 2020). Therefore, both the observed and predicted water temperature increments will expand the growth season with temperatures mostly remaining below or close to the optima for these species (paper I & II). However, inspection of the respective temperature-dependent growth curves stresses how the cool water species will benefit the most from the projected climate warming (Fig. 7). Other studies have also suggested that freshwater fish populations living north of the Arctic Circle have the potential to increase individual growth from moderate warming (Butzin & Pörtner 2016, Symons et al. 2019). Furthermore, both the observed and predicted growth increases are dependent on sufficient availability of food resources (paper II & III). Theory predicts that metabolic rates increase with warming, thus consumption needs to meet the elevated metabolic demands (Kingsolver & Huey 2019). Productivity will likely increase with warming at these latitudes (O`Bierne et al. 2017), possibly leading to an increase in food availability. Nevertheless, higher density of intraspecific competitors significantly reduced observed growth rates for all investigated species in this thesis (paper II & III), which is a common finding in ecological studies (Amundsen et al. 2007, Persson et al. 2007). Therefore, in high latitude populations where effects from increased temperature on somatic growth are not apparent, food availability might be the limiting factor (see paper II & III). With a reduction in food availability (e.g. by increase in consumer density) optimum temperature for growth will decrease as metabolic demands increase exponentially with temperature (Kingsolver & Huey 2019, Morrongiello et al. 2021). However, even though this effect was present in our modelling approach, it did not substantially affect the growth negatively, because the projected future water temperature remain beneath the optimum temperature of these species. To summarize, for both cold- and cool water fish located towards the northern edge of their distribution, somatic growth may increase with warming, assuming that productivity and food availability will meet the demands in a warmer ecosystem.

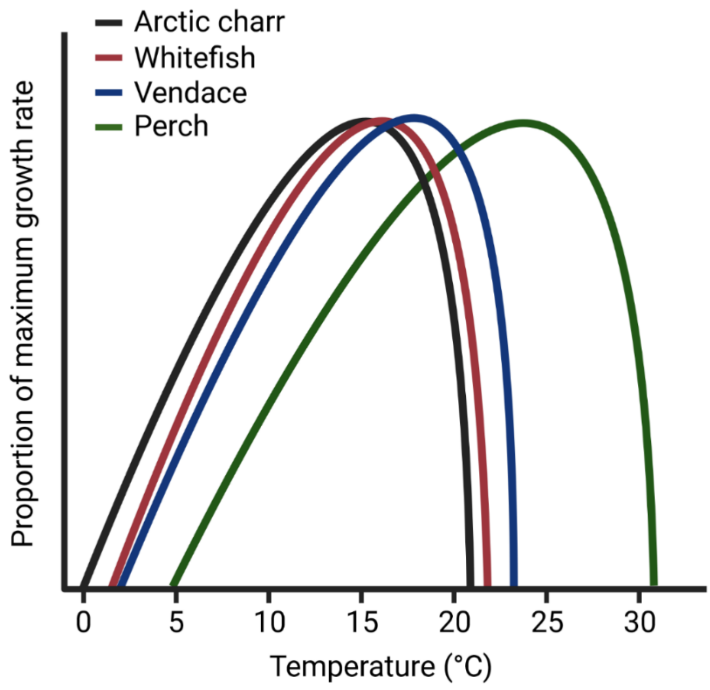


Figure 7. Temperature-dependent growth rates for both cold water (Arctic charr and whitefish) and cool water (vendace and perch) freshwater fish redrawn from existing literature on the relationship between somatic growth and temperature (paper I, II & III).

An increase in juvenile somatic growth rate will lead to larger size at age, which will mediate other life history responses affecting survival, maturation and reproduction (Wootton 1998, Heibo et al. 2005, Ohlberger et al. 2011). Mortality in fish is often size-dependent where smaller individuals are more vulnerable to both predation and mortality from starvation events (Elliott 1993, Gislason et al. 2010). If juvenile somatic growth increases with warming, individuals might reduce their time in predatory windows, resulting in avoidance of predators earlier in life. In addition, increased growth will lead to larger size at age, and larger fish will have higher resistance towards starvation than smaller fish (Bar 2014). Therefore, a rapid transition from these critical life stages might improve survival of juvenile fish. Favourable conditions and increased survival of juvenile individuals might lead to pulses of strong year classes that could dominate the population in the following years (Mills & Mann 1985). If these favourable growth conditions become more frequent in the future, overall population recruitment and abundance might increase especially for cool water fish at high latitudes (see paper III).

The present study provides evidence that an increase in growth leads to a plastic response in life history resulting in earlier maturation. The phenotypic plastic response in maturation age is adaptive (Roff 1992, Stearns 2000). Individuals with different growth trajectories mature at different sizes and ages dependent on the orientation of their maturation reaction norm (Heino et al. 2002, Dieckmann & Heino 2007, Heino & Dieckmann 2008). Paper I & II use population estimates of the maturation reaction norm for the different fish species, and given the projected increase in length at age from increased water temperature, individuals matured earlier contingent on their maturation reaction norm. Hence, maturation age is indirectly affected by the environment, where the "quality" of the environment affects the slope of growth directly (Dieckmann & Heino 2007, Nilsson-Örtman & Rowe 2021). The indirect environmental effect on maturation age, mediated by growth, demonstrated this theory empirically in paper III (Fig. 8). Similar results where an increase in juvenile growth led to a reduction in age at maturation have been seen in other freshwater fish, and also in marine fish species (Reznick 1990, Trip et al. 2014, Ward et al. 2017). Furthermore, for fish populations with a negatively sloped maturation reaction norm, size at maturation should also increase with faster juvenile growth (e.g. Fig. 8). Larger size at maturation will increase fecundity, since fecundity in fish is chiefly size-dependent (Berneche et al. 2018). In sum, for species where maturation size increases with faster juvenile growth rate, total population fecundity might increase as a consequence of climate warming.

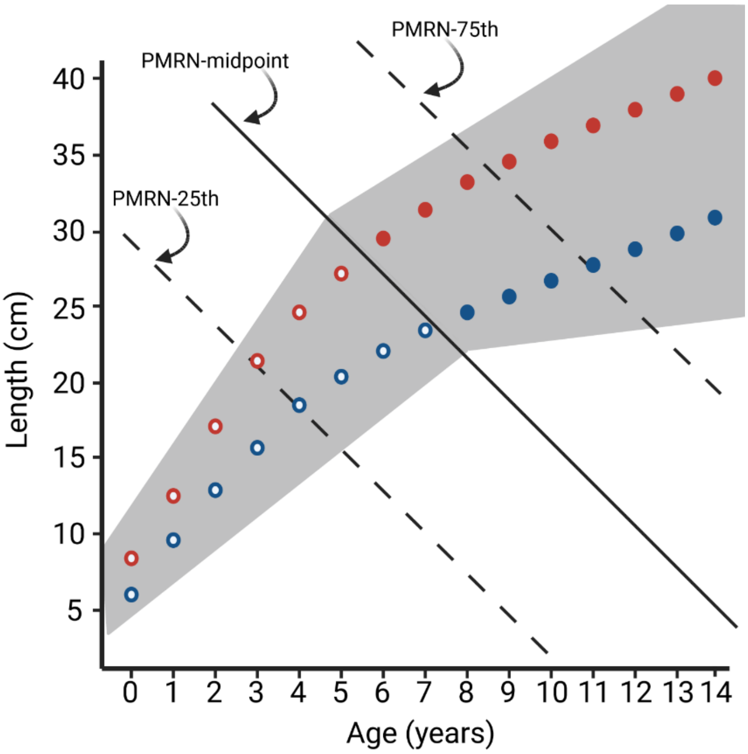


Figure 8. Schematic illustration of how difference in growth trajectories, with red and blue dots representing good and poor growth, respectively, will affect both age and size at maturation dependent on the maturation reaction norm of the species. The shaded area depicts the possible growth trajectories of the different individuals within the population, and the solid and stippled lines represents the probabilistic maturation reaction norm with midpoint, and 25th and 75th percentile, respectively.

4.2. Population level effects from climate warming

All three papers in this thesis show that the population level effects of climate change were mediated by the individual level responses to increasing ambient temperatures. The increased somatic growth led to a larger size at age and a reduction in age at maturity, which substantially increased stock biomass and yield (paper I & II). However, individual growth was also dependent on density (paper II & III), and under high density both stock biomass and yield increased less (paper II). The population level effects suggest that cold water fish populations at the latitudes investigated here might benefit from warming (paper 1 & II), at least in fish communities consisting of species from the same temperature guild. Other studies have also concluded that warming has the potential to increase both biomass and yield for cold water fish living at high latitudes (Reist et al. 2006, Campana et al. 2020, Jarvis et al. 2020). On the contrary, cold- and cool water fish populations living towards the southern end of the species distribution are already experiencing large negative impacts from climate warming (George et al. 2006, Rennie et al. 2009, Connor et al. 2019, Kelly et al. 2020). Hence, climate warming might change the outcome of ecological interactions. The IBMs used here are single species models and do not explicitly model effects from interspecific interactions. These complex interactions could have dramatic effects on the performance of especially cold water fish in the study area (Lindmark et al. 2019), making the future realized population growth to differ from the predictions presented here.

Furthermore, there are large regional differences in fish species compositions between western and eastern parts of northern Fennoscandia. Typically, lake ecosystems in western Fennoscandia consists of 2-3 species of cold water adapted salmonids, while ecosystems in eastern Fennoscandia can comprise 10 or more species from both cold (salmonids), cool (percids, pikes) and even warm (cyprinids) temperature guilds. For lakes with low species richness in western Fennoscandia, warming might benefit individual and population growth of cold water fish as predicted by the modelling effort in this thesis. However, in multispecies lakes in eastern Fennoscandia where species from different temperature guilds coexists, cold water fish might struggle under climate warming (paper II & III). Additionally, the rate of temperature increase is higher in eastern compared to western Fennoscandia. This means that the climate change impacts predicted in this thesis will take place earlier and be more severe in lake ecosystems in eastern-Fennoscandia, which could act as an early warning systems also for colder lakes located in the western parts.

Paper III documents that cool water fish have the potential to experience a substantial increase in density and importance relative to cold water fish with warming. With the rapid increase in water temperature witnessed in these high latitude areas (O`Reilly et al. 2015, paper III), an increase was not unexpected, but the speed and magnitude of the change were surprising. Similar increases in density of cool water fish above the Arctic Circle have been documented and predicted as a consequence of global warming in other studies (Ficke et al. 2007, Heino et al. 2009, Rolls et al. 2017). In addition, species from warmer temperature guilds are migrating northwards threatening native cold water species already existing in these high latitude areas (Reist et al. 2006, Comte et al. 2013, Campana et al. 2020). Simultaneously, cold water fish populations are suggested to be largely negatively affected by warming in the presence of cool water fish (Jeppesen et al. 2012, Morrissey-McCaffrey et al. 2019). Mass extirpations of cold water fish (Arctic charr) with warming in the presence of cool water predators (pike) are predicted in the future (Hein et al. 2014). Hence, cold water salmonids are classified as the most sensitive to future climate change (Blanchet et al. 2019). In sum, these predicted changes make cold water fish seem highly vulnerable to future climate change, regardless of the potential for increase in growth rate and biomass for cold water freshwater fish living in species poor systems, which hopefully can act as refuge areas.

The temperature-size rule predicts that populations living in colder environments will experience slower growth rates, mature later and reach larger adult body size than populations living in warmer ecosystems (Atkinson et al. 1994, Angilletta et al. 2004, Verberek et al. 2021). The results presented here concur with the general expectations of the rule, with the exception of a reduction in adult body size. However, in our modeled populations the temperature-growth relationship was constant with body size, but earlier research suggests that optimum temperature decreases with body size, as both oxygen and food demands increase disproportionally with body size under warming (Lindmark et al. 2018, Huss et al. 2019, Rubalcaba et al. 2020). Recent studies has however revealed that the temperature size-rule might not be as general as proposed, and that adult individuals in many species and populations actually become larger under warming (Audzijonyte et al. 2020). High latitude lakes are described as well-oxygenated and might become more productive in the future, which may contribute to sustain large individuals. Nevertheless, with the inclusion of a reduced thermal optima for growth with body size in the IBMs, mean adult body size could possibly decrease in the modelled populations experiencing the warmest temperature scenario towards year 2100. In addition, populations living in warmer environments are suggested to invest more energy in gonadosomatic growth at the expense of somatic growth (Heibo et al. 2005), which further could have reduced the realized adult growth if included in the modelling approach.

4.3. Cumulative effects of climate warming and size-selective harvesting

Paper I and paper II used a multiple stressor approach, by jointly addressing climate warming and size-selective fisheries. From earlier research we know that size-selective harvesting will truncate both age and size distributions, which will reduce recruitment rates in fish (Conover & Munch 2002, Heino & Godø 2002). In addition, large and old fish contribute the most to recruitment and can act as a buffer against environmental perturbations, and removing large fish will increase the vulnerability and decrease the resilience of exploited stocks (Anderson et al. 2008, Hsieh et al. 2010). Here, the impact of size-selective gill-net fisheries was modelled with different levels of fishing mortality. In the high fishing mortality scenarios (F>0.2), both age and size truncation were severe, and the age truncation was further increased with warming (paper I & II). Size truncation was not affected by warming (the used fishing scenario set a lower size threshold for catchability), but because of larger size at age, younger fish were susceptible to harvesting, increasing the age truncation within all study species. However, there was a large difference between species in the implications of the observed age truncation, contingent on their life history (paper II).

It is suggested that fish species with slow growth rates, with an old maturation age and large maturation size are more vulnerable to harvesting in combination with additional stressors than species with a faster turnover rate (Jennings et al. 1998, Wiedmann et al. 2014). The results presented here clearly support this earlier work, but further highlight that the steepness of the slope in the maturation reaction norm dictates the vulnerability towards the cumulative impact of climate warming and size-selective fisheries. Hence, fish species that have maturation schedules which depend relatively more on age than on size (steep negative maturation reaction norm slope), will be more vulnerable to size-selective harvesting under climate change. For example, Arctic charr experienced a substantial increase in size at age, which led to younger fish being susceptible to harvest. Thus, the orientation of the maturation reaction norm resulted in an increasing proportion of immature individuals in the catches with increasing water temperatures and faster somatic growth (paper I & II) (Fig. 9). Vendace on the other hand, have a gentler negative maturation reaction norm, which did not lead to an increase in catchability of immature individuals. The species therefore responded differently to the multiple stressor scenarios, and while for Arctic charr the cumulative pressure reduced the proportion of adults substantially, this was not evident in the vendace population (paper II). This suggests that Arctic charr would be more vulnerable and less resilient to size-selective harvesting under climate warming than vendace, which is a result of their difference in life history.

Both climate warming and size-selective harvesting might promote increased growth rates in high latitude fish populations as somatic growth increases with respectively higher water temperatures and lower population densities (Persson et al. 2007, Huey and Kingsolver 2019, Morrongiello et al. 2021). A reduction of competitors (i.e. reduced density) as a consequence of high fishing mortality promoted compensatory somatic growth in the modelled populations (paper I & II), in line with previous studies on density dependent growth (Rose et al. 2001, Amundsen et al. 2007, Evangelista et al. 2020). Density similarly affected growth in the wild populations investigated here (paper II & III). Therefore, an additional cumulative effect of climate warming and size-selective fisheries is that climate warming promotes an increase in individual growth, while harvesting, by reducing density, accentuates this effect in high latitude freshwater fish populations (paper II) (see Fig. 9). Such compensatory growth effects might increase juvenile survival, boosting reproductive rates and ultimately increase recruitment (Rose et al. 2001, Persson et al. 2007). However, as formerly mentioned, this is highly dependent on the life history of the species, as well as the fishing intensity or size-selectivity of the fisheries (paper I & II). The negative synergetic effects (age truncation and immature individuals caught) are worst with high exploitation rates because it releases the somatic growth potential from warming due to lower densities. In addition, high exploitation rates removes most of the large individuals that contribute the most to population recruitment (Anderson et al. 2008, Hsieh et al. 2010), and simultaneously harvests young, fast growing and possibly immature individuals, this harvest pattern combination contributes to increase vulnerability and decrease resilience (Fig. 9).

Paper I and paper II emphasize that fisheries might mask the effects of climate warming. Different levels of fishing mortality masked to a varying degree climate warming impacts both at the individual and population level in high latitude freshwater fish populations. The increase in both biomass and yield revealed for the low fishing mortality scenarios was not visible in the highest fishing mortality scenarios, because fisheries removes the largest individuals that contribute the most to an increase in biomass and yield. Hence, interpretations of population performance might wrongly conclude that climate warming has minor effects on these fish stocks. Proper management that includes age- and size distributions and maturation patterns in the monitoring would observe climate warming effects in the populations that are not visible when monitoring biomass and yield alone.

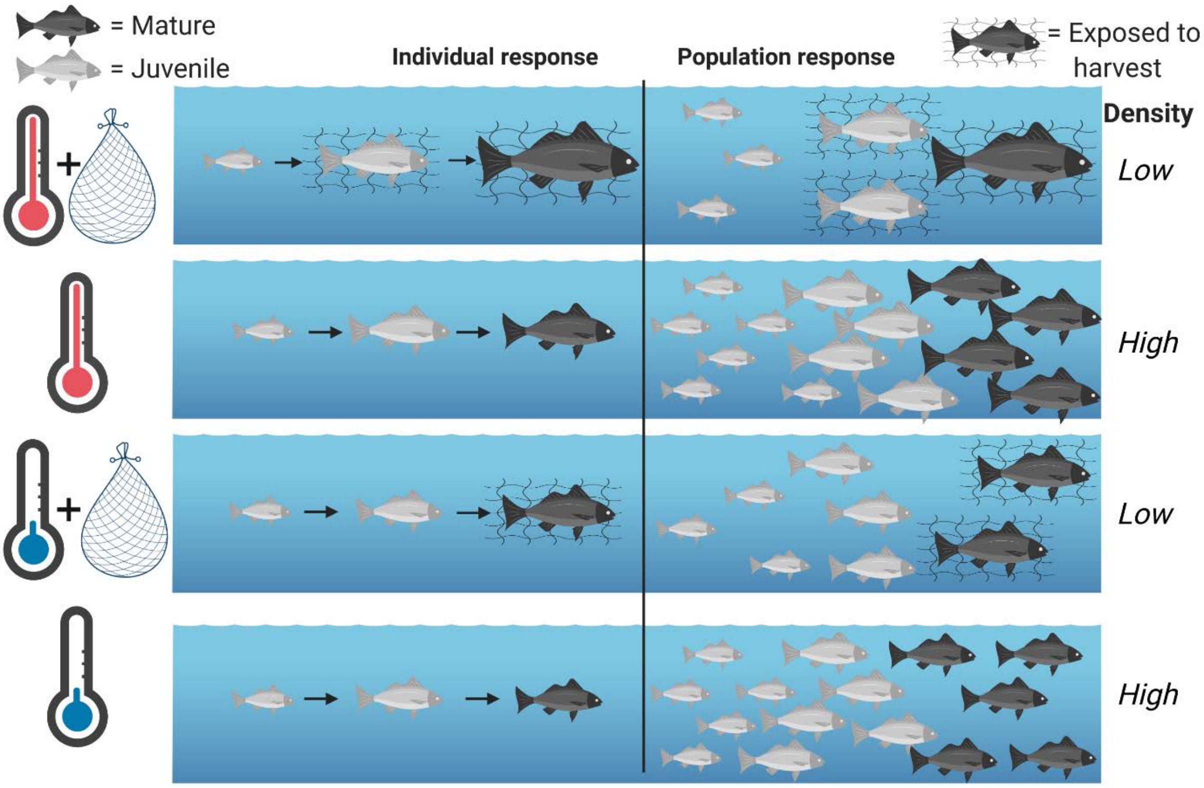


Figure 9. Theoretical representation of the combined effects of climate warming and size-selective harvesting in high latitude freshwater fish populations, exemplified with a life history described with slow juvenile growth, large size and old age at maturation. Panel 1 from the bottom: Cold water temperature without fisheries, leading to a high density situation that

combined with the low water temperature, results in slow juvenile and adult somatic growth. Panel 2 from the bottom: Cold water temperature with size-selective-fisheries, resulting in lower density of competitors promoting compensatory growth, leading to larger size at age compared to the scenario without fisheries. Panel 3 from the bottom: Warm water temperature without fishing, might lead to a relative high density of competitors, but the increase in temperature promotes increased juvenile somatic growth. Panel 4 from the bottom: Warm water temperature with size-selective fishing, resulting in "double" positive effect in individual growth caused by an increase in water temperature and low density of competitors from fisheries, resulting in increased vulnerability as also juveniles will be susceptible for harvest (paper I & II).

4.4. Implications for management and conservation

This thesis highlights two separate management challenges for future freshwater fish stocks at high latitudes. First, climate warming may accentuate the negative effects of size-selective harvesting, increasing vulnerability of exploited stocks (paper I & II). Secondly, cool water fish will benefit more than cold water fish in terms of increased individual growth (paper II), and increased density and relative importance in high latitude lakes (paper III). In northern lakes harvesting is important both for sustenance and recreational purposes (Reist et al. 2006), and large, active salmonids are particular vulnerable (Finstad et al. 2001), with many populations being under pressure from size-selective fisheries. It is important for future management to monitor changes in age and size structures to prevent further age truncation, which would increase vulnerability and decrease resilience in already fully exploited stocks under climate warming. Mitigation strategies must encompass such effects by setting a limitation in mesh-size of gill-nets and implement other strategies that protect large, adult individuals within harvested populations (e.g. catch and release, minimum body size limitation) (see Ahrens et al. 2020).

Climate adaptation must protect cold water fish in high latitude regions under climate change. Because, with warming, cool water fish will increase in density, relative importance (paper II & III), and might invade new areas where native cold water fish would be vulnerable. This thesis thus suggests that cool water fish might improve their overall performance in high latitude lakes and subsequently might threaten coexisting cold water fish. Therefore, it will be decisive to prevent future invasions or introductions of cool water fish into ecosystems where these species do not already coexist with cold water species. Introductions of species are already prohibited in many countries, but climate adaptation measures should involve strategies to prevent natural invasions of non-native fish as well. The native fish species already living in these ecosystems are very vulnerable towards invasions of non-native fish under climate warming (e.g. Bøhn et al. 2008, Morrissey-McCaffrey et al. 2018).

4.5. Future developments and perspectives

This thesis provides a causal understanding of how temperature affects individual growth and life history in fish, and the population level implications of these individual effects of climate warming in high latitude lakes. However, as these systems appear particularly vulnerable, it is important to further enhance the understanding of how climate warming may affect freshwater fish at high latitudes in the future. As demonstrated, both modelling efforts and long-term retrospective studies are important tools to investigate the complex implications of climate change. Furthermore, this thesis emphasizes the importance of studying climate change repercussions on the same temporal scale these effects unravel to obtain a strong causal understanding. To further increase complexity, climate warming seldom acts as the sole stressor on wild populations and including additional stressors makes the task of environmental impact assessment even more challenging. Modelling tools, like the IBM used here, may extricate the effects caused by multiple stressors, but we need more experimental studies to provide species-specific parameters that currently are unavailable in order to increase the realism and predictive power of these models. While filling knowledge gaps on species, we also need to adress whole ecosystem changes in climate change impact research. For instance, food web mediated effects, changes in productivity, and changes in ecological interactions both from coexisting species, but also from possible invading alien species need to be included in future modelling frameworks and research. The current study clearly reveals that climate-induced changes already are evident in northern lakes, and emphasizes the importance of learning from the past while making predictions and taking the necessary measures and precautions for a sustainable management of vulnerable freshwater fish.

References

Ahrens, R. N., Allen, M. S., Walters, C., & Arlinghaus, R. 2020. Saving large fish through harvest slots outperforms the classical minimum-length limit when the aim is to achieve multiple harvest and catch-related fisheries objectives. *Fish and Fisheries*, *21*, 483-510.

Allan, J. D., Abell, R., Hogan, Z., Revenga, C., Taylor, B. W., Welcomme, R. L., & Winemiller, K. 2005. Overfishing of inland waters. *Bioscience, 55,* 1041–1051.

Amundsen, P.-A., Klemetsen, A., & Grotnes, P. E. 1993. Rehabilitation of a stunted population of Arctic charr by intensive fishing. *North American Journal of Fisheries Management, 13*, 483-491.

Amundsen, P.-A., Knudsen, R., & Klemetsen, A. 2007. Intraspecific competition and density dependence of food consumption and growth in Arctic charr. *Journal of Animal Ecology, 76,* 149–158.

Amundsen, P.-A., Lafferty, K. D., Knudsen, R., Primicerio, R., Klemetsen, A., & Kuris, A. M. 2009. Food web topology and parasites in the pelagic zone of a subarctic lake. *Journal of Animal Ecology*, *78*, 563–572. https://doi.org/10.1111/j.1365-2656.2008.01518.x

Amundsen, P.-A., Primicerio, R., Smalås, A., Henriksen, E. H., Knudsen, R., Kristoffersen, R., & Klemetsen, A. 2019. Long-term ecological studies in northern lakes – challenges, experiences and accomplishments. *Limnology and Oceanography, 64*, 11-21.

Amundsen, P.-A., Bøhn, T., Popova, O. A., Staldvik, F. J., Reshetnikov, Y. S., Kashulin, N. A., & Lukin, A. A. 2003. Ontogenetic niche shifts and resource partitioning in a subarctic piscivore fish guild. *Hydrobiologia, 497,* 109-119.

Anderson, C. N. K., Hsieh, C. H., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., May, R. M., & Sugihara, G. 2008. Why fishing magnifies fluctuations in fish abundance. *Nature*, *452*, 835–839. https://doi.org/10.1038/nature06851

Angilletta, M. J., Steury, T. D., & Sears, M. W. 2004. Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. *Integrative and comparative biology, 44*, 498-509.

Arula, T., Shpilev, H., Raid, T., Vetemaa, M., & Albert, A. 2017. Maturation at a young age and small size of European smelt (*Osmerus eperlanus*): A consequence of population overexploitation or climate change? *Helgoland Marine Research*, *71,* 1-9.

Atkinson, D. 1994. Temperature and organism size - A biological law for ectotherms? *Advances in Ecological Research , 25*, 1-58.

Audzijonyte, A., Richards, S. A., Stuart-Smith, R. D., Pecl, G., Edgar, G. J., Barrett, N. S., Payne, N.,& Blanchard, J. L. 2020. Fish body sizes change with temperature but not all species shrink with warming. *Nature Ecology & Evolution*, *4*, 809-814.

Bar, N. 2014. Physiological and hormonal changes during prolonged starvation in fish. *Canadian Journal of Fisheries and Aquatic Sciences, 71*, 1447–1458.

Benateau, S., Gaudard, A., Stamm, C., & Altermatt, F. 2019. Climate change and freshwater ecosystems: Impacts on water quality and ecological status. *Hydro-CH2018Project*. Federal Office for the Environment (FOEN), Bern, Switzerland. pp.110.

Berkeley, S. A., Hixon, M. A., Larson, R. J., & Love, M. S. 2004. Fisheries Sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, *29*, 23–32.

Barneche, D. R., Robertson, D. R., White, C. R., & Marshall, D. J. 2018. Fish reproductive-energy output increases disproportionately with body size. *Science, 360*, 642-645.

Biro, P. A., Post, J. R., & Booth, D. J. 2007. Mechanisms for climate-induced mortality of fish populations in whole-lake experiments. *Proceedings of the National Academy of Sciences*, *104*, 9715–9719.

Blanchet, M.-A., Primicerio, R., Smalås, A., Arias-Hansen, J., & Aschan, M. 2019. How vulnerable is the European seafood production to climate warming? *Fisheries Research, 209*, 251–258.

Bonan, G. 2015. *Ecological Climatology: Concepts and Applications* (3rd ed.). Cambridge University Press.

Boukal, D. S., Dieckmann, U., Enberg, K., Heino, M., & Jørgensen, C. 2014. Life-history implications of the allometric scaling of growth. *Journal of Theoretical Biology*, *359*, 199–207.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. 2004. Toward a metabolic theory of ecology. *Ecology*, *85*, 1771–1789.

Burian, A., Nielsen, J. M., & Winder, M. 2020. Food quantity-quality interactions and their impact on consumer behavior and trophic transfer. *Ecological Monographs, 90*, pp. 19.

Butzin, M., & Pörtner, H. O. 2016. Thermal growth potential of Atlantic cod by the end of the 21st century. *Global Change Biology, 22,* 4162-4168.

Bøhn, T., Amundsen, P. A., & Sparrow, A. 2008. Competitive exclusion after invasion?. Biological Invasions, 10, 359-368.

Campana, S., Casselman, J., Jones, C., Black, G., Barker, O., Evans, M., Guzzo, M., Kilada, R., Muir, A., & Perry, R. 2020. Arctic freshwater fish productivity and colonization increase with climate warming. *Nature Climate Change, 10*, 428-433.

Cazelles, K., Bartley, T., Guzzo, M. M., Brice, M., MacDougall, A. S., Bennett, J. R., Esch, E. H., Kadoya, T., Kelly, J., Matsuzaki, S., Nilsson, K. A., & McCann, K. S. 2019. Homogenization of freshwater lakes: Recent compositional shifts in fish communities are explained by gamefish movement and not climate change. *Global Change Biology*, *25*, 4222–4233.

CBMP, Circumpolar Biodiversity Monitoring Programme. 2019. State of the Arctic Freshwater Biodiversity report: Fish. Conservation of Arctic Flora and Fauna report series. pp. 73-81.

Comte, L., Buisson, L., Daufresne, M., & Grenouillet, G. 2013. Climate-induced changes in the distribution of freshwater fish: observed and predicted trends. *Freshwater Biology*, *58*, 625–639.

Connor, L., Shephard, S., Rocks, K., & Kelly, F. L. 2019. Potential climate change impacts on Arctic char Salvelinus alpinus L. in Ireland. *Fisheries Management and Ecology, 26*, 527-539.

Conover, D. O., & Munch, S. B. 2002. Sustaining fisheries yields over evolutionary time scales. *Science*, *297*, 94–96.

Crook, D. A., Lowe, W. H., Allendorf, F. W., Eros, T., Finn, D. S., Gillanders, B. M., Hadwen, W. L., Harrod, C., Hermoso, V., Jennings, S., Kilada, R. W., Nagelkerken, I., Hansen, M. M., Page, T. J., Riginos, C., Fry, B., & Hughes, J. M. 2015. Human effects on ecological connectivity in aquatic ecosystems: Integrating scientific approaches to support management and mitigation. *Science of the Total Environment*, *534*, 52–64.

Dahlke, F. T., Wohlrab, S., Butzin, M., & Pörtner, H. O. 2020. Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science*, *369*, 65–70.

Deslauriers, D., Chipps, S. R., Breck, J. E., Rice, J. A., & Madenjian, C. P. 2017. Fish Bioenergetics 4.0: An R-based modeling application. *Fisheries*, *42*, 586–596.

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, *105,* 6668–6672.

Dieckmann, U., & Heino, M. 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. *Marine Ecology Progress Series*, *335,* 253–269.

Dodds, W. K., Perkin, J. S., & Gerken, J. E. 2013. Human impact on freshwater ecosystem services: A global perspective. *Environmental Science & Technology*, *47,* 9061–9068.

Dunlop, E. S., Heino, M., & Dieckmann, U. (2009). Eco-genetic modeling of contemporary life-history evolution. *Ecological Applications*, *19*, 1815–1834.

Edwards, P. N. 2011. History of climate modeling. *Wiley Interdisciplinary Reviews: Climate Change*, *2*, 128–139.

Elliott, J. M. 1993. The pattern of natural mortality throughout the life cycle in contrasting populations of brown trout, *Salmo trutta L. Fisheries Research, 17,* 123-136.

Enberg, K., Jørgensen, C., Dunlop, E. S., Heino, M., & Dieckmann, U. 2009. Implications of fisheries-induced evolution for stock rebuilding and recovery. *Evolutionary Applications, 2*, 394-414.

Evangelista, C., Vøllestad, L. A., Pauli, B. D., & Edeline, E. 2020. Density-dependent consequences of size-selective induced life-history changes to population fitness in medaka (*Oryzias latipes*). *Canadian Journal of Fisheries and Aquatic Sciences*, *77*, 1741–1748.

Fabens, A. J. 1965. Properties and fitting of von Bertalanffy growth curve. *Growth, 29*, 265-289.

Fenberg, P. B., & Roy, K. 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Molecular Ecology, 17,* 209–220.

Feuchtmayr, H., Moran, R., Hatton, K., Connor, L., Heyes, T., Moss, B., Harvey, I., & Atkinson, D. 2009. Global warming and eutrophication: Effects on water chemistry and autotrophic communities in experimental hypertrophic shallow lake mesocosms. *Journal of Applied Ecology, 46*, 713–723.

Ficke, A. D., Myrick, C. A., & Hansen, L. J. 2007. Potential impacts of global climate change on freshwater fisheries. *Reviews in Fish Biology and Fisheries*, *17,* 581–613.

Finstad, A. G., Jansen, P. A., & Langeland, L. 2001. Production and predation rates in a cannibalistic Arctic char (*Salvelinus alpinus L.*) population. *Ecology of Freshwater Fish*, 10, 220–226.

Finstad, A. G., Forseth, T., Jonsson, B., Bellier, E., Hesthagen, T., Jensen, A. J., Hessen, D. O., & Foldvik, A. 2011. Competitive exclusion along climate gradients: energy efficiency influences the distribution of two salmonid fishes. *Global Change Biology*, *17*, 1703–1711.

Finstad, A. G., Andersen, T., Larsen, S., Tominaga, K., Blumentrath, S., De Wit, H. A., Tømmervik, H., & Hessen, D. O. 2016. From greening to browning: Catchment vegetation development and reduced S-deposition promote organic carbon load on decadal time scales in Nordic lakes. *Scientific Reports*, *6*, 1–8.

George, D. G., Bell, V. A., Parker, J., & Moore, R. J. 2006. Using a 1-D mixing model to assess the potential impact of year-to-year changes in weather on the habitat of vendace (*Coregonus albula*) in Bassenthwaite Lake, Cumbria. *Freshwater Biology, 51*, 1407-1416.

Gerdaux, D. 1998. *Fluctuations in lake fisheries and global warming* (George D. G. (Ed): Management Workshop on management of lakes and reservoir during global climate change). Kluwer Academic Publishers.

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. 2001. Effects of size and temperature on metabolic rate. *Science, 293,* 2248–2251.

Gislason, H., Daan, N., Rice, J. C., & Pope, J. G. 2010. Size, growth, temperature and the natural mortality of marine fish. *Fish and Fisheries, 11*, 149-158.

Gissi, E., Manea, E., Mazaris, A. D., Fraschetti, S., Almpanidou, V., Bevilacqua, S., Coll, M., Guarnieri, G., Lloret-Lloret, E., Pascual, M., Petza, D., Rilov, G., Schonwald, M., Stelzenmüller, V., & Katsanevakis, S. 2021. A review of the combined effects of climate change and other local human stressors on the marine environment. *Science of the Total Environment, 755,* pp. 14.

Godiksen, J. A., Svenning, M.-A., Sinnatamby, R. N., Dempson, J. B., Borgstrøm, R., & Power, M. 2014. Stable isotope-based determinations of the average temperatures experienced by young-of-the-year Svalbard Arctic charr (*Salvelinus alpinus*). *Polar Biology, 34*, 591–596.

Green, P. A., Vörösmarty, C. J., Harrison, I., Farrell, T., Sáenz, L., & Fekete, B. M. 2015. Freshwater ecosystem services supporting humans: Pivoting from water crisis to water solutions. *Global Environmental Change, 34*, 108–118.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S. K., Huse, G., Huth, A., Jepsen, J. U., Jorgensen, C., Mooij, W. M., Muller, B., Pe'er, G., Piou, C., Railsback, S. F., Robbins, A. M., … DeAngelis, D. L. 2006. A standard protocol for describing individual-based and agent-based models. *Ecological Modelling*, *198*, 115–126.

Haddon, M. 2001. *Modelling and quantitative methods in fisheries.* Chapman & Hall/CRC.

Hansen, M. J., Madenjian, C. P., Selgeby, J. H., & Helser, T. E. 1997. Gillnet selectivity for lake trout (*Salvelinus namaycush*) in Lake Superior. *Canadian Journal of Fisheries and Aquatic Sciences, 54*, 2483–2490.

Harris, R. M. B., Grose, M. R., Lee, G., Bindoff, N. L., Porfirio, L. L., & Fox-Hughes, P. 2014. Climate projections for ecologists. *Wiley Interdisciplinary Reviews: Climate Change*, *5*, 621–637.

Hawley, K. L., Rosten, C. M., Haugen, T. O., Christensen, G., & Lucas, M. C. 2017. Freezer on, lights off! Environmental effects on activity rhythms of fish in the Arctic. *Biology Letters*, *13*, pp. 5.

Hayden, B., Harrod, C., Thomas, S. M., Eloranta, A. P., Myllykangas, J. -P., Siwertsson, A., Præbel, K., Knudsen, R., Amundsen, P. -A., & Kahilainen, K. K. 2019. From clear lakes to murky waters – tracing the functional response of high-latitude lake communities to concurrent 'greening' and 'browning.' *Ecology Letters*, *22,* 807–816.

Hayden, B., Holopainen, T., Amundsen, P. A., Eloranta, A. P., Knudsen, R., Præbel, K., & Kahilainen, K. K. 2013. Interactions between invading benthivorous fish and native whitefish in subarctic lakes. *Freshwater Biology*, *58*, 1234–1250.

Heermann, L., Eriksson, L. O., Magnhagen, C., & Borcherding, J. 2009. Size-dependent energy storage and winter mortality of perch. *Ecology of Freshwater Fish*, *18*, 560-571.

Heibo, E., Magnhagen, C., & Vøllestad, L. A. 2005. Latitudinal variation in life-history traits in Eurasian perch *Ecology*, *86*, 3377–3386.

Hein, C. L., Ohlund, G., & Englund, G. 2012. Future Distribution of Arctic Char Salvelinus alpinus in Sweden under Climate Change: Effects of Temperature, Lake Size and Species Interactions. *Ambio*, *41*, 303–312.

Heino, M., Dieckmann, U., & Godø O. R. 2002. Measuring probabilistic reaction norms for age and size at maturation. *Evolution*, *56*, 669–678.

Heino, M., & Godø, O. R. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. *Bulletin of Marine Science*, *70*, 639–656.

Heino, M., & Dieckmann, U. 2008. Detecting fisheries-induced life-history evolution: An overview of the reaction-norm approach. *Bulletin of Marine Science*, *83*, 69–93.

Heino, J., Virkkala, R., & Toivonen, H. 2009. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews*, *84*, 39–54.

Heino, M., Pauli, B. D., & Dieckmann, U. 2015. Fisheries-induced evolution. *Annual review of ecology, evolution, and systematics*, *46*, 461-480.

Hessen, D. O., Hindar, A., & Holtan, G. 1997. The significance of nitrogen runoff for eutrophication of freshwater and marine recipients. *Ambio*, *26*, 312–320.

Hipsey, M. R., Bruce, L. C., Hamilton, D. P., & Australia, T. U. of W. 2014. GLM - General Lake Model: Model overview and user information. In *AED Report #26*.

Hsieh, C. H., Yamauchi, A., Nakazawa, T., & Wang, W. F. 2010. Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences*, *72*, 165–178. https://doi.org/10.1007/s00027-009-0122-2

Huey, R. B., & Kingsolver, J. G. 2019. Climate warming, resource availability, and the metabolic meltdown of ectotherms. *American Naturalist*, *194*, 140-150.

Hughes, K. 2021. The world’s forgotten fishes. World Wide Fund for Nature, panda-report. pp. 46.

Huss, M., Lindmark, M., Jacobson, P., van Dorst, R. M., Gårdmark, A., & Gardmark, A. 2019. Experimental evidence of gradual size-dependent shifts in body size and growth of fish in response to warming. *Global Change Biology*, *25*, 2285–2295.

Hutchings, J. A., & Myers, R. A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, *51*, 2126-2146.

IPCC. 2013. *Climate change 2013: the physical science basis: Working Group I contribution to the Fifth assessment report of the Intergovernmental Panel on Climate Change.* (T. Stocker (Ed.)). Cambridge University Press.

IPCC. 2007. *Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC* (S. Salomon, M. Manning, M. Marquis, & D. Qin (Eds.)). Cambridge University Press.

Jacob, D., Petersen, J., Eggert, B., Alias, A., Christensen, O. B., Bouwer, L. M., Braun, A., Colette, A., Déqué, M., Georgievski, G., Georgopoulou, E., Gobiet, A., Menut, L., Nikulin, G., Haensler, A., Hempelmann, N., Jones, C., Keuler, K., Kovats, S., … Yiou, P. 2014. EURO-CORDEX: New high-resolution climate change projections for European impact research. *Regional Environmental Change, 14*, 563–578.

Jarvis, L. A., McMeans, B. C., Giacomini, H. C., & Chu, C. 2020. Species-specific preferences drive the differential effects of lake factors on fish production. *Canadian Journal of Fisheries and Aquatic Sciences, 77*, 1625–1637.

Jennings, S., Reynolds, J. D., & Mills, S. C. 1998. Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society B: Biological Sciences, 265*, 333-339.

Jeppesen, E., Mehner, T., Winfield, I. J., Kangur, K., Sarvala, J., Gerdeaux, D., Rask, M., Malmquist, H. J., Holmgren, K., Volta, P., Romo, S., Eckmann, R., Sandstrom, A., Blanco, S., Kangur, A., Stabo, H. R., Tarvainen, M., Ventela, A. M., Sondergaard, M., … Meerhoff, M. 2012. Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. *Hydrobiologia*, *694*, 1–39.

Jobling, M. 2002. Environmental factors and rates of development and growth. (P. J. B. Hart & J. D. Reynolds (Eds.)), *Handbook of fish biology and fisheries* (Vol. 2, pp. 97–122). Wiley-Blackwell.

Jobling, M. 1983. Towards an explanation of specific dynamic action (SDA). *Journal of Fish Biology, 23*, 549–555.

Johnson, T. B., & Evans, D. O. 1990. Size-dependent winter mortality of young-of-the-year white perch: Climate warming and invasion of the Laurentian Great Lakes. *Transactions of the American Fisheries Society, 119*, 301–313.

Judson, O. P. 1994. The Rise of the Individual-Based Model in Ecology. *Trends in Ecology & Evolution*, *9*, 9–14.

Katzav, J., & Parker, W. S. 2015. The future of climate modeling. *Climatic Change*, *132*, 475–487.

Kelly, S., Moore, T. N., de Eyto, E., Dillane, M., Goulon, C., Guillard, J., Lasne, E., McGinnity, P., Poole, R., Winfield, I. J., Woolway, R. I., & Jennings, E. 2020. Warming winters threaten peripheral Arctic charr populations of Europe. *Climatic Change*, 163, 599-618.

Killen, S. S., Atkinson, D., & Glazier, D. S. 2010. The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. *Ecology Letters*, *13*, 184–193.

Kingsolver, J. G., & Huey, R. B. 2008. Size, temperature, and fitness: three rules. *Evolutionary Ecology Research*, *10*, 251–268.

Kjellman, J., Lappalainen, J., Urho, L., & Hudd, R. 2003. Early determination of perch and pikeperch recruitment in the northern Baltic Sea. *Hydrobiologia*, *495*, 181–191.

Klemetsen, A., Amundsen, P. A., Muladal, H., Rubach, S. H., & Solbakken, J. I. 1989. Habitat shifts in a dense, resident Arctic charr *Salvelinus alpinus* population. *Physiology and Ecology, Japan Special Issue*, *1*, pp. 14.

Klemetsen, A., Amundsen, P. A., Grotnes, P. E., Knudsen, R., Kristoffersen, R., & Svenning, M. A. 2002. Takvatn through 20 years: long-term effects of an experimental mass removal of Arctic charr, *Salvelinus alpinus*, from a subarctic lake. In Ecology, behaviour and conservation of the charrs, genus Salvelinus (pp. 39-47). Springer, Dordrecht.

Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O’Connell, M. F., & Mortensen, E. 2003. Atlantic salmon *Salmo salar L.*, brown trout *Salmo trutta L.* and Arctic charr *Salvelinus alpinus (L.)*: A review of aspects of their life histories. *Ecology of Freshwater Fish*, *12*, 1-59.

Klemetsen, A. 2010. The charr problem revisited: exceptional phenotypic plasticity promotes ecological speciation in postglacial lakes. *Freshwater Reviews*, *3*, 49–74.

Koskela, J., Jobling, M., & Pirhonen, J. 1997. Influence of the length of the daily feeding period on feed intake and growth of whitefish, Coregonus lavaretus. *Aquaculture, 156, 35-44.*

Kristensen, D. M., Jørgensen, T. R., Larsen, R. K., Forchhammer, M. C., & Christoffersen, K. S. (2006). Inter-annual growth of Arctic charr (*Salvelinus alpinus* (L.)) in relation to climate variation. *BMC Ecology, 6*, 1–8.

Kuparinen, A., & Merilä, J. 2007. Detecting and managing fisheries-induced evolution. *Trends in ecology & evolution*, *22*, 652-659.

Landgren, O. A., & Haugen, J. E. 2016. Updated ranking of GCM-RCM results for five Scandinavian locations. *MET-Reports*, *7/2016*, 14.

Larsson, S., & Berglund, I. 1998. Growth and food consumption of 0+ Arctic charr fed pelleted or natural food at six different temperatures. *Journal of Fish Biology*, *52*, 230–242.

Larsson, S., & Berglund, I. 2005. The effect of temperature on the energetic growth efficiency of Arctic charr (*Salvelinus alpinus* L.) from four Swedish populations. *Journal of Thermal Biology*, *30*, 29–36. https://doi.org/10.1016/j.jtherbio.2004.06.001

Larsson, S., Forseth, T., Berglund, I., Jensen, A. J., Naslund, I., Elliott, J. M., & Jonsson, B. 2005. Thermal adaptation of Arctic charr: experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. *Freshwater Biology, 50*, 353–368.

Law, R. 2000. Fishing, selection, and phenotypic evolution. *Ices Journal of Marine Science*, *57*, 659–668.

Lindenmayer, D. B., & Likens, G. E. 2009. Adaptive monitoring: a new paradigm for long-term research and monitoring. *Trends in Ecology and Evolution*, *24*, 482–486.

Lindenmayer, D. B., & Likens, G. E. 2010. The science and application of ecological monitoring. *Biological Conservation*, *143*, 1317–1328.

Lindmark, M., Huss, M., Ohlberger, J., & Gardmark, A. 2018. Temperature-dependent body size effects determine population responses to climate warming. *Ecology Letters*, *21,* 181–189.

Lindmark, M., Ohlberger, J., Huss, M., & Gardmark, A. 2019. Size-based ecological interactions drive food web responses to climate warming. *Ecology Letters*, *22*, 778–786.

Lorenzen, K., & Enberg, K. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proceedings of the Royal Society B:Biological Sciences*, *269*, 49–54.

Maberly, S. C., O'Donnell, R. A., Woolway, R. I., Cutler, M. E. J., Gong, M., Jones, I. D., Merchant, C. J., Miller, C. A., Politi, E., Scott, E. M., Thackeray, S. J., & Tyler, A. N. 2020. Global lake thermal regions shift under climate change. *Nature Communications*, *11*, 1–9.

Maeda, E. E., Lisboa, F., Kaikkonen, L., Kallio, K., Koponen, S., Brotas, V., & Kuikka, S. 2019. Temporal patterns of phytoplankton phenology across high latitude lakes unveiled by long-term time series of satellite data. *Remote Sensing of Environment*, *221*, 609–620.

Magnuson, J. J., Crowder, L. B., & Medvick, P. A. 1979. Temperature as an ecological resource. *American Zoologist*, *19*, 331-343.

McMeans, B. C., Mccann, K. S., Guzzo, M. M., Bartley, T. J., Bieg, C., Blanchfield, P. J., Fernandes, T., Giacomini, H. C., Middel, T., Rennie, M. D., Ridgway, M. S., & Shuter, B. J. 2020. Winter in water: Differential responses and the maintenance of biodiversity. *Ecology letters*, *23*, 922-938.

Michaud, W. K., Dempson, J. B., & Power, M. 2010. Changes in growth patterns of wild Arctic charr (Salvelinus alpinus (L.)) in response to fluctuating environmental conditions. *Hydobiologia, 650,* 179–191.

Mills, C. A., & Mann, R. H. K. 1985. Environmentally-induced fluctuations in year-class strength and their implications for management. *Journal of Fish Biology, 27,* 209–226.

Morrissey-McCaffrey, E., Shephard, S., Kelly, F. L., & Kelly-Quinn, M. 2019. Non-native species and lake warming negatively affect Arctic char Salvelinus alpinus abundance; deep thermal refugia facilitate co-existence. *Journal of fish biology, 94,* 5-16.

Morrongiello, J. R., Horn, P. L., Ó Maolagáin, C., & Sutton, P. J. H. 2021. Synergistic effects of harvest and climate drive synchronous somatic growth within key New Zealand fisheries. *Global Change Biology, 27,* 1470–1484.

Moss, R. H., Edmonds, J. A., Hibbard, K. A., Manning, M. R., Rose, S. K., Van Vuuren, D. P., Carter, T. R., Emori, S., Kainuma, M., Kram, T., Meehl, G. A., Mitchell, J. F. B., Nakicenovic, N., Riahi, K., Smith, S. J., Stouffer, R. J., Thomson, A. M., Weyant, J. P., & Wilbanks, T. J. 2010. The next generation of scenarios for climate change research and assessment. *Nature 463,* 747–756).

Murdoch, A., & Power, M. 2013. The effect of lake morphometry on thermal habitat use and growth in Arctic charr populations: implications for understanding climate-change impacts. *Ecology of Freshwater Fish, 22,* 453–466.

Neuenhoff, R. D., Swain, D. P., Cox, S. P., McAllister, M. K., Trites, A. W., Walters, C. J., & Hammill, M. O. 2019. Continued decline of a collapsed population of Atlantic cod (*Gadus morhua*) due to predation-driven Allee effects. *Canadian Journal of Fisheries and Aquatic Sciences, 76,* 168-184.

Nilsson-Örtman, V., & Rowe, L. 2021. The evolution of developmental thresholds and reaction norms for age and size at maturity. *Proceedings of the National Academy of Sciences*, *118,* pp. 7.

O'Beirne, M. D., Werne, J. P., Hecky, R. E., Johnson, T. C., Katsev, S., & Reavie, E. D. 2017. Anthropogenic climate change has altered primary productivity in Lake Superior. *Nature Communications, 8,* 1-8.

Ohlberger, J. 2013. Climate warming and ectotherm body size - from individual physiology to community ecology. *Functional Ecology, 27,* 991–1001.

Ohlberger, J., Edeline, E., Vollestad, L. A., Stenseth, N. C., & Claessen, D. 2011. Temperature-Driven Regime Shifts in the Dynamics of Size-Structured Populations. *American Naturalist*, *177,* 211–223.

Okamoto, K. W., Whitlock, R., Magnan, P., & Dieckmann, U. 2009. Mitigating fisheries-induced evolution in lacustrine brook charr (Salvelinus fontinalis) in southern Quebec, Canada. *Evolutionary Applications, 2,* 415–437.

Olsen, E. M., Heino, M., Lilly, G. R., Morgan, M. J., Brattey, J., Ernande, B., & Dieckmann, U. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature, 428,* 932-935.

Olsen, E., Lilly, G. R., Heino, M., Morgan, M. J., Brattey, J., & Dieckmann, U. (2005). Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences, 62,* 811–823.

O'Reilly, C. M., Sharma, S., Gray, D. K., Hampton, S. E., Read, J. S., Rowley, R. J., Schneider, P., Lenters, J. D., McIntyre, P. B., Kraemer, B. M., Weyhenmeyer, G. A., Straile, D., Dong, B., Adrian, R., Allan, M. G., Anneville, O., Arvola, L., Austin, J., Bailey, J. L., … Zhang, G. Q. 2015. Rapid and highly variable warming of lake surface waters around the globe. *Geophysical Research Letters, 42,* 10773–10781.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology *Evolution and Systematics, 37,* 637–669.

Persson, L., Amundsen, P. A., De Roos, A. M., Klemetsen, A., Knudsen, R., & Primicerio, R. 2007. Culling prey promotes predator recovery - Alternative states in a whole-lake experiment. *Science, 316,* 1743–1746.

Persson, L., Amundsen, P. A., De Roos, A. M., Knudsen, R., Primicerio, R., & Klemetsen, A. 2013. Density-dependent interactions in an Arctic char - brown trout system: competition, predation, or both? *Canadian Journal of Fisheries and Aquatic Sciences, 70,* 610–616.

Pörtner, H. O., Berdal, B., Blust, R., Brix, O., Colosimo, A., De Wachter, B., Giuliani, A., Johansen, T., Fischer, T., Knust, R., Lannig, G., Naevdal, G., Nedenes, A., Nyhammer, G., Sartoris, F. J., Serendero, I., Sirabella, P., Thorkildsen, S., & Zakhartsev, M. 2001. Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Continental Shelf Research, 21,* 1975–1997.

Power, M., & van den Heuvel, M. R. 1999. Age-0 Yellow Perch Growth and Its Relationship to Temperature. *Transactions of the American Fisheries Society, 128,* 687–700.

Power, M., Dempson, J. B., Power, G., & Reist, J. D. 2000. Environmental influences on an exploited anadromous Arctic charr stock in Labrador. *Journal of Fish Biology, 57,* 82–98.

Railsback, S. F. 2001. Concepts from complex adaptive systems as a framework for individual-based modelling. *Ecological modelling, 139,* 47-62.

Ratkowsky, D. A., Lowry, R. K., McMeekin, T. A., Stokes, A. N., & Chandler, R. E. 1983. Model for bacterial culture growth rate throughout the entire biokinetic temperature range. *Journal of Bacteriology, 53, 122-126.*

Regier, H. A., & Meisner, J. D. 1990. Anticipated effects of climate change on freshwater fishes and their habitat. *Fisheries 15,* 10–15.

Reist, J. D., Wrona, F. J., Prowse, T. D., Power, M., Dempson, J. B., Beamish, R. J., King, J. R., Carmichael, T. J., & Sawatzky, C. D. 2006. General effects of climate change on Arctic fishes and fish populations. *Ambio, 35,* 370–380.

Rennie, M. D., Gary Sprules, W., & Johnson, T. B. 2009. Factors affecting the growth and condition of lake whitefish (*Coregonus clupeaformis*). *Canadian Journal of Fisheries and Aquatic Sciences. 66,* 2096-2108.

Reznick, D. N. 1990. Plasticity in age and size at maturity in male guppies (*Poecilia reticulata*): An experimental evaluation of alternative models of development. *Journal of Evolutionary Biology, 3,* 185–203.

Roff, D. A. 1992. The evolution of life histories. Theory and analysis. Chapman and hall, New york. 535 p.

Rose, K. A., Cowan Jr, J. H., Winemiller, K. O., Myers, R. A., & Hilborn, R. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries, 2,* 293-327.

Rubalcaba, J. G., E P Verberk, W. C., Jan Hendriks, A., Saris, B., & Arthur Woods, H. 2020. Oxygen limitation may affect the temperature and size dependence of metabolism in aquatic ectotherms. *Proceedings of the National Academy of Sciences 117,* 31963-31968.

Rummukainen, M. 2010. State-of-the-art with regional climate models. *Wiley Interdisciplinary Reviews: Climate Change, 1,* 82–96.

Sandlund, O. T., Gjelland, K. O., Bohn, T., Knudsen, R., & Amundsen, P. A. 2013. Contrasting population and life history responses of a young morph-pair of European whitefish to the invasion of a specialised coregonid competitor, vendace. *Plos One, 8,* pp. 13.

Schindler, D. W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. *Waters in Peril (pp. 165-186). Springer, Boston, MA.*

Sharma, S., Magnuson, J. J., Mendoza, G., & Carpenter, S. R. 2013. Influences of local weather, large-scale climatic drivers, and the ca. 11 year solar cycle on lake ice breakup dates; 1905-2004. *Climatic Change, 118,* 857–870.

Sharma, S., Blagrave, K., Magnuson, J. J., O'Reilly, C. M., Oliver, S., Batt, R. D., ... & Woolway, R. I. 2019. Widespread loss of lake ice around the Northern Hemisphere in a warming world. *Nature Climate Change, 9,* 227-231.

Siikavuopio, S. I., Saether, B. S., Skybakmoen, S., Uhlig, C., & Haugland, E. 2009. Effects of a simulated short winter period on growth in wild caught Arctic charr (Salvelinus alpinus L.) held in culture. *Aquaculture, 287,* 431–434.

Siikavuopio, S. I., Knudsen, R., & Amundsen, P. A. 2010. Growth and mortality of Arctic charr and European whitefish reared at low temperatures. *Hydrobiologia, 650,* 255–263.

Siikavuopio, S. I., Foss, A., Saether, B. S., Gunnarsson, S., & Imsland, A. K. 2013. Comparison of the growth performance of offspring from cultured versus wild populations of arctic charr, Salvelinus alpinus (L.), kept at three different temperatures. *Aquaculture Research, 44,* 995–1001.

Smalås, A., Strøm, J. F., Amundsen, P., Dieckmann, U., & Primicerio, R. 2020. Climate warming is predicted to enhance the negative effects of harvesting on high-latitude lake fish. *Journal of Applied Ecology, 57,* 270–282.

Stawitz, C. C., & Essington, T. E. 2018. Somatic growth contributes to population variation in marine fishes. *Journal of Animal Ecology, 88,* 315-329.

Stearns, S. C. 2000. Life history evolution: successes, limitations, and prospects. *Naturwissenschaften, 87,* 476-486.

Strand, Å., Magnhagen, C., & Alanärä, A. 2011. Growth and energy expenditures of eurasian perch *perca fluviatilis* (Linnaeus) in different temperatures and of different body sizes. *Journal of Aquaculture Research and Development, 2,* 114.

Strayer, D. L., & Dudgeon, D. 2010. Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society, 29,* 344-358.

Symons, C. C., Schulhof, M. A., Cavalheri, H. B., & Shurin, J. B. 2019. Antagonistic effects of temperature and dissolved organic carbon on fish growth in California mountain lakes. *Oecologia, 189,* 231-241.

L. Trip, E. D., Clements, K. D., Raubenheimer, D., & Choat, J. H. 2014. Temperature-related variation in growth rate, size, maturation and life span in a marine herbivorous fish over a latitudinal gradient. *Journal of Animal Ecology, 83,* 866–875.

van Dorst, R. M., Gardmark, A., Svanback, R., Beier, U., Weyhenmeyer, G. A., & Huss, M. 2019. Warmer and browner waters decrease fish biomass production. *Global Change Biology, 25,* 1395–1408.

van Zuiden, T. M., Chen, M. M., Stefanoff, S., Lopez, L., & Sharma, S. 2016. Projected impacts of climate change on three freshwater fishes and potential novel competitive interactions. *Diversity and Distributions, 22,* 603–614.

Verberk, W. C. E. P., Atkinson, D., Hoefnagel, K. N., Hirst, A. G., Horne, C. R., & Siepel, H. 2021. Shrinking body sizes in response to warming: explanations for the temperature–size rule with special emphasis on the role of oxygen. *Biological Reviews, 96,* 247–268.

Wang, H. Y., & Höök, T. O. 2009. Eco-genetic model to explore fishing-induced ecological and evolutionary effects on growth and maturation schedules. *Evolutionary Applications*, *2*, 438–455.

Ward, H. G. M., Post, J. R., Lester, N. P., Askey, P. J., & Godin, T. 2017. Empirical evidence of plasticity in life-history characteristics across climatic and fish density gradients. *Canadian Journal of Fisheries and Aquatic Sciences, 74,* 464–474.

Warne, C. P. K., McCann, K. S., Rooney, N., Cazelles, K., & Guzzo, M. M. 2020. Geography and Morphology Affect the Ice Duration Dynamics of Northern Hemisphere Lakes Worldwide. *Geophysical Research Letters, 47,* pp. 10.

Wiedmann, M. A., Primicerio, R., Dolgov, A., Ottesen, C. A. M., & Aschan, M. 2014. Life history variation in Barents Sea fish: implications for sensitivity to fishing in a changing environment. *Ecology and Evolution, 4,* 3596–3611.

Willis, K. J., & Birks, H. J. B. 2006. What is natural? The need for a long-term perspective in biodiversity conservation. *Science, 314*, 1261-1265.

Woodward, G., Perkins, D. M., & Brown, L. E. (2010). Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365,* 2093-2106.

Woolway, R. I., Kraemer, B. M., Lenters, J. D., Merchant, C. J., O'Reilly, C. M., & Sharma, S. 2020. Global lake responses to climate change. *Nature Reviews Earth & Environment, 1*, 388–403.

Woolway, R. I., & Merchant, C. J. 2019. Worldwide alteration of lake mixing regimes in response to climate change. *Nature Geoscience, 12,* 271–276.

Wootton, R. J. (1998). Ecology of teleost fishes. Springer Science & Business Media.

Wrona, F. J., Johansson, M., Culp, J. M., Jenkins, A., Mård, J., Myers-Smith, I. H., Prowse, T. D., Warwick, V. F., & Wookey, P. A. 2016. Transitions in Arctic ecosystems: Ecological implications of a changing hydrological regime. *Journal of Geophysical Research: Biogeosciences, 121*, 650-674.

Paper 1

Received: 18 February 2019 | Accepted: 7 October 2019

DOI: 10.1111/1365-2664.13535

RESEARCH ARTICLE

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

Climate warming is predicted to enhance the negative effects of harvesting on high-latitude lake fish

Aslak Smalås[1] | **John F. Strøm**[1] | **Per-Arne Amundsen**[1] | **Ulf Dieckmann**[2,3] | **Raul Primicerio**[1]

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

[2]Evolution and Ecology Program, International Institute for Applied Systems Analysis, Laxenburg, Austria

[3]Department of Evolutionary Studies of Biosystems, The Graduate University for Advanced Studies (Sokendai), Hayama, Japan

Correspondence
Aslak Smalås
Email: aslak.smalas@uit.no

Funding information
H2020 Food, Grant/Award Number: ClimeFish, 677039; UiT–The Arctic University of Norway

Handling Editor: Jani Heino

Abstract

1. Ecosystems at high latitudes are exposed to some of the highest rates of climate warming on earth, and freshwater ecosystems in those regions are already experiencing extended ice-free seasons and warmer waters. The dominant fish species in these ecosystems are cold-water salmonids, which play a central ecological role in lake ecosystems, where they are often exposed to size-selective fisheries that truncate their size and age distributions, making them potentially vulnerable to exploitation and environmental perturbations.
2. Here, we address the combined effects of climate-induced water temperature increase (using regionally downscaled climate models based on the RCP-4.5 and RCP-8.5 climate scenarios together with an air-to-water temperature model) and gillnet harvesting, over the period from 1950 to 2100, on the somatic growth, demography and vulnerability of Arctic charr *Salvelinus alpinus* (L.), using an eco-genetic individual-based model. The model captures successive annual life-history events, including the key processes of size-dependent mortality, age- and size-dependent maturation described by a probabilistic reaction norm, temperature-dependent growth, size-dependent reproduction and density-dependent recruitment.
3. Our model predicts that higher water temperatures will increase the somatic growth of Arctic charr, leading to larger body size at age and increased stock biomass: for RCP-8.5, we predict an 80% increase in stock biomass in the year 2100 relative to the year 2000 in the absence of fishing. Interestingly, this potential increase in biomass in future climate scenarios will be partially masked by harvesting: for a fishing mortality of 0.3 year^{-1}, we predict a mere 40% increase in stock biomass in 2100 relative to 2000. Despite the predicted increase in stock biomass, yield will increase substantially only when fishing mortality is low. In addition, climate warming will accentuate the age-truncation effect of harvesting, which will target younger individuals, including immatures, thus elevating the vulnerability of the population to environmental perturbations.

4. *Synthesis and applications*. Our model-based analyses highlight the combined effects of climate change and size-selective fishing, emphasizing the emerging vulnerability of fish populations to multiple stressors. We recommend carefully climate-adapted management strategies permitting only a narrow range of gillnet mesh sizes for inland fisheries at high latitudes.

KEYWORDS

age and size truncation, Arctic charr, climate change, ecological modelling, management of freshwater fish, population dynamics, salmonids, size-selective fishing

1 | INTRODUCTION

The effects of climate change on aquatic ecosystems have been studied extensively, and projections of future changes are presently under intense scrutiny (Bryndum-Buchholz et al., 2018; Parmesan, 2006). However, most studies do not incorporate additional anthropogenic stressors that are likely to interact with climatic effects, hindering understanding and predictions of the impact of multiple environmental stressors (Woodward, Perkins, & Brown, 2010). In ectotherms, temperature-dependent growth mediates some of the most notable effects of climate warming on individuals and populations (Deutsch et al., 2008; Ohlberger, 2013), and growth-mediated population-level effects are influenced by size-selective environmental pressures such as harvesting (Fenberg & Roy, 2008). Under climate warming in sub-Arctic regions, fish will experience increased temperatures, possibly favouring improved growth conditions at the northern limits of their distributional range (Deutsch et al., 2008; Ohlberger, 2013; Pörtner et al., 2001; Reist et al., 2006). Accordingly, the impacts of climate change and harvesting need to be addressed jointly (Brander, 2007).

The effects of increasing water temperature on the vital rates and demography of fish are primarily mediated by growth and reproduction (Ficke, Myrick, & Hansen, 2007; Wootton, 1998). In many fish species, growth may influence reproduction, because maturation schedules are phenotypically plastic, with the corresponding maturation reaction norms determining the age and size at maturation conditional on somatic growth (Heino, Dieckmann, & Godø, 2002). The changes in vital rates mediated by temperature-dependent growth have implications for fish demography, influencing population size, age structure and stock biomass. Harvesting of fish populations is often size-selective, targeting large individuals (Fenberg & Roy, 2008; Hansen, Madenjian, Selgeby, & Helser, 1997). A common outcome of size-selective harvesting is a truncation of size and age distributions as a consequence of the removal of large individuals (Conover & Munch, 2002; Heino & Godø, 2002), which may change the character of size structured interactions, leading to altered growth rates and changed ages and sizes at maturation of the fish that remain in the population (Law, 2000; Olsen et al., 2005). In many populations, large fish contribute the most to recruitment and may provide a buffer against environmental perturbations (Anderson et al., 2008; Berkeley, Hixon, Larson, & Love, 2004; Hsieh, Yamauchi, Nakazawa, & Wang, 2010). The use of efficient gears and the absence of sufficient regulation further increase the risk of overexploitation in freshwater fish populations (Allan et al., 2005; Post, Persson, Parkinson, & Kooten, 2008).

High latitudes are experiencing more rapid warming than temperate or tropical regions (Parmesan, 2006), and cold-water fish species, such as salmonids, are among the taxa most sensitive to climate change (Blanchet, Primicerio, Smalås, Arias-Hansen, & Aschan, 2019). Salmonids are also among the numerically dominant and ecologically most important freshwater fish in these regions (Klemetsen et al., 2003). Due to their large size and active behaviour, salmonids are vulnerable to size-selective gillnet fisheries (Finstad, Jansen, & Langeland, 2001). Among salmonids, Arctic charr *Salvelinus alpinus* (L.) has the northernmost distribution of all freshwater fish species (Klemetsen, 2010; Klemetsen et al., 2003). Arctic charr has been predicted to experience a large-scale extinction towards the southern end of its distribution; however, at higher latitudes and altitudes this pattern so far is not empirically evident (Hein, Öhlund, & Englund, 2012). On the contrary, it has been suggested that, in the latter locations, the somatic growth of Arctic charr might even increase under climate change, due to warmer water temperatures and a prolonged ice-free season (Pörtner et al., 2001; Reist et al., 2006), thereby opening new opportunities for their exploitation.

Here, we examine the combined effects of climate change and size-selective fishing on Arctic charr populations using an eco-genetic individual-based model (Dunlop, Heino, & Dieckmann, 2009). Arctic charr population dynamics are modelled over the period 1950–2100 for climate scenarios characterized by the representative concentration pathways (RCPs) RCP-4.5 and RCP-8.5, and for five different levels of size-selective harvesting. The model is parametrized and evaluated based on long-term data from a sub-Arctic lake (Amundsen, Knudsen, & Klemetsen, 2007; Amundsen et al., 2019; Persson et al., 2007). We investigate whether climate change will increase individual growth rates of Arctic charr in high-latitude lakes, as water temperatures approach the optimum for summer growth, resulting in larger size at age and higher stock biomass and production. We further address the truncation of size and age distributions by size-selective fishing and the effects on stock biomass and yield contingent on fishing effort and climate scenario. In light of our findings, we discuss climate-adaptation strategies for inland fisheries at high latitudes that can promote sustainable exploitation.

2 | MATERIALS AND METHODS

2.1 | Data sources and model parametrization

Our eco-genetic individual-based model for Arctic charr is forced by climate, using two different RCP scenarios, RCP-4.5 and RCP-8.5. These scenarios describe the projected increases, of either 4.5 or 8.5 W/m^2, in radiative forcing in the year 2100 resulting from rising greenhouse-gas concentrations in the atmosphere and their corresponding greenhouse effects on climate warming (IPCC, 2007). Climate variables are obtained at the finest grid resolution available (0.11°) from a regionally downscaled climate model (MPI-M-MPI-ESM-LR), forced by the global circulation model CLMcom-CCLM4-8-17. The climate model outcomes, made available through the EURO-CORDEX project, cover the period 1950–2100. To obtain daily lake water temperatures from the climate model outcomes, we adopt the one-dimensional air-to-water temperature model called 'General Lake Modelling,' using the R package GLM$_r$ (Hipsey, Bruce, & Hamilton, 2014). More detailed descriptions of the climate models and of the modelling of physical limnology are available in Appendix S2.

The eco-genetic model is parameterized and evaluated based on long-term data for the Arctic charr population of Lake Takvatn (69°07′N, 19°05′E). Lake Takvatn is located about 300 km north of the Arctic Circle in northern Norway, has an area of 15 km^2 and is situated 215 m above sea level. Data on Arctic charr have been collected yearly since the early 1980s (Amundsen et al., 2019) and include individual age, length, weight, maturation status, sex and fecundity data (Amundsen et al., 2007; Henriksen et al., 2019). Parameters used for our model are listed in Table S1 in Appendix S1, and data from Lake Takvatn charr are visualized in Figure S1 in Appendix S1. Analyses of robustness and sensitivity to changes in somatic growth and natural mortality are also available in Appendix S2.

2.2 | Eco-genetic model overview

We use an individual-based model designed according to the eco-genetic modelling framework introduced by Dunlop et al. (2009). Our model describes demographic processes without evolutionary effects on life-history traits. The model runs by accounting for successive life-history events during each annual cycle, including mortality, maturation, growth and reproduction (Dunlop et al., 2009). Growth is described by temperature-dependent daily length increments to capture climate-related growth effects. In each model run, the Arctic charr population is initialized with 3,000 individuals and traced for 150 years. Results are averaged over 50 replicate model runs.

2.3 | Mortality

Annual mortality is calculated as

$$Z = M + F, \tag{1a}$$

where Z is the total mortality, M the natural mortality, and F the fishing mortality (all expressed as instantaneous mortality rates). The natural mortality for many fishes, including salmonids, is assumed to be negatively correlated with their body size (Elliott, 1993; Gislason, Daan, Rice, & Pope, 2010), following an allometric relation,

$$M = M_\mathrm{r}(L/L_\mathrm{r})^{-c}, \tag{1b}$$

where L is the length of fish, M_r the natural mortality at the reference length L_r, and c the allometric exponent. The observed size distribution of Arctic charr in Lake Takvatn is used to calibrate L_r and c. To estimate M_r, we use the equation given by Pauly (1980),

$$\begin{aligned}\log\left(M_\mathrm{r}/\mathrm{year}^{-1}\right) = & -z_1 - z_2\log\left(L_\infty/\mathrm{cm}\right) \\ & + z_3\log\left(K/\mathrm{year}^{-1}\right) + z_4\log\left(\overline{T}/°\mathrm{C}\right),\end{aligned} \tag{1c}$$

where z-values are constants provided by Pauly (1980), all logarithms are natural logarithms, L_∞ (= 50 cm) and K (= 0.14 year^{-1}) are the asymptotic length and the growth rate of Lake Takvatn Arctic charr, respectively, both of which are estimated from empirical data using the von Bertalanffy growth model (Chen, Jackson, & Harvey, 1992), and $\overline{T}$ (= 4.4°C) is the observed mean water temperature of Lake Takvatn over the period 2017–2018.

We investigate five fishing-mortality scenarios, representing different levels of harvesting pressures by gillnets. Gillnet fishing is regulated by mesh size, which is recommended to be between 26 and 35 mm by the regional management institutions (Statskog, 2017). Size-selectivity of the minimum mesh size is modelled based on catch data for Lake Takvatn Arctic charr and used to parametrize the length-dependent fishing mortality,

$$F = F_0 + F_1 \frac{1}{1+\exp\left(-F_2\left(L-F_3\right)\right)}, \tag{1d}$$

where L is the length of fish, F_0 the size-independent component, F_1 scales the size-dependent component, F_2 the steepness of the size-dependent component, and F_3 the inflection point of the size-dependent component.

2.4 | Maturation

Age at maturation is assumed to be phenotypically plastic and determined by a probabilistic maturation reaction norm (PMRN) describing the length- and age-specific probabilities of maturation (Dieckmann & Heino, 2007; Heino et al., 2002). We estimate the PMRN from long-term data on Arctic charr in Lake Takvatn (Table S1 in Appendix S1) using the so-called demographic method assuming a linear reaction norm (Barot, Heino, O'Brien, & Dieckmann, 2004). Following Heino et al. (2002), we implement a PMRN that involves both age and size, and assume that these two variables have independent and linear effects,

$$P_{\mathrm{m}} = \frac{1}{1 + \exp\left(-\left(L - (i + as)\right)/d\right)}, \tag{2}$$

where L is the length of fish, a the age of fish, i the PMRN intercept, s the PMRN slope, and d the PMRN width.

2.5 | Temperature-dependent growth

We assume a temperature-dependent von Bertalanffy growth model,

$$L_{t+\Delta t} = L_t + (L_\infty - L_t)\left(1 - \exp\left(-K_t \Delta t\right)\right), \tag{3a}$$

where L_t is the length of fish at age t, Δt the time interval over which growth is considered, L_∞ is the asymptotic length at which growth is zero, and K_t is the temperature-dependent growth rate at age t (Equation 3b). Equation 3a uses the Fabens method for iteratively describing growth in the von Bertalanffy model (equation 4.1 in Fabens, 1965; see also Haddon, 2001, pp. 241–242). For our model, we account for daily variations in the growth rate K_t and accordingly consider daily growth increments, that is Δt = 1 day = 365.25^{-1} year = 0.0027379 year, with a year's growth beginning on 1 January and ending on 31 December. Growth starts at age 0 from an initial length randomly drawn from a normal distribution with mean $m\,(L_0)$ and $SD\ \sigma\,(L_0)$.

The temperature dependence of K_t follows a dome-shaped curve with a maximum of 0.35 ($K_{\max}$) at the temperature optimum (T_{opt}) of 14.1°C (Larsson & Berglund, 1998, 2005; Larsson et al., 2005; Siikavuopio, Foss, Sæther, Gunnarsson, & Imsland, 2013). The maximum growth rate, $K_{\max}$, is calibrated to the growth of Arctic charr in Lake Takvatn, and individual variability in growth rate is implemented by random sampling from a normal distribution centred on $K_{\max}$. The temperature-dependent growth coefficient K_t in year t is set to 0 if the temperature is smaller than 1˚C ($T_{\min}$) or larger than 20˚C ($T_{\max}$) (Larsson & Berglund, 1998, 2005; Larsson et al., 2005; Siikavuopio, Knudsen, & Amundsen, 2010; Siikavuopio, Skybakmoen, & Sæther, 2009). Otherwise, K_t is calculated as follows,

$$K_t = K_{\max} \frac{\left(T_t - T_{\min}\right)\left(T_t - T_{\max}\right)}{\left(T_t - T_{\min}\right)\left(T_t - T_{\max}\right) - \left(T_t - T_{\mathrm{opt}}\right)^2}, \tag{3b}$$

where $K_{\max}$ is the maximum growth rate parameterized for the Takvatn charr population using the average von Bertalanffy growth rate (K) and the average annual water temperature (from the GLMr) for the last 10 years of the long-term data series, T_t is the average water temperature for the upper ten metres on day t, and $T_{\min}$, $T_{\max}$ and T_{opt} are the minimum, maximum and optimum water temperatures for Arctic charr, respectively (Table S1 in Appendix S1). Arctic charr at high latitudes predominantly utilize the shallow-water habitat, especially during the ice-free season (Hawley, Rosten, Haugen, Christensen, & Lucas, 2017), and therefore, we use the average water temperature for the upper 10 m.

2.6 | Reproduction and recruitment

The fecundity f of individual adult females is described by an allometric function estimated for the fecundity–length relationship,

$$f = f_{\mathrm{r}} L^{\mathrm{b}}, \tag{4a}$$

where L is the length of fish, f_{r} is the fecundity–length relationship coefficient, and b is the allometric exponent.

Annual recruitment is dependent on the size of the spawning stock, as well as on the fecundity of adult fish and the density-dependent mortality of eggs and hatchlings (Haddon, 2001). The latter density dependence is assumed to follow a Beverton–Holt stock–recruitment relationship,

$$R_t = R_{\max} \frac{f_{\mathrm{tot},t}}{f_{\mathrm{tot},t} + f_{\mathrm{tot},1/2}}, \tag{4b}$$

where R_t is the total number of recruits, that is surviving offspring, to the population in year t, $f_{\mathrm{tot},t}$ the stock's total fecundity in year t (given by the sum of the fecundities f according to Equation 4a of all adult females reproducing in that year), $R_{\max}$ the maximal number of recruits, and $f_{\mathrm{tot},1/2}$ the total fecundity at which density-dependent recruitment mortality kills 50% of the offspring. This Beverton–Holt stock–recruitment model predicts a saturating relationship between the total population fecundity f_t and the total number R_t of recruits.

2.7 | Limitations of model assumptions

The model description above is limited by simplifying assumptions regarding mechanisms and processes. Realistic models of intermediate complexity are suggested to enhance ecological understanding and are thereby considered advisable (Van Nes & Scheffer, 2005). In our model, we simplified the effects of density dependence on growth to facilitate the analysis of how water temperature and fishing mortality affect populations of Arctic charr. Density dependence is assumed to influence recruitment through a Beverton–Holt relationship, thus affecting the annual recruitment. Ignoring density-dependent growth will affect model outcomes for individual-level growth rates and population-level biomass and yield, particularly in low-fishing-mortality scenarios when abundance is relatively high. However, the maximum temperature-dependent growth coefficient $K_{\max}$ is calibrated to Arctic charr growth from Lake Takvatn (von Bertalanffy growth curve, Figure S1 in Appendix S1), thereby implicitly taking into account resource availability. Interspecific interactions are omitted, as Arctic

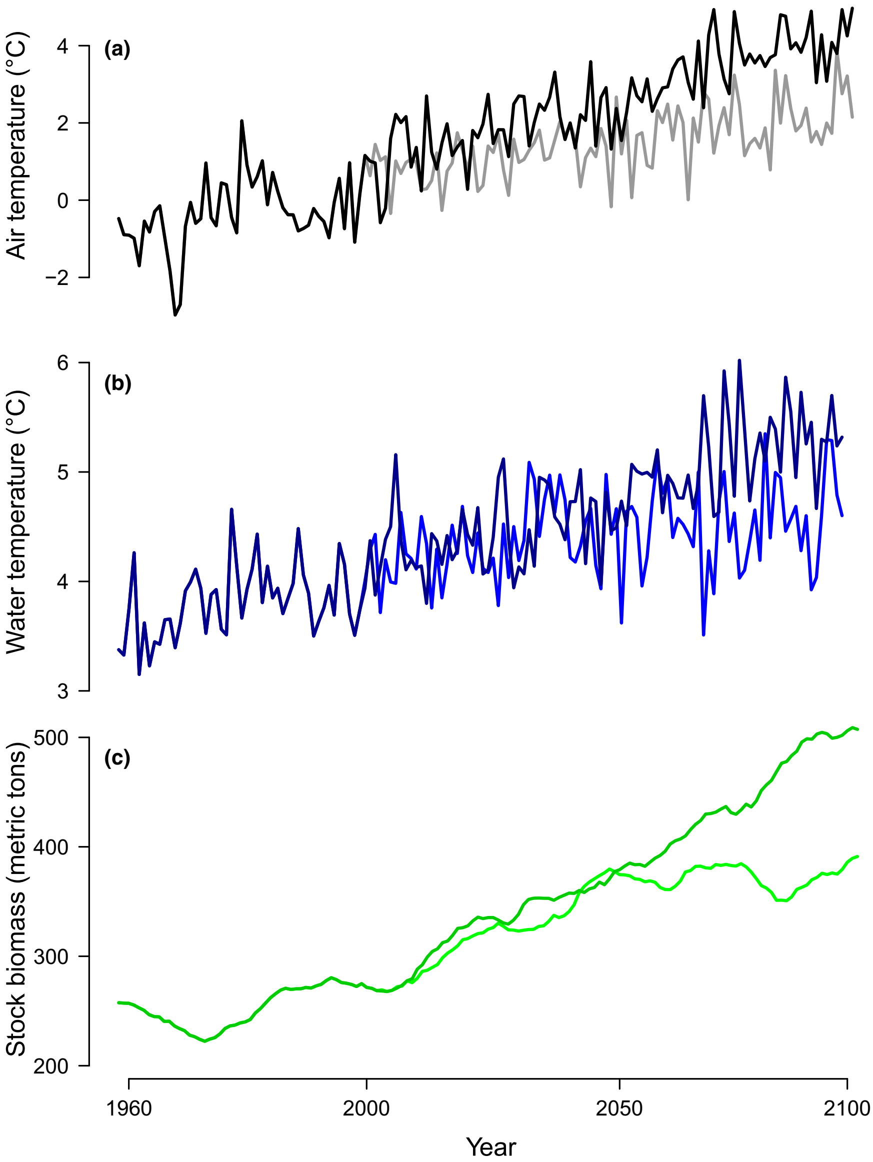


FIGURE 1 Time series of (a) air temperature, (b) water temperature and (c) stock biomass of Arctic charr in Lake Takvatn without harvesting for two climate scenarios (light shades for RCP-4.5, dark shades for RCP-8.5) from 1953 to 2005 (hindcasted model-predicted) and from 2006 to 2100 (scenario-projected and model-predicted)

charr populations are often allopatric in high-latitude lakes (Klemetsen et al., 2003).

3 | RESULTS

3.1 | Climate warming increases somatic growth and stock biomass

Our model predicts that an increase in water temperature (Figure 1) substantially increases the length at age of Arctic charr (Figure 2). For example, the mean length of 4-year-old Arctic charr in the RCP-8.5 climate scenario shows a significant increase from an average of 20.7 cm in the year 2000 to 23.3 cm in the year 2050 (Wilcox non-parametric *W* test, $W = 44{,}289$, $p < .001$) and to 25.5 cm in the year 2100 ($W = 12{,}663$, $p < .001$). For the RCP-4.5 climate scenario, the increase of length at age is small, but significant; for 4-year-old charr, the average length increases to 22.8 cm in the year 2050 ($W = 59{,}873$, $p < .001$) and to 23.2 cm in the year 2100 ($W = 55{,}658$, $p < .001$). The stock biomass of Arctic charr is influenced by growth rate, increasing with time along with temperature (Figures 1 and 3). The biomass increase since the year 2000 is 34% and 37% by the year 2050, and 35% and 80% by the year 2100 in the RCP-4.5 and RCP-8.5 climate scenarios, respectively.

3.2 | Increased harvesting masks the temperature effects on stock biomass and yield

Increased harvesting masks the positive effects of temperature on stock biomass: for the year 2100, a fishing mortality of $F = 0.0$ year^{-1} results in a ratio of $\overline{B}_{\text{RCP-8.5}}/\overline{B}_{\text{RCP-4.5}} = 1.25$ (comparing RCP-8.5 and RCP-4.5), $F = 0.1$ year^{-1} results in $\overline{B}_{\text{RCP-8.5}}/\overline{B}_{\text{RCP-4.5}} = 1.22$, $F = 0.2$ year^{-1} results in $\overline{B}_{\text{RCP-8.5}}/\overline{B}_{\text{RCP-4.5}} = 1.14$,

$F = 0.3$ year^{-1} results in $\overline{B}_{\text{RCP-8.5}}/\overline{B}_{\text{RCP-4.5}} = 1.09$, and $F = 0.5$ year^{-1} results in $\overline{B}_{\text{RCP-8.5}}/\overline{B}_{\text{RCP-4.5}} = 1.03$. This masking effect occurs because the predicted stock biomass of Arctic charr is strongly affected by the level of fishing; for example, the predicted biomass in the year 2100 for $F = 0.5$ year^{-1} is only 5% of the biomass predicted without fishing.

Yield is substantially affected by increased somatic growth rates (Figure 4). For the lowest fishing mortality (0.1 year^{-1}) in the RCP-4.5 climate scenario, yield increases by 28% by the year 2050 and did not increase further by the year 2100. For the same fishing mortality in the RCP-8.5 climate scenario, yield increases by 33% by the year 2050 and by 67% by the year 2100. Yield is largest for the lowest considered non-zero fishing mortality of $F = 0.1$ year^{-1} and decreases significantly as harvesting is increased: the yield for $F = 0.5$ year^{-1} is on average only 40% of the yield for $F = 0.1$ year^{-1}. For the hindcast period 1950–2005, there is no significant difference in yield between the fishing mortalities 0.1 and 0.2 year^{-1} ($W = 405{,}670$, $p = .12$). However, with increasing temperature, yield increases more for $F = 0.1$ year^{-1} than for $F = 0.2$ year^{-1}, and the difference is significant for the forecast period 2006–2100 in the RCP-8.5 climate scenario ($W = 1{,}175{,}400$, $p < .001$), during which average yield is 13% larger for $F = 0.1$ year^{-1} than for $F = 0.2$ year^{-1}.

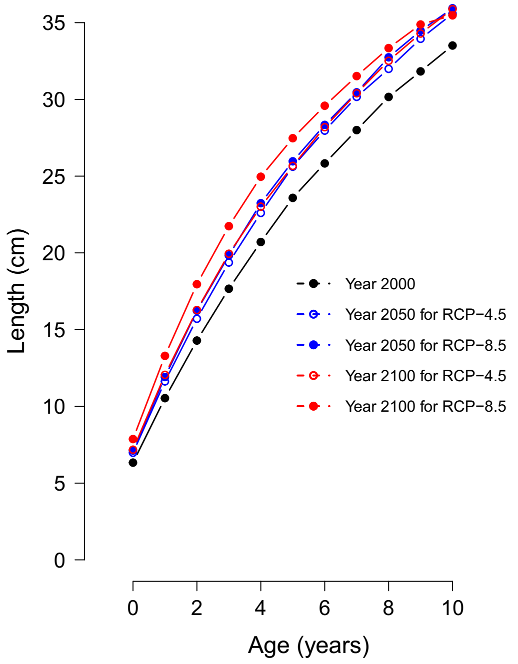


FIGURE 2 Model predictions of lengths at age of Arctic charr in Lake Takvatn for two climate scenarios without harvesting

3.3 | Climate warming increases the vulnerability of harvested populations

The enhanced growth rates of Arctic charr lead to shifts in the age distributions of all individuals and harvested individuals (Figure 5a,c). Thus, relative to the year 2000, the age distribution in the Arctic charr population for a given fishing mortality (e.g. $F = 0.2$ year^{-1}, mean age = 4.3 years) is significantly shifted towards younger individuals in the years 2050 (mean age = 4.0 years, $W = 961{,}160$, $p = .008$) and 2100 (mean age = 3.8 years, $W = 12{,}037{,}000$, $p < .001$). Similarly, relative to the year 2000, the age distribution of harvested Arctic charr (e.g. $F = 0.2$ year^{-1}, mean age = 8.6 years) is significantly shifted towards younger individuals in the years 2050 (mean age = 7.7 years, $W = 49{,}375$,

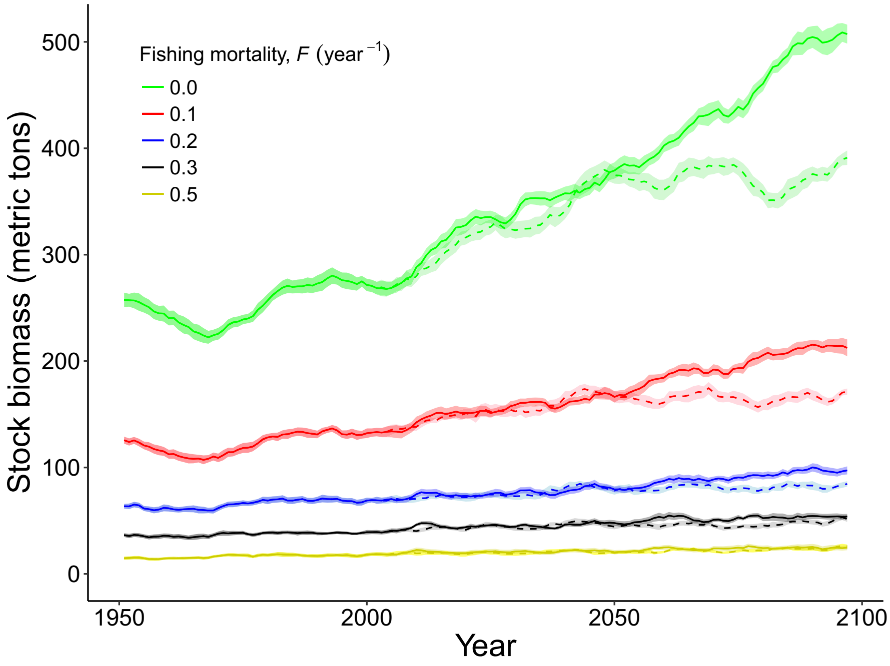


FIGURE 3 Model predictions of stock biomass of Arctic charr in Lake Takvatn for two climate scenarios (dashed lines for RCP-4.5, continuous lines for RCP-8.5) and five fishing mortalities (0.0, 0.1, 0.2, 0.3 and 0.5 year^{-1}) from 1953 to 2005 (hindcasted) and from 2006 to 2100 (forecasted) with 95% confidence intervals indicated by shading

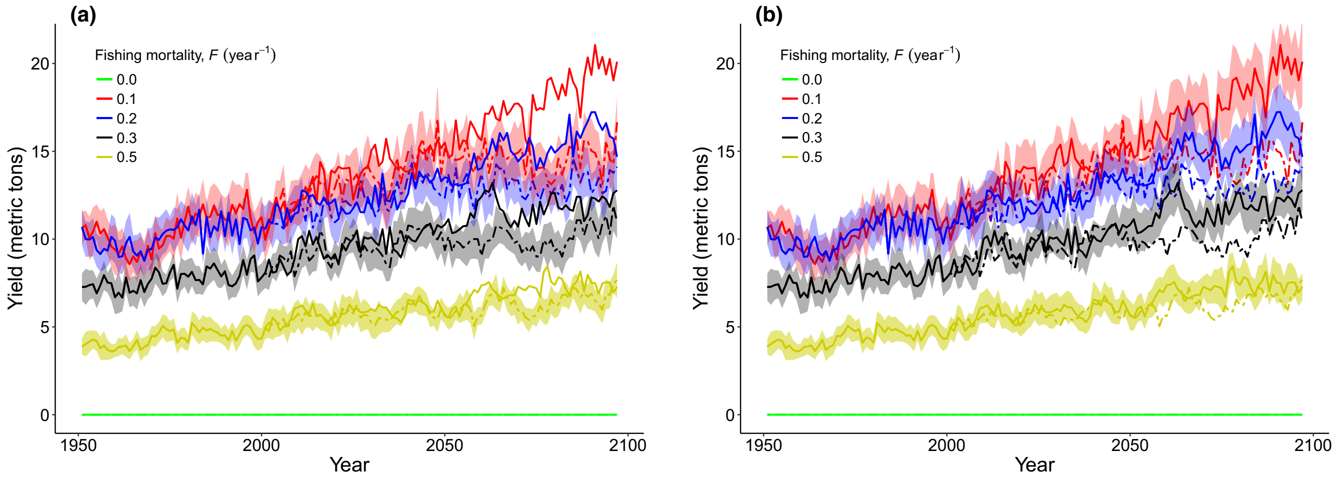


FIGURE 4 Model predictions of yield of Arctic charr in Lake Takvatn for two climate scenarios (dashed lines for RCP-4.5, continuous lines for RCP-8.5) and five fishing mortalities (0.0, 0.1, 0.2, 0.3 and 0.5 year^{-1}) from 1953 to 2005 (hindcasted) and from 2006 to 2100 (forecasted). (a) Focus on RCP-4.5 climate scenario and (b) focus on RCP-8.5 climate scenario, with 95% confidence intervals indicated by shading

$p < .001$) and 2100 (mean age = 7.2 years, W = 74,782, $p < .001$). The size distribution of the Arctic charr population does not change with climate warming (Figure S4 in Appendix S4). The age distributions of all individuals and harvested individuals are truncated as fishing mortality is increased (Figure 5b,d); the same truncation effect is also empirically observed in the size distribution of Artic charr in Lake Takvatn (Figure S4 in Appendix S4). The mean age of the remaining population in the year 2100 for F = 0.1 year^{-1} (RCP-8.5) is 5.1 years, but decreases to 2.5 years for F = 0.5 year^{-1}. The five levels of fishing mortalities result in significantly different mean ages in the Arctic charr population in the year 2100 (F = 0.0 year^{-1} vs. F = 0.1 year^{-1}, W = 52,667,000, $p < .001$; F = 0.1 year^{-1} vs. F = 0.2 year^{-1}, W = 2,2036,000, $p < .001$; F = 0.2 year^{-1} vs. F = 0.3 year^{-1}, W = 1,0,137,000, $p < .001$; and F = 0.3 year^{-1} vs. F = 0.5 year^{-1}, W = 5,516,800, $p < .001$). The mean age of the harvested Arctic charr in the year 2100 for F = 0.1 year^{-1} (RCP-8.5) is 8.6 years and decreases to 5.4 years for F = 0.5 year^{-1}.

The numbers of mature individuals and recruits increase with climate warming for low fishing mortality ($F < 0.2$ year^{-1}), especially under the RCP-8.5 climate scenario. For instance, for F = 0.1 year^{-1} and RCP-8.5, the number of mature individuals increases by 19.9% (W = 46,920, $p < .001$), and the number of recruits increases by 7.2% (W = 48,400, $p < .001$) from the year 2000 to the year 2100. However, for high fishing mortality ($F > 0.2$ year^{-1}), the numbers of mature individuals and recruits decrease with climate warming. For instance, for F = 0.3 year^{-1} and RCP-8.5, the numbers of mature individuals and recruits in the year 2100, compared to the year 2000, are only 83.1% (W = 10,662, $p < .001$) and 88.3% (W = 11,696, $p < .001$), respectively. Through climate warming, the proportion of immature individuals included in the catches increases over time. For instance, for F = 0.2 year^{-1} and RCP-8.5, this proportion equals 20.1% in the year 2000, 29.7% in the year 2050 and 33.9% in the year 2100, corresponding to a 69% increase during the century.

4 | DISCUSSION

Our model predicts that higher water temperatures will accelerate the somatic growth of Arctic charr at high latitudes, leading to larger body size at age and increased stock biomass. Interestingly, the potential increase in biomass with future climate warming is masked by harvesting, which has a strong negative effect on biomass due to the increase in the fishing mortality of larger individuals. According to our model, yield will increase substantially under climate warming only when fishing mortality is low, and the sensitivity of yield to fishing mortality will increase as water temperature rises. In addition, under climate warming, harvesting will target younger individuals, resulting in a more pronounced age truncation and a larger proportion of immature individuals in the catches, which might elevate the vulnerability of the population to environmental perturbations.

Despite a significant increase in mean annual water temperature (by 1.5°C in the RCP-8.5 climate scenario for 2000–2100), the projected water temperatures are unlikely to exceed Arctic charr's optimum for somatic growth for the majority of the growing season in sub-Arctic areas: only 10.2 days above optimum are predicted for the year 2100. Temperature-dependent somatic growth in high-latitude Arctic charr populations has been studied extensively and has revealed positive somatic growth between about 1°C and about 20°C, with an optimum temperature of about 14°C (Larsson & Berglund, 1998, 2005; Siikavuopio et al., 2010, 2009). According to our study, the projected rise in water temperature will result in a significant increase in mean size at age and stock

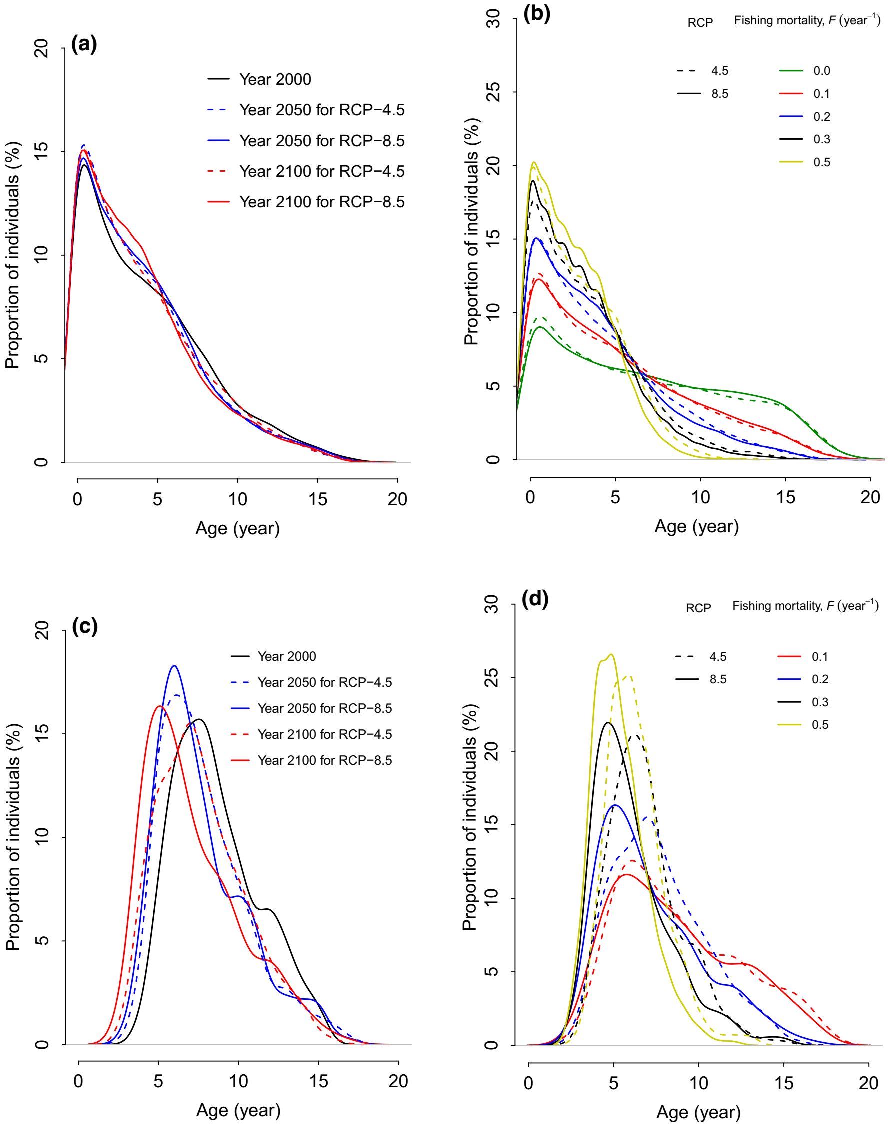


FIGURE 5 Model predictions of the age distributions of the population of Arctic charr in Lake Takvatn (a, b) and among the harvested individuals (c, d). (a, c) Age distributions in the years 2000, 2050 and 2100 for a fishing mortality of $F = 0.2\ \text{year}^{-1}$ and two climate scenarios (dashed lines for RCP-4.5, continuous lines for RCP-8.5). (b, d) Age distributions in the year 2100 for five fishing mortalities (0.0, 0.1, 0.2, 0.3 and 0.5 year^{-1}) and two climate scenarios (dashed lines for RCP-4.5, continuous lines for RCP-8.5)

biomass. Higher growth rates and production have been suggested to be a consequence of climate warming for freshwater fish populations living in high-latitude lakes (Brander, 2007; Reist et al., 2006). There are few studies testing the impact of climate warming on somatic growth in salmonids; however, a study on rainbow trout revealed that a 2°C increase in water temperature enhanced growth throughout most of the growing season (Morgan, McDonald, & Wood, 2001). This is further supported by a recent study showing that freshwater salmonid populations experiencing climate warming within their temperature tolerance range will exhibit increased growth rates (Symons, Schulhof, Cavalheri, & Shurin, 2019). It is therefore likely that Arctic charr inhabiting areas where current water temperatures are substantially lower than the optimum for somatic growth will experience increased somatic growth and production from climate warming (Karlsson, Jonsson, & Jansson, 2005). This expectation assumes that the outcomes of interactions with other species do not change. For instance, studies on Arctic charr closer to the southern border of its distributional range indicate that an experienced temperature rise alone did not affect the production of such an Arctic charr population, but when non-native fish (percids) were abundant, Arctic charr population's production decreased with increasing temperature (Morrissey-McCaffrey, Shephard, Kelly, & Kelly-Quinn, 2018). Our projections of changes in growth and stock biomass are robust to small (±5%) changes in growth parameters (L_∞ and K_{max}) and qualitatively consistent across the investigated range of natural-mortality parameters (Appendix S3). Our model results are based on the assumption that individual growth is not dependent on the density of the Arctic charr population. Hence, the empirical effects of increasing water temperatures on growth and stock biomass may be less pronounced than what is predicted by our model.

Our model shows that higher water temperatures will increase the production and stock biomass of Arctic charr substantially only when fishing mortality is low. The substantial positive temperature effect on stock biomass and yield predicted for low fishing mortalities ($F < 0.2\ \text{year}^{-1}$) is largely reduced at higher levels of harvesting. A comparison between model results for the two considered climate scenarios and different levels of fishing mortality reveals that the positive temperature effect on production also diminishes at higher levels of fishing mortality. Including density-dependent growth in the model may somewhat compensate for loss of production to fishing mortality, thereby reducing the negative impact of increased harvesting on yield. Interestingly, the yields our model predicts for the hindcast period 1950–2005 are quantitatively similar for the two lowest non-zero levels of fishing mortality we have considered (F = 0.1 year^{-1} and 0.2 year^{-1}), whereas with future climate warming, these yields will diverge, resulting in substantially higher yield for F = 0.1 year^{-1} than for F = 0.2 year^{-1}. Brander (2007) suggested that yield may increase in high-latitude fisheries as a consequence of increasing water temperatures, but emphasized the need to reduce fishing mortality in fully exploited stocks as a mitigation strategy against climate change. Our results suggest that climate-warming effects in highly exploited stocks might be hard to detect, because they will be masked by harvesting.

Long-term empirical studies (with study periods longer than 10 years; Lindenmayer & Likens, 2010) are especially important for assessing population impacts of climate warming. However, such studies are rare and often examine systems simultaneously impacted by other anthropogenic stressors such as harvesting (Amundsen et al., 2019). A review of long-term empirical time series of freshwater fish in Europe indicates that declines in Arctic charr populations can be attributed to climate warming, even though somatic growth rates have often increased over time (Jeppesen et al., 2012). Indeed, in addition to experiencing climate warming, most of the studied populations were also influenced by other anthropogenic stressors including harvesting (Jeppesen et al., 2012). Climate-change effects might therefore be hard to disentangle from the impacts of other factors. Our model-based analyses help identify possible negative effects of the combined exposure to warming and harvesting.

We have found severe demographic effects of size-selective harvesting on Arctic charr, a phenomenon documented for many harvested fish populations (Anderson et al., 2008; Jørgensen et al., 2007; Longhurst, 2006). Our model predictions show a sharper truncation of the age and size distribution as harvesting is increased. A population experiencing size and age truncation typically becomes more vulnerable and less resilient to environmental perturbations and stochastic events (Anderson et al., 2008; Heino & Godø, 2002). Larger and older (and thus more experienced) individuals tend to tolerate fluctuating environmental pressures and survive hard times better through bet-hedging strategies than smaller and younger individuals (Bobko & Berkeley, 2004; Marteinsdottir & Steinarsson, 1998). Higher vulnerability due to size and age truncation by fisheries might be particularly detrimental under the widely predicted increase in the frequency of extreme climate events (Beniston et al., 2007). Arctic charr individuals are extremely vulnerable to gillnet fisheries, and only a few gillnets with large mesh sizes can remove the production of large piscivorous individuals (Finstad et al., 2001). In addition to ecological effects of size and age truncation, evolutionary effects that might not be easily reversed are found in populations of fish under size-selective harvesting (Enberg, Jørgensen, Dunlop, Heino, & Dieckmann, 2009; Jørgensen et al., 2007; Olden et al., 2010).

The combined effects of fishing and climate warming seem severe, highlighting the importance of considering multiple stressors affecting structured fish populations. With higher water temperatures, somatic growth increases, resulting in younger fish becoming available to gillnet fisheries. Our model predicts that the proportion of young, immature individuals in the catches

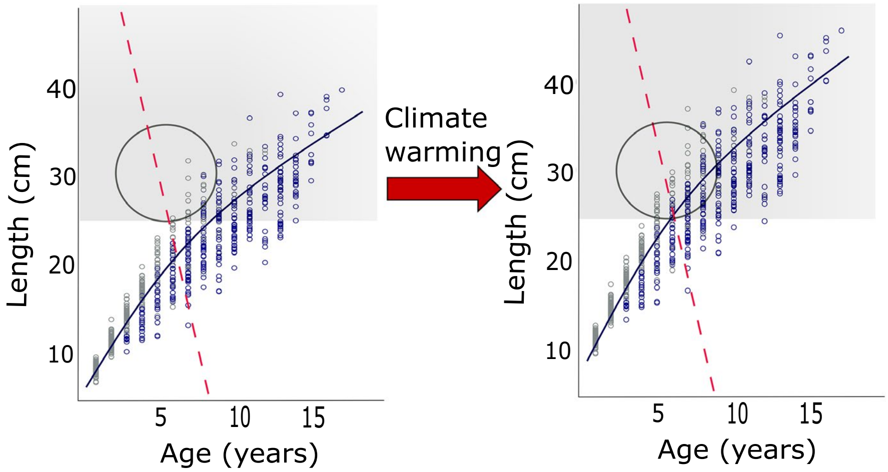


FIGURE 6 Conceptual illustration of the demographic changes caused by the combination of climate warming and size-dependent harvesting. The grey shading shows the size range of the fishery, the dashed red line shows the age-dependent probabilistic maturation reaction norm (PMRN) midpoints, and the blue lines show the mean growth trajectories (a) before (dashed blue line) and (b) after (continuous blue line) a period of climate warming. Open grey circles represent immature individuals, and open blue circles represent mature individuals, as predicted by our model. The two large black circles highlight the increased risks of large immature individuals (to the left of the dashed red line) and of small mature individuals (to the right of the dashed red line) to be harvested. This shows how the climate-induced changes in the demographic distribution of the population might increase its vulnerability, as a larger proportion of the population becomes susceptible to harvesting, including more large immature individuals and more young mature individuals

will increase with climate warming: this effect is particularly pronounced for fishing mortalities $F > 0.2$ year^{-1} and in fish populations with steeply negatively sloped maturation reaction norms, for which maturation is largely influenced by age, as in the present study. For such fishing mortalities, climate warming does not change the population's size distribution, but causes a decline in the numbers of mature individuals and recruits. In turn, such an erosion in recruitment increases the population's vulnerability to environmental perturbations, which are expected to increase in frequency and intensity under climate warming. Further, the sharp decrease in the number of older mature individuals with climate warming results in a spawning stock that by the year 2100 consists mainly of young individuals (3–5 years old). Older individuals typically produce larger, higher-quality eggs, resulting in offspring that may better withstand starvation and survive a broader suite of negative environmental conditions (Anderson et al., 2008; Berkeley et al., 2004; Hsieh et al., 2010). In Arctic charr, older individuals produce larger eggs (Lasne, Leblanc, & Gillet, 2018), and thus larger larvae, which have faster initial growth and higher survival than their smaller counterparts (Leblanc, Benhaïm, Hansen, Kristjánsson, & Skúlason, 2011). Also, the stronger age truncation of adults induced by climate warming results in a very narrow adult age range, which implies that weak cohorts will have a greater negative impact on recruitment. In addition to the ecological effects, removing a high proportion of immature, fast-growing fish might lead to fisheries-induced selection towards smaller size at maturation (Enberg et al., 2009). The decline in the number of mature individuals and recruits eventually leads to a reduction in population abundance for high fishing mortality, further increasing vulnerability (see Figure 6 for a conceptual summary of the possible combined effects of climate warming and size-dependent harvesting).

For the management of exploited stocks under climate change, our results suggest that monitoring should address not only stock abundances and biomasses, but also size and age distributions, as well as maturation status, to detect demographic changes triggered by increased water temperatures. In many freshwater systems, monitoring of populations is based on catch statistics, which often do not include information about the age of fish, and climate-change effects may therefore be difficult to detect. In light of our findings, we recommend a moderation of fishing effort (i.e. limiting the number of gillnets/night or licensed fishermen, or establishing a temporal window for harvesting) and a narrow range of gillnet mesh sizes (excluding large mesh sizes, thus protecting larger individuals), as climate adaptations of the management of inland fisheries at high latitudes. Such mitigation strategies will help maintain the old and large individuals in the population and limit the harvesting of juvenile individuals. Current regulations in northern Scandinavia are highly variable; however, decision-makers are increasingly realizing that climate-adaptation plans are necessary for sustainable harvest.

Our model ignores temperature-driven changes in other candidate parameters that may mitigate or exacerbate the combined effects of climate warming and size-selective fisheries. One candidate parameter related to growth is the asymptotic length L_∞, which might increase with climate warming (Quince, Abrams, Shuter, & Lester, 2008). This would mitigate some of the negative demographic effects for high levels of harvesting if older, larger individuals could survive harvesting. To the extent that the maximum recruitment $R_{\max}$ may be limited by basal production available to the larvae, $R_{\max}$ might increase with climate warming due to higher production (Karlsson et al., 2005). Such an increase in $R_{\max}$ would mitigate the increased vulnerability associated with high levels of fishing mortality and climate warming.

The effects of multiple anthropogenic stressors on freshwater fish populations are presently poorly understood and hard to predict (Olden, Hogan, & Zanden, 2007). Scenario-based modelling helps to understand how combined pressures might interact (Folt, Chen, Moore, & Burnaford, 1999), which aids the future management and preservation of harvested freshwater fish stocks. The present study demonstrates that the combined effects of climate warming and size-selective fishing can be large, influencing both stock biomass and yield, as well as the size- and age structure of exploited Arctic charr populations. Harvested fish populations may thereby become less resilient and more vulnerable to climate warming.

ACKNOWLEDGEMENTS

Thanks are due to the Freshwater Ecology Group at UiT–The Arctic University of Norway, for collecting and sharing their long-term time series from Lake Takvatn. Thanks are also due to Prof. Malcolm Jobling for thorough and helpful revisions of earlier versions of the manuscript. A.S. was supported by UiT–The Arctic University of Norway. A.S. and R.P. acknowledge funding by the EU-H2020 project ClimeFish (project ID 677039). U.D. acknowledges funding by the EU-H2020 project COMFORT (project ID 820989). No conflict of interest are to be reported.

AUTHORS' CONTRIBUTIONS

A.S. and R.P. conceived the ideas and planned the paper. A.S., R.P., J.F.S. and U.D. contributed significantly to model development. P.-A.A., A.S. and R.P. collected data. A.S. and R.P. analysed model results with substantial input from P.-A.A. and U.D. A.S. led the writing. All authors contributed significantly to the drafts and approved the final manuscript.

DATA AVAILABILITY STATEMENT

Data used for model parameterization is available through the Dryad Digital Repository at https://doi.org/10.5061/dryad.bd10668 (Henriksen et al., 2019). Fish culling reduces tapeworm burden in Arctic charr by increasing parasite mortality rather than by reducing density-dependent transmission). Output data from the individual-based model used here is available through Dryad: https://doi.org/10.5061/dryad.jdfn2z370. (Smalås et al. 2020).

ORCID

Aslak Smalås https://orcid.org/0000-0002-6316-2811
John F. Strøm https://orcid.org/0000-0002-9456-3976
Per-Arne Amundsen https://orcid.org/0000-0002-2203-8216
Ulf Dieckmann https://orcid.org/0000-0001-7089-0393
Raul Primicerio https://orcid.org/0000-0002-1287-0164

REFERENCES

Allan, J. D., Abell, R., Hogan, Z. E. B., Revenga, C., Taylor, B. W., Welcomme, R. L., & Winemiller, K. (2005). Overfishing of inland waters. *AIBS Bulletin*, *55*, 1041–1051. https://doi.org/10.1641/0006-3568(2005)055[1041:OOIW]2.0.CO;2

Amundsen, P.-A., Knudsen, R., & Klemetsen, A. (2007). Intraspecific competition and density dependence of food consumption and growth in Arctic charr. *Journal of Animal Ecology*, *76*, 149–158. https://doi.org/10.1111/j.1365-2656.2006.01179.x

Amundsen, P.-A., Primicerio, R., Smalås, A., Henriksen, E. H., Knudsen, R., Kristoffersen, R., & Klemetsen, A. (2019). Long-term ecological studies in northern lakes – challenges, experiences and accomplishments. *Limnology and Oceanography*, *64*, 11–21. https://doi.org/10.1002/lno.10951

Anderson, C. N. K., Hsieh, C.-H., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., … Sugihara, G. (2008). Why fishing magnifies fluctuations in fish abundance. *Nature*, *452*, 835–839. https://doi.org/10.1038/nature06851

Barot, S., Heino, M., O'Brien, L., & Dieckmann, U. (2004). Estimating reaction norms for age and size at maturation when age at first reproduction is unknown. *Evolutionary Ecology Research*, *6*, 659–678.

Beniston, M., Stephenson, D. B., Christensen, O. B., Ferro, C. A. T., Frei, C., Goyette, S., … Woth, K. (2007). Future extreme events in European climate: An exploration of regional climate model projections. *Climatic Change*, *81*, 71–95. https://doi.org/10.1007/s10584-006-9226-z

Berkeley, S. A., Hixon, M. A., Larson, R. J., & Love, M. S. (2004). Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, *29*, 23–32. https://doi.org/10.1577/1548-8446(2004)29[23:fsvpoa]2.0.co;2

Blanchet, M.-A., Primicerio, R., Smalås, A., Arias-Hansen, J., & Aschan, M. (2019). How vulnerable is the European seafood production to climate warming? *Fisheries Research*, *209*, 251–258. https://doi.org/10.1016/j.fishres.2018.09.004

Bobko, S. J., & Berkeley, S. A. (2004). Maturity, ovarian cycle, fecundity, and age-specific parturition of black rockfish (*Sebastes melanops*). *Fishery Bulletin*, *102*, 418–429.

Brander, K. M. (2007). Global fish production and climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 19709–19714. https://doi.org/10.1073/pnas.0702059104

Bryndum-Buchholz, A., Tittensor, D. P., Blanchard, J. L., Cheung, W. W., Coll, M., Galbraith, E. D., … Lotze, H. K. (2018). Twenty-first-century climate change impacts on marine animal biomass and ecosystem structure across ocean basins. *Global Change Biology*, *25*, 459–472. https://doi.org/10.1111/geb.14512

Chen, Y., Jackson, D. A., & Harvey, H. H. (1992). A comparison of von Bertalanffy and polynomial functions in modeling fish growth data. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*, 1228–1235. https://doi.org/10.1139/f92-138

Conover, D. O., & Munch, S. B. (2002). Sustaining fisheries yields over evolutionary time scales. *Science*, *297*, 94–96. https://doi.org/10.1126/science.1074085

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 6668–6672. https://doi.org/10.1073/pnas.0709472105

Dieckmann, U., & Heino, M. (2007). Probabilistic maturation reaction norms: Their history, strengths, and limitations. *Marine Ecology Progress Series*, *335*, 253–269. https://doi.org/10.3354/meps335253

Dunlop, E. S., Heino, M., & Dieckmann, U. (2009). Eco-genetic modeling of contemporary life-history evolution. *Ecological Applications*, *19*, 1815–1834. https://doi.org/10.1890/08-1404.1

Elliott, J. M. (1993). The pattern of natural mortality throughout the life cycle in contrasting populations of brown trout, *Salmo trutta* L. *Fisheries Research*, *17*, 123–136. https://doi.org/10.1016/0165-7836(93)90012-v

Enberg, K., Jørgensen, C., Dunlop, E. S., Heino, M., & Dieckmann, U. (2009). Implications of fisheries-induced evolution for stock rebuilding and recovery. *Evolutionary Applications*, *2*, 394–414. https://doi.org/10.1111/j.1752-4571.2009.00077.x

Fabens, A. J. (1965). Properties and fitting of the von Bertalanffy growth curve. *Growth*, *29*, 265–289.

Fenberg, P. B., & Roy, K. (2008). Ecological and evolutionary consequences of size-selective harvesting: How much do we know? *Molecular Ecology*, *17*, 209–220. https://doi.org/10.1111/j.1365-294x.2007.03522.x

Ficke, A. D., Myrick, C. A., & Hansen, L. J. (2007). Potential impacts of global climate change on freshwater fisheries. *Reviews in Fish Biology and Fisheries*, *17*, 581–613. https://doi.org/10.1007/s11160-007-9059-5

Finstad, A. G., Jansen, P. A., & Langeland, L. (2001). Production and predation rates in a cannibalistic arctic char (*Salvelinus alpinus* L.) population. *Ecology of Freshwater Fish*, *10*, 220–226. https://doi.org/10.1034/j.1600-0633.2001.100404.x

Folt, C. L., Chen, C. Y., Moore, M. V., & Burnaford, J. (1999). Synergism and antagonism among multiple stressors. *Limnology and Oceanography*, *44*, 864–877. https://doi.org/10.4319/lo.1999.44.3_part_2.0864

Gislason, H., Daan, N., Rice, J. C., & Pope, J. G. (2010). Size, growth, temperature and the natural mortality of marine fish. *Fish and Fisheries*, *11*, 149–158. https://doi.org/10.1111/j.1467-2979.2009.00350.x

Haddon, M. (2001). *Modelling and quantitative methods in fisheries*. Boca Raton, FL: Chapman & Hall/CRC.

Hansen, M. J., Madenjian, C. P., Selgeby, J. H., & Helser, T. E. (1997). Gillnet selectivity for lake trout (*Salvelinus namaycush*) in Lake Superior. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*, 2483–2490. https://doi.org/10.1139/cjfas-54-11-2483

Hawley, K. L., Rosten, C. M., Haugen, T. O., Christensen, G., & Lucas, M. C. (2017). Freezer on, lights off! Environmental effects on activity rhythms of fish in the Arctic. *Biology Letters*, *13*, 20170575. https://doi.org/10.1098/rsbl.2017.0575

Hein, C. L., Öhlund, G., & Englund, G. (2012). Future distribution of Arctic char *Salvelinus alpinus* in Sweden under climate change: Effects of temperature, lakes size and species interactions. *Ambio*, *41*, 303–312. https://doi.org/10.1007/s13280-012-0308-z

Heino, M., Dieckmann, U., & Godø, O. R. (2002). Measuring probabilistic reaction norms for age and size at maturation. *Evolution*, *56*, 669–678. https://doi.org/10.1111/j.0014-3820.2002.tb01378.x

Heino, M., & Godø, O. R. (2002). Fisheries-induced selection pressures in the context of sustainable fisheries. *Bulletin of Marine Science*, *70*, 639–656.

Henriksen, E. H., Frainer, A., Knudsen, R., Kristoffersen, R., Kuris, A. M., Lafferty, K. D., & Amundsen, P.-A. (2019). Fish culling reduces tapeworm burden in Arctic charr by increasing parasite mortality rather than by reducing density-dependent transmission. *Journal of Applied Ecology*, *56*, 1482–1491. https://doi.org/10.1111/1365-2664.13369

Hipsey, M. R., Bruce, L. C., & Hamilton, D. P. (2014).GLM – General Lake Model: Model overview and user information. AED Report #26. University of Western Australia, Perth, Australia, p. 42.

Hsieh, C. H., Yamauchi, A., Nakazawa, T., & Wang, W. F. (2010). Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences*, *72*, 165–178. https://doi.org/10.1007/s00027-009-0122-2

IPCC; Solomon, S., Qin, D., Manning, M., & Averyt, K. (2007).Climate Change 2007 – The Physical Science Basis: Working Group I Contribution to the Fourth Assessment Report of the IPCC (vol. 4). Cambridge University Press.

Jeppesen, E., Mehner, T., Winfield, I. J., Kangur, K., Sarvala, J., Gerdeaux, D., … Meerhoff, M. (2012). Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. *Hydrobiologia*, *694*, 1–39. https://doi.org/10.1007/s10750-012-1182-1

Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., … Rijnsdorp, A. D. (2007). Managing evolving fish stocks. *Science*, *318*, 1247–1248. https://doi.org/10.1126/science.1148089

Karlsson, J., Jonsson, A., & Jansson, M. (2005). Productivity of high-latitude lakes: Climate effect inferred from altitude gradient. *Global Change Biology*, *11*, 710–715. https://doi.org/10.1111/j.1365-2486.2005.00945.x

Klemetsen, A. (2010). The charr problem revisited: Exceptional phenotypic plasticity promotes ecological speciation in postglacial lakes. *Freshwater Review*, *3*, 49–74. https://doi.org/10.4290/frj-3.1.3

Klemetsen, A., Amundsen, P.-A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F., & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): A review of aspects of their life histories. *Ecology of Freshwater Fish*, *12*, 1–59. https://doi.org/10.1034/j.1600-0633.2003.00010.x

Larsson, S., & Berglund, I. (1998). Growth and food consumption of 0+ Arctic charr fed pelleted or natural food at six different temperatures. *Journal of Fish Biology*, *52*, 230–242. https://doi.org/10.1006/jfbi.1997.0575

Larsson, S., & Berglund, I. (2005). The effect of temperature on the energetic growth efficiency of Arctic charr (*Salvelinus alpinus* L.) from four Swedish populations. *Journal of Thermal Biology*, *30*, 29–36. https://doi.org/10.1016/j.jtherbio.2004.06.001

Larsson, S., Forseth, T., Berglund, I., Jensen, A. J., Näslund, I., Elliott, J. M., & Jonsson, B. (2005). Thermal adaptation of Arctic charr: Experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. *Freshwater Biology*, *50*, 353–368. https://doi.org/10.1111/j.1365-2427.2004.01326.x

Lasne, E., Leblanc, C. A. L., & Gillet, C. (2018). Egg size versus number of offspring trade-off: Female age rather than size matters in a domesticated Arctic charr population. *Evolutionary Biology*, *45*, 105–112. https://doi.org/10.1007/s11692-017-9433-8

Law, R. (2000). Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Sciences*, *57*, 659–668. https://doi.org/10.1006/jmsc.2000.0731

Leblanc, C. A. L., Benhaïm, D., Hansen, B. R., Kristjánsson, B. K., & Skúlason, S. (2011). The importance of egg size and social effects for behaviour of Arctic charr juveniles. *Ethology*, *117*, 664–674. https://doi.org/10.1111/j.1439-0310.2011.01920.x

Lindenmayer, D. B., & Likens, G. E. (2010). The science and application of ecological monitoring. *Biological Conservation*, *143*, 1317–1328. https://doi.org/10.1016/j.biocon.2010.02.013

Longhurst, A. (2006). The sustainability myth. *Fisheries Research*, *81*, 107–112. https://doi.org/10.1016%2Fj.fishres.2006.06.022

Marteinsdottir, G., & Steinarsson, A. (1998). Maternal influence on the size and viability of Iceland cod *Gadus morhua* eggs and larvae. *Journal of Fish Biology*, *52*, 1241–1258. https://doi.org/10.1111/j.1095-8649.1998.tb00969.x

Morgan, I. J., McDonald, D. G., & Wood, C. M. (2001). The cost of living for freshwater fish in a warmer, more polluted world. *Global Change Biology*, *7*, 345–355. https://doi.org/10.1046/j.1365-2486.2001.00424.x

Morrissey-McCaffrey, E., Shephard, S., Kelly, F. L., & Kelly-Quinn, M. (2018). Non-native species and lake warming negatively affect Arctic char *Salvelinus alpinus* abundance; deep thermal refugia facilitate co-existence. *Journal of Fish Biology*, *94*, 5–16. https://doi.org/10.1111/jfb.13837

Ohlberger, J. (2013). Climate warming and ectotherm body size – From individual physiology to community ecology. *Functional Ecology*, *27*, 991–1001. https://doi.org/10.1111/1365-2435.12098

Olden, J. D., Hogan, Z. S., & Zanden, M. J. V. (2007). Small fish, big fish, red fish, blue fish: Size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography*, *16*, 694–701. https://doi.org/10.1111/j.1466-8238.2007.00337.x

Olden, J. D., Kennard, M. J., Leprieur, F., Tedesco, P. A., Winemiller, K. O., & García-Berthou, E. (2010). Conservation biogeography of freshwater fishes: Recent progress and future challenges. *Diversity and Distribution*, *16*, 496–513. https://doi.org/10.1111/j.1472-4642.2010.00655.x

Olsen, E. M., Lilly, G. R., Heino, M., Morgan, M. J., Brattey, J., & Dieckmann, U. (2005). Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, *62*, 811–823. https://doi.org/10.1139/f05-065

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Pauly, D. (1980). On the interrelationships between natural mortality, growth-parameters, and mean environmental-temperature in 175 fish stocks. *ICES Journal of Marine Sciences*, *39*, 175–192. https://doi.org/10.1093/icesjms/39.2.175

Persson, L., Amundsen, P.-A., de Roos, A. M., Klemetsen, A., Knudsen, R., & Primicerio, R. (2007). Culling prey promotes predator recovery – Alternative states in a whole-lake experiment. *Science*, *316*, 1743–1746. https://doi.org/10.1126/science.1141412

Pörtner, H. O., Berdal, B., Blust, R., Brix, O., Colosimo, A., De Wachter, B., … Zakhartsev, M. (2001). Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: Developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Continental Shelf Research*, *21*, 1975–1997. https://doi.org/10.1016/s0278-4343(01)00038-3

Post, J. R., Persson, L., Parkinson, E. V., & van Kooten, T. (2008). Angler numerical response across landscapes and the collapse of freshwater fisheries. *Ecological Applications*, *18*, 1038–1049. https://doi.org/10.1890/07-0465.1

Quince, C., Shuter, B. J., Abrams, P. A., & Lester, N. P. (2008). Biphasic growth in fish II: Empirical assessment. *Journal of Theoretical Biology*, *254*, 207–214. https://doi.org/10.1016/j.jtbi.2008.05.030

Reist, J. D., Wrona, F. J., Prowse, T. D., Power, M., Dempson, J. B., King, J. R., & Beamish, R. J. (2006). An overview of effects of climate change on selected Arctic freshwater and anadromous fishes. *Ambio*, *35*, 381–387. https://doi.org/10.1579/0044-7447(2006)35[381:aooeoc]2.0.co;2

Siikavuopio, S. I., Foss, A., Sæther, B. S., Gunnarsson, S., & Imsland, A. K. (2013). Comparison of the growth performance of offspring from cultured versus wild populations of arctic charr, *Salvelinus alpinus* (L.), kept at three different temperatures. *Aquaculture Research*, *44*, 995–1001. https://doi.org/10.1111/j.1365-2109.2012.03112.x

Siikavuopio, S. I., Knudsen, R., & Amundsen, P.-A. (2010). Growth and mortality of Arctic charr and European whitefish reared at low temperatures. *Hydrobiologia*, *650*, 255–263. https://doi.org/10.1007/s10750-010-0192-0

Siikavuopio, S. I., Skybakmoen, S., & Sæther, B. S. (2009). Comparative growth study of wild- and hatchery-produced Arctic charr (*Salvelinus alpinus* L.) in a coldwater recirculation system. *Aquaculture Engineering*, *41*, 122–126. https://doi.org/10.1016/j.aquaeng.2009.06.006

Smalås, A., Strøm, J., Amundsen, P. A., Dieckmann, U., & Primicerio, R. (2020). Data from: Climate warming is predicted to enhance the negative effects of harvesting on high-latitude lake fish populations. v2. *Dryad*. Dataset. https://doi.org/10.5061/dryad.jdfn2z370.

Statskog. (2017). Fiskeregler for Troms (in Norwegian). https://statskog.s3.amazonaws.com/pdf_word/fiske/Fiskeregler_Troms.pdf?mtime=20181214132321

Symons, C. C., Schulhof, M. A., Cavalheri, H. B., & Shurin, J. B. (2019). Antagonistic effects of temperature and dissolved organic carbon on fish growth in California mountain lakes. *Global Change Ecology*, *189*, 231–241. https://doi.org/10.1007/s00442-018-4298-9

Van Nes, E. H., & Scheffer, M. (2005). A strategy to improve the contribution of complex simulation models to ecological theory. *Ecological Modelling*, *185*, 153–164. https://doi.org/10.1016/j.ecolmodel.2004.12.001

Woodward, G., Perkins, D. M., & Brown, L. E. (2010). Climate change and freshwater ecosystems: Impacts across multiple levels of organization. *Philosophical Transaction of the Royal Society B: Biological Sciences*, *365*, 2093–2106. https://doi.org/10.1098/rstb.2010.0055

Wootton, R. J. (1998). *Ecology of teleost fishes*. Netherlands: Springer Science & Business Media, https://doi.org/10.1007/978-94-009-0829-1

SUPPORTING INFORMATION

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

How to cite this article: Smalås A, Strøm JF, Amundsen P-A, Dieckmann U, Primicerio R. Climate warming is predicted to enhance the negative effects of harvesting on high-latitude lake fish. *J Appl Ecol*. 2019;00:1–13. https://doi.org/10.1111/1365-2664.13535

Paper 2

Temperature affinities and life history determine vulnerability of freshwater fish to multiple stressors in a warming Arctic

Aslak Smalås[1], Raul Primicerio[1], Ulf Dieckmann[2,3], John F. Strøm[4] and Per-Arne Amundsen[1]

[1]Faculty of Bioscience, Fisheries and Economy, UiT – The Arctic University of Norway.

[2]Evolution and Ecology Program & Advancing Systems Analysis Program, International Institute for Applied Systems Analysis, Laxenburg, Austria.

[3]Department of Evolutionary Studies of Biosystems, The Graduate University for Advanced Studies (Sokendai), Hayama, Kanagawa 240-0193, Japan.

[4]Institute of Marine Research, Tromsø, Norway.

Corresponding author: Aslak Smalås, e-mail: aslak.smalas@uit.no

Abstract

The effects of climate change on fish are increasingly well documented but have so far largely been overlooked in high-latitude freshwater ecosystems. High latitudes experience more rapid warming than any other area on the planet, and freshwater ecosystems appear to be more vulnerable than both marine and terrestrial environments. Here, we study how past and projected climate warming, together with anthropogenic harvesting pressures, affect lacustrine salmonids north of the Arctic Circle. We combine retrospective analyses of four decades of field data on temperature-dependent growth with individual based models (IBMs) forced by observed and modelled climate variability to assess how climate warming affects somatic growth in three salmonid species – Arctic charr, whitefish, and vendace – differing in their life histories and temperature preferences. The IBMs enable us to address different multi-stressor scenarios of climate warming (RCP 4.5 and RCP 8.5, as defined by the Intergovernmental Panel on Climate Change), density dependence, and size-selective harvesting. We find that all three salmonid species increase somatic growth under climate warming in both observed and modelled populations. We project that size at age and population biomass will increase for these populations. Vendace, which is the least cold-water-adapted species in our study, stands to benefit significantly more, in terms of somatic growth and population biomass, from climate warming than the more cold-water-adapted species Arctic charr and whitefish. Arctic charr, on the other hand, is the species most sensitive to climate warming and has a life history most vulnerable to size-selective harvesting. Our results highlight how the cumulative effects of global climate warming and local anthropogenic harvesting pressures are threatening for many populations of cold-water-adapted freshwater fish.

Keywords: climate warming, salmonids, climate change, ecological modelling, population dynamics, size-selective fishing.

Introduction

Climate change affects freshwater environments and biota via the rapid warming of water temperatures (O’Reilly et al. 2015), leading to shifts in species distributions (Hickling et al. 2006, Comte et al. 2013, Campana et al. 2020), altering vital rates (Biro et al. 2007, Arula et al. 2017, Huss et al. 2019), and affecting ecosystem services and functioning (Dodds et al. 2013, Benateau et al. 2019). The rates of climate warming in Arctic and sub-Arctic regions are higher than elsewhere on the planet (Parmesan 2006), and freshwater environments might be more exposed than terrestrial and marine environments (Woodward et al. 2010). For ectotherms like fish, physiological processes are influenced by ambient temperatures, and somatic growth rates thus change with climate warming (Huss et al. 2019). Somatic growth rates, in turn, influence maturation, survival, and reproduction (Biro et al. 2007), and increased temperatures therefore comprehensively impact the ecology and population dynamics of freshwater fish. The population effects of climate warming will vary depending on species-specific traits, community composition, and geographic area, but also on the presence and strength of other human stressors like size-selective fisheries (Smalås et al. 2020). Even though cold-water-adapted freshwater fishes at high latitudes are expected to respond strongly to ongoing and future climate warming, there is a lack of long-term studies and prospective model-based investigations to evaluate and quantify such expectations. This knowledge gap is concerning as it hinders possible climate action in pursuit of sustainable management and conservation.

In fish, temperature-dependent somatic growth mediates many individual-level and population-level effects of climate change (Deutsch et al. 2008, Ohlberger 2013). Ambient temperature affects both food intake and metabolic costs, with their balance determining net energy gain and somatic growth (Jobling 2002). Food consumption increases with ambient temperature up to an optimum before it steeply drops (Jobling 1981, Koskela et al. 1997). In contrast, metabolic expenses increase exponentially with temperature (Brown et al. 2004). Somatic growth rates are thus highest at an intermediate temperature within the thermal tolerance range of a fish species. Net energy gain and somatic growth also depend on food availability (Huey & Kingsolver 2019), which in turn is affected by ecosystem productivity and consumer abundance (Lorenzen & Enberg 2002, Amundsen et al. 2007). Whereas climate warming is projected to reduce productivity in temperate and tropical areas, climate warming is expected to raise productivity in cold, high-latitude environments (Deutsch et al. 2008, O’Beirne et al. 2017). Since present water temperatures in high-latitude freshwater systems are relatively low, somatic growth is often slow in the typically late-maturing and long-lived species of freshwater fish living there (Reist et al. 2013). If climate warming significantly increases somatic growth rates, the ecological implications for individuals and populations will be wide-ranging: ages and sizes at maturation might change, mortality patterns might be altered, and reproduction and recruitment might be impacted.

Additional stressors affecting fish populations can either mitigate or accentuate the effects of climate warming. One such stressor is size-selective fishing, which greatly affects harvested populations (Ernande et al. 2004). Humans are important predators in species-poor high-latitude ecosystems and can reduce the abundance of fish competitors, thereby indirectly promoting density-dependent somatic growth (Amundsen et al. 2007, Persson et al. 2007). Although fisheries might thus increase somatic growth through the release of density dependence, size-selective harvesting reduces recruitment via the truncation of age and size distributions (Conover & Munch 2002, Heino & Godø 2002). Despite positive effects on somatic growth resulting from climate warming and size-selective harvesting, their cumulative effect may increase the vulnerability of exploited fish populations (Smalås et al. 2020). Multiple anthropogenic stressors already threaten fish populations at high latitudes, and climate warming may intensify the resultant risk via synergistic effects (Dodds et al. 2013, Green et al. 2015). Synergistic effects of climate warming and size-selective harvesting mediated by their effects on somatic growth crucially depend on the thermal preferences and life histories of the affected species (Smalås et al. 2020). The changes in vital rates mediated by temperature-dependent growth have implications for demography, influencing population size, age structure, and maturation schedules (Biro et al. 2007). Therefore, with climate warming, size-selective harvesting may shift from targeting primarily adult fish to targeting both adults and juveniles, and will exacerbate age truncation, reducing both the proportion of adults in the population and the recruitment potential (Smalås et al. 2020). The latter will increase population vulnerability to environmental perturbations. For instance, fish species with fast development, early maturation, and maturation reaction norms dependent more on size than on age might be less vulnerable and vice versa (Jennings et al. 1998, Wiedmann et al. 2014). Therefore, the combined effects of climate warming and size-selective harvesting must be expected to differ between species, depending on their temperature preferences and life histories.

Freshwater salmonids living at high latitudes vary substantially in their temperature preferences and life histories (Klemetsen et al. 2003, Reist et al. 2006). Here, we focus on three salmonid species with wide geographical distributions in northern Eurasia that differ in their temperature preferences, life histories, and exploitability, to assess their differential responses to climate warming and to investigate the synergistic effects of climate warming and size-selective harvesting. First, Arctic charr (*Salvelinus alpinus*) is the most cold-water-adapted of all freshwater fish species, with relative high longevity, slow juvenile growth, large adult size, and late maturation, and is an important but vulnerable target for sustenance and recreational fisheries (Klemetsen et al. 2003, 2010). Second, European whitefish (*Coregonus lavaretus*) is also cold-water-adapted, although it thrives at slightly higher temperatures than Arctic charr (Siikavuopio et al. 2010). Whitefish tend to mature at younger ages and smaller sizes than Arctic charr, have a greater juvenile growth capacity, and an on average smaller adult body size (e.g., Amundsen et al. 2002, Sandlund et al. 2013). Third, vendace (*Coregonus albula*) is a cool-water-adapted fish and differs from the other two species by maturing at very young age and relatively small size while accomplishing very fast juvenile growth (Sandlund et al. 2013). Vendace often displace whitefish from the pelagic zone of lakes when originally coexisting there (Sandlund et al. 2013). Thus, there is a gradient both in temperature preferences and in life histories among these three species. The present study’s objectives are to (i) assess the effect of climate warming on somatic growth based on long-term empirical studies of the three aforementioned salmonids using backcalculated sizes at age, (ii) model past and future effects of climate warming based on climate-forced individual-based models (IBMs) of these species, and (iii) compare the synergistic effects of climate warming and size-selective harvesting across these species. We expect that less cold-water-adapted species will display stronger positive responses to climate warming in terms of accelerated juvenile somatic growth, while more cold-water-adapted species will experience stronger negative synergistic effects of climate warming and size-selective harvesting.

Material and Methods

Empirical data and climate modelling

To estimate temperature-dependent growth, we used long-term datasets from two of the best-studied watercourses at high latitudes, including three different species of freshwater fish, Arctic charr, whitefish, and vendace (Amundsen et al. 2019). Growth estimates for Arctic charr (n = 680) are from Lake Takvatn in the Målselv watercourse, covering the period 1986-2018. Growth estimates for whitefish (n = 331) and vendace (n = 199) are from two lakes, Lake Skrukkebukta and Lake Vaggatem, in the Pasvik watercourse, covering the period 1991-2007. For the Pasvik watercourse, water temperatures were available from an automated logger at the Skogfoss hydropower plant situated 25 km upstream from Lake Skrukkebukta and 23 km downstream from Lake Vaggatem. For Lake Takvatn, continuous water temperature data were not available, and we therefore used climate data from the nearby meteorological station at Bardufoss, situated 20 km southwest of the lake, to force a one-dimensional air-to-water temperature model, called General Lake Modelling (Hipsey et al. 2014, Appendix E), calibrated and validated using measured lake water temperature data. To assess water temperature change over time, we used linear regression.

The eco-genetic individual-based model (IBM) specified below was forced by climate, using two different Representative Concentration Pathways (RCP) scenarios, RCP-4.5 and

RCP-8.5, as defined by the Intergovernmental Panel on Climate Change. These scenarios describe the projected increases, of either 4.5 or 8.5 W/m^2, in radiative forcing in 2100 resulting from rising greenhouse-gas concentrations in the atmosphere and their corresponding greenhouse effects on climate warming (IPCC 2007). Climate variables were obtained at the finest grid resolution available (0.11°) from a regionally downscaled climate model (MPI-M-MPI-ESM-LR), forced by the global circulation model CLMcom-CCLM4-8-17. The climate model outcomes, made available through the EURO-CORDEX project, cover the period 1950-2100. To obtain daily lake water temperatures from the climate model outcomes, we again adopted the one-dimensional air-to-water temperature model, called General Lake Modelling, using the R package GLMr (Hipsey et al. 2014). A more detailed description of the climate models and of the modelling of physical limnology are available in the Supplementary Information (Appendix E).

The longitudes and latitudes of the chosen lakes allow us to address the temperature difference between the western and eastern regions in northern Norway while representatively accounting for the zoogeography of freshwater fish in northern Scandinavia (Lake Takvatn, 69°06’N, 19°05’E, and Lake Skrukkebukta, 69°33’N, 30°07’E; Supplementary Information, Table E1). Long-term data from fish populations in Lake Takvatn (Arctic charr) and Lake Skrukkebukta (whitefish and vendace) covering the last 30 years were used to parameterize the eco-genetic IBM as described below. Data include individual age, length, weight, maturation status, sex, and fecundity in addition to relative density in form of catch-per-unit-effort (CPUE) measurements. All resultant model parameters are listed in Table B1 in the Supplementary Information (Appendix B). Analyses of robustness and sensitivity to changes in somatic growth and natural mortality are also available in the Supplementary Information (Appendix C).

Empirical growth estimates

To estimate empirical temperature-dependent growth, we backcalculated length at age for individuals of the three salmonid species using measurements of annulus radii in sagittal otoliths according to the backcalculation model described by Finstad (2003), which includes an interaction term between age and length,

$$L_a = \left[O_a O_A^{-1}(\beta_0 + \beta_1 L_a + \beta_2 A + \beta_3 L_A A) - \beta_0 \beta_2 a\right](\beta_1 + \beta_3 a)^{-1}, \tag{1}$$

were L_a is the backcalculated length at age a, A is the age at capture, O_a is the measured otolith radius at age a, O_A is the observed otolith radius at time of capture, and L_A is the observed fish length at time of capture. The coefficients β_0, β_1, β_2, and β_3 are estimated by least-square multiple regression (Finstad 2003). The lengths at age 1 year of Arctic charr (*n* = 680), whitefish (*n* = 331), and vendace (*n* = 199) were backcalculated from immature fish ranging in age from 2 to 6 years and covering the whole time period described above. To estimate how growth (or equivalently, the length at age 1 year) is affected by water temperature, we controlled for difference in food availability between years by accounting for differences in the relative density of competitors (catch per unit effort, CPUE) for the respective populations and years. Linear mixed-effect models were used with individual growth or length increment as the response variable, predicted by mean annual water temperature and mean annual relative density of competitors (CPUE) as fixed effects and age at capture and lakes (for the coregonids in the Pasvik watercourse) as random effects. Computations, statistical analyses, and graphical outputs were implemented in R (R version 3.6.0).

Eco-genetic model overview

We used the eco-genetic individual-based model (IBM) developed by Dunlop et al. (2009) and modified for climate-change impact applications by Smalås et al. (2020), parametrized for Arctic charr, whitefish, and vendace. For each annual cycle, the model specifies successive population-level processes, including mortality, maturation, somatic growth, and reproduction, from which the corresponding individual-level events are derived (Dunlop et al. 2009). The initial population in each model run was set to 3000 individuals, and 50 replicate model runs for 150 years were used. Figure 1 shows a schematic illustration of the modeled annual cycle.

The somatic-growth model estimates a yearly length increment, but to capture climate-related growth effects the model accumulates daily temperature-dependent effects on net intake rate over the year. Since the main aim of the present study is to investigate how temperature- and density-dependent growth affect population dynamics under climate warming and size-selective harvesting (Figures 1 & 2), we describe the somatic-growth model in greater detail below. A detailed description of all other components of the IBM is provided in the Supplementary Information (Appendix B); see also Smalås et al. (2020).

Somatic-growth model

We used the Quince-Boukal-Dieckmann (QBD) biphasic growth model (Boukal et al. 2014) to describe juvenile and adult growth trajectories,

$$L_{a+1} = \sqrt[(1-\beta)\alpha]{\frac{L_a^{(1-\beta)\alpha} + (1-\beta)cb^{-(1-\beta)}}{1+q^{-1}(1-\beta)\, r_{a+1}}}, \tag{2}$$

where L_a is the length at age a, β is the allometric exponent relating the rate cW_a^β of net energy intake – measured in terms of weight gain – to the weight W_a, c scales this rate, q is the ratio between the energetic costs per unit of weight of producing gonadic versus somatic tissue, r_{a+1} is the ratio between somatic and gonadic weight at the end of the growth season at age $a+1$, α is the allometric exponent relating the weight $W_a = bL_a^\alpha$ to the length L_a, and b scales this weight. For juveniles, all available energy is allocated to growth, i.e., $r_a = 0$. For adults, a fraction of the net energy intake is allocated to reproduction, i.e., $r_a > 0$. We assumed that r_a does not change with age a; therefore, we set $r_a = r$ and use the closed form of the QBD model for adult growth (Boukal et al. 2014). Figure 3 compares estimates of the biphasic somatic-growth model with the observed length at age data for the different species. We used empirically derived parameters from the QBD growth model for the different species in combination with the corresponding water-temperature and density experienced by the different populations to scale c_{max} to the optimum temperature for growth for the different species (see Supplementary Information, Appendix B).

The coefficient c was jointly determined by a temperature- and density-dependent consumption rate, scaled by $I(T, D)$, and a temperature-dependent metabolic rate, scaled by $m(T)$, where T and D denote temperature and density, respectively. In other words, the consumption rate depends both on temperature and – indirectly, through the density of competitors – on food availability, while the metabolic rate depends only on temperature. This implies that the optimum temperature for growth is lower when the density of competitors is higher (Huey and Kingsolver 2019). In addition to $m(T)$, three different processes (Deslauriers et al. 2017) diminish c: egestion E is the fraction of the consumed energy that is not ingested and leaves the fish as feces, specific dynamic action SDA is the fraction of W_a^β used for processing the food to energy or storage (Jobling 1983), and excretion U is the fraction of W_a^β

lost as nitrogen waste (Deslauriers et al. 2017). Therefore, c was calculated using the following bioenergetic relationship,

$$c = I(T, D)(1 - E) - SDA - U - m(T), \tag{3}$$

For eq. 4-7 (see below), the calculated values are given in kJ day^{-1}, but c in the QBD model have the unit of $g^{1-\beta}$ year^{-1} and we therefore first accumulated the daily energy intake over the 365 days and subsequently used a conversion factor $c = \frac{c}{z}$ to model growth on the correct scale used in QBD growth model framework. To reflect individual variation in energy acquisition, individual values of c were distributed normally around the mean value given by eq. (3).

The temperature-dependent scaling of the consumption rate follows a Ratkowsky-type growth model (Ratkowsky et al. 1983, Larsson et al. 2005, Finstad et al. 2011), useful to describe consumption rate in salmonid fish,

$$I(T) = d(T - T_{\min})\left(1 - e^{g(T - T_{\max})}\right), \tag{4}$$

where T is the experienced water temperature, $T_{\min}$ and $T_{\max}$ are the minimum and maximum temperatures for ingestion, respectively, and d and g are constants.

The density-dependent scaling of the consumption rate follows a negative power law described by Amundsen et al. (2007); see also Lorenzen & Enberg (2002),

$$I(D) = \delta_1 D / {d_c}^{\delta_2}, \tag{5}$$

where D is the total density of competitors, d_c is the conversion factor from the catch-per-unit-effort scale used in Amundsen et al. 2007 to density of competitors in the model, and δ_1 and δ_2 are constants. For densities below the minimum density described in Amundsen et al. (2007)

(catch-per-unit-effort (CPUE) = 4.8), $I(D)$ was set to a maximum $I_{\max}$, where $I_{\max}$= 3.35 is the maximum consumption rate seen in Amundsen et al. 2007.

To capture the combined effects of temperature and density on the consumption rate, we used the following equation,

$$I(T,D) = I(T)(\frac{I(D)}{I_{\max}}), \tag{6}$$

where $I(T,D)$ reaches its maximum when the water temperature is optimal and the population density is lower than the minimum density described by Amundsen et al. (2007).

The temperature-dependent scaling of the metabolic rate follows the Arrhenius function (Gillooly et al. 2001, Lindmark et al. 2018),

$$m(T) = m_0 \omega e^{-\frac{E_{\mathrm{m}}(T-t_0)}{kTt_0}}, \tag{7}$$

where m_0 is the metabolic scaling constant in terms of oxygen consumption, ω is the conversion factor from oxygen consumption to energy consumption, E_{m} is the mean activation energy of biochemical reactions in fish, k is the Boltzmann constant, T is the temperature in terms of the Kelvin scale, and t_0 is the conversion factor from Kelvin scale to Celsius scale.

Field studies of the relationship between water temperature and growth are not available for freshwater salmonids at high latitudes, while corresponding lab experiments have frequently been conducted for the most common high-latitude freshwater fish species. Therefore, we used data from lab experiments to parameterize eq. (3): specifically, bioenergetic studies have provided estimates of the energies lost to egestion, specific dynamic action, and excretion and of the temperature-dependent metabolic rate (Deslauriers et al. 2017). For the corresponding species-specific parameterizations, see the Supplementary Information (Appendix B).

Results

Climate warming increases water temperature in high latitude lakes

Water temperature has increased over the last 30 years in both study systems (Fig. 4a). For Lake Skrukkebukta, in the eastern part of the study area, annual mean water temperature increased by 0.42 ˚C per decade (F=8.61, $p< 0.01$, adj-R^2=0.241). In Lake Takvatn in the western part of northern Norway, the increment was lower than for Lake Skrukkebukta with an increase of 0.28 ˚C per decade (F=19.66, $p< 0.01$, adj-R^2=0.361). Climate warming is predicted to increase both air- and water temperatures in northern parts of Europe towards year 2100 (Fig. 4b, & Supplementary Information, Fig. E1 & E3). Annual mean water temperature is projected to increase by 0.29 ˚C (F=331, $p< 0.001$, adj-R^2 =0.77) and 0.15 ˚C (F=163.1, $p< 0.001$, adj-R^2 =0.62) per decade (year 2000-2100) under the RCP-8.5 climate scenario in Skrukkebukta and Takvatn, respectively. In addition, number of days with significant surplus growth (length of growth season, water temperature between 2-18 ˚C) are also projected to increase by 2.5 days per decade (RCP-4.5, F=93.67, $p< 0.001$, adj-R^2=0.39) or by 4.2 days per decade (RCP-8.5, F=307, $p< 0.001$, adj-R^2=0.68) for Arctic charr in Lake Takvatn. For whitefish and vendace in Lake Skrukkebukta, length of growth season is projected to increase by 2.2 days per decade (RCP-4.5, F=93.67, $p< 0.001$, adj-R^2=0.39) or 3.7 days per decade (RCP-8.5, F=307, $p< 0.001$, adj-R^2=0.68) (Supplementary Information, Appendix E, Fig. E4 & E5).

Length at age increases with temperature in wild fish populations

Increase in mean annual water temperature led to a significant increase in observed length at age 1-year for all three species. Vendace in Lake Skrukkebukta showed the greatest increase of length with 8.6 mm per degree (˚C) increase in mean annual water temperature. Whitefish from Lake Skrukkebukta and Arctic charr from Lake Takvatn showed a significant, but lower increment in length at age 1-year with 4.7 mm per degree (˚C) and 3.4 mm per degree (˚C) increase in mean annual water temperature, respectively (Fig. 5, Supplementary Information, Table A2, A3 & A6). An increase in relative density of competitors (CPUE) led to a significant decrease in length at age for all three species, but the effect size was low for vendace in the Pasvik watercourse (Fig. 5). An increase of one standard deviation in CPUE led to very similar effects on length at age for all three species ranging between -0.97 to -1.11 mm per increase in SD of CPUE (Supplementary Information, Table A4, A5 & A7). Comparison between the effects of water temperature and relative density on length at age showed that the change in temperature was more important in explaining length increment than relative density within the observed range experienced by these fishes using standardized variables (Supplementary Information, Table A1 & A5).

The least cold-water adapted species benefits the most from projected warming

Our individual based model predicted that length at age increases for all three species, but the least cold-water adapted fish species benefits the most from warming in terms of increase in somatic growth (Fig. 6a-c). For example, with intermediate fishing pressure (F= 0.2 yr^{-1}) and thus with intermediate densities, a 4-year old vendace was on average 41 % larger in year 2100 compared to year 2000 under the RCP-8.5 climate scenario (Wilcox non-parametric W-test, W=2626, p< 0.001). For Arctic charr and whitefish this predicted increase was in contrast smaller with a length increment of 32.6 % (Wilcox non-parametric W-test, W=664,091, p< 0.001) and 28.4 % (Wilcox non-parametric W-test, W=486,772, p< 0.001), respectively. This general trend was true for most fishing mortality scenarios under both climate scenarios (Supplementary Information, Appendix C, Tables C1-C15 & Fig. C1-C5 for summary results including all fishing mortality and climate scenarios). However, under the highest fishing mortality scenario (*F*= 0.4 yr^{-1}) the faster growing and largest vendace individuals were removed from the population through fishing, therefore the climate effect was masked by the size-selective harvest, and the more cold water adapted species had larger increase in length at age (Supplementary information, Tables C13-C15).

Stock biomass also increased substantially with warming for all three species in our modelled populations due to increased individual somatic growth (Fig. 6d). With intermediate fishing mortality (*F*= 0.2 yr^{-1}) and thus intermediate densities, vendace stock biomass was predicted to increase by 119 % from year 2000 to year 2100 under the RCP-8.5 climate scenario (Wilcox non-parametric W-test, W=250,000, p< 0.001). The more cold-water adapted fish species, Arctic charr and whitefish, benefited less than vendace from warming with a biomass increase of 88 % (Wilcox non-parametric W-test, W=250,000, p< 0.001) and 89 % (Wilcox non-parametric W-test, W=250,000, p< 0.001), respectively. Similar trend in biomass increase was evident also for other fishing mortality scenarios (see Supplementary Information, Appendix C, Fig. C1-C6).

Increased vulnerability caused by the joint effect of multiple stressors

The modelled populations differ in their response to multiple stressors. High size-selective harvest (*F*> 0.2 yr^{-1}) combined with climate warming altered the age-distribution of all three species (Fig. 7). The age-truncation was severe and led to a decrease in both mean age and mean age of mature individuals in all three populations. For instance, for fishing mortality *F*= 0.2 yr^{-1}, mean age of the Arctic charr population decreased by 7.3 % from 3.01 years in year 2000 to 2.79 years in year 2100 (Wilcox non-parametric W-test, W=47,983.143, p< 0.001). For the whitefish population, mean age decreased by 10.1 % from 1.81 years in year 2000 to 1.64 years in year 2100 (Wilcox non-parametric W-test, W=43,085,751, p< 0.001), while the mean age in the vendace population decreased by 30 % from 0.62 years in year 2000 to 0.48 years in year 2100 (Wilcox non-parametric W-test, W=20,984,348, $p < 0.001$). With warming all three species increased their length at age, which reduced age at maturation contingent on their respective maturation reaction norm. For Arctic charr ($F = 0.2$ yr^{-1}), the mean age at maturation decreased from 6.0 to 5.6 years and mean adult age decreased from 7.2 to 6.5 years from year 2000 to the year 2100 (Wilcox non-parametric W-test, W=1,744,764, $p < 0.001$). Whereas for whitefish ($F = 0.2$ yr^{-1}), the mean age at maturation decreased from 4.5 to 3.9 years and mean adult age decreased from 5.3 to 4.8 years from year 2000 to the year 2100 (Wilcox non-parametric W-test, W=45.583.587, $p < 0.01$). For vendace ($F = 0.2$ yr^{-1}), the mean age at maturation decreased from 1.1 years in year 2000 to 0.9 years in year 2100, and the mean adult age decreased from 1.9 to 1.5 years (Wilcox non-parametric W-test, W=1.817.218, $p < 0.001$). For all investigated species, there is no significant sharpening of the size-truncation with warming under high fishing mortality scenarios (see Supplementary Information, Appendix C for more detailed description of the individual based model outcomes and results).

The cumulative effects of warming and harvesting increased population vulnerability by reducing the proportion of adults due to increased age-specific fishing mortality. Earlier maturation age did somewhat mitigate the reduction in the proportion of adults, but the degree of compensation differs among the three species. The proportion of mature individuals decreased for both Arctic charr and whitefish, but not for vendace in the multiple stressor scenarios considered here. For vendace, the proportion of mature individuals was stable or increased with warming for all fishing mortality scenarios (Fig. 7c.). Even for the highest fishing mortality scenario ($F = 0.4$ yr^{-1}), the proportion of mature individuals in the population was not decreasing with warming (year 2000 vs. year 2100: Wilcox non-parametric W-test, W=124.771, $p = 0.96$). For the whitefish and the Arctic charr populations the negative cumulative effect on adult proportion was substantial. For example, under the highest fishing mortality scenario (F = 0.4 yr^{-1}), the proportion of mature individuals in the Arctic charr population decreased by 24.5 % from year 2000 to year 2100 (Wilcox non-parametric W-test, W=545.5, p< 0.001) (Fig. 7a-b). For the whitefish population the effect was less pronounced, with a decrease of 16.5 % in the proportion of mature individuals from year 2000 to year 2100 (Wilcox non-parametric W-test, W=24.455, p< 0.001).

Discussion

Our study shows that climate warming affects freshwater fish life history at high latitudes via increased temperature-dependent somatic growth. Backcalculations of length at age show an increase in somatic growth with warming for the three investigated species. The cool-water adapted species vendace, increased length at age with temperature substantially more than the cold-water adapted Arctic charr and whitefish. The stronger warming effects detected in vendace were also seen in the model outcomes, with different growth performance projections among species due to their different temperature affinities. Our results highlight that the difference in temperature preferences between cold- and cool-water adapted fish will be more advantageous for the latter in a warming Arctic. The variation in life-history between species explained their different population sensitivity to the multiple stressors, where Arctic charr, with the slowest juvenile growth rate and oldest age at maturity, will be more heavily affected than vendace by size-selective harvesting under climate warming.

We provide compelling evidence that cold- and cool-water salmonids benefitted from the rapid warming experienced during the last three decades in terms of increased juvenile somatic growth. However, a large difference between species in 0+ growth increase with temperature was evident. The cool-water adapted vendace grew twice as fast (8.6 mm) as the cold-water adapted Arctic charr (3.4 mm) and whitefish (4.7 mm) per degree (°C) of warming.

Our individual based models predict that the somatic growth rates will continue to increase towards year 2100 under the two climate scenarios investigated. At the population level, production and biomass are predicted to increase, more so for the least cold-water adapted species, vendace, than for Arctic charr and whitefish. Our findings are consistent with expectation that individuals living in ecosystems where the ambient temperature is considerably lower than optimum may improve somatic growth under warming, especially for juvenile fish (Van Dorst et al. 2019, Huss et al. 2019). Our study systems are located well above the Arctic Circle and the projected warming will therefore prolong the temperature-dependent growth season towards year 2100. Number of days between 2-18 ˚C are predicted to increase by 4.2 (in Takvatn) and 3.7 (in Skrukkebukta) days per decade (RCP-8.5). Under the projected warming, ambient temperatures will get closer to optimum temperatures for growth of salmonids during the open water season. On the contrary, populations living towards the southern end of the investigated species' distribution are already experiencing large negative impacts from climate warming (George et al. 2006, Rennie et al. 2009, Connor et al. 2019, Kelly et al. 2020). For instance, Arctic charr in Ireland and vendace in the UK are currently struggling because their preferred thermal habitat is greatly reduced, affecting not only growth but also survival (George et al. 2006, Connor et al. 2019). Similarly, other studies associate climate warming with a decrease in population biomass and production at lower latitudes (Cohen et al. 2016, van Dorst et al. 2019), whereas systems located in the Arctic or sub-Arctic are expected to have a rise in population production of freshwater fish (Reist et al. 2006, Campana et al. 2020), in line with our findings.

Somatic growth in the three salmonid species was affected by temperature but also by density of competitors, stressing the importance of food availability for growth performance. As expected, consumer density affected somatic growth negatively in our wild fish populations, however, the magnitude of this effect was smaller than that of temperature in all three populations. At high densities food intake rates will be reduced substantially, limiting the scope for somatic growth variation (Amundsen et al. 2007), which may mask the positive effects on growth driven by warming at high latitudes. With warming, metabolic activity increases and food intake rate will therefore have to rise to meet the higher metabolic demands (Huey & Kingsolver 2019). In our models, productivity and prey availability are only considered implicitly, as food intake rate is dependent on number of competitors, and productivity is assumed to be constant. However, primary productivity will likely increase with warming in cold areas (Karlsson et al. 2005, Schindler et al. 2005, O`Bierne et al. 2017), and greater prey density may help satisfy the increased metabolic needs caused by warming (Kao et al. 2015, Huss et al. 2019), as also shown for other salmonids in high latitude ecosystems (Rich et al. 2009). The negative effects that lower food availability has on somatic growth are well documented in harvested populations, where higher fishing mortality reduces consumer density resulting in compensatory growth (Evangelista et al. 2020), an effect also observed in the wild populations investigated here (Amundsen et al. 2007).

Our modelling results show how synergistic effects mediated by compensatory and temperature-dependent growth increase the cumulative risk of harvesting and warming for wild salmonid populations. Under higher fishing pressure, compensatory growth increases the risk of size-selective fishing mortality in younger fish, including immatures, a phenomenon that is amplified by the growth acceleration induced by warming. The growth acceleration also leads to more pronounced age truncation and reduced proportion of adults (Jørgensen et al. 2007, Anderson et al. 2008, Smalås et al. 2020), resulting in cumulative effects that threaten exploited wild fish populations under warming. The severity of the cumulative risk depends on the thermal affinities and life history of the fish species. For instance, populations that are slow growing and late maturing, with a large maturation size, are more vulnerable to cumulative effects than populations with a faster life history (Jennings et al. 1998, Wiedmann et al. 2014).

The shape of the maturation reaction norm further determines vulnerability, with steep negative slopes resulting in greater risk of fishing mortality for immatures and a larger reduction in the proportion of adults, as seen for Arctic charr. Vendace, on the other hand, has a fast turnover rate and a gentler negative slope of the maturation reaction norm, and the population did not experience a reduction in the proportion of mature individuals even for the highest fishing mortality scenario. The difference in life history and vulnerability to cumulative effects among salmonids has also implications for their evolutionary responses to multiple stressors, with warming being likely to affect selection pressure from size-selective harvesting (Fenberg & Roy 2008). Climate adaptation plans for the management of salmonids should thereby address ecological and evolutionary cumulative effects when considering mitigation measures concerning fishing effort and gear selectivity.

The predictions on warming impact and cumulative effects based on our individual based models are influenced by a number of simplifying assumptions. The temperature-dependence in somatic growth capacity was assumed constant during ontogeny, however fish respond differently to temperature depending on size and life stage (Huss et al. 2019, Dahlke et al. 2020). Different temperature-performance relationships have been suggested for fish of different sizes, with larger fish being more negatively affected by warming than smaller ones (Lindmark et al. 2018). Also, embryos, larvae and spawners are especially vulnerable life stages with narrow thermal windows (Dahlke et al. 2020). Our projected changes in growth, age-distribution and stock biomass are qualitatively robust to small (±5%) pairwise changes in both growth parameters (d and g) and natural-mortality parameters (Supplementary information, Appendix D). Yet, these projections do not factor in other indirect, ecological effects of warming mediated by interactions with other species or changes in environmental conditions. The negative impact of warming on cold water adapted salmonids will likely be magnified by interspecific interactions with species adapted to warmer waters (Comte et al. 2013, Rolls et al.

2017), which will experience a greater increase in performance in a warming Arctic (Lindmark et al. 2019).

Conclusion

We show how the cumulative effects of warming and size-selective harvesting at high latitudes are contingent on a species thermal niche and life history. Salmonid species adapted to warmer waters displayed the greater increase in growth performance, and cold water species with slow life history suffered the greatest cumulative effects. Such ecological factors contributing to the cumulative risk from climate warming and local anthropogenic pressures must be taken into account in climate adaptation strategies that attempt to mitigate impact on populations of cold-water adapted freshwater fish.

Authors' Contributions

A.S. and R.P. conceived the ideas and planned the paper. A.S., R.P., J.F.S. and U.D. contributed significantly to model development. P.-A.A., A.S. and R.P. collected data. A.S. and R.P. analyzed model results with substantial input from J.F.S., P.-A.A. and U.D. A.S. led the writing.

Acknowledgements

Thanks are due to the Freshwater Ecology Group at UiT–The Arctic University of Norway, for collecting and sharing their long-term time series from Lake Takvatn and the Pasvik watercourse. A.S. was supported by UiT–The Arctic University of Norway. A.S. and R.P. acknowledge funding by the EU-H2020 project ClimeFish (project ID 677039). U.D. acknowledges funding by the EU-H2020 project COMFORT (project ID 820989). P.-A.A.

acknowledges funding by the Norwegian Research Council (project no. 213610 and 183984). No conflict of interest are to be reported.

Data availability statement

Summary data on population level properties from the individual based model outcomes and summary information on individual empirical data will be available upon acceptance of the MS.

References

Amundsen, A., Kristoffersen, R., Knudsen, R., & Klemetsen, A. (2002). Long-term effects of a stock depletion programme: The rise and fall of a rehabilitated whitefish population. *Advances in Limnology, 57*, 577-58.

Amundsen, P. A., Knudsen, R., & Klemetsen, A. (2007). Intraspecific competition and density dependence of food consumption and growth in Arctic charr. *Journal of Animal Ecology, 76*, 149–158. https://doi.org/10.1111/j.1365-2656.2006.01179.x

Amundsen, P.-A., Primicerio, R., Smalås, A., Henriksen, E. H., Knudsen, R., Kristoffersen, R., & Klemetsen, A. (2019). Long-term ecological studies in northern lakes – challenges, experiences and accomplishments. *Limnology and Oceanography, 64*, 11-21. https://doi.org/10.1002/lno.10951

Anderson, C. N. K., Hsieh, C.-H., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., … Sugihara, G. (2008). Why fishing magnifies fluctuations in fish abundance. *Nature, 452*, 835–839. https ://doi. org/10.1038/natur e06851

Arula, T., Shpilev, H., Raid, T., Vetemaa, M., & Albert, A. (2017). Maturation at a young age and small size of European smelt (*Osmerus eperlanus*): A consequence of population overexploitation or climate change? *Helgoland Marine Research, 71*, 7. https://doi.org/10.1186/s10152-017-0487-x

Benateau, S., Gaudard, A., Stamm, C., & Altermatt, F. (2019). Climate change and freshwater ecosystems: Impacts on water quality and ecological status. Zürich: *Federal Office for the Environment (FOEN) Eawag,* 1-110.

Biro, P. A., Post, J. R., & Booth, D. J. (2007). Mechanisms for climate-induced mortality of fish populations in whole-lake experiments. *Proceedings of the National Academy of Sciences, 104*, 9715–9719. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1887605/pdf/zpq9715.pdf

Boukal, D. S., Dieckmann, U., Enberg, K., Heino, M., & Jorgensen, C. (2014). Life-history implications of the allometric scaling of growth. *Journal of Theoretical Biology, 359*, 199–207. https://doi.org/10.1016/j.jtbi.2014.05.022

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology, 85*, 1771–1789. https://doi.org/Doi 10.1890/03-9000

Campana, S. T., Casselman, J. M., Jones, C. M., Black, G., Barker, O., Evans, M., Guzzo, M. M., Kilada, R., Muir, A. M., & Perry, R. (2020). Arctic freshwater fish productivity and colonization increase with climate warming. *Nature Climate Change, 10,* 428-433. https://www.nature.com/articles/s41558-020-0744-x

Cohen, A., Gergurich, E., Kraemer, B. M., McGlue, M. M., McIntyre, P. B. Russell, J. M., Simmons, J. D. & Swarzenski P. W. (2016). Climate warming reduces fish production and benthic habitat in Lake Tanganyika, one of the most biodiverse freshwater ecosystems. *Proceedings of the National Academy of Sciences*, *113*, 9563-9568. https://www.pnas.org/content/113/34/9563.short

Comte, L., Buisson, L., Daufresne, M., & Grenouillet, G. (2013). Climate-induced changes in the distribution of freshwater fish: observed and predicted trends. *Freshwater Biology*, *58*, 625–639. https://doi.org/10.1111/fwb.12081

Conover, D. O., & Munch, S. B. (2002). Sustaining fisheries yields over evolutionary time scales. *Science, 297*, 94–96. https://doi.org/DOI 10.1126/science.1074085

Connor, L., Shephard, S., Rocks, K., & Kelly, F. L. (2019). Potential climate change impacts on Arctic char *Salvelinus alpinus* L. in Ireland. *Fisheries Management and Ecology, 26,* 527–539. https://doi.org/10.1111/fme.12327

Dahlke, F. T., Wohlrab, S., Butzin, M., & Pörtner, H. O. (2020). Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science, 369*, 65–70. https://doi.org/10.1126/science.aaz3658

Deslauriers, D., S.R. Chipps, J.E. Breck, J.A. Rice and C.P. Madenjian. (2017). Fish Bioenergetics 4.0: An R-based modelling application. *Fisheries, 42,* 586-596.

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, *105*, 6668–6672. https://doi.org/10.1073/pnas.0709472105

Dodds, W. K., Perkin, J. S., & Gerken, J. E. (2013). Human Impact on Freshwater Ecosystem Services: A Global Perspective. *Environmental science & technology, 47*, 9061–9068. https://doi.org/10.1021/es4021052

Dunlop, E. S., Heino, M., & Dieckmann, U. (2009). Eco-genetic modeling of contemporary life-history evolution. *Ecological Applications, 19*, 1815–1834. https://doi.org/Doi 10.1890/08-1404.1

Ernande, B., Dieckmann, U., & Heino, M. (2004). Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 271*, 415–423. https://doi.org/10.1098/rspb.2003.2519

Evangelista, C., Vøllestad, L. A., Pauli, B. D., & Edeline, E. (2020). Density-dependent consequences of size-selective induced life-history changes to population fitness in medaka (*Oryzias latipes*). *Canadian Journal of Fisheries and Aquatic Sciences, 77*, 1741–1748. https://doi.org/10.1139/cjfas-2019-0406

Fenberg, P. B., & Roy, K. (2008). Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Molecular Ecology, 17*, 209–220. https://doi.org/10.1111/j.1365-294X.2007.03522.x

Finstad, A. G. (2003). Growth backcalculations based on otoliths incorporating an age effect: Adding an interaction term. *Journal of Fish Biology, 62*, 1222-1225. https://doi.org/10.1046/j.1095-8649.2003.00102.x

Finstad, A. G., Forseth, T., Jonsson, B., Bellier, E., Hesthagen, T., Jensen, A. J., Hessen, D. O., & Foldvik, A. (2011). Competitive exclusion along climate gradients: energy efficiency influences the distribution of two salmonid fishes. *Global Change Biology, 17,* 1703–1711. https://doi.org/10.1111/j.1365-2486.2010.02335.x

George, D. G., Bell, V. A., Parker, J., & Moore, R. J. (2006). Using a 1-D mixing model to assess the potential impact of year-to-year changes in weather on the habitat of vendace (*Coregonus albula*) in Bassenthwaite Lake, Cumbria. *Freshwater Biology*, *51,* 1407-1416. https://doi.org/10.1111/j.1365-2427.2006.01572.x

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science, 293,* 2248–2251. https://doi.org/10.1126/science.1061967

Green, P. A., Vörösmarty, C. J., Harrison, I., Farrell, T., Sáenz, L., & Fekete, B. M. (2015). Freshwater ecosystem services supporting humans: Pivoting from water crisis to water solutions. *Global Environmental Change, 34,* 108–118.

Heino, M., & Godo, O. R. (2002). Fisheries-induced selection pressures in the context of sustainable fisheries. *Bulletin of Marine Science, 70,* 639–656.

Hickling, R., Roy, D. B., Hill, J. K., Fox, R., & Thomas, C. D. (2006). The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology, 12,* 450–455. https://doi.org/10.1111/j.1365-2486.2006.01116.x

Hipsey, M. R., Bruce, L. C., Hamilton, D. P., & Australia, T. U. of W. (2014). GLM - General Lake Model: Model overview and user information. In *AED Report #26.*

Huey, R. B., & Kingsolver, J. G. (2019). Climate warming, resource availability, and the metabolic meltdown of ectotherms. *American Naturalist, 194,* 140-150. https://doi.org/10.1086/705679

Huss, M., Lindmark, M., Jacobson, P., van Dorst, R. M., Gårdmark, A., & Gardmark, A. (2019). Experimental evidence of gradual size-dependent shifts in body size and growth of fish in response to warming. *Global Change Biology*, *25*, 2285–2295. https://doi.org/10.1111/gcb.14637

IPCC; Solomon, S., Qin, D., Manning, M., & Averyt, K. (2007). Climate Change 2007 – The Physical Science Basis: Working Group I Contribution to the Fourth Assessment Report of the IPCC (vol. 4). Cambridge University Press.

Jennings, S., Reynolds, J. D., & Mills, S. C. (1998). Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society B: Biological Sciences*, *265,* 333-339. https://doi.org/10.1098/rspb.1998.0300

Jobling, M. (1981). Temperature tolerance and the final preferendum—rapid methods for the assessment of optimum growth temperatures. *Journal of Fish Biology, 19*, 439-455. https://doi.org/10.1111/j.1095-8649.1981.tb05847.x

Jobling, M. (1983). Towards an explanation of specific dynamic action (SDA). *Journal of Fish Biology, 23,* 549–555. https://doi.org/10.1111/j.1095- 8649.1983.tb02934.x

Jobling, M. (2002). Environmental factors and rates of development and growth. In P. J. B. Hart & J. D. Reynolds (Eds.), *Handbook of fish biology and fisheries* (Vol. 2, pp. 97–122). Wiley-Blackwell.

Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande, B., Gårdmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M., & Rijnsdorp, A.D. (2007). Managing evolving fish stocks. *Science, 318,* 1247–1248.

Kao, Y. C., Madenjian, C. P., Bunnell, D. B., Lofgren, B. M., & Perroud, M. (2015). Potential effects of climate change on the growth of fishes from different thermal guilds in Lakes Michigan and Huron. *Journal of Great Lakes Research, 41,* 423–435. https://doi.org/10.1016/j.jglr.2015.03.012

Karlsson, J., Jonsson, A., & Jansson, M. (2005). Productivity of high-latitude lakes: climate effect inferred from altitude gradient. *Global Change Biology, 11,* 710–715. https://doi.org/10.1111/j.1365-2486.2005.00945.x

Kelly, S., Moore, T. N., de Eyto, E., Dillane, M., Goulon, C., Guillard, J., Lasne, E., McGinnity, P., Poole, R., Winfield, I. J., Woolway, R. I., & Jennings, E. (2020). Warming winters threaten peripheral Arctic charr populations of Europe. *Climatic Change, 163,* 599-618. https://doi.org/10.1007/s10584-020-02887-z

Klemetsen, A. (2010). The charr problem revisited: exceptional phenotypic plasticity promotes ecological speciation in postglacial lakes. *Freshwater Reviews, 3,* 49–74.

Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O’Connell, M. F., & Mortensen, E. (2003). Atlantic salmon Salmo salar L., brown trout Salmo trutta L. and Arctic charr *Salvelinus alpinus* (L.): A review of aspects of their life histories. *Ecology of Freshwater Fish, 12,* 1-59. https://doi.org/10.1034/j.1600-0633.2003.00010.x

Koskela J., Jobling M. & Pirhonen J. (1997). Influence of the length of daily feeding period on feed intake and growth of whitefish, *Coregonus lavaretus*. *Aquaculture 156,* 35–44.

Larsson, S., Forseth, T., Berglund, I., Jensen, A. J., Naslund, I., Elliott, J. M., & Jonsson, B. (2005). Thermal adaptation of Arctic charr: experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. *Freshwater Biology, 50,* 353–368.

Lindmark, M., Huss, M., Ohlberger, J., & Gardmark, A. (2018). Temperature-dependent body size effects determine population responses to climate warming. *Ecology Letters, 21,* 181–189. https://doi.org/10.1111/ele.12880

Lindmark, M., Ohlberger, J., Huss, M., & Gardmark, A. (2019). Size-based ecological interactions drive food web responses to climate warming. *Ecology Letters, 22,* 778–786. https://doi.org/10.1111/ele.13235

Lorenzen, K., & Enberg, K. (2002). Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proceedings of the Royal Society B-Biological Sciences, 269,* 49–54. https://doi.org/10.1098/rspb.2001.1853

O’Beirne, M. D., Werne, J. P., Hecky, R. E., Johnson, T. C., Katsev, S., & Reavie, E. D. (2017). Anthropogenic climate change has altered primary productivity in Lake Superior. *Nature Communications, 8,* 1-8. https://doi.org/10.1038/ncomms15713

Ohlberger, J. (2013). Climate warming and ectotherm body size - from individual physiology to community ecology. *Functional Ecology, 27,* 991–1001. https://doi.org/10.1111/1365-2435.12098

O’Reilly, C. M., Sharma, S., Gray, D. K., Hampton, S. E., Read, J. S., Rowley, R. J., Schneider, P., Lenters, J. D., McIntyre, P. B., Kraemer, B. M., Weyhenmeyer, G. A., Straile, D., Dong, B., Adrian, R., Allan, M. G., Anneville, O., Arvola, L., Austin, J., Bailey, J. L., … Zhang, G. Q. (2015). Rapid and highly variable warming of lake-surface waters around the globe. *Geophysical Research Letters, 42,* 10773–10781. https://doi.org/10.1002/2015gl066235

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics, 37,* 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Persson, L., Amundsen, P. A., De Roos, A. M., Klemetsen, A., Knudsen, R., & Primicerio, R. (2007). Culling prey promotes predator recovery - Alternative states in a whole-lake experiment. *Science, 316,* 1743–1746. https://doi.org/10.1126/science.1141412

Ratkowsky, D. A., Lowry, R. K., McMeekin, T. A., Stokes, A. N., & Chandler, R. E. (1983). Model for bacterial culture growth rate throughout the entire biokinetic temperature range. *Journal of Bacteriology, 53,* 122-126.

Rich, H. B., Quinn, T. P., Scheuerell, M. D., & Schindler, D. E. (2009). Climate and intraspecific competition control the growth and life history of juvenile sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences, 66*, 238-246. https://doi.org/10.1139/F08-210

Reist, J. D., Wrona, F. J., Prowse, T. D., Power, M., Dempson, J. B., Beamish, R. J., King, J. R., Carmichael, T. J., & Sawatzky, C. D. (2006). General effects of climate change on Arctic fishes and fish populations. *Ambio, 35,* 370–380. https://doi.org/Doi 10.1579/0044-7447(2006)35

Reist, J. D., Power, M., & Dempson, J. B. (2013). Arctic charr (*Salvelinus alpinus*): a case study of the importance of understanding biodiversity and taxonomic issues in northern fishes. *Biodiversity, 14*, 45-56. https://doi.org/10.1080/14888386.2012.725338

Rennie, M. D., Gary Sprules, W., & Johnson, T. B. (2009). Factors affecting the growth and condition of lake whitefish (*Coregonus clupeaformis*). *Canadian Journal of Fisheries and Aquatic Sciences, 66*, 2096-2108. https://doi.org/10.1139/F09-139

Rolls, R. J., Hayden, B., & Kahilainen, K. K. (2017). Conceptualising the interactive effects of climate change and biological invasions on subarctic freshwater fish. *Ecology and Evolution, 7,* 4109-4128. https://doi.org/10.1002/ece3.2982

Sandlund, O. T., Gjelland, K. O., Bohn, T., Knudsen, R., & Amundsen, P. A. (2013). Contrasting Population and Life History Responses of a Young Morph-Pair of European Whitefish to the Invasion of a Specialised Coregonid Competitor, Vendace. *Plos One*, *8*, pp.13. https://doi.org/ARTN e68156 10.1371/journal.pone.0068156

Schindler, D. E., Rogers, D. E., Scheuerell, M. D., & Abrey, C. A. (2005). Effects of changing climate on zooplankton and juvenile sockeye salmon growth in southwestern Alaska. *Ecology, 86*, 198-209. https://doi.org/10.1890/03-0408

Siikavuopio, S. I., Knudsen, R., & Amundsen, P. A. (2010). Growth and mortality of Arctic charr and European whitefish reared at low temperatures. *Hydrobiologia, 650,* 255–263. https://doi.org/10.1007/s10750-010-0192-0

Smalås, A., Strøm, J. F., Amundsen, P., Dieckmann, U., & Primicerio, R. (2020). Climate warming is predicted to enhance the negative effects of harvesting on high-latitude lake fish. *Journal of Applied Ecology*, *57*, 270–282. https://doi.org/10.1111/1365-2664.13535

van Dorst, R. M., Gardmark, A., Svanback, R., Beier, U., Weyhenmeyer, G. A., & Huss, M. (2019). Warmer and browner waters decrease fish biomass production. *Global Change Biology*, *25*, 1395–1408. https://doi.org/10.1111/gcb.14551

Wang, H., Botsford, L., White, J., Fogarty, M., Juanes, F., Hastings, A., Holland, M., & Brander, K. (2014). Effects of temperature on life history set the sensitivity to fishing in Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series*, *514*, 217–229. https://doi.org/10.3354/meps10943

Wiedmann, M. A., Primicerio, R., Dolgov, A., Ottesen, C. A. M., & Aschan, M. (2014). Life history variation in Barents Sea fish: implications for sensitivity to fishing in a changing environment. *Ecology and Evolution, 4*, 3596–3611. https://doi.org/10.1002/ece3.1203

Woodward, G., Perkins, D. M., & Brown, L. E. (2010). Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *365*, 2093–2106. https://doi.org/10.1098/rstb.2010.0055

Figure Legends

Figure 1. Schematic representation of the four successive events in the annual cycle of the individual based model. 1) Mortality, modelled as two different size-dependent components ($Z = \text{natural } (M) + \text{fishing } (F)$). 2) Maturation specified by a linear probabilistic maturation reaction norm (PMRN), depending on both length and age. 3) Growth, modelled as biphasic growth which is both density- and temperature-dependent. 4) Reproduction, with size dependent fecundity, and density-dependent recruitment.

Figure 2. a) Theoretical representation of temperature-dependent rates affecting growth performance in the individual based model, 100% (solid line) and 75% (stippled line) of maximum ration. b) Temperature-dependent growth at maximum ration for Arctic charr (*Salvelinus alpinus*) (—), whitefish (*Coregonus lavaretus*) (—) and Vendace (*Coregonus albula*) (—).

Figure 3. Fit of the Quince-Boukal-Dieckmann biphasic growth model to the observed length at age data with the estimated probabilistic maturation reaction norm midpoint, the 25th and 75th percentile (dashed lines) for a) Arctic charr in Takvatn, and b) whitefish and c) vendace in Lake Skrukkebukta.

Figure 4. a) Historical annual mean water temperature for Lake Skrukkebukta (—) (1991-2016), eastern part of northern Norway, and Lake Takvatn (—) (1985-2016), western part of northern Norway. Solid lines show the linear development in temperature over time. b) Projected annual mean water temperature for the upper ten meters for Lake Skrukkebukta (—), eastern part of northern Norway, and Lake Takvatn (—), western part of northern Norway. Solid lines represent the RCP-8.5 climate scenario and dashed lines represent the RCP-4.5 climate scenario.

Figure 5. Backcalculated length for one-year-old Arctic charr (*Salvelinus alpinus*) from Lake Takvatn, and one-year-old whitefish (*Coregonus lavaretus*) and vendace (*Coregonus albula*) from the Pasvik watercourse. Grey points represent the mean, whiskers represent the bootstrapped 95 % confidence interval of the mean, line with shading represent linear regression with standard error. Left panels: Length at age 1-year dependent on annual mean water temperature (˚C). Right panels: Length at age 1-year dependent on annual mean Catch-Per-Unit-Effort.

Figure 6. Model predictions of length at age for a) Arctic charr in Takvatn, and b) whitefish and c) vendace in Skrukkebukta under two climate scenarios, RCP (4.5 & 8.5), for intermediate fishing mortality (F= 0.2 yr^{-1}). d) Model predictions of percentage change in stock biomass for Arctic charr (—) in Lake Takvatn, and whitefish (—) and vendace (—) in Lake Skrukkebukta under the RCP-4.5 (dashed line) and RCP-8.5 (solid line) climate scenarios from year 1950 to year 2100 for intermediate fishing mortality (F= 0.2 yr^{-1}).

Figure 7. Model predictions of the demographic changes in a) Arctic charr in Lake Takvatn, and b) whitefish and c) vendace in Lake Skrukkebukta. Left panels: Proportion of mature individuals for five different fishing mortality scenarios (F= 0.0-0.4 yr^{-1}) from year 1950-2100 under the RCP-4.5 (dashed line) and RCP-8.5 (solid line) climate scenarios. Right panels: Age-distribution with immature (grey bars) and mature individuals (black bars) for three different fishing mortality scenarios (F= 0.0-, 0.2- & 0.4 yr^{-1}) for the RCP-8.5 climate scenario in year 2000, year 2050 and year 2100.

Figures

Fig. 1

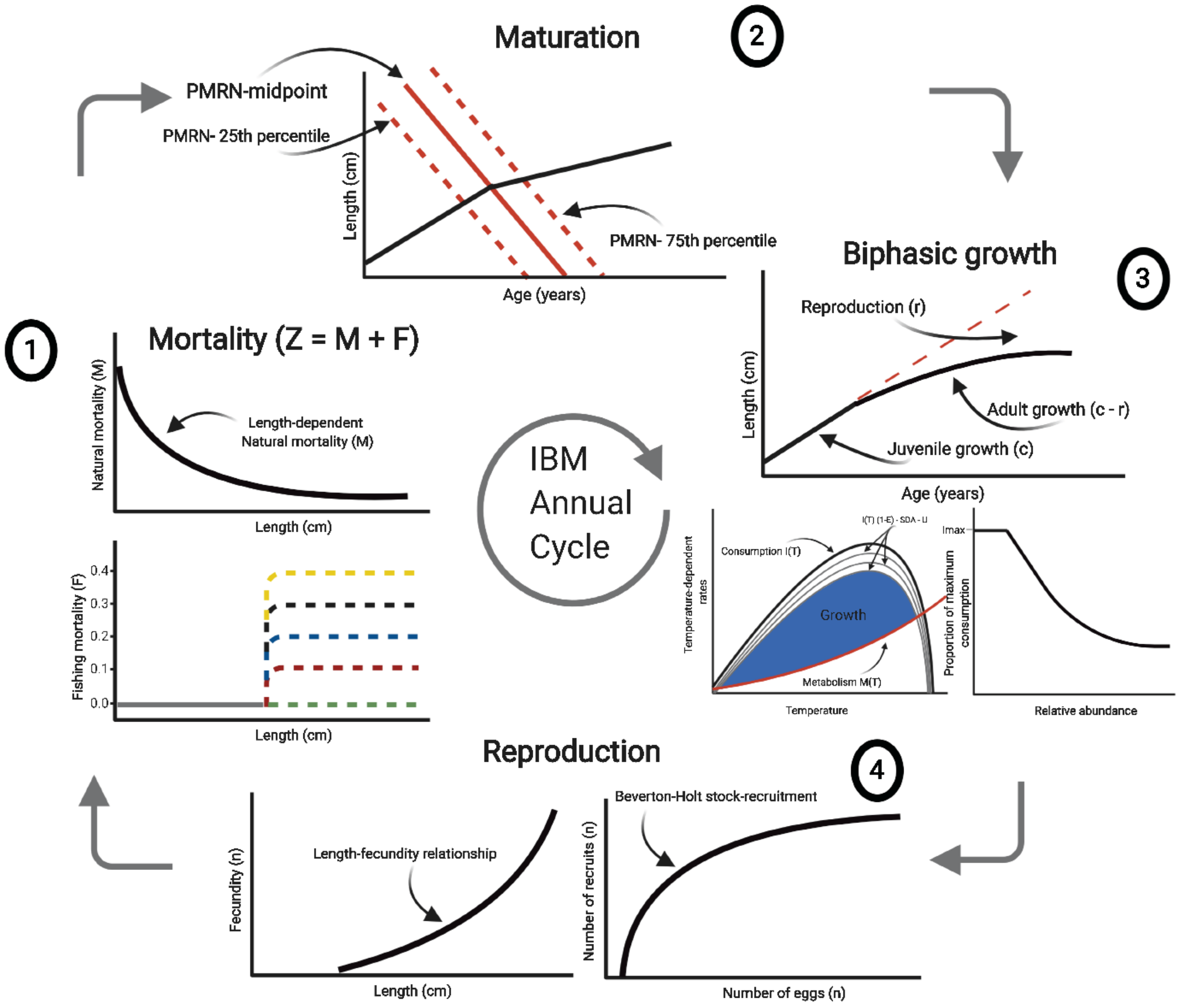


Fig. 2

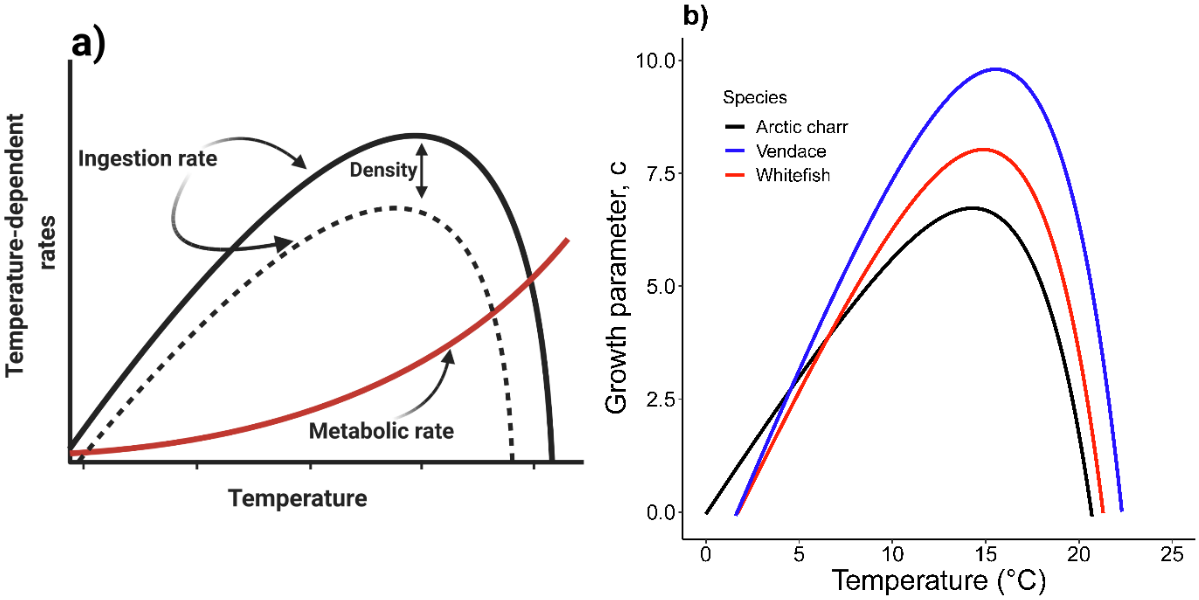

a)
Temperature-dependent rates
Ingestion rate
Density
Metabolic rate
Temperature
b)
Growth parameter, c
10.0
7.5
5.0
2.5
0.0
Species
Arctic charr
Vendace
Whitefish
0
5
10
15
20
25
Temperature (°C)

Fig. 3

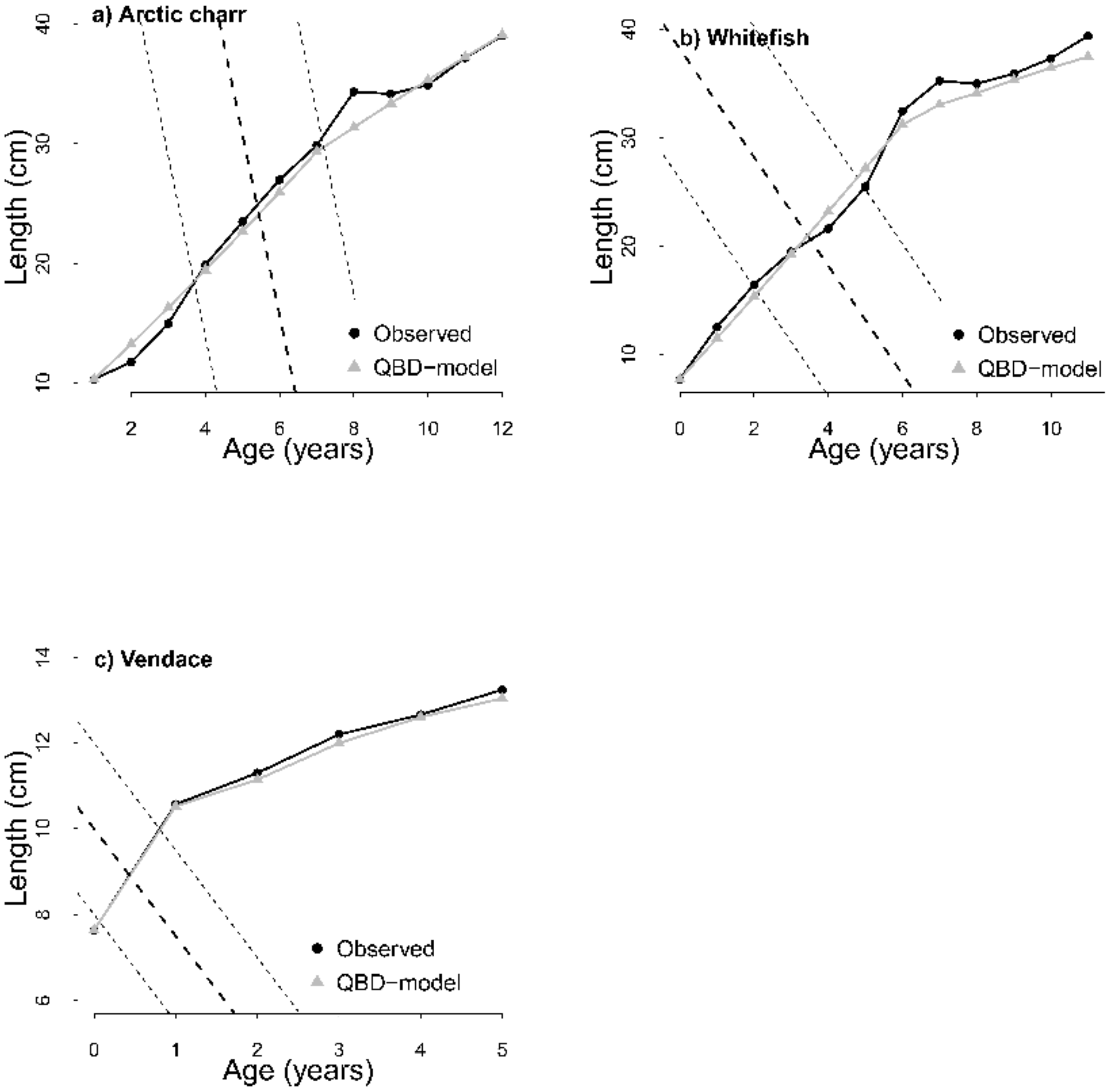

a) Arctic charr
Length (cm)
Age (years)
10
20
30
40
2
4
6
8
10
12
Observed
QBD−model
b) Whitefish
Length (cm)
Age (years)
10
20
30
40
0
2
4
6
8
10
Observed
QBD−model
c) Vendace
Length (cm)
Age (years)
6
8
10
12
14
0
1
2
3
4
5
Observed
QBD−model

Fig. 4

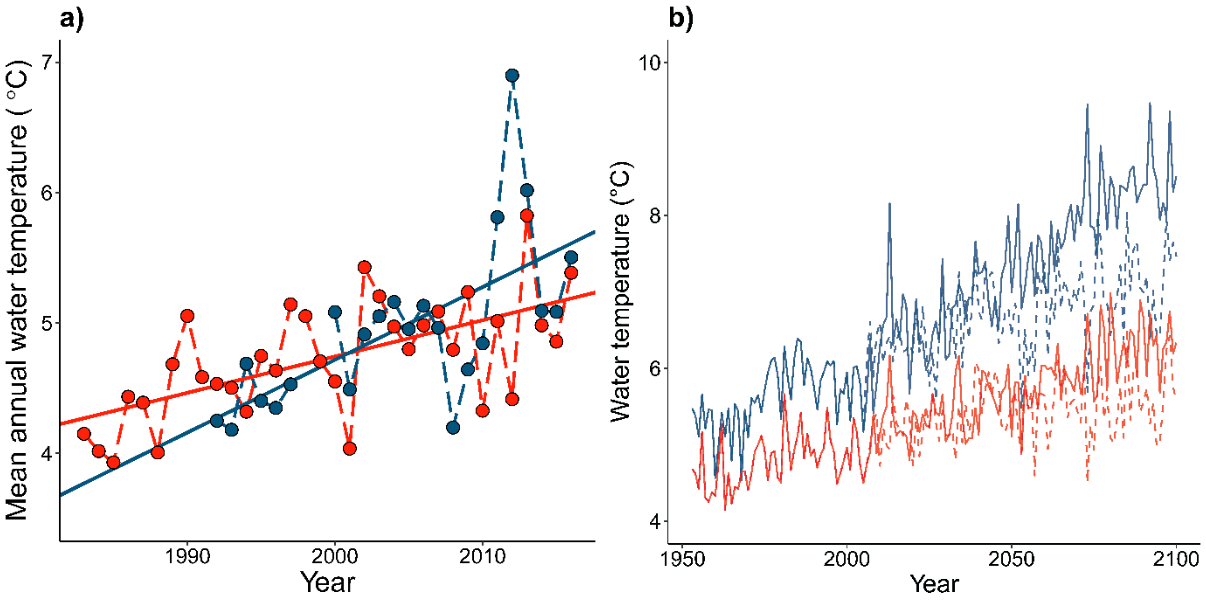

a)
Mean annual water temperature (°C)
7
6
5
4
1990
2000
2010
Year
b)
Water temperature (°C)
10
8
6
4
1950
2000
2050
2100
Year

Fig. 5

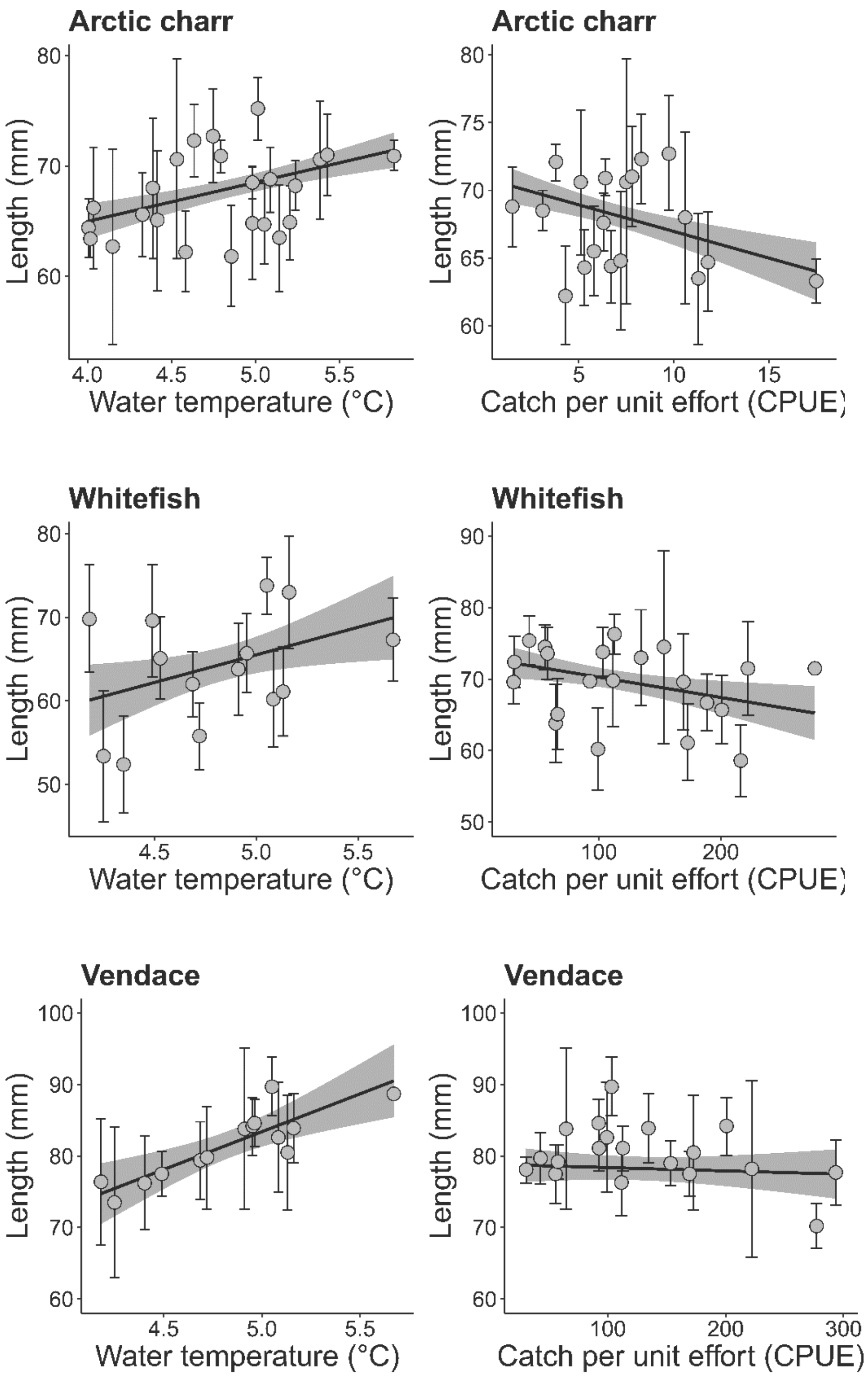

Arctic charr
Length (mm)
80
70
60
4.0
4.5
5.0
5.5
Water temperature (°C)
Arctic charr
Length (mm)
80
75
70
65
60
5
10
15
Catch per unit effort (CPUE)
Whitefish
Length (mm)
80
70
60
50
4.5
5.0
5.5
Water temperature (°C)
Whitefish
Length (mm)
90
80
70
60
50
100
200
Catch per unit effort (CPUE)
Vendace
Length (mm)
100
90
80
70
60
4.5
5.0
5.5
Water temperature (°C)
Vendace
Length (mm)
100
90
80
70
60
100
200
300
Catch per unit effort (CPUE)

Fig. 6

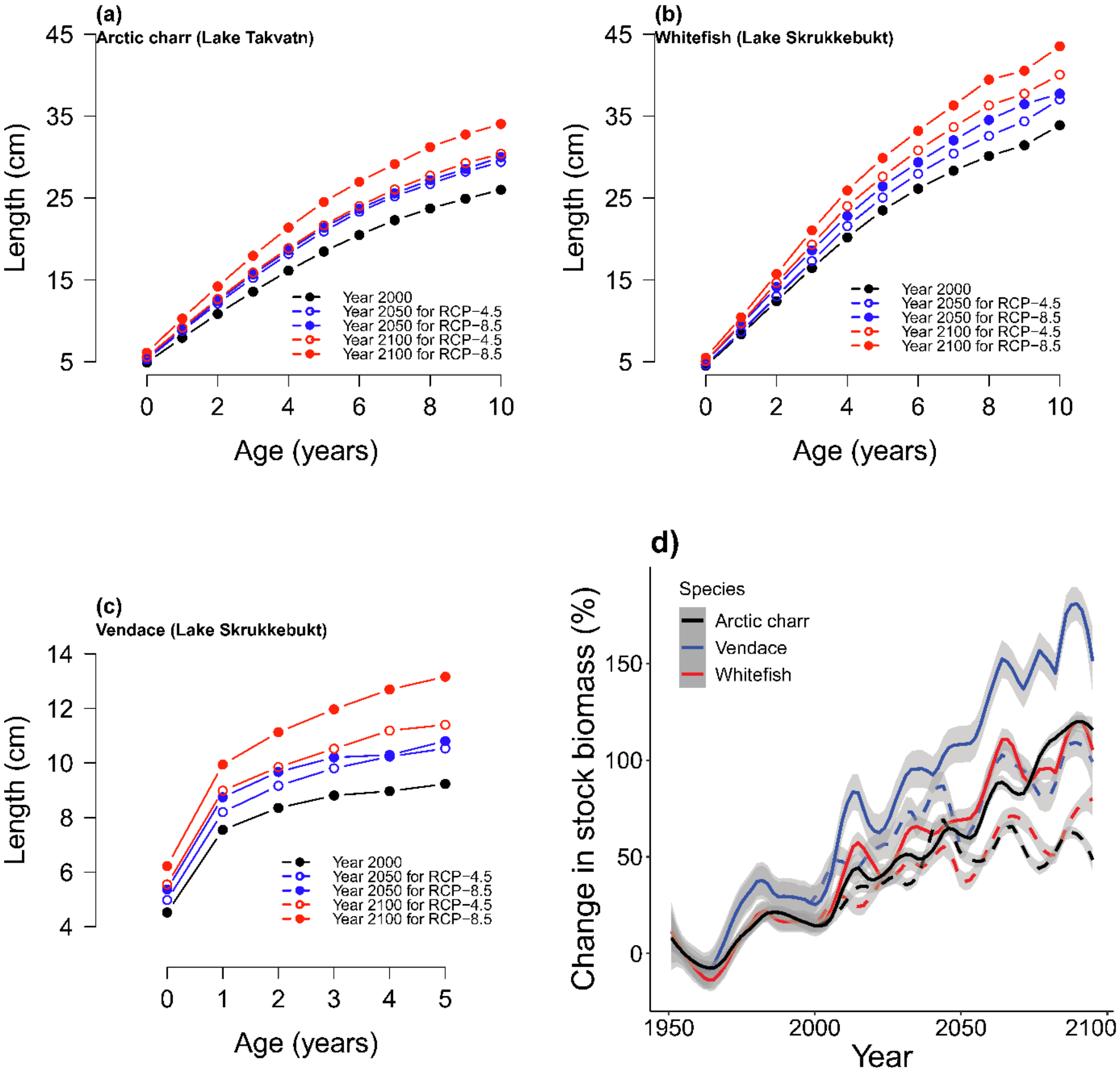
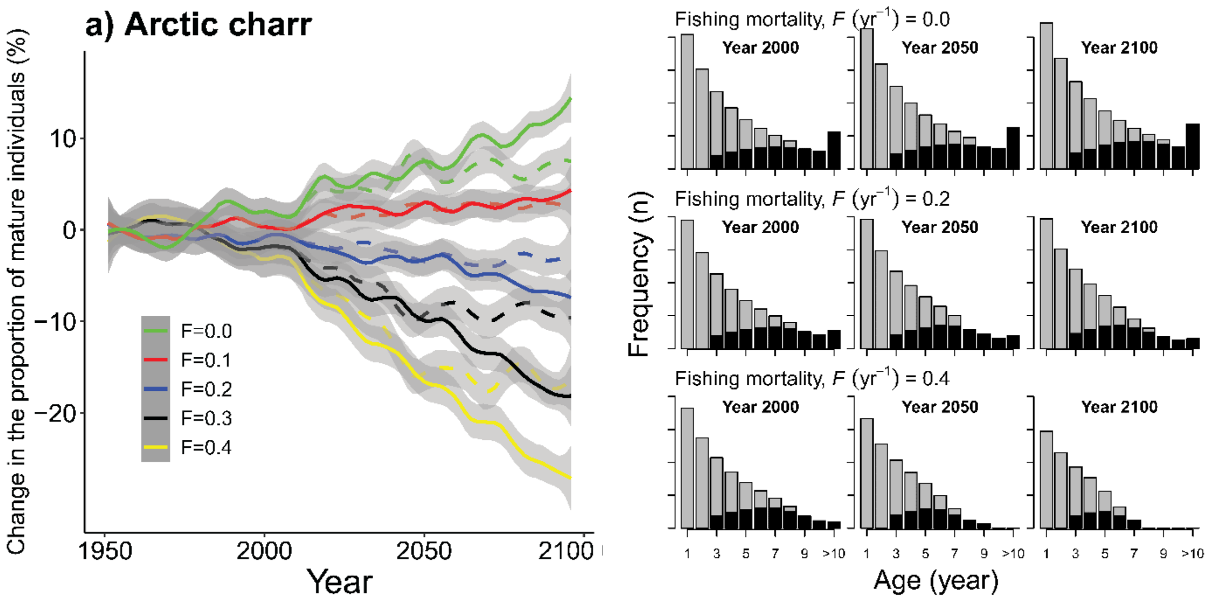
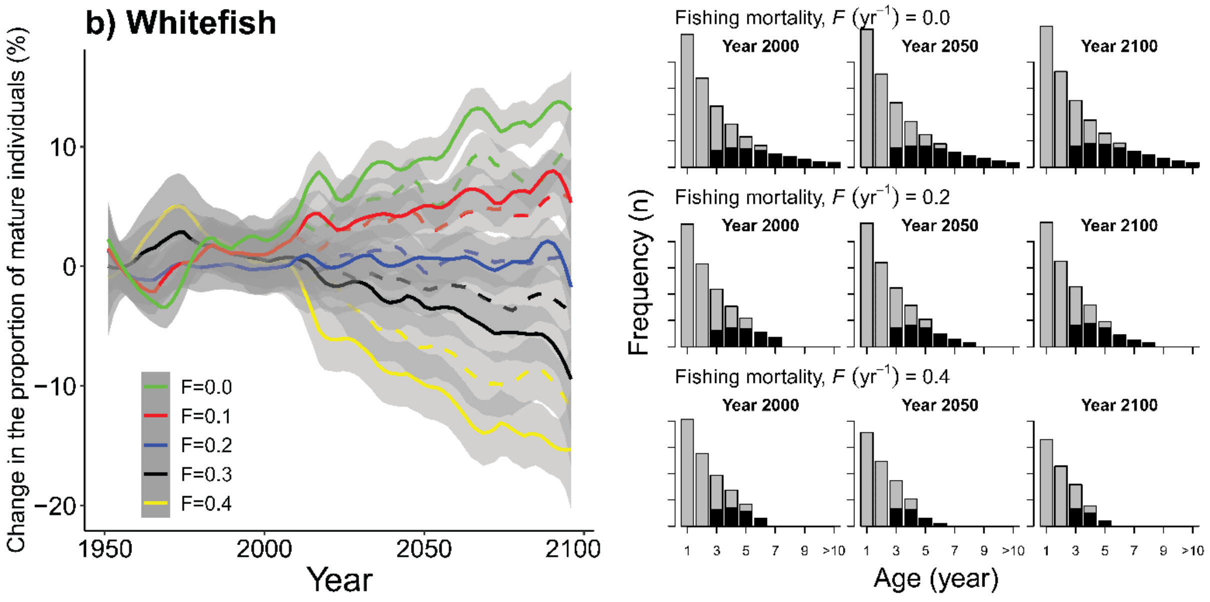
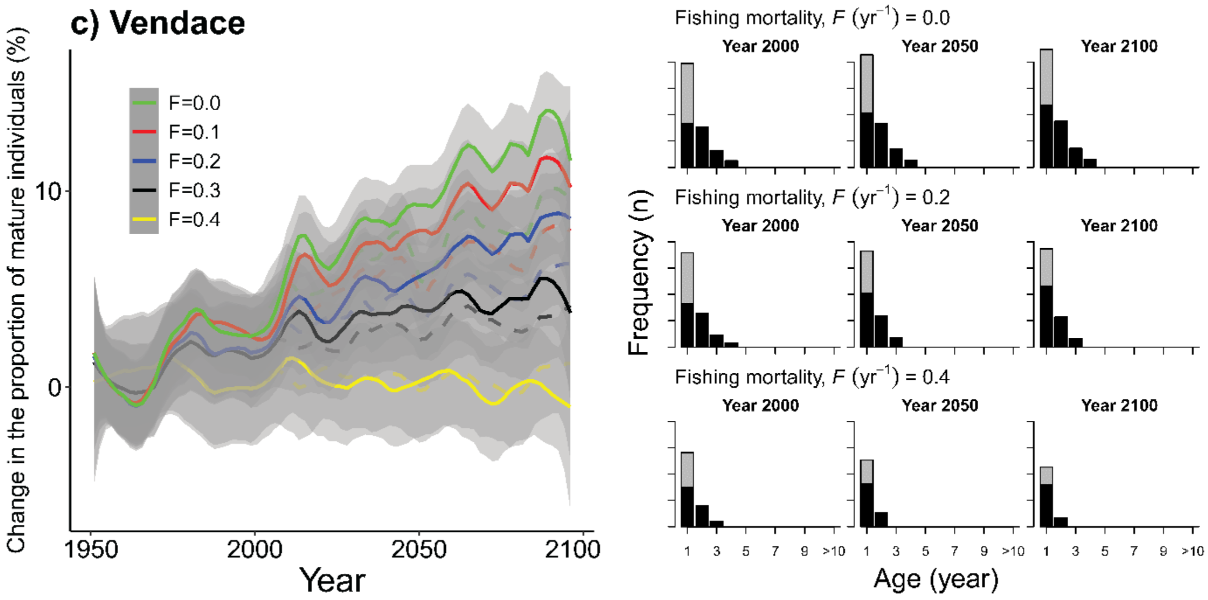

(a)
Arctic charr (Lake Takvatn)
Length (cm)
Age (years)
Year 2000
Year 2050 for RCP−4.5
Year 2050 for RCP−8.5
Year 2100 for RCP−4.5
Year 2100 for RCP−8.5
(b)
Whitefish (Lake Skrukkebukt)
Length (cm)
Age (years)
(c)
Vendace (Lake Skrukkebukt)
Length (cm)
Age (years)
d)
Change in stock biomass (%)
Year
Species
Arctic charr
Vendace
Whitefish

Fig. 7


a) Arctic charr
Change in the proportion of mature individuals (%)
10
0
−10
−20
1950
2000
2050
2100
Year
F=0.0
F=0.1
F=0.2
F=0.3
F=0.4
Fishing mortality, F (yr−1) = 0.0
Fishing mortality, F (yr−1) = 0.2
Fishing mortality, F (yr−1) = 0.4
Year 2000
Year 2050
Year 2100
Frequency (n)
1
3
5
7
9
>10
Age (year)


b) Whitefish
Change in the proportion of mature individuals (%)
10
0
−10
−20
1950
2000
2050
2100
Year
F=0.0
F=0.1
F=0.2
F=0.3
F=0.4
Fishing mortality, F (yr−1) = 0.0
Fishing mortality, F (yr−1) = 0.2
Fishing mortality, F (yr−1) = 0.4
Year 2000
Year 2050
Year 2100
Frequency (n)
1
3
5
7
9
>10
Age (year)


c) Vendace
Change in the proportion of mature individuals (%)
10
0
1950
2000
2050
2100
Year
F=0.0
F=0.1
F=0.2
F=0.3
F=0.4
Fishing mortality, F (yr⁻¹) = 0.0
Year 2000
Year 2050
Year 2100
Fishing mortality, F (yr⁻¹) = 0.2
Year 2000
Year 2050
Year 2100
Fishing mortality, F (yr⁻¹) = 0.4
Year 2000
Year 2050
Year 2100
Frequency (n)
1
3
5
7
9
>10
Age (year)

Supplementary Information

Appendix A: Temperature and density effect on backcalculated length for 1-year-old fish.

Table A1. Summary results of the linear mixed-effect model (LME) for the effects of water-temperature (˚C) and relative density (catch-per-unit-effort, CPUE) (centered and standardized) on 1-year-old vendace (*Coregonus albula*) and whitefish (*Coregonus lavaretus*) from the Pasvik watercourse from 1991 to 2007. The full model includes fish from both Lake Skrukkebukt and Lake Vaggatem, to have enough data that includes both water-temperature and relative density.

	Length (one-year-old)		
Predictors	*Estimates*	*CI*	*p*
Intercept (Vendace)	82.67	77.48 – 87.86	**<0.001**
Annual Mean Water-temperature (WTa) (	1.42	0.18 – 2.66	**0.025**
Whitefish	-9.89	-13.27 – -6.52	**<0.001**
Total Catch Per Unit Effort (Coregonids)	-0.90	-1.70 – -0.10	**0.028**
WTa * Whitefish	-0.64	-2.24 – 0.97	0.436
Random Effects			
N $_{\text{Age}}$	6		
Observations	500		
Marginal R^2 / Conditional R^2	0.192/0.404		

Table A2. Summary results of the linear mixed-effect model (LME) for the effects of water-temperature (˚C) (centered and standardized) on 1-year-old vendace (*Coregonus albula*) and whitefish (*Coregonus lavaretus*) from Lake Skrukkebukta from 1991 to 2007.

	Length (one-year-old)		
Predictors	*Estimates*	*CI*	*p*
Intercept (Vendace)	85.67	79.40 – 91.94	**<0.001**
Annual Mean Water-temperature (WTa)	3.08	1.25 – 4.90	**0.001**
Whitefish	-18.30	-23.64 – -12.97	**<0.001**
WTa * Whitefish	-2.11	-4.50 – 0.27	0.082
N $_{Age}$	6		
Observations	230		
Marginal R^2 / Conditional R^2	0.44/0.57		

Table A3. Summary results of the linear mixed-effect model (LME) for the effects of water-temperature (˚C) on 1-year-old vendace (*Coregonus albula*) and whitefish (*Coregonus lavaretus*) from Lake Skrukkebukta from 1991 to 2007.

	Length (one-year-old)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	44.20	23.66 – 64.73	**<0.001**
Vendace	8.60	4.52 – 12.68	**<0.001**
Whitefish	4.72	0.66 – 8.79	**0.023**
N $_{Age}$	6		
Observations	230		
Marginal R^2 / Conditional R^2	0.45/0.59		

Table A4. Summary results of the linear mixed-effect model (LME) for the effects of relative density (catch-per-unit-effort, CPUE) (centered and standardized) on 1-year-old vendace (*Coregonus albula*) and whitefish (*Coregonus lavaretus*) from Lake Skrukkebukta from 1991 to 2007.

	Length (one-year-old)		
Predictors	*Estimates*	*CI*	*p*
(Intercept) (Vendace)	82.16	77.28 – 87.04	**<0.001**
Whitefish	-9.62	-12.95 – -6.28	**<0.001**
Total Catch Per Unit Effort (Coregonids)	-1.11	-1.89 – -0.32	**0.006**
N $_{Age}$	6		
Observations	500		
Marginal R^2 / Conditional R^2	0.18/0.37		

Table A5. Summary results of the linear mixed-effect model (LME) for the effects of water-temperature (˚C) and relative density (catch-per-unit-effort, CPUE) (centered and standardized) on one-year-old Arctic charr (*Salvelinus alpinus*) from Lake Takvatn from 1986 to 2016.

	Length (one-year-old)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	67.75	66.33 – 69.16	**<0.001**
Annual Mean Water-temperature (WTa)	1.38	0.68 – 2.09	**<0.001**
Catch Per Unit Effort (Arctic charr)	-0.97	-1.69 – -0.25	**0.008**
Random Effects			
N $_{Age}$	6		
Observations	680		
Marginal R^2 / Conditional R^2	0.247 / 0.264		

Table A6. Summary results of the linear mixed-effect model (LME) for the effects of water-temperature (˚C) on one-year-old Arctic charr (*Salvelinus alpinus*) from Lake Takvatn from 1986 to 2016.

	Length (one-year-old)

Predictors	*Estimates*	*CI*	*p*
(Intercept)	51.22	45.42 – 57.02	**<0.001**
Annual Mean Water-temperature (WTa)	3.37	2.22 – 4.52	**<0.001**
Random Effects			
N_{Age}	6		
Observations	680		
Marginal R^2 / Conditional R^2	0.05 / 0.08		

Table A7. Summary results of the linear mixed-effect model (LME) for the effects of relative density (catch-per-unit-effort, CPUE) on one-year-old Arctic charr (*Salvelinus alpinus*) from Lake Takvatn from 1986 to 2016.

	Length (one-year-old)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	70.05	68.21 – 71.90	**<0.001**
Catch Per Unit Effort (Arctic charr)	-0.37	-0.52 – -0.23	**<0.001**
Random Effects			
N_{Age}	6		
Observations	680		
Marginal R^2 / Conditional R^2	0.04 / 0.07		

Appendix B: Individual Based Model description and parameters

Eco-genetic model overview

We used an individual-based model (IBM) relying on the eco-genetic framework developed by Dunlop et al. (2009). The IBM was modified to omit evolutionary effects on life-history traits, retaining only demographic processes. The model runs using successive events for each annual cycle, which includes mortality, maturation, growth, and reproduction (Dunlop et al., 2009). The growth routine in our model uses a temperature-dependent daily length increment to capture climate-related growth effects. The initial population in each simulation was set to 3000 individuals, and 50 replicate model runs for 150 years were used for every simulation.

Mortality

Annual mortality is calculated as

$$Z = M + F, \tag{1a}$$

where Z is total mortality, M is natural mortality, and F is fishing mortality. The natural mortality for many fishes, including salmonids, is assumed to be negatively correlated with their body size (Elliott, 1993; Gislason et al. 2010), following an allometric relation,

$$M = M_{\mathrm{r}}(L/L_{\mathrm{r}})^{-m_{\mathrm{b}}}\,, \tag{1b}$$

where L is the length of fish, M_{r} is the natural mortality at the reference length L_{r}, and m_{b} is the allometric exponent. For whitefish and vendace in the Pasvik watercourse, M_{r} is taken from Sandlund et al. 2013, and for Arctic charr the M_{r} is estimated using the equation given by Pauly (1980) (For details see Smalås et al. 2020). The observed size-distribution of the different populations is used to calibrate L_{r} and m_{b}.

We investigated five fishing-mortality scenarios, representing different levels of harvesting pressures by gillnets (F = 0.1-0.4 yr^{-1}). Gillnet fishing is regulated by mesh-size, which is recommended to be between 26 and 35 mm in Lake Takvatn by the regional management institutions (Statskog, 2017). In the Pasvik watercourse gill-net fishing is not regulated by mesh-size, but fishermen seldom uses nets with mesh-size under 30 mm. For vendace, harvesting with gill-nets in the Pasvik watercourse is rare, however we wanted to investigate effects of fishing since this is common in neighboring areas in Finland, and there vendace under 10 cm is rarely caught. Known mesh-size selectivity were than used to estimate which size-classes were vulnerable under the given regulations and habits used by fishermen to parametrize the length-dependent fishing mortality,

$$F = F_0 + \frac{F_1}{1+\exp(-F_2(L-F_3))} \quad , \tag{1c}$$

where F_0 is the size-independent component, F_1 scales the size-dependent component, F_2 is the steepness of the size-dependent component, L is the length of the fish, and F_3 is the inflection point of the size-dependent component.

Maturation

Age at maturation is assumed to be plastic and depends on a probabilistic maturation reaction norm (PMRN) describing the length- and age-specific probabilities of maturation (Heino et al., 2002; Dieckmann & Heino, 2007). We calculated the PMRN from long-term data on Arctic charr in Lake Takvatn, and whitefish and vendace in Lake Skrukkebukta (Table B1) by the demographic method assuming a linear reaction norm (Barot et al. 2004). We implemented a model that involves both age and size, and assumed that these two variables have independent and linear effects, following Heino et al. (2002),

$$P_{\mathrm{m}} = 1/\left\{1 + \exp\left(- \frac{L-(a+as)}{d}\right)\right\}, \tag{2}$$

where L is the length of fish, i is the PMRN intercept, a is the age of fish, s is the PMRN slope, and d is the PMRN width.

Growth

Biphasic growth model

We used the Quince-Boukal-Dieckmann (QBD) biphasic growth model (Boukal et al. 2014) to describe juvenile and adult growth trajectories,

$$L_{a+1} = \sqrt[(1-\beta)\alpha]{\frac{L_a^{(1-\beta)\alpha}+(1-\beta)cb^{-(1-\beta)}}{1+q^{-1}(1-\beta)\, r_{a+1}}}, \tag{3a}$$

where L_a is the length at age a, β is the allometric exponent relating the rate cW_a^{β} of net energy intake – measured in terms of weight gain – to the weight W_a, c scales this rate, q is the ratio between the energetic costs per unit of weight of producing gonadic versus somatic tissue, r_{a+1} is the ratio between somatic and gonadic weight at the end of the growth season at age $a + 1$, α is the allometric exponent relating the weight $W_a = bL_a^{\alpha}$ to the length L_a, and b scales this weight. For juveniles, all available energy is allocated to growth, i.e., $r_a = 0$. For adults, a fraction of the net energy intake is allocated to reproduction, i.e., $r_a > 0$. We assumed that r_a does not change with age a; therefore, we set $r_a = r$ and use the closed form of the QBD model for adult growth (Boukal et al. 2014). We used empirically derived parameters from the QBD growth model for the different species in combination with the corresponding water-temperature and density experienced by the different populations to scale c_{max} to the optimum temperature for growth for the different species (see below).

The coefficient c was jointly determined by a temperature- and density-dependent consumption rate, scaled by $I(T,D)$, and a temperature-dependent metabolic rate, scaled by $m(T)$, where T and D denote temperature and density, respectively. In other words, the consumption rate depends both on temperature and – indirectly, through the density of competitors – on food availability, while the metabolic rate depends only on temperature. This implies that the optimum temperature for growth is lower when the density of competitors is higher (Huey and Kingsolver 2019). In addition to $m(T)$, three different processes (Deslauriers et al. 2017) diminish c: egestion E is the fraction of the consumed energy that is not ingested and leaves the fish as feces, specific dynamic action SDA is the fraction of W_a^{β} used for processing the food to energy or storage (Jobling 1983), and excretion U is the fraction of W_a^{β} lost as nitrogen waste (Deslauriers et al. 2017). Therefore, c was calculated using the following bioenergetic relationship,

$$c = I(T,D)(1-E) - SDA - U - m(T), \qquad (3b)$$

For eq. 3c-3f (see below), the calculated values are given in kJ day^{-1}, but c in the QBD model have the unit of $g^{1-\beta}$ year^{-1} and we therefore first accumulated the daily energy intake over the 365 days and subsequently used a conversion factor $c = \frac{c}{z}$ to model growth on the correct scale used in QBD growth model framework. To reflect individual variation in energy acquisition, individual values of c were distributed normally around the mean value given by eq. (3b).

The temperature-dependent scaling of the consumption rate follows a Ratkowsky-type growth model (Ratkowsky et al. 1983, Larsson et al. 2005, Finstad et al. 2011), useful to describe consumption rate in salmonid fish,

$$I(T) = d(T - T_{\min})\left(1 - e^{g(T - T_{\max})}\right), \qquad (3c)$$

where T is the experienced water temperature, T_{min} and T_{max} are the minimum and maximum temperatures for ingestion, respectively, and d and g are constants.

The density-dependent scaling of the consumption rate follows a negative power law described by Amundsen et al. (2007); see also Lorenzen & Enberg (2002),

$$I(D) = \delta_1 D/{d_c}^{\delta_2}, \tag{3d}$$

where D is the total density of competitors, d_c is the conversion factor from the catch-per-unit-effort scale used in Amundsen et al. 2007 to density of competitors in the model, and δ_1 and δ_2 are constants. For densities below the minimum density described in Amundsen et al. (2007) (catch-per-unit-effort (CPUE) = 4.8), $I(D)$ was set to a maximum I_{max}, where I_{max}= 3.35 is the maximum consumption rate seen in Amundsen et al. 2007.

To capture the combined effects of temperature and density on the consumption rate, we used the following equation,

$$I(T, D) = I(T)(\frac{I(D)}{I_{\mathrm{max}}}), \tag{3e}$$

where $I(T, D)$ reaches its maximum when the water temperature is optimal and the population density is lower than the minimum density described by Amundsen et al. (2007).

The temperature-dependent scaling of the metabolic rate follows the Arrhenius function (Gillooly et al. 2001, Lindmark et al. 2018),

$$m(T) = m_0 \omega e^{-\frac{E_{\mathrm{m}}(T-t_0)}{kTt_0}}, \tag{3f}$$

where m_0 is the metabolic scaling constant in terms of oxygen consumption, ω is the conversion factor from oxygen consumption to energy consumption, E_{m} is the mean activation energy of biochemical reactions in fish, k is the Boltzmann constant, T is the temperature in terms of the Kelvin scale, and t_0 is the conversion factor from Kelvin scale to Celsius scale.

Field studies of the relationship between water temperature and growth are not available for freshwater salmonids at high latitudes, while corresponding lab experiments have frequently been conducted for the most common high-latitude freshwater fish species. Therefore, we used data from lab experiments to parameterize eq. (3c): specifically, bioenergetic studies have provided estimates of the energies lost to egestion, specific dynamic action, and excretion and of the temperature-dependent metabolic rate (Deslauriers et al. 2017).

Bioenergetic parameterization

Field studies of the relationship between water temperature and growth is limiting for freshwater salmonids at high latitudes, however lab experiment are conducted frequently for the most common high latitude freshwater fish species. Therefore, we used data from laboratory experiments to parameterize the different compartments in our growth routine. Bioenergetic studies have provided parameters for the estimation of temperature-dependent metabolic rate and the proportion of energy intake that is lost to assimilation, excretion and egestion (see Deslauriers et al. 2017).

Arctic charr (*Salvelinus alpinus*)

For Arctic charr temperature-growth relationship are studied extensively in laboratory experiments. Arctic charr exhibit positive growth from 0.3 ˚C to 20-23 ˚C with an optimum between 14-16 ˚C (Jobling 1983b, Brännäs & Wiklund 1992, Larsson & Berglund 1998, Larsson & Berglund 2005, Larsson et al. 2005, Siikavuopio et al. 2010, Siikavuopio et al. 2013, Sæther et al. 2016). To calibrate the parameters used to estimate consumption (eq. 3c), we used existing estimates for temperature-dependent food intake rate (see Larsson & Berglund 2005), and calibrated them to fit the observed growth in Lake Takvatn (see next paragraph) and the above for mentioned temperature-dependent growth relationships (see Fig. 1, original paper).

We ran the QBD-Biphasic model (Boukal et al. 2014) on the existing data from Lake Takvatn, and model results show that using data from 2006-2018 where the average annual water temperature was 4.4 ˚C, and with an average Catch-Per-Unit-Effort of 4.8 giving 89% of the maximum temperature-dependent growth curve in Amundsen et al. (2007). The estimated net energy intake rate from the data, $c = 2.55 \pm 0.08$ (95% CI) and $r = 0.158 \pm 0.031$ (See Fig. 2a in the original paper for comparison of observed length-at-age and the QBD-modelled length-at-age). The estimated values from the individual based model using the above for mentioned parameter values gave a $c = 2.51$, with $r = 0.15$ which is well within the confidence interval of the observed values for the population.

Whitefish (*Coregonus lavaretus*)

For whitefish temperature-growth relationship under laboratory experiments are well documented. Whitefish, in laboratory settings, grow from 1-3 ˚C to 21-23 ˚C with an optimum between 15-16 ˚C (Tolonen 1998, Siikavuopio et al. 2010, Siikavuopio et al. 2012). To calibrate the parameters used to estimate consumption (eq. 3c), we used existing estimates for temperature-dependent food intake rate, and calibrated them to fit the observed growth in the Pasvik watercourse (see next paragraph) and the above for mentioned temperature-dependent growth relationships (see Fig. 1, original paper).

We ran the QBD-Biphasic model (Boukal et al. 2014) on the existing data from Lake Skrukkebukta, and model results show that using data from 2007-2009 where the average annual water temperature was 5.2 ˚C, and with an average Catch-Per-Unit-Effort of 63.8 assuming 85 % of the maximum temperature-dependent growth curve. The estimated net energy intake rate from the data, c = 2.25 ± 0.13 (95% CI) and r = 0.266 ± 0.05 (see Fig. 2b in the original paper for comparison of observed length-at-age and the QBD-modelled length-at-age). The estimated values from the individual based model using the above for mentioned parameter values gave a c = 2.36, with r = 0.27 which is within the confidence interval of the observed values for the population.

Vendace (*Coregonus albula*)

For vendace temperature-growth relationship are to a lesser extent studied in laboratory experiments compared to both Arctic charr and whitefish, but some information exists. Vendace show positive growth from 1-3 ˚C to 22-24 ˚C with an optimum between 15-17 ˚C (Helminen et al. 1990, Luczynski 1991). To calibrate the parameters used to estimate consumption (eq. 3c), we used existing estimates for temperature-dependent food intake rate, and calibrated them to fit the observed growth in the Pasvik watercourse (see next paragraph) and the above for mentioned temperature-dependent growth relationships (see Fig. 1, original paper).

We ran the QBD-Biphasic model (Boukal et al. 2014) on the existing data from Lake Skrukkebukta in Pasvik, and model results show that using data from 2007-2009 where the average annual water temperature was 5.2 ˚C, and with an average Catch-Per-Unit-Effort of 63.2 assuming 85 % of the maximum temperature-dependent growth curve. The estimated net energy intake rate from the data, c = 2.87 ± 0.22 (95% CI) and r = 1.04 ± 0.096 (95% CI) (see Fig. 2c in the original paper for comparison of observed length-at-age and the QBD-modelled length-at-age). The estimated values from the individual based model using the above for mentioned parameter values gave a c = 2.86, with r = 1.04 which is well within the confidence interval of observed values for the population.

Recruitment and reproduction

Annual recruitment is dependent on the size of the spawning stock, as well as on the fecundity of adult fish and the density-dependent mortality of eggs and hatchlings (Haddon, 2001). The latter density dependence is assumed to follow a Beverton-Holt stock-recruitment relationship,

$$R_{\mathrm{t}} = \frac{R_{\max} f_{\mathrm{t}}}{f_{\mathrm{t}} + \vartheta}, \tag{4a}$$

where R_{t} is the total number of surviving offspring or recruits to the population in year t, f_{t} is the total fecundity of the mature female population in year t, $R_{\max}$ is the maximal number of surviving offspring or recruits, and ϑ defines the strength of the density-dependent recruitment mortality. The Beverton-Holt stock-recruitment model predicts an asymptotic relationship between total population fecundity and number of surviving recruits. The fecundity F_{c} of adult females is described by an allometric function estimated from the fecundity-length relationship,

$$F_{\mathrm{c}} = a_f \, L^{b_f}, \tag{4b}$$

where L is the length of fish, and a_f and b_f are constants.

Limitations and caveats of model assumptions

The model description above is limited by simplifying assumptions regarding mechanisms and processes. Realistic models of intermediate complexity are suggested to enhance ecological understanding, and are thereby considered advisable (Van Nes & Scheffer, 2005). In our modelling effort, the main focus is temperature-dependent growth, therefore we assume that temperature do not affect other processes like mortality and reproduction directly. Also, in order to investigate these populations we ignore interspecific interactions, but we include them indirectly since parameters are from systems were these populations interact with other fish species. In addition, we ignore evolutionary processes and thus some of the effects presented here might be compensated for through evolution.

References

Amundsen, P. A., Knudsen, R., & Klemetsen, A. (2007). Intraspecific competition and density dependence of food consumption and growth in Arctic charr. *Journal of Animal Ecology*, *76*, 149–158. https://doi.org/10.1111/j.1365-2656.2006.01179.x

Barot, S., Heino, M., O`Brien, L., & Dieckmann, U. (2004). Estimating reaction norms for age and size at maturation when age at first reproduction is unknown. Evolutionary Ecology Research, 6, 659–678.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. Ecology, 85, 1771–1789. https://doi.org/Doi 10.1890/03-9000

Brännäs, E., & Wiklund, B. (1992). Low temperature growth potential of Arctic charr and rainbow trout. *Nordic Journal of Freshwater Research*, *67*, 77–81. https://gupea.ub.gu.se/bitstream/2077/48954/1/gupea_2077_48954_1.pdf#page=80

Deslauriers, D., S.R. Chipps, J.E. Breck, J.A. Rice and C.P. Madenjian. 2017. Fish Bioenergetics 4.0: An R-based modeling application. Fisheries 42: 586-596

Dieckmann, U., & Heino, M. (2007). Probabilistic maturation reaction norms: their history, strengths, and limitations. Marine Ecology Progress Series, 335, 253–269. https://doi.org/DOI 10.3354/meps335253

Dunlop, E. S., Heino, M., & Dieckmann, U. (2009). Eco-genetic modeling of contemporary life-history evolution. Ecological Applications, 19, 1815–1834. https://doi.org/Doi 10.1890/08-1404.1

Finstad, A. G., Forseth, T., Jonsson, B., Bellier, E., Hesthagen, T., Jensen, A. J., Hessen, D. O., & Foldvik, A. (2011). Competitive exclusion along climate gradients: energy efficiency influences the distribution of two salmonid fishes. Global Change Biology, 17, 1703–1711. https://doi.org/10.1111/j.1365-2486.2010.02335.x

Gislason, H., Daan, N., Rice, J. C., & Pope, J. G. (2010). Size, growth, temperature and the natural mortality of marine fish. Fish and Fisheries, 11, 149–158. https://doi.org/10.1111/j.1467-2979.2009.00350.x

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science*, *293*, 2248–2251. https://doi.org/10.1126/science.1061967

Haddon, M. (2001). Modelling and quantitative methods in fisheries. Chapman & Hall/CRC.

Heino, M., Dieckmann, U., & Godo, O. R. (2002). Measuring probabilistic reaction norms for age and size at maturation. Evolution, 56, 669–678. https://doi.org/DOI 10.1111/j.0014-3820.2002.tb01378.x

Helminen, H., Sarvala, J., & Hirvonen, A. (1990). Growth and food consumption of vendace (Coregonus albula (L.)) in Lake Pyhäjärvi, SW Finland: a bioenergetics modeling analysis. Hydrobiologia, 200–201, 511–522. https://doi.org/10.1007/BF02530368

Huey, R. B., & Kingsolver, J. G. (2019). Climate warming, resource availability, and the metabolic meltdown of ectotherms. American Naturalist. https://doi.org/10.1086/705679

Jobling, M. (1983a). Towards an explanation of specific dynamic action (SDA). Journal of Fish Biology, 23, 549–555. https://doi.org/10.1111/j.1095-8649.1983.tb02934.x

Jobling, M. (1983b). Influence of Body-Weight and Temperature on Growth-Rates of Arctic Charr, Salvelinus-Alpinus (L). *Journal of Fish Biology*, *22*, 471–475. https://doi.org/Doi 10.1111/J.1095-8649.1983.Tb04767.X

Larsson, S., Forseth, T., Berglund, I., Jensen, A. J., Naslund, I., Elliott, J. M., & Jonsson, B. (2005). Thermal adaptation of Arctic charr: experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. Freshwater Biology, 50, 353–368.

Larsson, S., & Berglund, I. (1998). Growth and food consumption of 0+ Arctic charr fed pelleted or natural food at six different temperatures. Journal of Fish Biology, 52, 230–242.

Larsson, S., & Berglund, I. (2005). The effect of temperature on the energetic growth efficiency of Arctic charr (Salvelinus alpinus L.) from four Swedish populations. Journal of Thermal Biology, 30, 29–36. https://doi.org/10.1016/j.jtherbio.2004.06.001

Lorenzen, K., & Enberg, K. (2002). Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proceedings of the Royal Society B-Biological Sciences, 269, 49–54. https://doi.org/10.1098/rspb.2001.1853

Luczynski, M. (1991). Temperature requirements for growth and survival of larval vendace, Coregonus albula (L.). Journal of Fish Biology, 38, 29–35. https://doi.org/10.1111/j.1095-8649.1991.tb03088.x

Pauly, D. (1980). On the Interrelationships between Natural Mortality, Growth-Parameters, and Mean Environmental-Temperature in 175 Fish Stocks. Journal Du Conseil, 39, 175–192.

Ratkowsky, D. A., Lowry, R. K., McMeekin, T. A., Stokes, A. N., & Chandler, R. E. (1983). Model for bacterial culture growth rate throughout the entire biokinetic temperature range. Journal of Bacteriology. https://doi.org/10.1128/jb.154.3.1222-1226. 1983

Saether, B. S., Siikavuopio, S. I., & Jobling, M. (2016). Environmental conditions required for intensive farming of Arctic charr (Salvelinus alpinus (L.)). Hydrobiologia, 783, 347–359. https://doi.org/10.1007/s10750-015-2572-y

Sandlund, O. T., Gjelland, K. O., Bohn, T., Knudsen, R., & Amundsen, P. A. (2013). Contrasting Population and Life History Responses of a Young Morph-Pair of European Whitefish to the Invasion of a Specialised Coregonid Competitor, Vendace. Plos One, 8. https://doi.org/ARTN e68156 10.1371/journal.pone.0068156

Siikavuopio, S. I., Foss, A., Saether, B. S., Gunnarsson, S., & Imsland, A. K. (2013). Comparison of the growth performance of offspring from cultured versus wild populations of arctic charr, Salvelinus alpinus (L.), kept at three different temperatures. Aquaculture Research, 44, 995–1001. https://doi.org/10.1111/j.1365-2109.2012.03112.x

Siikavuopio, S. I., Knudsen, R., & Amundsen, P. A. (2010). Growth and mortality of Arctic charr and European whitefish reared at low temperatures. Hydrobiologia, 650, 255–263. https://doi.org/10.1007/s10750-010-0192-0

Siikavuopio, S. I., Knudsen, R., Amundsen, P. A., Saether, B. S., & James, P. (2012). Effects of high temperature on the growth of European whitefish (Coregonus lavaretus L.). Aquaculture Research, 44, 8–12. https://doi.org/10.1111/j.1365-2109.2011.02999.x

Smalås, A., Strøm, J. F., Amundsen, P., Dieckmann, U., & Primicerio, R. (2020). Climate warming is predicted to enhance the negative effects of harvesting on high-latitude lake fish. *Journal of Applied Ecology*, *57*, 270–282. https://doi.org/10.1111/1365-2664.13535

Statskog. (2017). Fiskeregler for Troms (in Norwegian). https ://statskog. s3.amazo naws.com/pdf_word/fiske/ Fiske regler_Troms.pdf?mtime =20181 21413 2321

Tolonen, A. (1998). Application of a bioenergetics model for analysis of growth and food consumption of subarctic whitefish Coregonus lavaretus (L.) in Lake Kilpisjarvi, Finnish Lapland. *Hydrobiologia*, *390*, 153–169. https://doi.org/10.1023/A:1003525008870

Van Nes, E. H., & Scheffer, M. (2005). A strategy to improve the contribution of complex simulation models to ecological theory. *Ecological Modelling*, *185*, 153–164. https://doi.org/10.1016/j.ecolmodel.2004.12.001

Table B1. Model parameters, equation number and symbol in equation and reference to source of parameter value for Arctic charr, whitefish and vendace.

Description	*Symbol*	*Equation*	*Arctic charr*	*Source Arctic charr*	*Whitefish*	*Source Whitefish*	*Vendace*	*Source Vendace*	*Unit*
Mean initial size	t_0	-	1.664	1	0.978	5	0.77	5	cm
Variance initial size	t_0 σ^2	-	0.047	1	0.15	5	0.07	5	cm
Start population	-	-	3000	-	3000	-	3000	-	n
Simulation length	-	-	100+150	-	100+150	-	100+150	-	yr
Maximum number of recruits	R_{max}	4a	800	-	1000	-	3000	-	n
Beverton-Holt parameter	ϑ	4a	0.2	-	0.1	-	0.1	-	-
Allometric scaling exponent in the growth rate-weight relationship	β	3a	0.748	4	0.712	4^*	0.712	4	-
Conversion factor between gonadic and somatic investment	q	3a	1	-	1	-	1	-	-
Relative reproductive investment	r	3a	0.18	1	0.27	2	1.23	3	-
Length-weight relationship coefficient	α	3a	0.00372	1	0.0054	2	0.0051	3	g cm^{-b}
Length-weight relationship exponent	b	3a	3.3288	1	3.1281	2	3.2092	3	-
Maximum value for the allometric scaling coefficient in the growth rate-weight relationship	c_{max}	-	6.72	1 (10)	8.02	2	9.8	3	$g^{1-\beta}$ yr^{-1}
Conversion factor between kJ and $g^{1-\beta}$	z	-	50	-	50	-	50	-	-
Ratkowsky model constant	d	3c	0.14	1 (9,10)	0.2	2	0.2	3	-
Ratkowsky model constant	g	3c	0.23	1 (9,10)	0.21	2	0.23	3	-
Minimum temp for ingestion	T_{min}	3c	-0.3	1 (9,10)	1	2	1	3	˚C
Maximum temp for ingestion	T_{max}	3c	21	1 (9,10)	22	2	23	3	˚C
Minimum temp for growth	G_{min}	-	0.3	6,7	1.9	7	1.8	24	˚C
Maximum temp for growth	G_{max}	-	20.6	8-10	21.3	26,27	22.4	25	˚C
Optimum temp for ingestion	T_{opt}	-	14.1	11-13	15	27	15.6	24,25	˚C
Metabolic scaling constant	m_0	3f	0.0024	14	0.00584	21	0.006235	23	O_2 g^{-1} d^{-1}
Activation energy	E_m	3f	6.57E-17	15	6.57E-17	15	6.57E-17	15	kJ
Conversion factor, O_2 to kJ	ω	3f	13.56	17^*	13.56	17^*	13.56	17^*	J g^{-1} O_2
Boltzmann's constant	k	3f	1.18E-20	15,16	1.18E-20	15,16	1.18E-20	15,16	kJ K^{-1}
Kelvin factor	t_0	3f	273.15	15	273.15	15	273.15	15	K
Egestion	E	3b	21	17^*,18	19	21,18	19	23,18	%
Excretion	U	3b	3.14	17^*,18	7	21,18	7	23,18	%
Specific Dynamic Action (SDA)	SDA	3b	17	17^*,18	17	21,18	17	23,18	%
Density-dependent growth coefficient	δ_1	3d	7.23	19	7.23	19^*	7.23	19^*	-
Density-dependent growth exponent	δ_2	3d	-0.556	19	-0.556	19^*	-0.556	19^*	-
Conversion factor between CPUE and density of competitors in the model	d_c	3d	200	-	200	-	200	-	-
Allometric fecundity coefficient	a_f	4b	4×10^{-5}	1	4×10^{-5}	1^*	4×10^{-5}	1^*	-
Allometric fecundity exponent	b_f	4b	2.9425	1	2.9425	1^*	2.9425	1^*	-
PMRN Intercept	i_p	2a	106.25	1	38.2	2	10	3	cm
PMRN Intercept (SD)	i_{pSD}	2a	5.3125	1	1.91	2	0.5	3	cm
PMRN Slope	s_p	2a	-15.083	1	-5	2	-5	3	cm yr^{-1}
PMRN Width	d	2a	31.98	1	12	2	2	3	cm
Natural mortality for L_r	M_r	1b	0.17	1	0.3	22	0.6	22	yr^{-1}
Reference length in natural mortality	L_r	1b	20	1	15	2	-	22,3	cm
Allometric exponent in natural mortality	m_{b}	1b	0.2	1	0.1	2	0	22,3	-
Size-independent component of fishing mortality (F)	F_0	1c	0	20	0	20	0	20	yr^{-1}
Size-dependent component of F	F_1	1c	0.0-0.5, step 0.1	20	0.0-0.5, step 0.1	20	0.0-0.5, step 0.1	20	yr^{-1}
Steepness of size-dependent component of F	F_2	1c	1	20	1	20	1	20	
Inflection point of size-dependent component of F	F_3	1c	25	20	25	14	10	14	cm

Source: 1) Estimated from the Arctic charr population in Lake Takvatn. 2) Estimated from the whitefish population in the Pasvik watercourse. 3) Estimated from the vendace population in the Pasvik watercourse. 4) Killen et al. 2010 (Supplementary information) Used vendace parameter value for whitefish. 5) Urpanen et al. 2005. 6) Brännäs & Wiklund 1992. 7) Siikavuopio et al. 2010. 8) Larsson & Berglund 1998. 9) Larsson & Berglund 2005. 10) Larsson et al. 2005.11) Jobling 1983. 12) Siikavuopio et al. 2013. 13) Sæther et al. 2016. 14) FEFO, 2019. 15) Gillooly et al. 2001. 16) Brown et al. 2004. 17) Stewart et al. 1983 (Estimated using Lake trout data). 18) Deslauriers et al. 2017 (Fish Bioenergetics 4.0). 19) Amundsen et al. 2007 (Used Arctic charr values for both whitefish and vendace. 20) Statskog 2017 (see Smalås et al. 2020). 21) Huuskonen et al. 1998. 22) Sandlund et al. 2013. 23) Karjalainen et al. 1997. 24) Helminen et al. 1990. 25) Luczynski 1991. 26) Siikavuopio et al. 2012. 27) Tolonen 1998.

References:

4) Killen, S. S., Atkinson, D., & Glazier, D. S. (2010). The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. *Ecology Letters, 13*, 184–193.

5) Urpanen, O., Huuskonen, H., Marjomaki, T. J., & Karjalainen, J. (2005). Growth and size-selective mortality of vendace (Coregonus albula (L.)) and whitefish (C. lavaretus L.) larvae. *Boreal Environment Research*, *10*, 225–238.

6) Brännäs, E., & Wiklund, B. (1992). Low temperature growth potential of Arctic charr and rainbow trout. *Nordic Journal of Freshwater Research, 67*, 77–81. https://gupea.ub.gu.se/bitstream/2077/48954/1/gupea_2077_48954_1.pdf#page=80

7) Siikavuopio, S. I., Knudsen, R., & Amundsen, P. A. (2010). Growth and mortality of Arctic charr and European whitefish reared at low temperatures. *Hydrobiologia, 650,* 255–263. https://doi.org/10.1007/s10750-010-0192-0

8) Larsson, S., & Berglund, I. (1998). Growth and food consumption of 0+ Arctic charr fed pelleted or natural food at six different temperatures. *Journal of Fish Biology, 52,* 230–242.

9) Larsson, S., & Berglund, I. (2005). The effect of temperature on the energetic growth efficiency of Arctic charr (Salvelinus alpinus L.) from four Swedish populations. *Journal of Thermal Biology, 30,* 29–36. https://doi.org/10.1016/j.jtherbio.2004.06.001

10) Larsson, S., Forseth, T., Berglund, I., Jensen, A. J., Naslund, I., Elliott, J. M., & Jonsson, B. (2005). Thermal adaptation of Arctic charr: experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. *Freshwater Biology, 50,* 353–368.

11) Jobling, M. (1983). Influence of Body-Weight and Temperature on Growth-Rates of Arctic Charr, Salvelinus-Alpinus (L). *Journal of Fish Biology, 22,* 471–475. https://doi.org/Doi 10.1111/J.1095-8649.1983.Tb04767.X

12) Siikavuopio, S. I., Foss, A., Saether, B. S., Gunnarsson, S., & Imsland, A. K. (2013). Comparison of the growth performance of offspring from cultured versus wild populations of arctic charr, Salvelinus alpinus (L.), kept at three different temperatures. *Aquaculture Research, 44,* 995–1001. https://doi.org/10.1111/j.1365-2109.2012.03112.x

13) Saether, B. S., Siikavuopio, S. I., & Jobling, M. (2016). Environmental conditions required for intensive farming of Arctic charr (Salvelinus alpinus (L.)). *Hydrobiologia, 783,* 347–359. https://doi.org/10.1007/s10750-015-2572-y

14) FEFO. (2019). https://www.fefo.no/fiske/innlandsfiske/

15) Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science, 293*, 2248–2251. https://doi.org/10.1126/science.1061967

16) Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology, 85*, 1771–1789. https://doi.org/Doi 10.1890/03-9000

17) Stewart, D. J., Weininger, D., Rottiers, D. V, & Edsall, T. A. (1983). An Energetics Model for Lake Trout, Salvelinus namaycush: Application to the Lake Michigan Population. *Article in Canadian Journal of Fisheries and Aquatic Sciences*, *40*, 681–698. https://doi.org/10.1139/f83-091

18) Deslauriers, D., S.R. Chipps, J.E. Breck, J.A. Rice and C.P. Madenjian. (2017). Fish Bioenergetics 4.0: An R-based modeling application. *Fisheries, 42,* 586-596.

19) Amundsen, P. A., Knudsen, R., & Klemetsen, A. (2007). Intraspecific competition and density dependence of food consumption and growth in Arctic charr. Journal of Animal *Ecology, 76,* 149–158. https://doi.org/10.1111/j.1365-2656.2006.01179.x

20) Statskog. (2017). Fiskeregler for Troms (in Norwegian).

21) Huuskonen, H., Karjalainen, J., Medgyesy, N., & Wieser, W. (1998). Energy allocation in larval and juvenile Coregonus lavaretus: validation of a bioenergetics model. *Journal of Fish Biology, 52*, 962–972. https://doi.org/10.1111/j.1095-8649.1998.tb00596.x

22) Sandlund, O. T., Gjelland, K. O., Bohn, T., Knudsen, R., & Amundsen, P. A. (2013). Contrasting Population and Life History Responses of a Young Morph-Pair of European

Whitefish to the Invasion of a Specialised Coregonid Competitor, Vendace. *Plos One, 8*. https://doi.org/ARTN e68156 10.1371/journal.pone.0068156

23) Karjalainen, J., Ylonen, O., & Huuskonen, H. (2003). Additive budgeting of metabolic costs in larval coregonids. *Proceedings of the 26th Annual Larval Fish Conference*.

24) Helminen, H., Sarvala, J., & Hirvonen, A. (1990). Growth and food consumption of vendace (Coregonus albula (L.)) in Lake Pyhäjärvi, SW Finland: a bioenergetics modeling analysis. *Hydrobiologia, 200–201*, 511–522. https://doi.org/10.1007/BF02530368

25) Luczynski, M. (1991). Temperature requirements for growth and survival of larval vendace, Coregonus albula (L.). *Journal of Fish Biology, 38*, 29–35. https://doi.org/10.1111/j.1095-8649.1991.tb03088.x

26) Siikavuopio, S. I., Knudsen, R., Amundsen, P. A., Saether, B. S., & James, P. (2012). Effects of high temperature on the growth of European whitefish (Coregonus lavaretus L.). *Aquaculture Research, 44*, 8–12. https://doi.org/10.1111/j.1365-2109.2011.02999.x

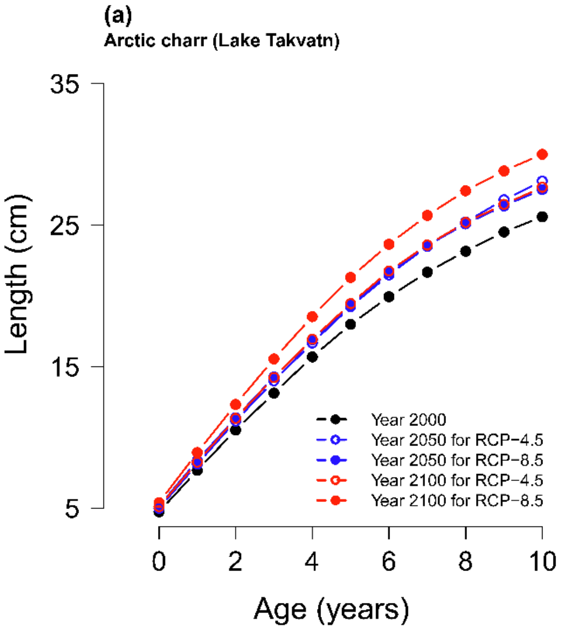
27) Tolonen, A. (1998). Application of a bioenergetics model for analysis of growth and food consumption of subarctic whitefish Coregonus lavaretus (L.) in Lake Kilpisjarvi, Finnish Lapland. *Hydrobiologia, 390*, 153–169.

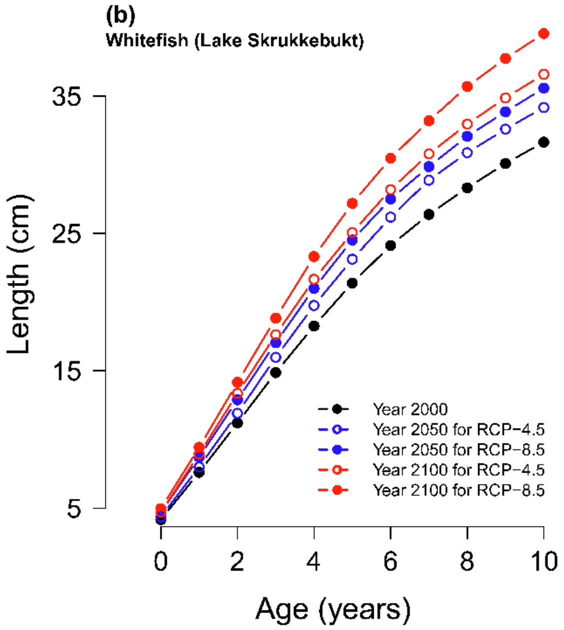
https://doi.org/10.1023/A:1003525008870

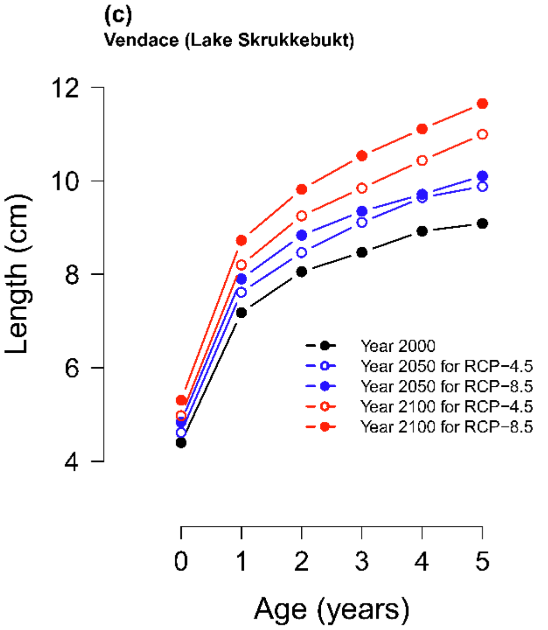
Appendix C: Individual based model results

Length at age and stock biomass development with warming under two climate scenarios (RCP-4.5 & RCP-8.5) and five fishing mortality scenarios (*F*= 0.0-0.4 yr^{-1}).

F = 0.0 yr^{-1}







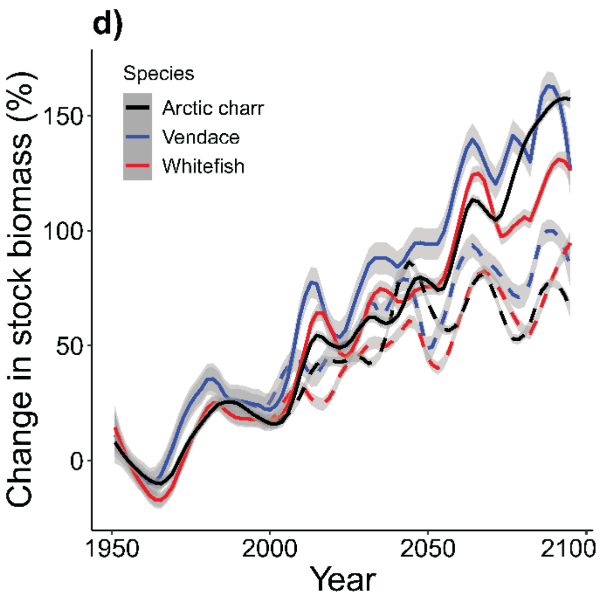


Figure C1. Individual based model predictions of length-at-age for a) Arctic charr in Takvatn, and b) whitefish and c) vendace in Skrukkebukta under two RCP (-4.5 & -8.5) climate scenarios for fishing mortality, F= 0.0 yr^{-1}. d) Model predictions of percentage change in stock biomass for Arctic charr (—) in Takvatn, whitefish (—) and vendace (—) in Skrukkebukta under the RCP-4.5 (dashed line) and RCP-8.5 (solid line) climate scenarios from year 1950 to year 2100 for fishing mortality, F= 0.0 yr^{-1}.

Table C1. Change in length-at-age for Arctic charr in Takvatn from year 2000 to year 2100 under RCP-4.5 and RCP-8.5 climate scenarios and fishing mortality of F= 0.0 yr^{-1}.

RCP-4.5 *RCP-8.5,*

	Length at age (cm) year 2000	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*	*Length at age (cm) year 2000*	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*
Age 1 year	**7.67 (7.63-7.71)**	**8.25 (8.2-8.3)**	**0.58 (0.51-0.64)** W=2.312.906, p>0.001	**7.6 %**	**7.67 (7.63-7.71)**	**8.93 (8.87-8.98)**	**1.26 (1.19-1.33)** W=2.992.363, p>0.001	**16.4 %**
Age 2 year	**10.52 (10.46-10.58)**	**11.34 (11.27-11.41)**	**0.83 (0.73-0.92)** W=1.320.584, p>0.001	**7.8 %**	**10.52 (10.46-10.58)**	**12.3 (12.2-12.4)**	**1.82 (1.72-1.91)** W=1.752.392, p>0.001	**17.2 %**
Age 3 year	**13.1 (13.05-13.21)**	**14.23 (14.14-14.32)**	**1.09 (0.97-1.22)** W=818.609, p>0.001	**8.4 %**	**13.1 (13.05-13.21)**	**15.55 (15.45-18.64)**	**2.44 (2.31-2.56)** W=1.147.789, p>0.001	**18.4 %**
Age 4 year	**15.7 (15.59-15.78)**	**16.9 (16.8-17.04)**	**1.24 (1.08-1.39)** W=524.789, p>0.001	**7.9 %**	**15.7 (15.59-15.78)**	**18.5 (18.4-18.65)**	**2.87 (2.72-3.03)** W=731.068, p>0.001	**18.2 %**
Age 5 year	**17.98 (17.87-18.1)**	**19.45 (19.31-19.59)**	**1.46 (1.28-1.65)** W=364.484, p>0.001	**8.2 %**	**17.98 (17.87-18.1)**	**21.3 (21.16-21.44)**	**3.33 (3.14-3.51)** W=513.525, p>0.001	**18.5 %**

Table C2. Change in length-at-age for whitefish in Skrukkebukta from year 2000 to year 2100 under RCP-4.5 and RCP-8.5 climate scenarios and fishing mortality of F= 0.0 yr^{-1}.

RCP-4.5 *RCP-8.5,*

	Length at age (cm) year 2000	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*	*Length at age (cm) year 2000*	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*
Age 1 year	**7.61 (7.57-7.65)**	**8.95 (8.9-9.0)**	**1.33 (1.27-1.4)** W=4.331.115, p>0.001	**17.6 %**	**7.61 (7.57-7.65**	**9.43 (9.36-9.5)**	**1.79 (1.71-1.87)** W=4.504.359, p>0.001	**24.0 %**
Age 2 year	**11.2 (11.14-11.27)**	**13.36 (13.27-13.44)**	**2.11 (2.01-2.21)** W=2.108.306, p>0.001	**19.2 %**	**11.2 (11.14-11.27)**	**14.2 (14.05-14.27)**	**2.91 (2.78-3.04)** W=1.183.831, p>0.001	**26.4 %**
Age 3 year	**14.87 (14.78-14.95)**	**17.63 (17.51-17.74)**	**2.72 (2.58-2.86)** W=1.005.780, p>0.001	**18.5 %**	**14.87 (14.78-14.95)**	**18.83 (18.68-18.99)**	**3.91 (3.74-4.09)** W=1.101.752, p>0.001	**27.0 %**
Age 4 year	**18.26 (18.14-18.38)**	**21.66 (21.51-21.81)**	**3.38 (3.19-3.57)** W=512.699, p>0.001	**18.6 %**	**18.26 (18.14-18.38)**	**23.32 (23.12-23.52)**	**5.02 (4.79-5.26)** W=534.539, p>0.001	**27.7 %**
Age 5 year	**21.39 (21.24-21.54)**	**25.1 (24.86-25.27)**	**3.67 (3.42-3.92)** W=259.559, p>0.001	**17.2 %**	**21.39 (21.24-21.54)**	**27.2 (26.94-27.43)**	**5.75 (5.46-6.03)** W=282.099, p>0.001	**27.1 %**

Table C3. Change in length-at-age for vendace in Skrukkebukta from year 2000 to year 2100 under RCP-4.5 and RCP-8.5 climate scenarios and fishing mortality of $F = 0.0$ yr^{-1}.

RCP-4.5 *RCP-8.5,*

	Length at age (cm) year 2000	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*	*Length at age (cm) year 2000*	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*
Age 1 year	**7.18 (7.12-7.24)**	**8.2 (8.13-8.27)**	**1.02 (0.93-1.11)** W=2.238.131, p>0.001	**14.2 %**	**7.18 (7.12-7.24)**	**8.73 (8.65-8.81)**	**1.49 (1.39-1.6)** W=2.516.140, p>0.001	**21.6 %**
Age 2 year	**8.06 (7.97-8.14)**	**9.25 (9.15-9.35)**	**1.2 (1.06-1.33)** W=366.631, p>0.001	**14.8 %**	**8.06 (7.97-8.14)**	**9.82 (9.71-9.93)**	**1.72 (1.58-1.87)** W=465.922, p>0.001	**21.9 %**
Age 3 year	**8.47 (8.34-8.6)**	**9.84 (9.69-9.99)**	**1.37 (1.16-1.57)** W=61.622, p>0.001	**16.2 %**	**8.47 (8.34-8.6)**	**10.54 (10.38-10.69)**	**2.09 (1.87-2.3)** W=73.289, p>0.001	**24.4 %**
Age 4 year	**8.92 (8.72-9.12)**	**10.44 (10.22-10.65)**	**1.54 (1.25-1.83)** W=9.265, p>0.001	**16.9 %**	**8.92 (8.72-9.12)**	**11.11 (10.88-11.34)**	**2.52 (1.94-2.57)** W=10.304, p>0.001	**24.5 %**
Age 5 year	**9.09 (8.75-9.42)**	**11.0 (10.7-11.3)**	**1.95 (1.48-2.33)** W=1.583, p>0.001	**21.0 %**	**9.09 (8.75-9.42**	**11.65 (11.3-12.0)**	**2.51 (2.03-3.02)** W=1.737, p>0.001	**28.2 %**

F = 0.1 yr^{-1}

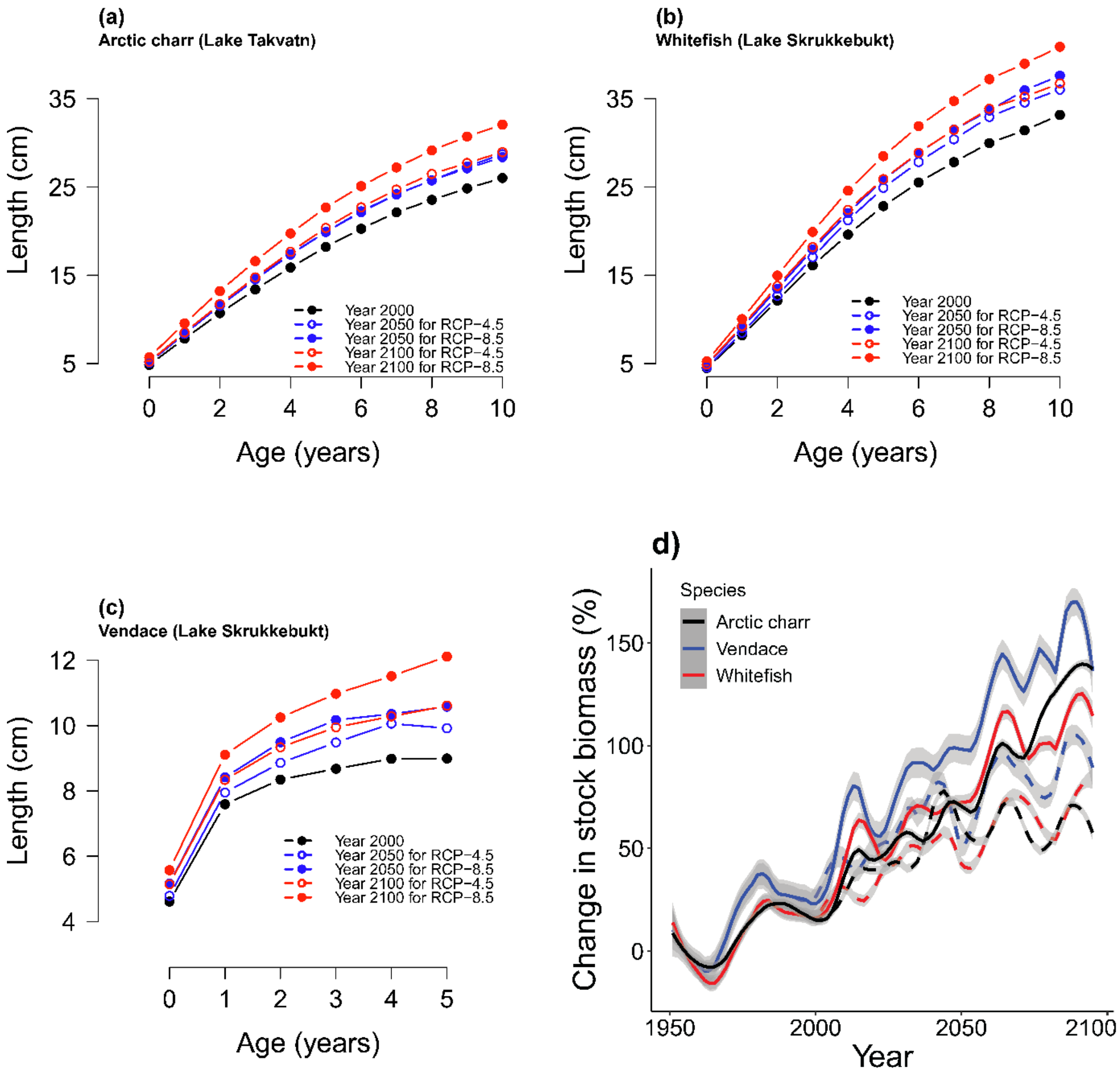


Figure C2. Individual based model predictions of length-at-age for a) Arctic charr in Takvatn, and b) whitefish and c) vendace in Skrukkebukta under two RCP (-4.5 & -8.5) climate scenarios for fishing mortality, F= 0.1 yr^{-1}. d) Model predictions of percentage change in stock biomass for Arctic charr (—) in Takvatn, and whitefish (—) and vendace (—) in Skrukkebukta under the RCP-4.5 (dashed line) and RCP-8.5 (solid line) climate scenarios from year 1950 to year 2100 for fishing mortality, F= 0.1 yr^{-1}.

Table C4. Change in length-at-age for Arctic charr in Takvatn from year 2000 to year 2100 under RCP-4.5 and RCP-8.5 climate scenarios and fishing mortality of *F*= 0.1 yr^{-1}.

	RCP-4.5				*RCP-8.5,*			
	Length at age (cm) year 2000	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*	*Length at age (cm) year 2000*	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*
Age 1 year	**7.67 (7.63-7.71)**	**8.25 (8.2-8.3)**	**0.58 (0.51-0.64)** W=2.312.906, p>0.001	**7.6 %**	**7.67 (7.63-7.71)**	**8.93 (8.87-8.98)**	**1.26 (1.19-1.33)** W=2.992.363, p>0.001	**16.4 %**
Age 2 year	**10.52 (10.46-10.58)**	**11.34 (11.27-11.41)**	**0.83 (0.73-0.92)** W=1.320.584, p>0.001	**7.8 %**	**10.52 (10.46-10.58)**	**12.3 (12.2-12.4)**	**1.82 (1.72-1.91)** W=1.752.392, p>0.001	**17.2 %**
Age 3 year	**13.1 (13.05-13.21)**	**14.23 (14.14-14.32)**	**1.09 (0.97-1.22)** W=818.609, p>0.001	**8.4 %**	**13.1 (13.05-13.21)**	**15.55 (15.45-18.64)**	**2.44 (2.31-2.56)** W=1.147.789, p>0.001	**18.4 %**
Age 4 year	**15.7 (15.59-15.78)**	**16.9 (16.8-17.04)**	**1.24 (1.08-1.39)** W=524.789, p>0.001	**7.9 %**	**15.7 (15.59-15.78)**	**18.5 (18.4-18.65)**	**2.87 (2.72-3.03)** W=731.068, p>0.001	**18.2 %**
Age 5 year	**17.98 (17.87-18.1)**	**19.45 (19.31-19.59)**	**1.46 (1.28-1.65)** W=364.484, p>0.001	**8.2 %**	**17.98 (17.87-18.1)**	**21.3 (21.16-21.44)**	**3.33 (3.14-3.51)** W=513.525, p>0.001	**18.5 %**

Table C5. Change in length-at-age for whitefish in Skrukkebukta from year 2000 to year 2100 under RCP-4.5 and RCP-8.5 climate scenarios and fishing mortality of *F*=0.1 yr^{-1}.

	RCP-4.5				*RCP-8.5,*			
	Length at age (cm) year 2000	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*	*Length at age (cm) year 2000*	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*
Age 1 year	**7.61 (7.57-7.65)**	**8.95 (8.9-9.0)**	**1.33 (1.27-1.4)** W=4.331.115, p>0.001	**17.6 %**	**7.61 (7.57-7.65**	**9.43 (9.36-9.5)**	**1.79 (1.71-1.87)** W=4.504.359, p>0.001	**24.0 %**
Age 2 year	**11.2 (11.14-11.27)**	**13.36 (13.27-13.44)**	**2.11 (2.01-2.21)** W=2.108.306, p>0.001	**19.2 %**	**11.2 (11.14-11.27)**	**14.2 (14.05-14.27)**	**2.91 (2.78-3.04)** W=1.183.831, p>0.001	**26.4 %**
Age 3 year	**14.87 (14.78-14.95)**	**17.63 (17.51-17.74)**	**2.72 (2.58-2.86)** W=1.005.780, p>0.001	**18.5 %**	**14.87 (14.78-14.95)**	**18.83 (18.68-18.99)**	**3.91 (3.74-4.09)** W=1.101.752, p>0.001	**27.0 %**
Age 4 year	**18.26 (18.14-18.38)**	**21.66 (21.51-21.81)**	**3.38 (3.19-3.57)** W=512.699, p>0.001	**18.6 %**	**18.26 (18.14-18.38)**	**23.32 (23.12-23.52)**	**5.02 (4.79-5.26)** W=534.539, p>0.001	**27.7 %**
Age 5 year	**21.39 (21.24-21.54)**	**25.1 (24.86-25.27)**	**3.67 (3.42-3.92)** W=259.559, p>0.001	**17.2 %**	**21.39 (21.24-21.54)**	**27.2 (26.94-27.43)**	**5.75 (5.46-6.03)** W=282.099, p>0.001	**27.1 %**

Table C6. Change in length-at-age for vendace in Skrukkebukta from year 2000 to year 2100 under RCP-4.5 and RCP-8.5 climate scenarios and fishing mortality of $F = 0.1\ \text{yr}^{-1}$.

	RCP-4.5				*RCP-8.5,*			
	Length at age (cm) year 2000	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*	*Length at age (cm) year 2000*	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*
Age 1 year	**7.18 (7.12-7.24)**	**8.2 (8.13-8.27)**	**1.02 (0.93-1.11)** W=2.238.131, p>0.001	**14.2 %**	**7.18 (7.12-7.24)**	**8.73 (8.65-8.81)**	**1.49 (1.39-1.6)** W=2.516.140, p>0.001	**21.6 %**
Age 2 year	**8.06 (7.97-8.14)**	**9.25 (9.15-9.35)**	**1.2 (1.06-1.33)** W=366.631, p>0.001	**14.8 %**	**8.06 (7.97-8.14)**	**9.82 (9.71-9.93)**	**1.72 (1.58-1.87)** W=465.922, p>0.001	**21.9 %**
Age 3 year	**8.47 (8.34-8.6)**	**9.84 (9.69-9.99)**	**1.37 (1.16-1.57)** W=61.622, p>0.001	**16.2 %**	**8.47 (8.34-8.6)**	**10.54 (10.38-10.69)**	**2.09 (1.87-2.3)** W=73.289, p>0.001	**24.4 %**
Age 4 year	**8.92 (8.72-9.12)**	**10.44 (10.22-10.65)**	**1.54 (1.25-1.83)** W=9.265, p>0.001	**16.9 %**	**8.92 (8.72-9.12)**	**11.11 (10.88-11.34)**	**2.52 (1.94-2.57)** W=10.304, p>0.001	**24.5 %**
Age 5 year	**9.09 (8.75-9.42)**	**11.0 (10.7-11.3)**	**1.95 (1.48-2.33)** W=1.583, p>0.001	**21.0 %**	**9.09 (8.75-9.42**	**11.65 (11.3-12.0)**	**2.51 (2.03-3.02)** W=1.737, p>0.001	**28.2 %**

F = 0.2 yr^{-1}

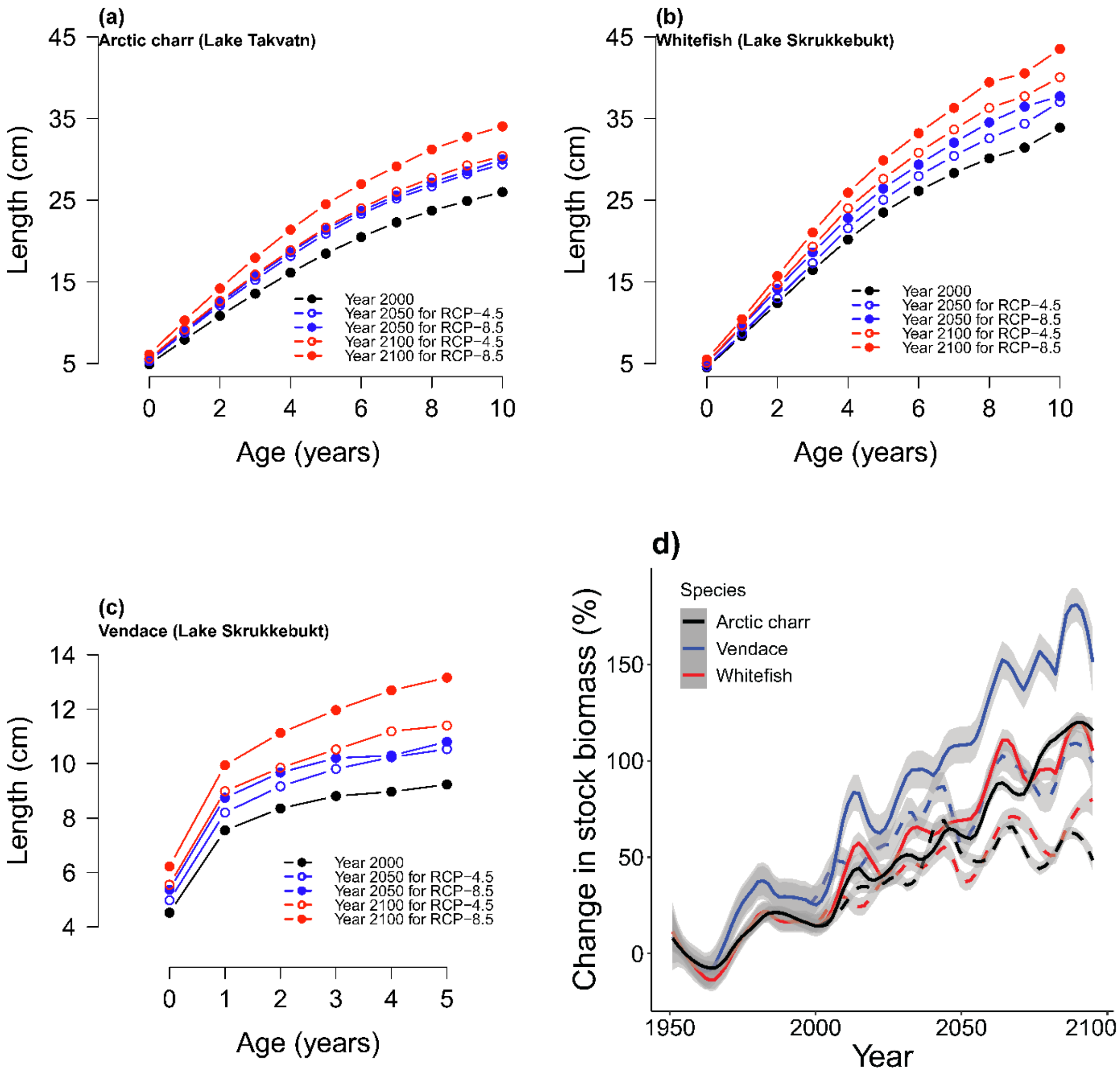


Figure C3. Individual based model predictions of length-at-age for a) Arctic charr in Takvatn, and b) whitefish and c) vendace in Skrukkebukta under two RCP (-4.5 & -8.5) climate scenarios for fishing mortality, F= 0.2 yr^{-1}. d) Model predictions of percentage change in stock biomass for Arctic charr (—) in Takvatn, and whitefish (—) and vendace (—) in Skrukkebukta under the

RCP-4.5 (dashed line) and RCP-8.5 (solid line) climate scenarios from year 1950 to year 2100 for fishing mortality, F= 0.2 yr^{-1}.

Table C7. Change in length-at-age for Arctic charr in Takvatn from year 2000 to year 2100 under RCP-4.5 and RCP-8.5 climate scenarios and fishing mortality of F= 0.2 yr^{-1}.

	RCP-4.5				*RCP-8.5,*			
	Length at age (cm) year 2000	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*	*Length at age (cm) year 2000*	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*
Age 1 year	**7.92 (7.88-7.97)**	**9.17 (9.11-9.24)**	**1.25 (1.17-1.33)** W=2.351.663, p>0.001	**15.8 %**	**7.92 (7.88-7.97)**	**10.27 (10.2-10.3)**	**2.35 (2.26-2.44)** W=2.731.753, p>0.001	**29.6 %**
Age 2 year	**10.85 (10.79-10.91)**	**12.65 (12.57-12.73)**	**1.82 (1.72-1.92)** W=1.344.183, p>0.001	**16.6 %**	**10.85 (10.79-10.91)**	**14.2 (14.1-14.3)**	**3.37 (3.25-3.48)** W=1.609.976, p>0.001	**30.1 %**
Age 3 year	**13.55 (13.47-13.63)**	**15.89 (15.79-15.99)**	**2.35 (2.22-2.48)** W=840.592, p>0.001	**17.2 %**	**13.55 (13.47-13.63)**	**17.94 (17.8-18.07)**	**4.39 (4.24-4.53)** W=1.028.223, p>0.001	**32.3 %**
Age 4 year	**16.1 (16.0-16.2)**	**18.9 (18.7-19.0)**	**2.73 (2.56-2.9)** W=530.560, p>0.001	**17.0 %**	**16.1 (16.0-16.2)**	**21.4 (21.2-21.5)**	**5.29 (5.1-5.47)** W=664.091, p>0.001	**32.6 %**
Age 5 year	**18.46 (18.32-18.6)**	**21.6 (21.48-21.8)**	**3.16 (2.95-3.38)** W=353.935, p>0.001	**17.2 %**	**18.46 (18.32-18.6)**	**24.5 (24.33-24.7)**	**6.07 (5.84-6.3)** W=426.501, p>0.001	**32.8 %**

Table C8. Change in length-at-age for whitefish in Skrukkebukta from year 2000 to year 2100 under RCP-4.5 and RCP-8.5 climate scenarios and fishing mortality of F= 0.2 yr^{-1}.

	RCP-4.5				*RCP-8.5,*			
	Length at age (cm) year 2000	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*	*Length at age (cm) year 2000*	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*
Age 1 year	**8.36 (8.31-8.4)**	**9.7 (9.63-9.75)**	**1.33 (1.25-1.41)** W=3.528.810, p>0.001	**16.0 %**	**8.36 (8.31-8.4)**	**10.43 (10.36-10.51)**	**2.04 (1.95-2.13)** W=3.836.122, p>0.001	**24.8 %**
Age 2 year	**12.4 (12.33-12.46)**	**14.65 (14.56-14.74)**	**2.26 (2.15-2.38)** W=1.803.484, p>0.001	**18.2 %**	**12.4 (12.33-12.46)**	**15.7 (15.6-15.82)**	**3.24 (3.11-3.37)** W=1.935.018, p>0.001	**26.7 %**
Age 3 year	**16.44 (16.35-16.54)**	**19.31 (19.17-19.44)**	**2.88 (2.71-3.04)** W=890.521, p>0.001	**17.4 %**	**16.44 (16.35-16.54)**	**21.04 (20.89-21.2)**	**4.53 (4.34-4.72)** W=946.124, p>0.001	**27. %**

Age 4 year	**20.18 (20.05-20.31)**	**24.0 (23.8-24.2)**	**3.81 (3.6-4.04)** W=468.506, p>0.001	**18.9 %**	**20.18 (20.05-20.31)**	**25.91 (25.7-26.1)**	**5.69 (5.45-5.92)** W=486.772, p>0.001	**28.4 %**
Age 5 year	**23.5 (23.32-23.65)**	**27.6 (27.38-27.84)**	**4.08 (3.8-4.37)** W=219.924, p>0.001	**17.5 %**	**23.5 (23.32-23.65)**	**29.87 (29.6-30.1)**	**6.35 (6.03-6.67)** W=213.206, p>0.001	**27.2 %**

Table C9. Change in length-at-age for vendace in Skrukkebukta from year 2000 to year 2100 under RCP-4.5 and RCP-8.5 climate scenarios and fishing mortality of $F = 0.2\ \text{yr}^{-1}$.

RCP-4.5 *RCP-8.5,*

	Length at age (cm) year 2000	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*	*Length at age (cm) year 2000*	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*
Age 1 year	**7.55 (7.5-7.6)**	**9.0 (8.9-9.1)**	**1.42 (1.31-1.53)** W=1.991.453, p>0.001	**19.1 %**	**7.55 (7.5-7.6)**	**9.94 (9.84-10.04)**	**2.27 (2.15-2.4)** W=2.302.043, p>0.001	**31.7 %**
Age 2 year	**8.35 (8.26-8.44)**	**9.85 (9.71-9.98)**	**1.43 (1.26-1.60)** W=272.332, p>0.001	**17.9 %**	**8.35 (8.26-8.44)**	**11.12 (10.95-11.3)**	**2.68 (2.48-2.87)** W=283.722, p>0.001	**33.2 %**
Age 3 year	**8.81 (8.68-8.93)**	**10.52 (10.27-10.77)**	**1.61 (1.37-1.87)** W=30.822, p>0.001	**19.5 %**	**8.81 (8.68-8.93)**	**11.97 (11.6-12.29)**	**3.09 (2.77-3.43)** W=26.632, p>0.001	**35.9 %**
Age 4 year	**8.97 (8.76-9.17)**	**11.18 (10.64-11.73)**	**2.11 (1.61-2.58)** W=2778, p>0.001	**24.7 %**	**8.97 (8.76-9.17)**	**12.69 (12.17-13.2)**	**3.71 (3.24-4.24)** W=2626, p>0.001	**41.5 %**
Age 5 year	**9.23 (8.9-9.57)**	**11.4 (10.4-12.4)**	**2.19 (1.55-3.07)** W=201, p>0.001	**23.4 %**	**9.23 (8.9-9.57**	**13.15 (11.7-14.6)**	**4.06 (2.73-5.03)** W=210, p>0.001	**42.5 %**

$F = 0.3$ yr^{-1}

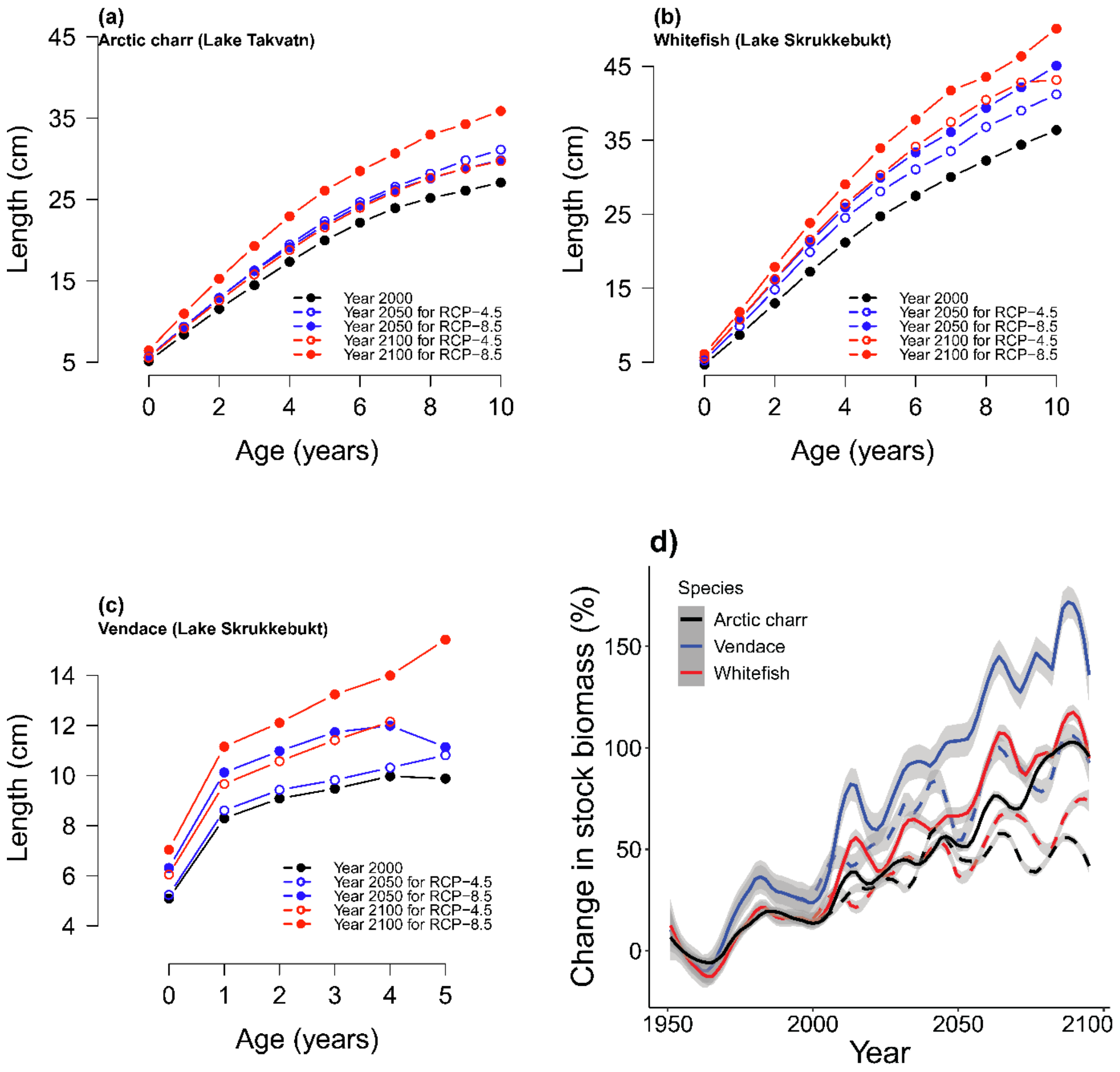


Figure C4. Individual based model predictions of length-at-age for a) Arctic charr in Takvatn, and b) whitefish and c) vendace in Skrukkebukta under two RCP (-4.5 & -8.5) climate scenarios and fishing mortality, F= 0.3 yr^{-1}. d) Model predictions of percentage change in stock biomass for Arctic charr (—) in Takvatn, and whitefish (—) and vendace (—) in Skrukkebukta under the RCP-4.5 (dashed line) and RCP-8.5 (solid line) climate scenarios from year 1950 to year 2100 for fishing mortality, F= 0.3 yr^{-1}.

Table C10. Change in length-at-age for Arctic charr in Takvatn from year 2000 to year 2100 under RCP-4.5 and RCP-8.5 climate scenarios and fishing mortality of $F= 0.3\ yr^{-1}$.

RCP-4.5 *RCP-8.5,*

	RCP-4.5				*RCP-8.5,*			
	Length at age (cm) year 2000	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*	*Length at age (cm) year 2000*	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*
Age 1 year	**8.41 (8.36-8.46)**	**9.14 (9.08-9.2)**	**0.72 (0.64-0.8)** W=1.827.569, p>0.001	**8.7 %**	**8.41 (8.36-8.46)**	**10.96 (10.88-11.04)**	**2.55 (2.46-2.65)** W=2.203.354, p>0.001	**30.3 %**
Age 2 year	**11.55 (11.48-11.62)**	**12.58 (12.49-12.66)**	**1.03 (0.92-1.14)** W=1.041.649, p>0.001	**8.9 %**	**11.55 (11.48-11.62)**	**14.6 (14.4-14.6)**	**3.72 (3.6-3.85)** W=1.328.405, p>0.001	**32.0 %**
Age 3 year	**14.47 (14.39-14.57)**	**15.78 (15.68-15.89)**	**1.33 (1.19-1.47)** W=1.041.649, p>0.001	**9.0 %**	**14.47 (14.39-14.57)**	**19.28 (19.15-19.4)**	**4.83 (4.67-4.99)** W=939.367, p>0.001	**33.2 %**
Age 4 year	**17.35 (17.23-17.46)**	**18.79 (18.66-18.92)**	**1.46 (1.28-1.63)** W=459.440, p>0.001	**8.3 %**	**17.35 (17.23-17.46)**	**22.9 (22.8-23.1)**	**5.59 (5.39-5.78)** W=634.732, p>0.001	**32.2 %**
Age 5 year	**19.96 (19.83-20.09)**	**21.6 (21.42-21.73)**	**1.63 (1.43-1.84)** W=327.339, p>0.001	**8.1 %**	**19.96 (19.83-20.09)**	**26.1 (25.9-26.3)**	**6.13 (5.89-6.36)** W=413.577, p>0.001	**30.7 %**

Table C11. Change in length-at-age for whitefish in Skrukkebukta from year 2000 to year 2100 under RCP-4.5 and RCP-8.5 climate scenarios and fishing mortality of $F= 0.3\ yr^{-1}$.

	RCP-4.5				*RCP-8.5,*			
	Length at age (cm) year 2000	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*	*Length at age (cm) year 2000*	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*
Age 1 year	**8.68 (8.63-8.73)**	**10.8 (10.73-10.87)**	**2.09 (2.0-2.17)** W=3.353.592, p>0.001	**24.4 %**	**8.68 (8.63-8.73)**	**11.8 (11.7-11.89)**	**3.08 (2.97-3.18)** W=3.533.177, p>0.001	**35.9 %**
Age 2 year	**12.97 (12.9-13.04)**	**14.65 (14.56-14.74)**	**3.23 (3.1-3.37)** W=1.618.781, p>0.001	**25.2 %**	**12.97 (12.9-13.04)**	**17.9 (17.73-18.01)**	**4.81 (4.65-4.97)** W=1.727.318, p>0.001	**37.8 %**
Age 3 year	**17.2 (17.13-17.33)**	**21.56 (21.41-21.7)**	**4.3 (4.12-4.47)** W=821.631, p>0.001	**25.1 %**	**17.2 (17.13-17.33)**	**23.8 (23.6-24.0)**	**6.55 (6.33-6.77)** W=869.437, p>0.001	**38.3 %**
Age 4 year	**21.2 (21.04-21.32)**	**26.4 (26.2-26.6)**	**5.21 (4.97-4.45)** W=407.095, p>0.001	**24.7 %**	**21.2 (21.04-21.32)**	**29.1 (28.8-29.3)**	**7.87 (7.58-8.16)** W=391.084, p>0.001	**37.1 %**
Age 5 year	**24.7 (24.5-24.9)**	**30.3 (30.02-30.59)**	**5.56 (5.22-5.9)** W=149.250, p>0.001	**22.6 %**	**24.7 (24.5-24.9)**	**33.9 (33.55-34.3)**	**9.2 (8.79-9.6)** W=138.061, p>0.001	**37.2 %**

Table C12. Change in length-at-age for vendace in Skrukkebukta from year 2000 to year 2100 under RCP-4.5 and RCP-8.5 climate scenarios and fishing mortality of *F*= 0.3 yr^{-1}.

RCP-4.5

RCP-8.5,

	Length at age (cm) year 2000	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*	*Length at age (cm) year 2000*	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*
Age 1 year	**8.29 (8.21-8.37)**	**9.65 (9.56-9.76)**	**1.33 (1.2-1.46)** W=1.467.052, p>0.001	**16.5 %**	**8.29 (8.21-8.37)**	**11.15 (11.02-11.28)**	**2.73 (2.58-2.89)** W=2.400.128, p>0.001	**34.5 %**
Age 2 year	**9.08 (8.97-9.2)**	**10.57 (10.39-10.75)**	**1.47 (1.25-1.67)** W=135.016, p>0.001	**16.4 %**	**9.08 (8.97-9.2)**	**12.1 (11.84-12.37)**	**2.99 (2.73-3.26)** W=92.466, p>0.001	**33.3 %**
Age 3 year	**9.5 (9.28-9.66)**	**11.4 (11.12-11.7)**	**1.91 (1.56-2.24)** W=10.776, p>0.001	**20.5 %**	**9.5 (9.28-9.66)**	**13.2 (12.62-13.85)**	**3.64 (3.09-4.19)** W=5.094, p>0.001	**39.8 %**
Age 4 year	**9.97 (9.63-10.29)**	**12.15 (11.52-12.77)**	**2.11 (1.45-2.73)** W=772, p>0.001	**21.8 %**	**9.97 (9.63-10.29)**	**13.99 (13.78-14.19)**	**4.01 (2.75-5.25)** W=141, p>0.001	**40.3 %**
Age 5 year	**9.87 (9.4-10.35)**	**NA (NA-NA)**	**NA**	**NA**	**9.87 (9.4-10.35)**	**15.42 (NA-NA)**	**5.72 (4.66-6.39)** W=8, p=0.22	**56.2 %**

F = 0.4 yr^{-1}

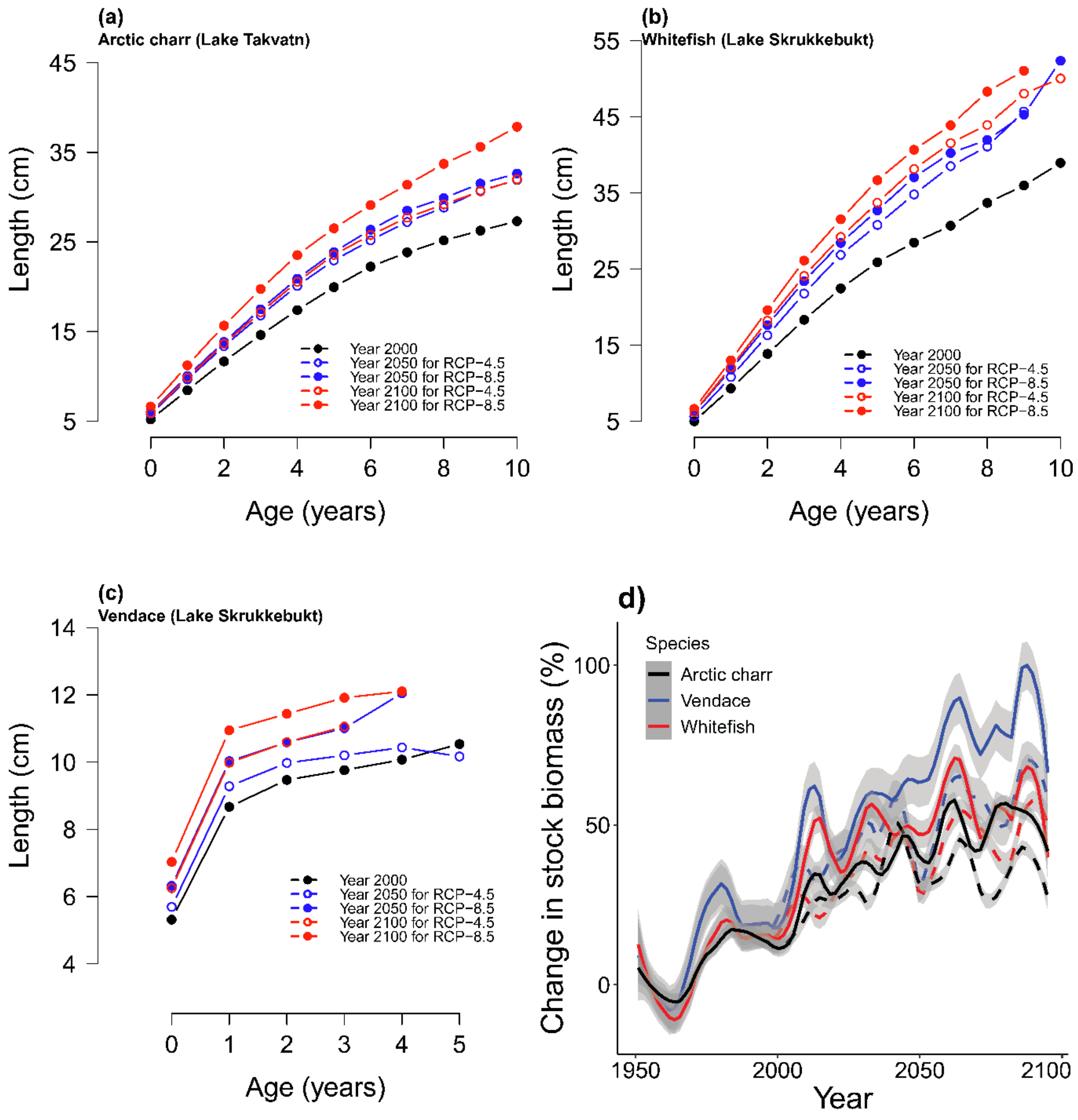


Figure C5. Individual based model predictions of length-at-age for a) Arctic charr in Takvatn, and b) whitefish and c) vendace in Skrukkebukta under two RCP (-4.5 & -8.5) climate scenarios for fishing mortality, F= 0.4 yr^{-1}. d) Model predictions of percentage change in stock biomass for Arctic charr (—) in Takvatn, and whitefish (—) and vendace (—) in Skrukkebukta under the

RCP-4.5 (dashed line) and RCP-8.5 (solid line) climate scenarios from year 1950 to year 2100 for fishing mortality, F= 0.4 yr^{-1}.

Table C13. Change in length-at-age for Arctic charr in Takvatn from year 2000 to year 2100 under RCP-4.5 and RCP-8.5 climate scenarios and fishing mortality of F= 0.4 yr^{-1}.

RCP-4.5 *RCP-8.5,*

	Length at age (cm) year 2000	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*	*Length at age (cm) year 2000*	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*
Age 1 year	**8.45 (8.4-8.5)**	**9.86 (9.79-9.93)**	**1.42 (0.64-0.8)** W=1.827.569, $p>0.001$	**16.7 %**	**8.45 (8.4-8.5)**	**11.22 (11.14-11.31)**	**2.78 (2.68-2.88)** W=2.842.472, $p>0.001$	**32.8 %**
Age 2 year	**11.67 (11.6-11.74)**	**13.64 (13.55-13.73)**	**1.97 (1.86-2.09)** W=1.172.859, $p>0.001$	**16.9 %**	**11.67 (11.6-11.74)**	**15.67 (15.55-15.78)**	**3.98 (3.84-4.11)** W=1.146.946, $p>0.001$	**34.2 %**
Age 3 year	**14.62 (14.53-14.71)**	**17.15 (17.03-17.27)**	**2.52 (2.36-2.67)** W=757.070, $p>0.001$	**17.3 %**	**14.62 (14.53-14.71)**	**19.75 (19.6-19.9)**	**5.13 (4.96-5.3)** W=787.279, $p>0.001$	**35.1 %**
Age 4 year	**17.4 (17.29-17.51)**	**20.56 (20.41-20.71)**	**3.13 (2.94-3.31)** W=515.122, $p>0.001$	**18.2 %**	**17.4 (17.29-17.51)**	**23.5 (23.35-23.71)**	**6.11 (5.89-6.32)** W=502.943, $p>0.001$	**35.2 %**
Age 5 year	**19.95 (19.81-20.09)**	**23.56 (23.38-23.74)**	**3.63 (6.3-6.86)** W=343.255, $p>0.001$	**18.1 %**	**19.95 (19.81-20.09**	**26.52 (25.3-26.73)**	**6.55 (6.3-6.81)** W=307.138, $p>0.001$	**32.9 %**

Table C14. Change in length-at-age for whitefish in Skrukkebukta from year 2000 to year 2100 under RCP-4.5 and RCP-8.5 climate scenarios and fishing mortality of F= 0.4 yr^{-1}.

RCP-4.5 *RCP-8.5,*

	Length at age (cm) year 2000	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*	*Length at age (cm) year 2000*	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*
Age 1 year	**9.32 (9.26-9.37)**	**12.1 (12.0-12.17)**	**2.78 (2.68-2.88)** W=2.877.347, $p>0.001$	**29.8 %**	**9.32 (9.26-9.37)**	**12.99 (12.88-13.11)**	**3.65 (3.52-3.78)** W=2.504.952, $p>0.001$	**39.5 %**
Age 2 year	**13.85 (13.76-13.94)**	**18.19 (18.06-18.32)**	**4.35 (4.2-4.51)** W=1.396.644, $p>0.001$	**31.4 %**	**13.85 (13.76-13.94**	**19.6 (19.42-19.78)**	**5.67 (5.47-5.87)** W=1.247.140, $p>0.001$	**41.6 %**
Age 3 year	**18.32 (18.21-18.44)**	**23.1 (23.9-24.26)**	**5.8 (5.58-6.02)** W=694.799, $p>0.001$	**31.4 %**	**18.32 (18.21-18.44)**	**26.2 (25.85-26.4)**	**7.8 (7.52-8.1)** W=577.753, $p>0.001$	**42.5 %**

Age 4 year	**22.4 (22.28-22.6)**	**29.2 (28.96-29.49)**	**6.74 (6.44-7.06)** W=280.941, p>0.001	**30.2 %**	**22.4 (22.28-22.6)**	**31.53 (31.15-31.9)**	**8.87 (8.47-9.26)** W=205.809, p>0.001	**40.5 %**
Age 5 year	**25.9 (25.68-26.1)**	**33.7 (33.2-34.19)**	**7.69 (7.19-8.18)** W=70.435, p>0.001	**30.2 %**	**25.9 (25.68-26.1**	**36.7 (36.03-37.31)**	**10.7 (10.0-11.3)** W=46.627, p>0.001	**41.6 %**

Table C15. Change in length-at-age for vendace in Skrukkebukta from year 2000 to year 2100 under RCP-4.5 and RCP-8.5 climate scenarios and fishing mortality of *F*= 0.4 yr^{-1}.

RCP-4.5 *RCP-8.5,*

	Length at age (cm) year 2000	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*	*Length at age (cm) year 2000*	*Length at age (cm) year 2100*	*Change in length at age (cm)*	*Change in length at age*
Age 1 year	**8.67 (8.58-8.75)**	**9.98 (9.87-10.09)**	**1.27 (1.13-1.42)** W=1.022.442, p>0.001	**15.2 %**	**8.67 (8.58-8.75)**	**10.94 (10.81-11.08)**	**2.17 (2.0-2.33)** W=986.743, p>0.001	**26.3 %**
Age 2 year	**9.47 (9.33-9.61)**	**10.59 (10.3-10.78)**	**1.1 (0.88-1.33)** W=65.008, p>0.001	**11.8 %**	**9.47 (9.33-9.61)**	**11.43 (11.14-11.73)**	**1.87 (1.58-2.18)** W=43.200, p>0.001	**20.7 %**
Age 3 year	**9.76 (9.55-9.97)**	**11.05 (10.76-11.35)**	**1.34 (0.96-1.71)** W=3.230,5, p>0.001	**13.3 %**	**9.76 (9.55-9.97)**	**11.91 (10.78-13.05)**	**1.93 (1.05-3.19)** W=889, p>0.001	**22.1 %**
Age 4 year	**10.07 (9.65-10.49)**	**NA (NA-NA)**	**NA**	**NA**	**10.07 (9.65-10.49)**	**12.1 (11.54-12.66)**	**2.08 (0.86-3.00)** W=35, p=0.021	**20.2 %**
Age 5 year	**10.54 (9.77-11.3)**	**NA (NA-NA)**	**NA**	**NA**	**10.54 (9.77-11.3)**	**NA (NA-NA)**	**NA**	**NA**

Development of stock biomass and yield for two climate scenarios and five different fishing mortality scenarios

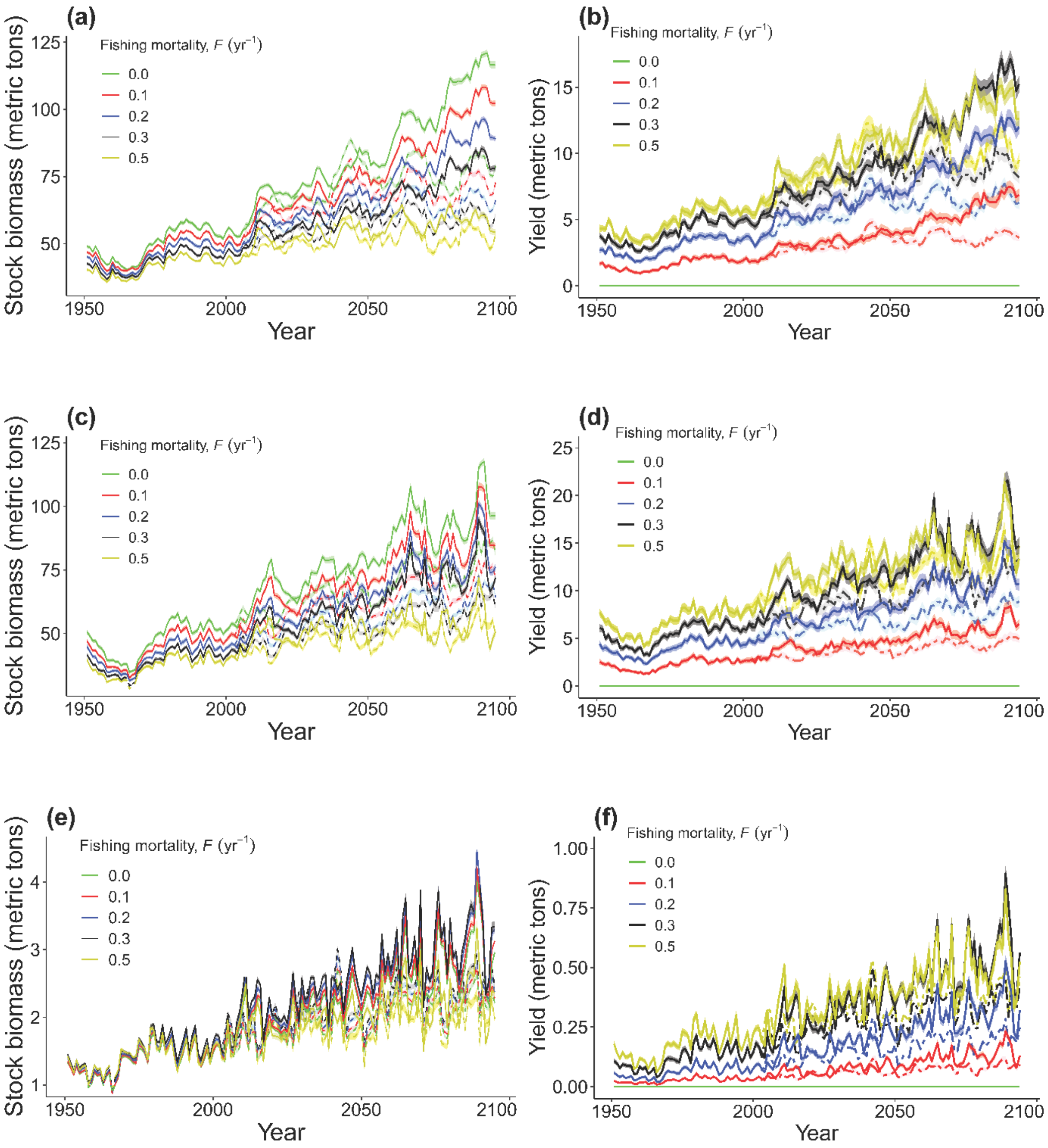


Figure C6. Development of stock biomass (a, c and e) and yield (b, d and f) for Arctic charr (a and b) in Takvatn, and whitefish (c and d) and vendace (e and F) in Skrukkebukta from year 1950 to year 2100 for climate scenarios RCP-4.5 (dashed line) and RCP-8.5 (solid line).

Development in age- and size-distribution and number of recruits and adult individuals from year 1950-2100

Arctic charr in Lake Takvatn

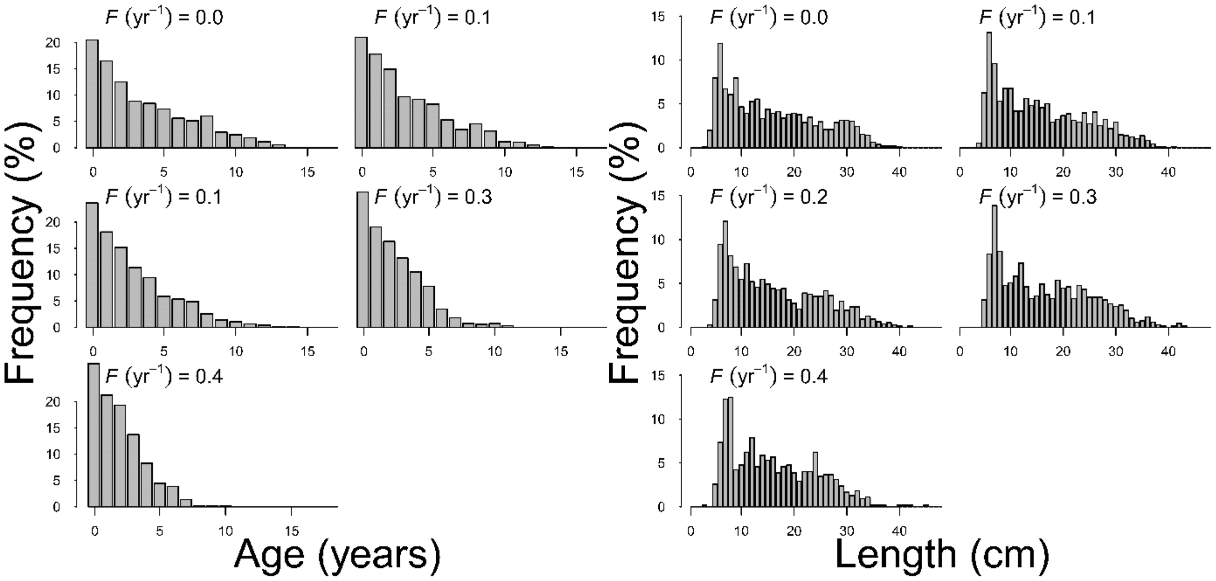


Figure C7. Age-distribution (right) and size-distribution (left) for five different levels of fishing mortality (F = 0.1-0.4) under the RCP-8.5 climate scenario in year 2100 for Arctic charr in Lake Takvatn predicted in the individual based model.

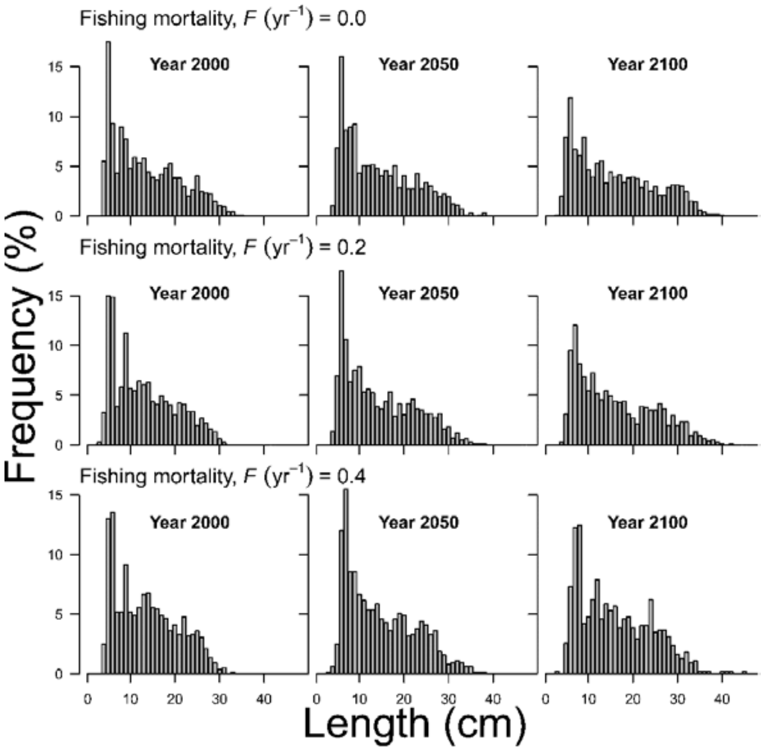


Figure C8. Individual based model predictions of size-distribution in the Arctic charr population in Lake Takvatn for three different fishing mortality scenarios (*F*= 0.0-, 0.2- & 0.4 yr^{-1}) in the year 2000 (left), year 2050 (middle) and year 2100 (right) for the RCP-8.5 climate scenario.

Proportion of mature individuals and number of recruits increases significantly with warming (RCP=8.5) for the low fishing mortality scenarios (*F*< 0.2 yr^{-1}) (Fig. C9), for *F*= 0.0 yr^{-1} proportion of mature individuals increases with 8.9% (W=230,743, p<0.001) and number of recruits increases with 5.8% from year 2000 to the year 2100 (W=39,954, p<0.001). For *F*= 0.1 yr^{-1} proportion of mature individuals increases with 2.4% (W=158,311, p<0.001), and number of recruits increases with 9.2% from year 2000 to the year 2100 (W=216,278, p<0.001). However, for *F*>= 0.2 yr^{-1} proportion of mature individuals and number of recruits decreases with warming (RCP-8.5), and for *F*= 0.4 yr^{-1} the decrease is severe. For *F*= 0.2 yr^{-1} proportion of mature individuals are only 94.2% (W=55,499, p<0.001), and number of recruits are only 92.6% in the year 2100 compared to the year 2000 (W=53,779, p<0.001). For *F*= 0.3 yr^{-1}

proportion of mature individuals are only 83.6% (W=5,927, p<0.001), and number of recruits are only 88.4% in the year 2100 compared to the year 2000 (W=134.5, p<0.001). For *F*= 0.4 yr^{-1} proportion of mature individuals are only 75.3% (W=433, p<0.001), and number of recruits are only 76.4% in the year 2100 compared to the year 2000 (W=0, p<0.001) (Fig. C9).

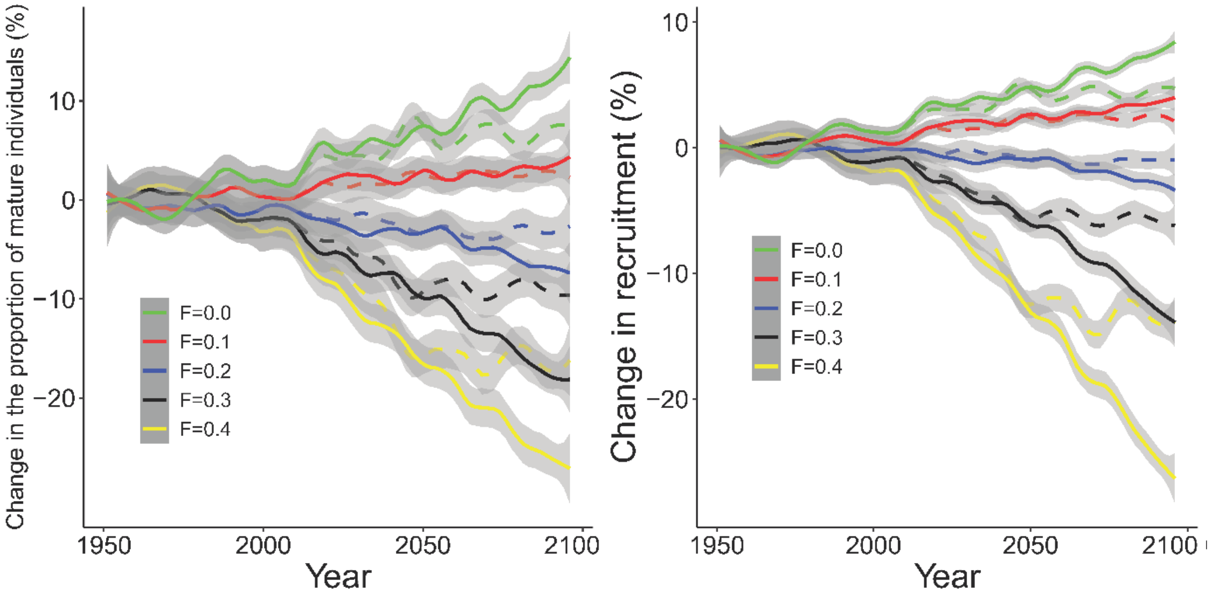


Figure C9. Proportion of mature individuals (left) and number of recruits (right) in the Arctic charr population in Takvatn from the year 1950-2100 for five different fishing mortalities (yr^{-1}) and two different climate scenarios, RCP-4.5 (dashed line) and RCP-8.5 (solid line) predicted in the individual based model.

Whitefish in Lake Skrukkebukta

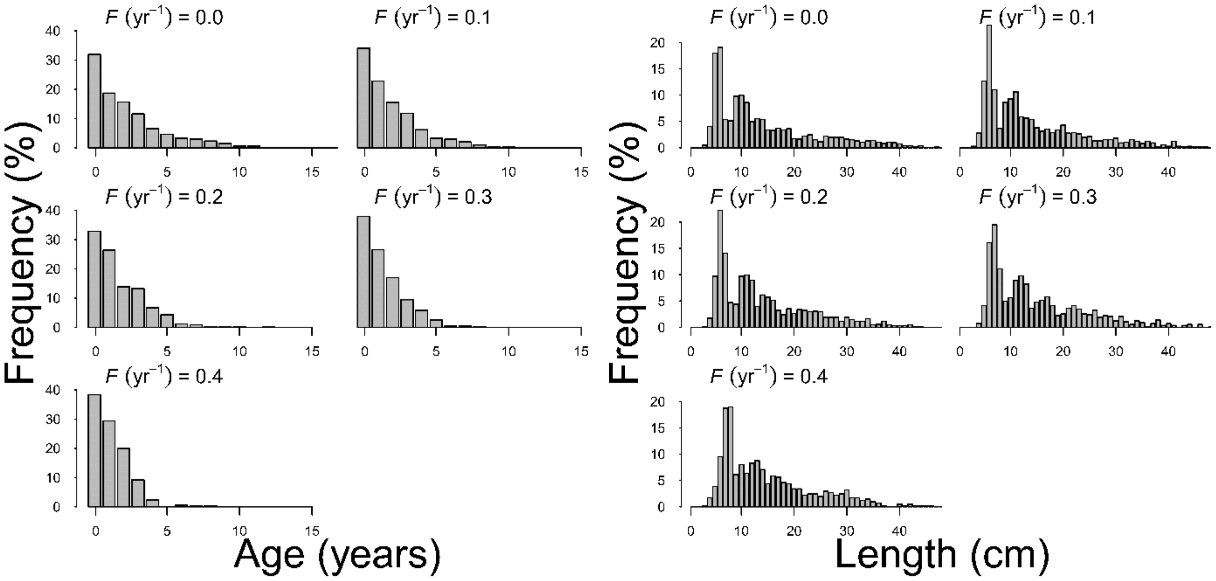


Figure C10. Age-distribution (right) and size-distribution (left) for five different levels of fishing mortality (F= 0.1-0.4 yr^{-1}) under the RCP-8.5 climate scenario in year 2100 for whitefish in Lake Skrukkebukt predicted in the individual based model.

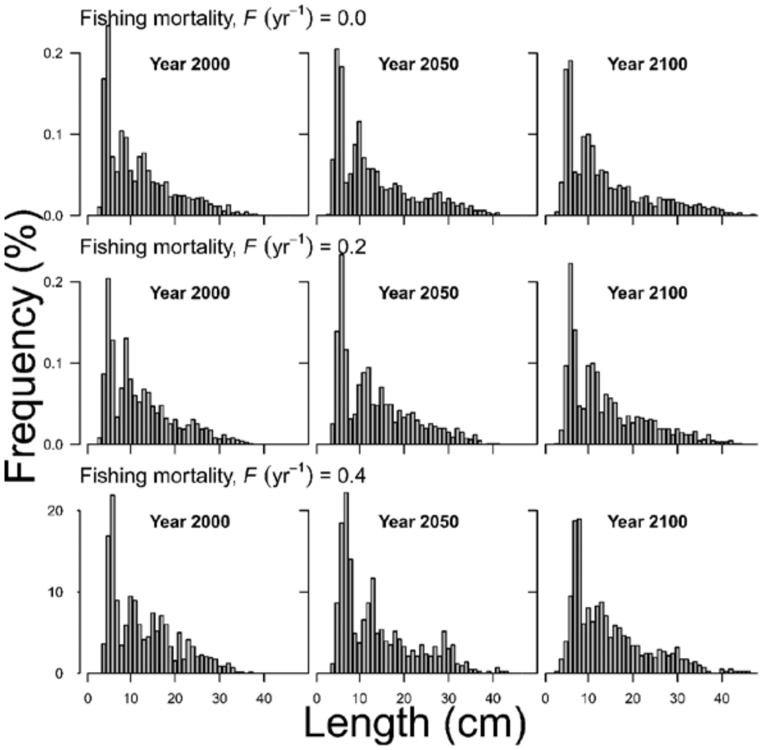


Figure C11. Individual based model predictions of size-distribution in the Arctic charr population in Lake Takvatn for three different fishing mortality scenarios (F= 0.0-, 0.2- & 0.4

yr^{-1}) in the year 2000 (left), year 2050 (middle) and year 2100 (right) for the RCP-8.5 climate scenario.

Proportion of mature individuals and number of recruits increases significantly or have no change with warming (RCP=8.5) for the low to medium fishing mortality scenarios (*F*< 0.3 yr^{-1}), for *F*= 0.0 yr^{-1} proportion of mature individuals increases with 11.1% (W=231,179, p<0.001) and number of recruits increases with 5.1% from year 2000 to the year 2100 (W=38,493, p<0.001). For *F*= 0.1 yr^{-1} proportion of mature individuals increases with 6.8% (W=195,455, p<0.001), and number of recruits increases with 11.1% from year 2000 to the year 2100 (W=211,028, p<0.001). However, for *F*= 0.2 yr^{-1} proportion of mature individuals and number of recruits are stabile with warming (RCP=8.5), and for *F*> 0.2 yr^{-1} both decreases with warming. For *F*= 0.2 yr^{-1} proportion of mature individuals increases by 1.8% (W=145,366, p<0.001), and number of recruits does not change in the year 2100 compared to the year 2000 (W=131,463, p=0.157). For *F*= 0.3 yr^{-1} proportion of mature individuals are only 92.4% (W=55,546, p<0.001), and number of recruits are only 91.1% in the year 2100 compared to the year 2000 (W=2,369, p<0.001). For *F*= 0.4 yr^{-1} proportion of mature individuals are only 83.4% (W=24,057, p<0.001), and number of recruits are only 77.8% in the year 2100 compared to the year 2000 (W=517.5, p<0.001) (Fig. C12).

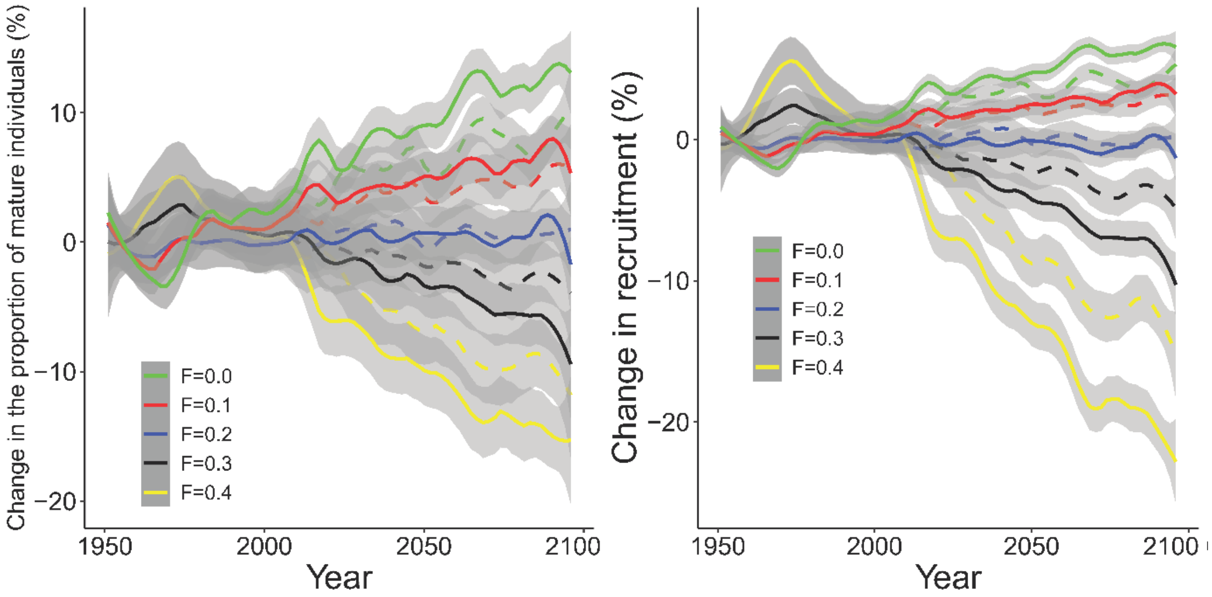


Figure C12. Proportion of mature individuals (left) and number of recruits (right) in the whitefish population in Skrukkebukta from the year 1950-2100 for five different fishing mortalities and two different climate scenarios, RCP-4.5 (dashed line) and RCP-8.5 (solid line) predicted in the individual based model.

Vendace

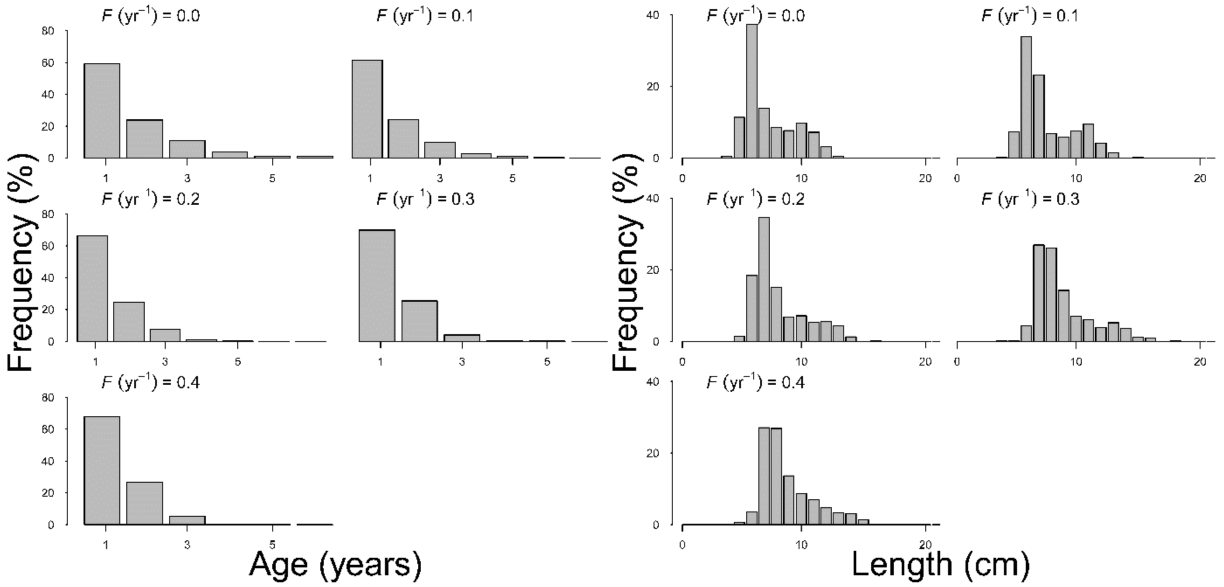


Figure C13. Age-distribution (right) and size-distribution (left) for five different levels of fishing mortality (F= 0.1-0.4 yr^{-1}) under the RCP-8.5 climate scenario in year 2100 for vendace in Lake Skrukkebukt predicted in the individual based model.

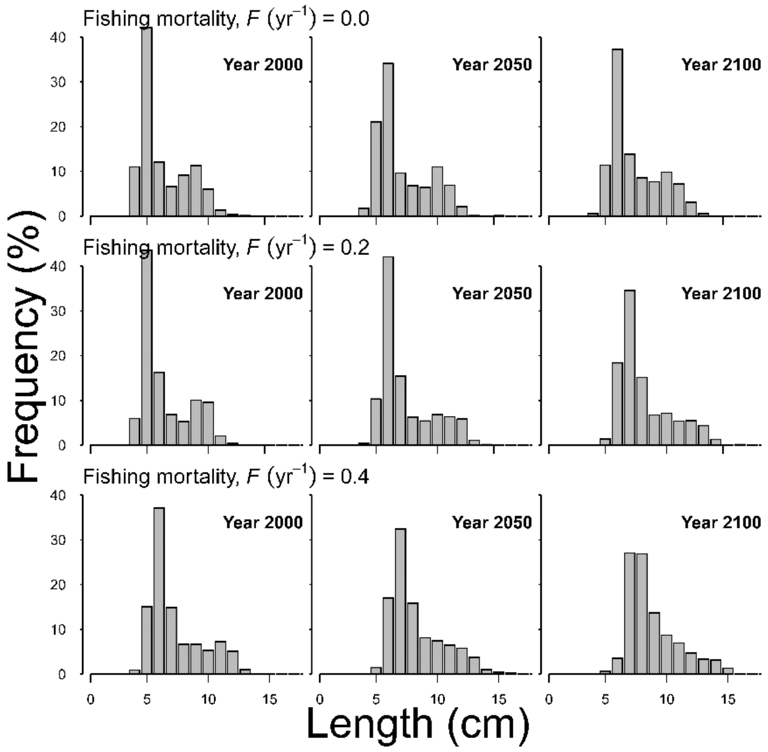


Figure C14. Individual based model predictions of size-distribution in the Arctic charr population in Lake Takvatn for three different fishing mortality scenarios (F= 0.0-, 0.2- & 0.4 yr^{-1}) in the year 2000 (left), year 2050 (middle) and year 2100 (right) for the RCP-8.5 climate scenario.

Proportion of mature individuals increases significantly with warming for all fishing mortality scenarios except for the highest scenario of F= 0.4 yr^{-1}, where proportion of mature individuals stays constant with warming. Number of recruits increases significantly with warming for low and medium fishing mortality scenarios (F< 0.3 yr^{-1}), but decreases with warming for high fishing mortality scenarios (F> 0.2 yr^{-1}). For F= 0.0 yr^{-1} proportion of mature individuals increases with 10.5% (W=217,692, p<0.001) and number of recruits increases with 13.9% from year 2000 to the year 2100 (W=39,533, p<0.001). For F= 0.1 yr^{-1} proportion of mature individuals increases with 7.6% (W=195,180, p<0.001), and number of recruits increases with 15.2% from year 2000 to the year 2100 (W=225,651, p<0.001). For F= 0.2 yr^{-1} proportion of mature individuals increases with 6.4% (W=185,580, p<0.001), and number of recruits increases with 7.1% from year 2000 to the year 2100 (W=178,779, p<0.001). For F= 0.3 yr^{-1} proportion of mature individuals increases with 3.1% (W=154,088, p<0.001), but number of recruits decreases with 5.2% from the year 2100 compared to the year 2000 (W=12,440, p<0.001). For F= 0.4 yr^{-1} proportion of mature individuals stays constant with warming (W=120,664, p=0.342), and number of recruits decreases to only 84.1% in the year 2100 compared to the year 2000 (W=27,516, p<0.001) (Fig. C15).

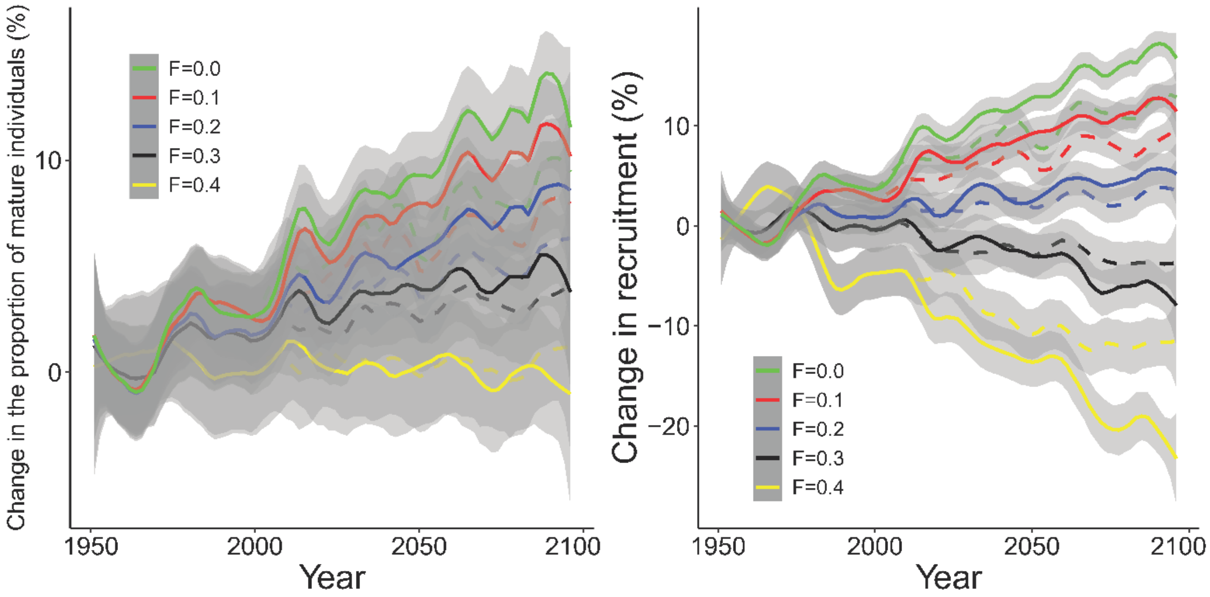


Figure C15. Proportion of mature individuals (left) and number of recruits (right) in the vendace population in Skrukkebukta from the year 1950-2100 for five different fishing mortalities and two different climate scenarios, RCP-4.5 (dashed line) and RCP-8.5 (solid line) predicted in the individual based model.

Density-dependent growth

Our model assumes that consumption rate is dependent on both temperature and density. Maximum consumption is thus fractioned by number of competitors (see original paper), which will affect individual growth rate. In addition, it will also affect the optimum temperature of growth (Fig. C16). Thus, density affects individual somatic growth rate, and the development over time in density-factor is visualized in Figure C17 for all three species, both climate scenarios and five different fishing mortality scenarios. Fishing mortality affects the density of competitors, but warming is also influencing abundance and therefore also density in the populations (Fig. C17). However, the three different species are similarly affected in the development of density by both warming and fisheries.

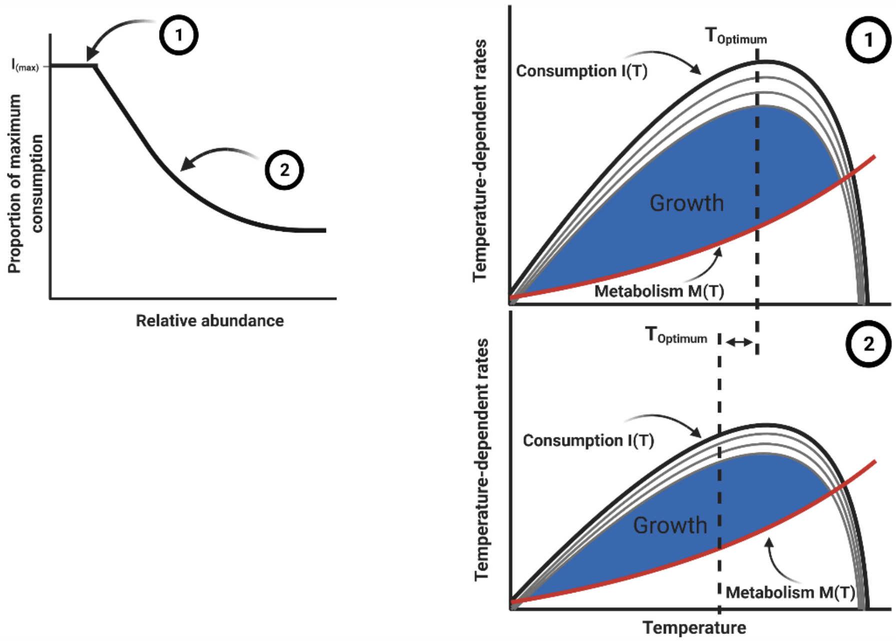


Figure C16. Theoretical representation on how temperature and density affects individual somatic growth in our individual based model. Black line (—): Energy acquired through consumption ($I(T, D)$), Grey lines (—): Represent energy lost to Standard Dynamic Action (SDA), Egestion (E) and Excretion (U). Red line (—): Energy lost through metabolic processes (m(T)). The blue filled area (—): Energy available for somatic growth and/or reproduction (Inspired by Deslauriers et al. 2017).

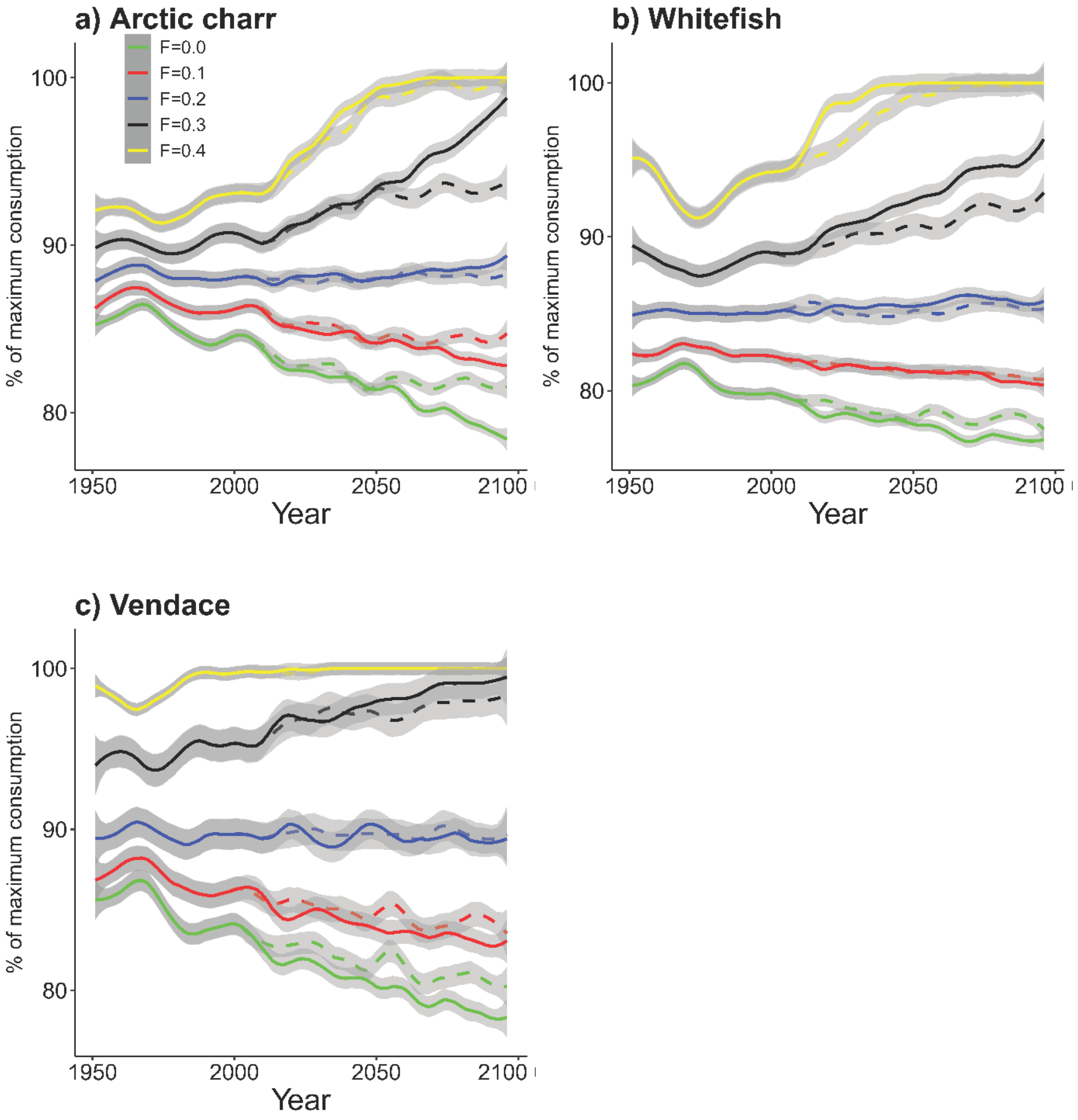


Figure C17. Development in the density-dependent factor from year 1950 to year 2100 with five different fishing mortality scenarios and two different climate scenarios, RCP-4.5 (dashed line) and RCP-8.5 (solid line) for a) Arctic charr in Takvatn, and b) whitefish and c) vendace in Skrukkebukta.

Appendix D: Robustness and sensitivity analyses

For the robustness and sensitivity analysis, we focus on the growth parameters, which are temperature- and density dependent and thus particularly important for our study. We modified consumption rate parameters d and g in eq. 4 in the original paper (or Supplementary Information eq. 3c, Appendix B) to reflect a 5% increase or decrease in the growth parameter c in eq. 2 and 3 in the original paper (or Supplementary Information eq. 3a and 3b, Appendix B). In addition, we focus simultaneously on the natural-mortality parameter M_r that will affect growth indirectly through density-dependence, and modified M_r to reflect 5% increase or decrease in natural mortality (yr^{-1}). We assess how a variation in these parameters affects the individual based model-predicted population stock biomass (Fig. D1, D4 & D7), population age-distribution (Fig. D2, D5 & D8), and individual somatic growth (Fig. D3, D6 & D9). The sensitivity analysis show that small changes in parameter values have no qualitative effects and do not change our conclusions, but could have relative large quantitative effects for some combinations of parameter values. It is also evident that the change in natural mortality have larger effect on both individual level and population level outcomes than a change in growth parameters.

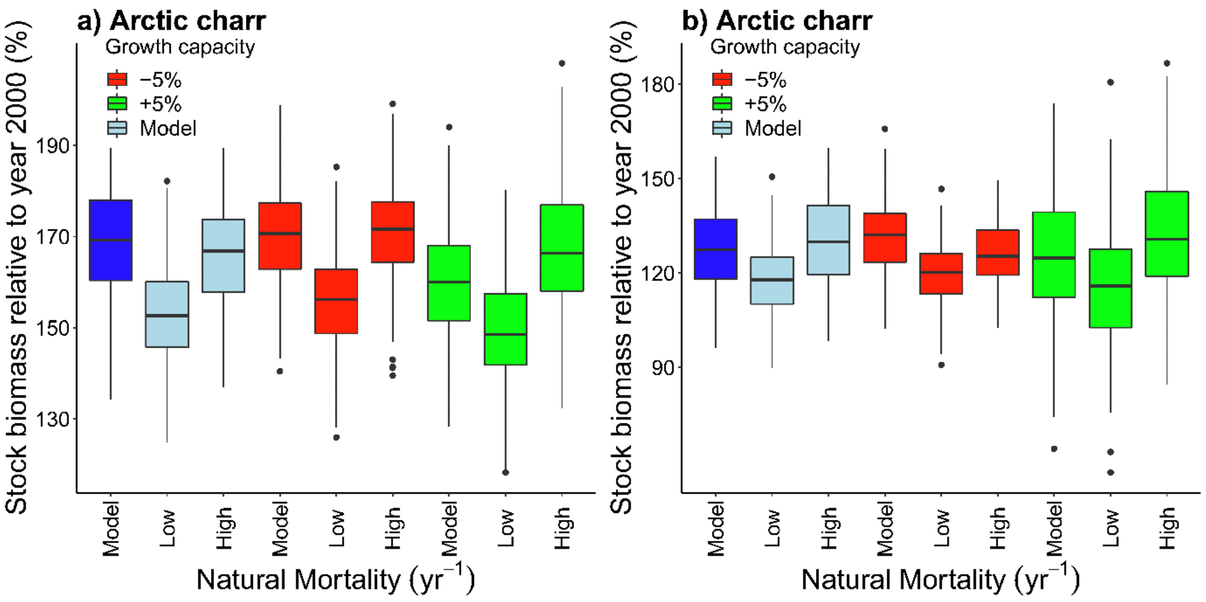


Figure D1. Change in stock biomass from year 2000 to year 2100 for the RCP-8.5 climate scenario with the pairwise combination of three levels of the growth parameter (c) and natural mortality (yr^{-1}) for Arctic charr in Takvatn, a) *F*= 0.0 yr^{-1} and b) *F*= 0.2 yr^{-1}.

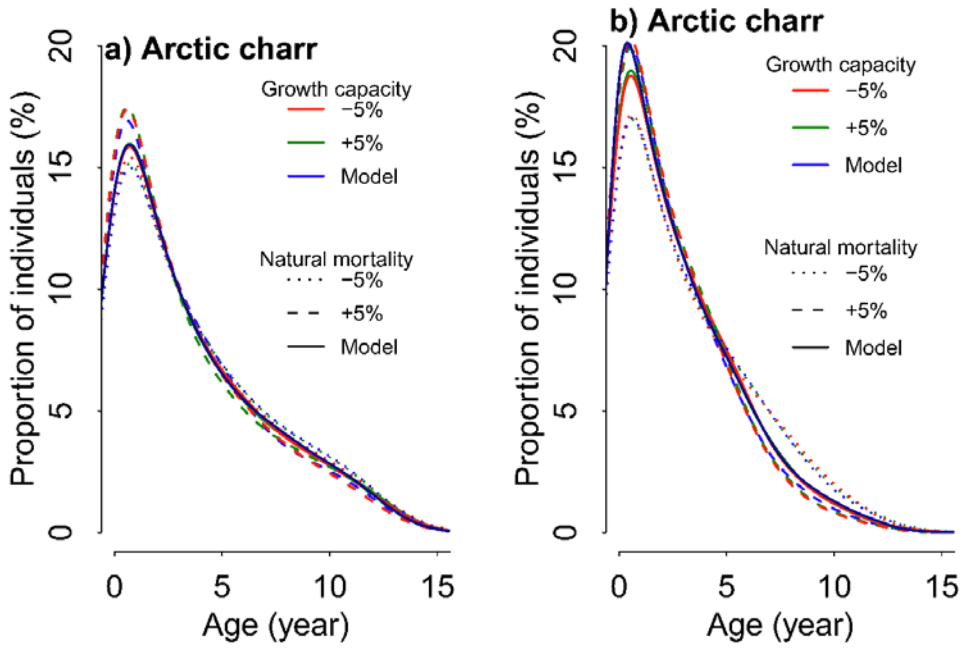


Figure D2. Difference in age-distribution in year 2100 for the RCP-8.5 climate scenario between the pairwise combination of three levels of the growth parameter (c) and natural mortality (yr^{-1}) for Arctic charr in Takvatn, a) *F*= 0.0 yr^{-1} and b) *F*= 0.2 yr^{-1}.

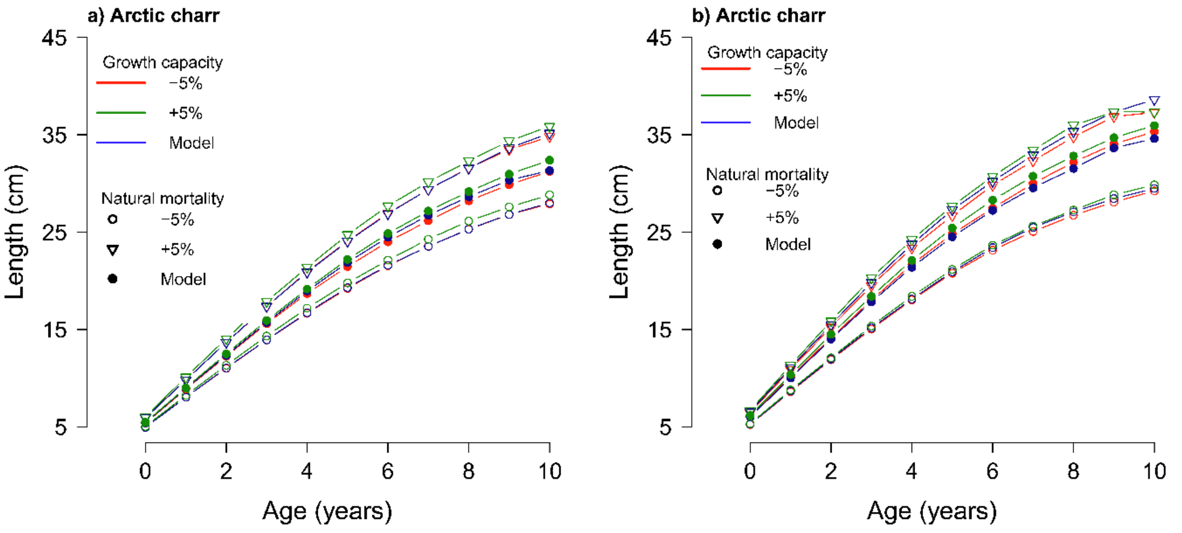


Figure D3. Difference in length-at-age in year 2100 for the RCP-8.5 climate scenario between the pairwise combination of three levels of the growth parameter (c) and natural mortality (yr^{-1}) for Arctic charr in Takvatn, a) F= 0.0 yr^{-1} and b) F= 0.2 yr^{-1}.

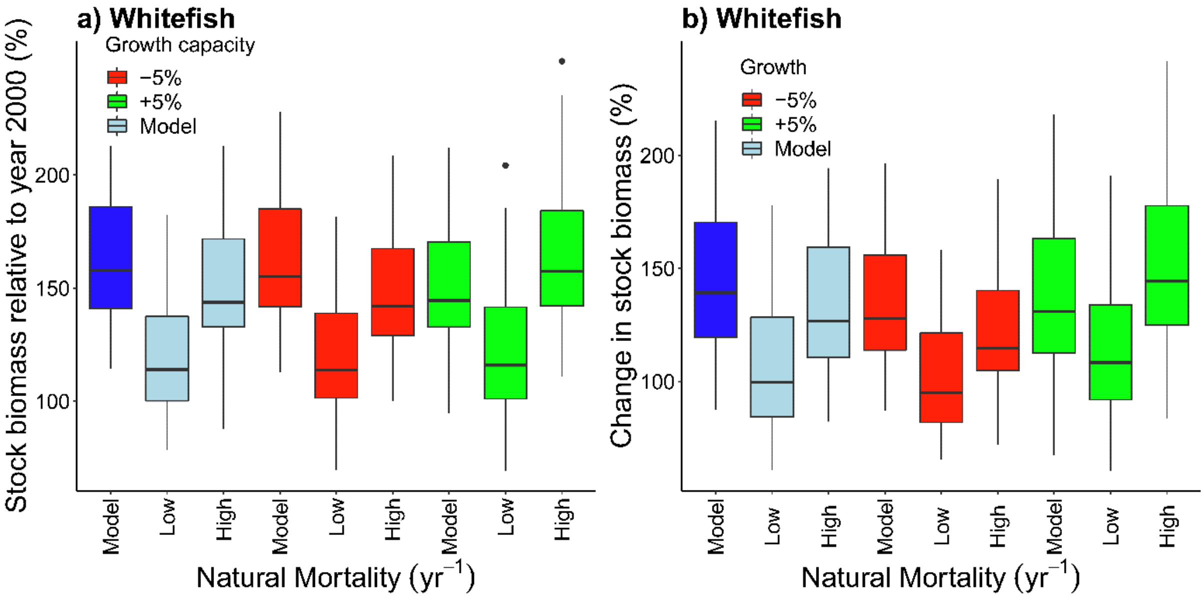


Figure D4. Change in stock biomass from year 2000 to year 2100 for the RCP-8.5 climate scenario with the pairwise combination of three levels of the growth parameter (c) and natural mortality (yr^{-1}) for Whitefish in Skrukkebukta, a) F= 0.0 yr^{-1} and b) F= 0.2 yr^{-1}.

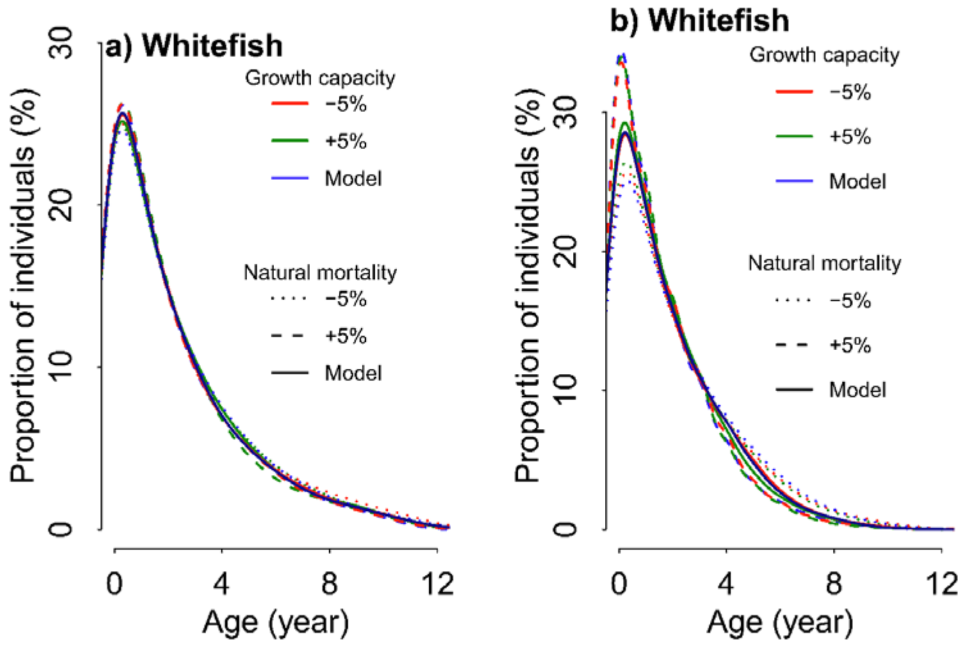


Figure D5. Difference in age-distribution in year 2100 for the RCP-8.5 climate scenario between the pairwise combination of three levels of the growth parameter (c) and natural mortality (yr^{-1}) for whitefish in Skrukkebukta, a) F= 0.0 yr^{-1} and b) F= 0.2 yr^{-1}.

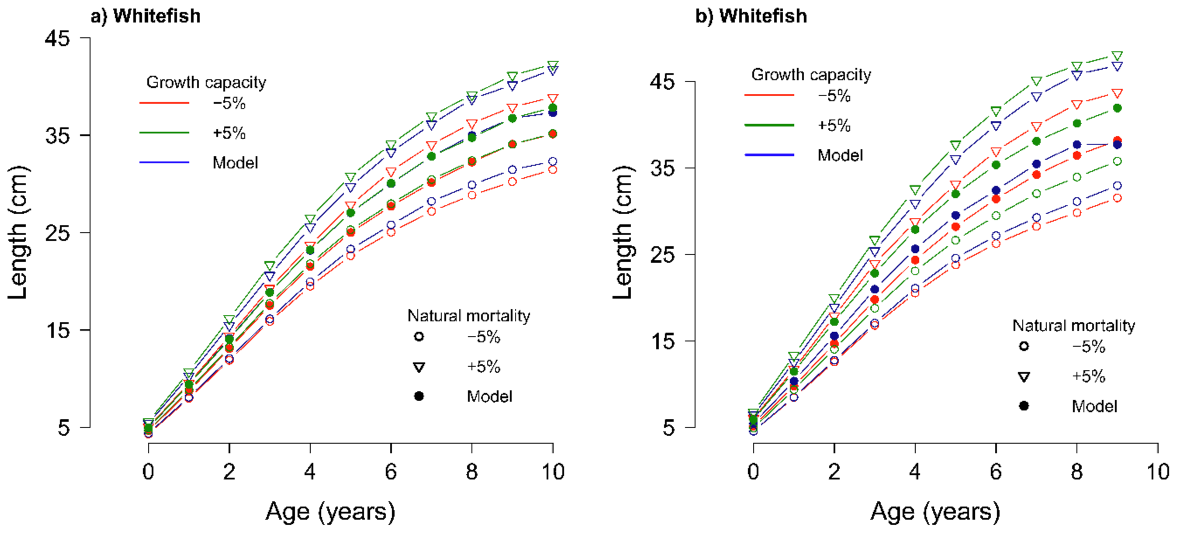


Figure D6. Difference in length-at-age in year 2100 for the RCP-8.5 climate scenario between the pairwise combination of three levels of the growth parameter (c) and natural mortality (yr^{-1}) for whitefish in Skrukkebukta, a) F= 0.0 yr^{-1} and b) F= 0.2 yr^{-1}.

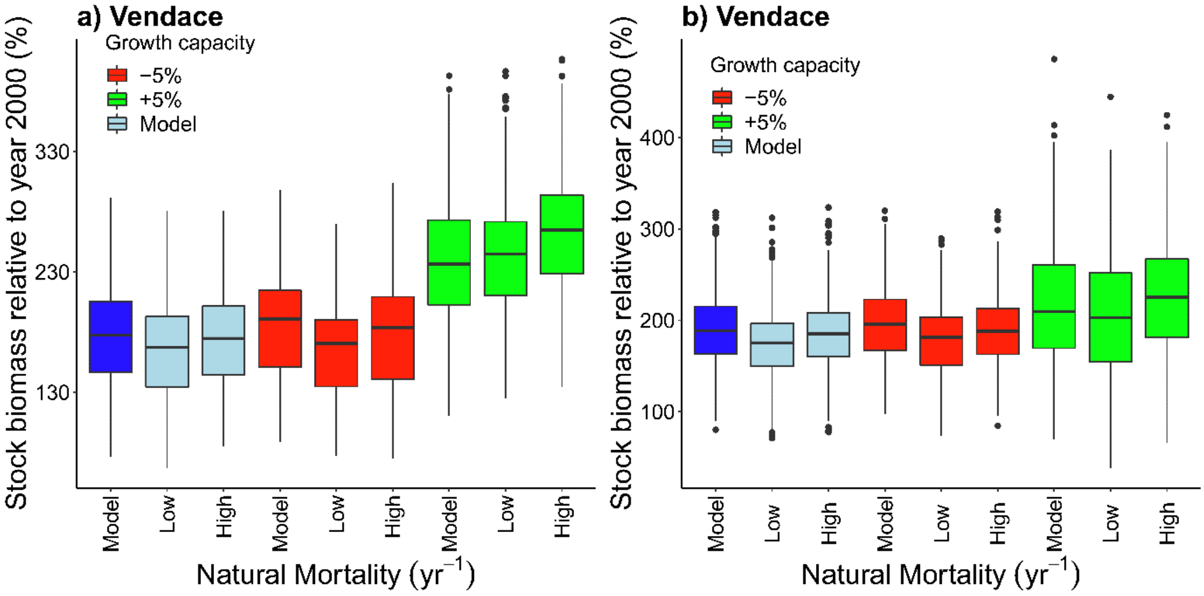


Figure D7. Change in stock biomass from year 2000 to year 2100 for the RCP-8.5 climate scenario with the pairwise combination of three levels of the growth parameter (c) and natural mortality (yr^{-1}) for vendace in Skrukkebukta, a) F= 0.0 yr^{-1} and b) F= 0.2 yr^{-1}.

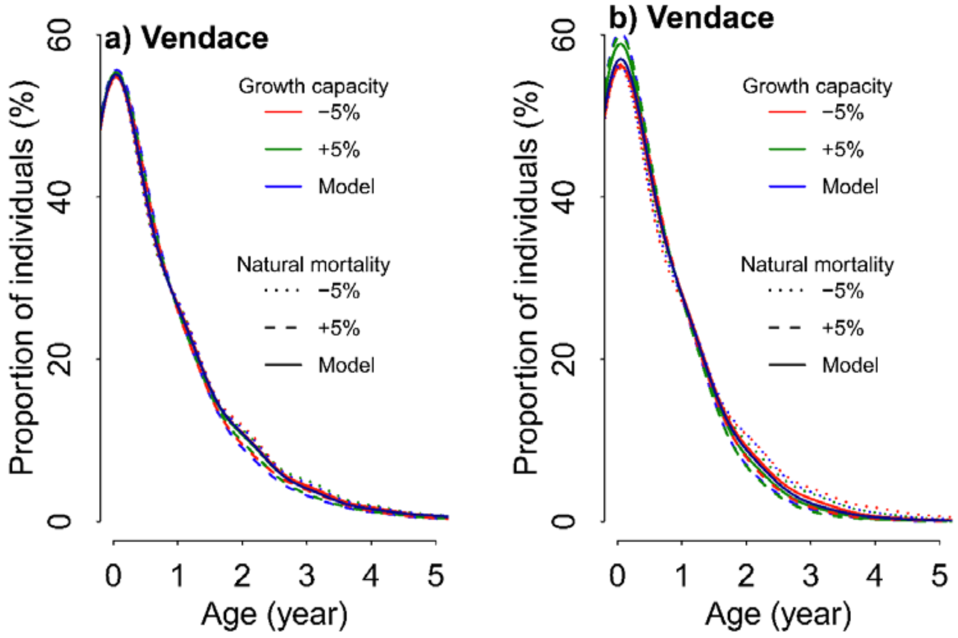


Figure D8. Difference in age-distribution in year 2100 for the RCP-8.5 climate scenario between the pairwise combination of three levels of the growth parameter (c) and natural mortality (yr^{-1}) for vendace in Skrukkebukta, a) F= 0.0 yr^{-1} and b) F= 0.2 yr^{-1}.

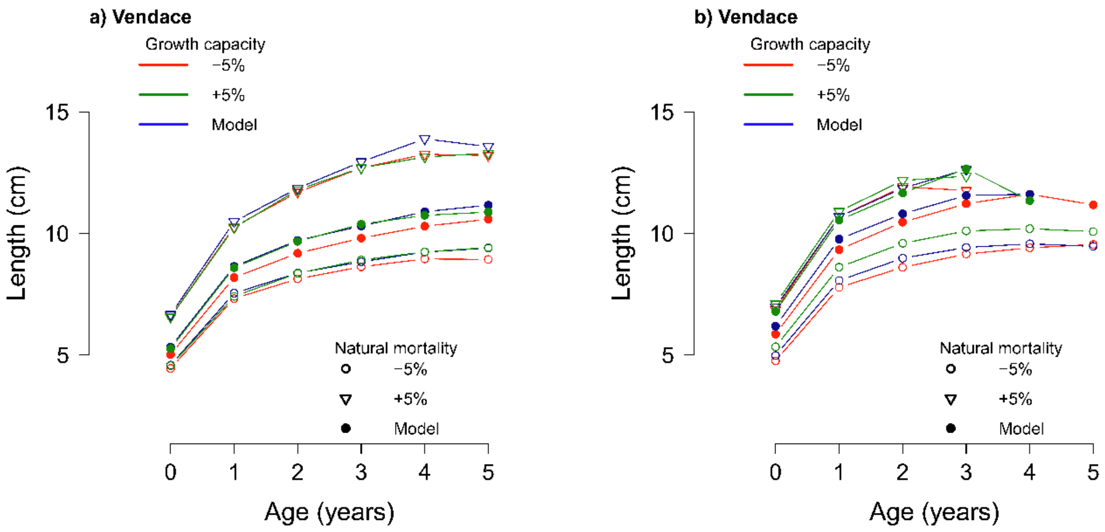


Figure D9. Difference in length-at-age in year 2100 for the RCP-8.5 climate scenario between the pairwise combination of three levels of the growth parameter (c) and natural mortality (yr^{-1}) for vendace in Skrukkebukta, a) F= 0.0 yr^{-1} and b) F= 0.2 yr^{-1}.

Appendix E: Air- and water temperature, General Lake model parameterization, calibration and evaluation and Lake morphometries.

To demonstrate both historic and future climate at high latitude regions in Europe. We used the WorldClim database to show both historic air-temperature and projected future air-temperature (Fig. E1). The WorldClim data we used has high spatial resolution (30 seconds or ~1 km^2 resolution tiles) of both historic measured and future modelled climate (Fick & Hijmans 2017). For the future air-temperature projections, WorldClim uses results from the Coupled Model Intercomparison Project phase 6 (CMIP6), and for mean air-temperature comparison in Figure E1, we used the SSP-8.5 scenario with a regionally downscaled climate model (MPI-ESM) from year 2061-2080. Both for the historical and the projected air-temperature it is a large difference between the western and the eastern part of Fenno-Scandia. To illustrate temperature differences between coastal areas in the west and more inland areas in the east of northern-Norway we used air temperature data from the Worldclim database (Fick & Hijmans 2017). Both historical and projected air temperature data are available in 30 Arc-seconds resolution and we used the same climate model (MPI-ESM) for the projected air temperature data as for the water temperature estimation routine described below (average from 2061-2080). In addition, we used water temperature loggers (HOBO® Pendant temp/light, Part #UA-002-64) deployed at both Lake Skrukkebukta and Lake Takvatn to illustrate how the difference in climatic variables translate into difference in water temperatures from June 2018 to September 2019 (Fig. E2).

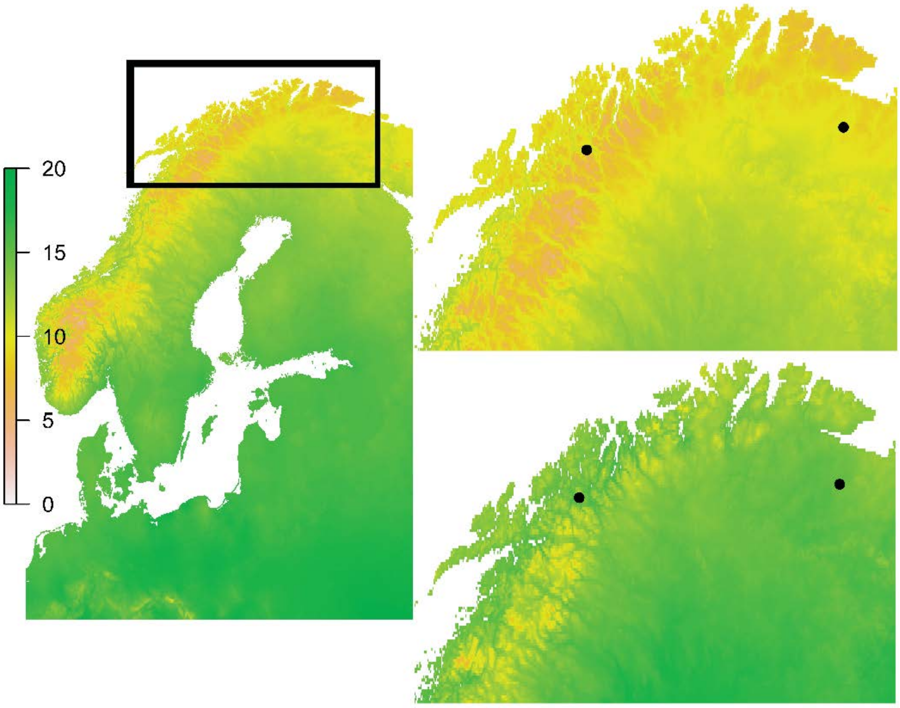


Figure E1. Left: Map of northern Europe with average (1960-2000) July air temperature. Right: Northern Fenno-Scandia with (top) average (1960-2000) July air temperature and (bottom) average projected (year 2061-2081) July air temperature under the RCP-8.5 climate scenario. Black dots represent Takvatn (left) in the Målselv watercourse and Skrukkebukta (right) in the Pasvik watercourse.

We measured water-temperature in both Lake Takvatn and Lake Skrukkebukta with temperature loggers. We measured water-temperature at 1m, 3m, 5m, 7m, 9m, 12m, 15m, 20m, 25m and 30m depth with two different types of HOBO loggers (HOBO® Pendant temp/light, Part #UA-002-64 and HOBO® Water Temp Pro v2, Part #U22-001 for greater depths (20-30 m)) to illustrate how the difference in climatic variables translate into difference in water temperatures from June 2018 to September 2019. In addition, we used this data to validate the GLMr model used to project future water-temperature (see below). There is a clear difference in summer water-temperature between Takvatn and Skrukkebukt, where Skrukkebukt has significantly higher summer water-temperature (mean of top ten meters) than Takvatn (Fig. E2).

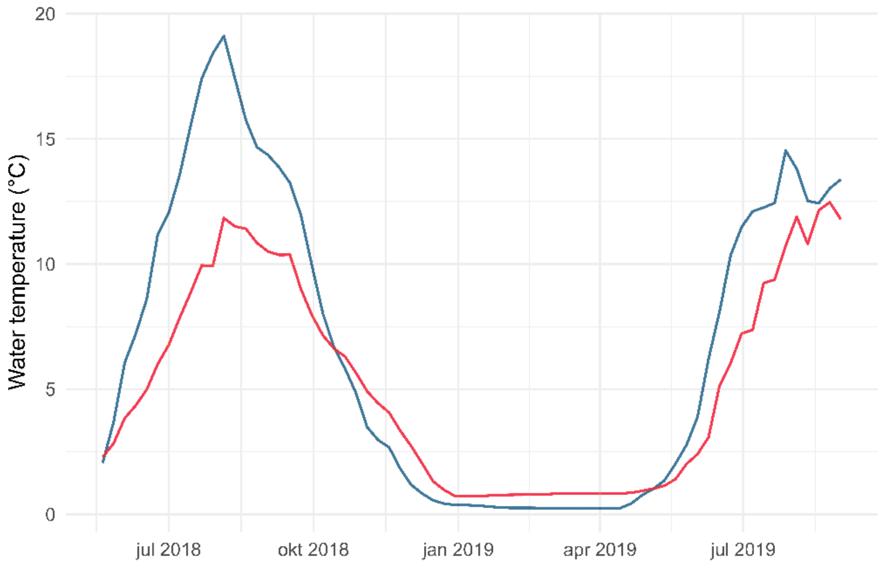


Figure E2. Average water-temperature of the top ten meters in Takvatn in the western part of northern Norway (—) and Skrukkebukta in the eastern part of northern Norway (—) from June 2018 to September 2019 measured with temperature loggers.

Climate scenarios RCP-4.5 and RCP-8.5 were obtained for both the historic period and for future projections (1950–2100) from the EURO-CORDEX project and the Earth System Grid Federation (ESGF) project. The chosen climate model was a regionally downscaled implementation at the finest grid resolution (0.11°) (MPI-M-MPI-ESM-LR), forced by the global circulation model CLMcom-CCLM4-8-17. This climate model has been ranked as the one best fitting our study area in a report by the Norwegian Meteorological Institute (Landgren & Haugen 2016). Air-temperature derived from this climate model is visualized in Figure E3a.

The climate model's outcomes were used to force a one-dimensional air-to-water temperature model implemented by the General Lake Modelling approach, using the R package GLMr (Hipsey et al., 2014). This temperature model assumes no horizontal temperature variability within the water body and computes vertical temperature profiles by accounting for surface heating, surface cooling, and vertical mixing. The model also includes the effects of ice-cover formation and subsequent melting on heating and mixing processes within the lake (Hipsey et al., 2014). We calibrated and evaluated the model using water-temperature data from Lake Takvatn for the years 1982, 1992, 1994, 1997, 2017, 2018 and 2019, and for Lake Skrukkebukta we used water-temperature data from year 2000 to year 2017 obtained from the Skogfoss hydro-power plant to calibrate the model, and water-temperature data from our loggers years 2018 and 2019 to evaluate the model. The GLMr-implemented temperature model requires input data for climatic variables (air temperature, precipitation, solar radiation, wind speed, cloud cover, and relative humidity) and lake-morphometric variables (see Fig. E10 and Table E1) (Hipsey et al., 2014). Model evaluation summary can be found below (Fig. E6-E9).

Climate warming is predicted to increase both air- and water temperature in northern parts of Europe towards year 2100 (Fig. E3a). The summer air temperature difference between lakes in western and eastern part of northern-Norway is relative large and the difference will maintain with warming (Fig. E3a), therefore lakes in eastern part of northern-Norway have significantly warmer water temperature during the summer than their counterparts in the west (Fig. E3b). Annual mean air temperature increases with 0.46 ˚C (t-value=32.74, $p<0.001$, adj-R^2 =0.88) and 0.40 ˚C (t-value=27.69, $p<0.001$, adj-R^2 =0.84) per decade (year 1950-2100) under the RCP-8.5 climate scenario in Skrukkebukta and Takvatn, respectively. Modelled water-temperature show similar difference between lakes in eastern (Skrukkebukta) and western (Takvatn) part of northern Fennoscandia as air-temperature (Fig. E3b). In addition, length of growth season increases substantially for both study systems and for both climate scenarios.

Lake Skrukkebukta has a significantly longer growth season than Lake Takvatn both for the retrospective and the prospective time period (Fig. E3 and E4). In Lake Takvatn number of growth days (water-temperature between 2-18 ˚C) increases with 2.5 days ($F=93.67_{1,146}$, $R^2=0.39$) and 4.2 ($F=307_{1,146}$, $R^2=0.68$) days per decade for the RCP-4.5 and RCP-8.5 climate scenarios, respectively. For Lake Skrukkebukta the increase is in growth season (water-temperature between 2-18 ˚C) is also substantial, with 2.2 days ($F=120.8_{1,146}$, $R^2=0.45$) and 3.7 days ($F=216.6_{1,146}$, $R^2=0.595$) per decade for the RCP-4.5 and RCP-8.5 climate scenarios, respectively. In addition, the period with water temperature within the 20 % of the maximum of the temperature-dependent growth curve are increasing for all three species. For Arctic charr in the cold western, part of northern Norway the increase is 3.3 days per decade. For whitefish and vendace, in the warmer eastern part of northern Norway, the increase is lower but substantial with 1.7- and 2.9 days per decade, respectively.

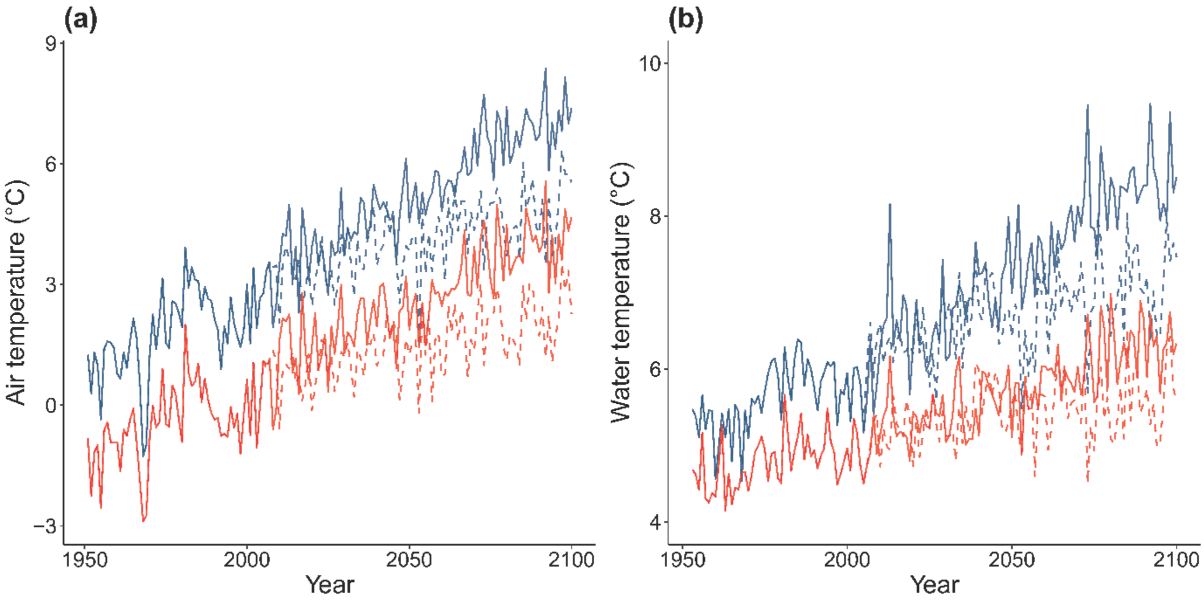


Figure E3. Annual mean air temperature (a) and annual mean water temperature for the upper ten meters (b) for Lake Skrukkebukta (—), eastern part of northern Norway, and Lake Takvatn (—), western part of northern Norway. Solid line represent the RCP-8.5 climate scenario and dashed line represent the RCP-4.5 climate scenario.

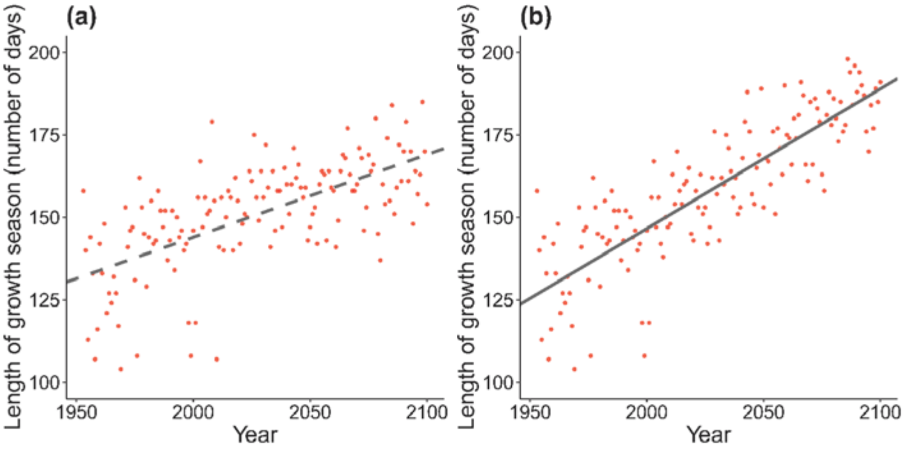


Figure E4. Number of days with water temperature between 2-18 ˚C (length-of-growth-season) for Arctic charr in Takvatn under two different climate scenarios a) RCP-4.5 and b) RCP-8.5.

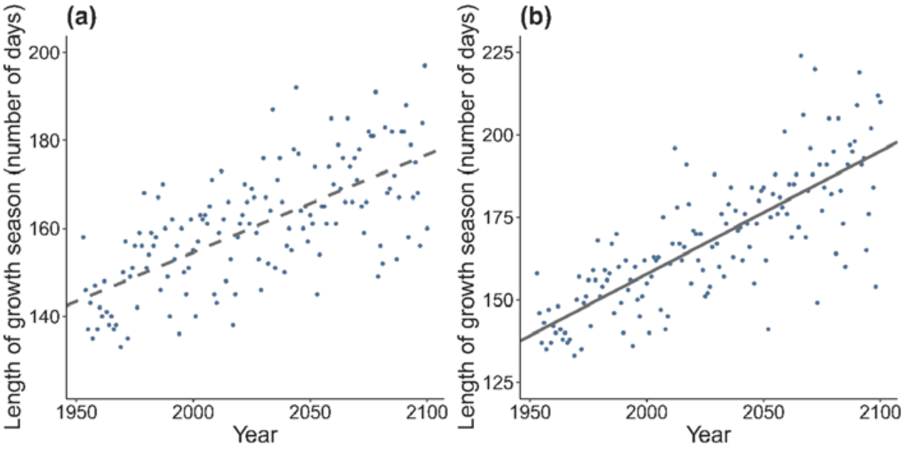


Figure E5. Number of days with water temperature between 2-18 ˚C (length-of-growth-season) for whitefish and vendace in Skrukkebukta under two different climate scenarios a) RCP-4.5 and b) RCP-8.5.

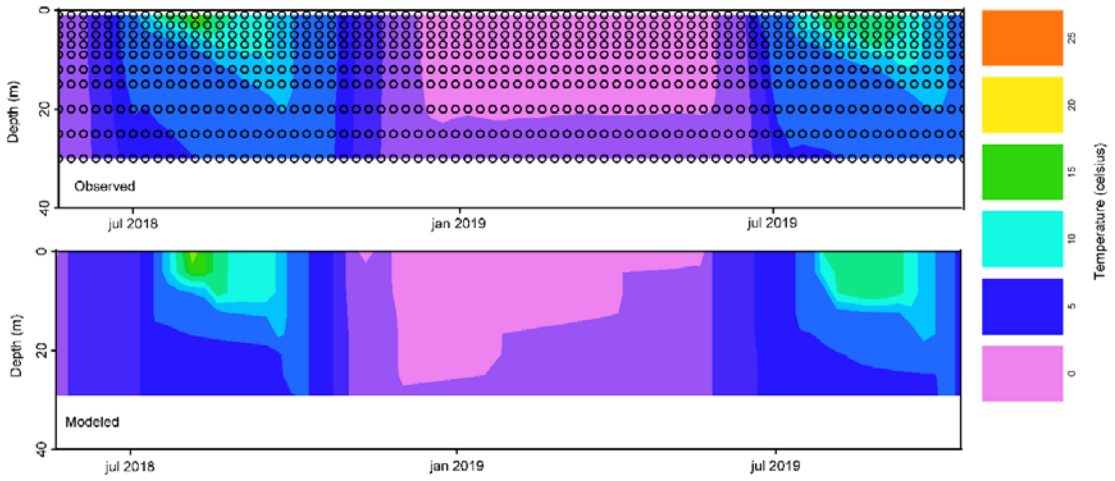


Figure E6. Comparison of observed (top panel) and modelled (bottom panel) water temperature in Lake Takvatn from May 2018 to October 2019. Open circles depicts the individual measurements of water temperature by temperature loggers.

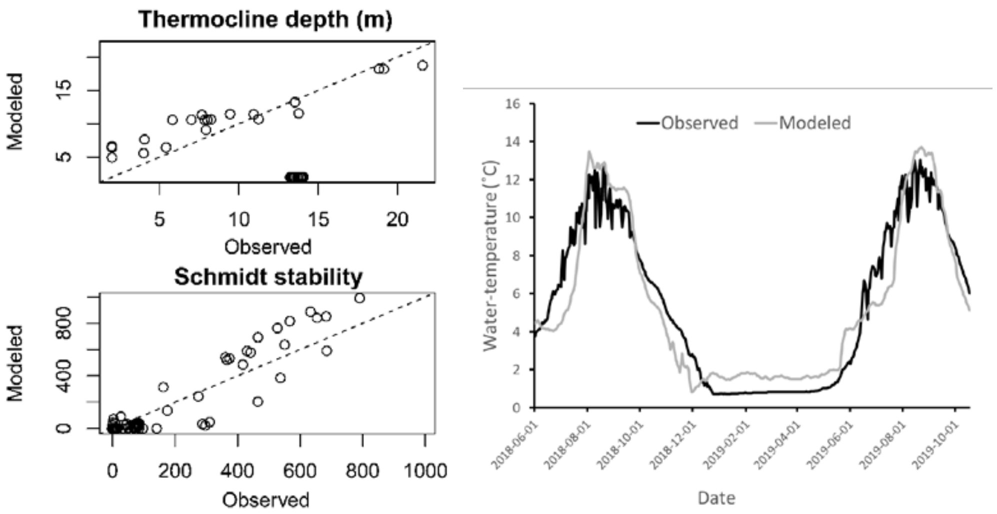


Figure E7. Observed vs. modelled thermocline depth (top left), Schmidt stability (bottom left) and average water temperature (right) for the top ten meters in Lake Takvatn from June 2018 to November 2019.

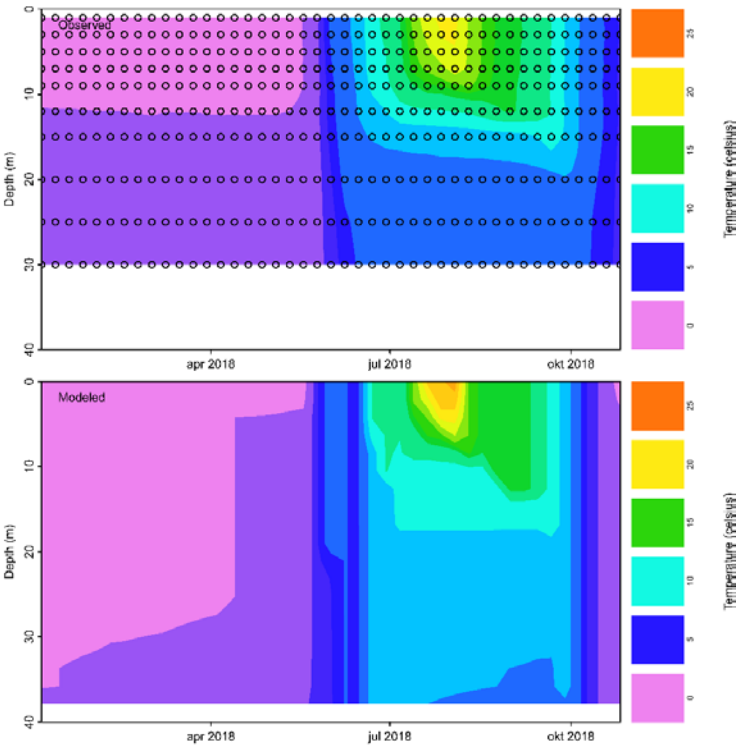


Figure E8. Comparison of observed (top panel) and modelled (bottom panel) water temperature in Lake Skrukkebukta from March 2018 to October 2018. Open circles depicts the individual measurements of water temperature by temperature loggers.

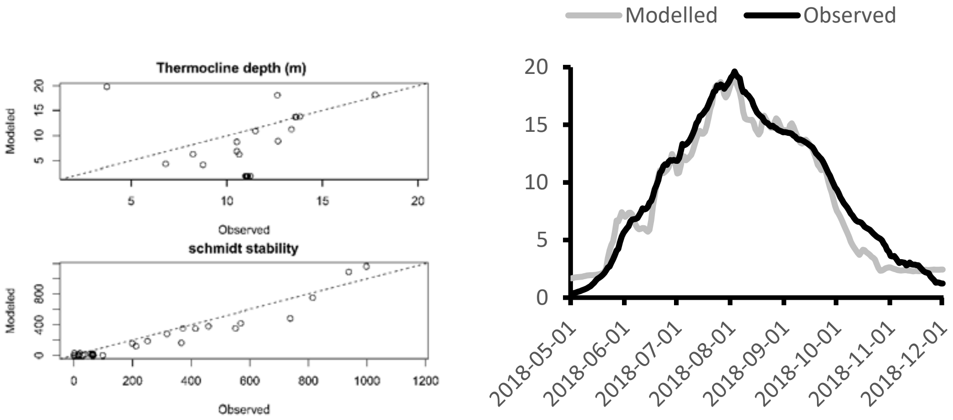


Figure E9. Observed vs. modelled thermocline depth (top left), Schmidt stability (bottom left) and average water temperature (right) for the top ten meters in Lake Skrukkebukta from May 2018 to December 2018.

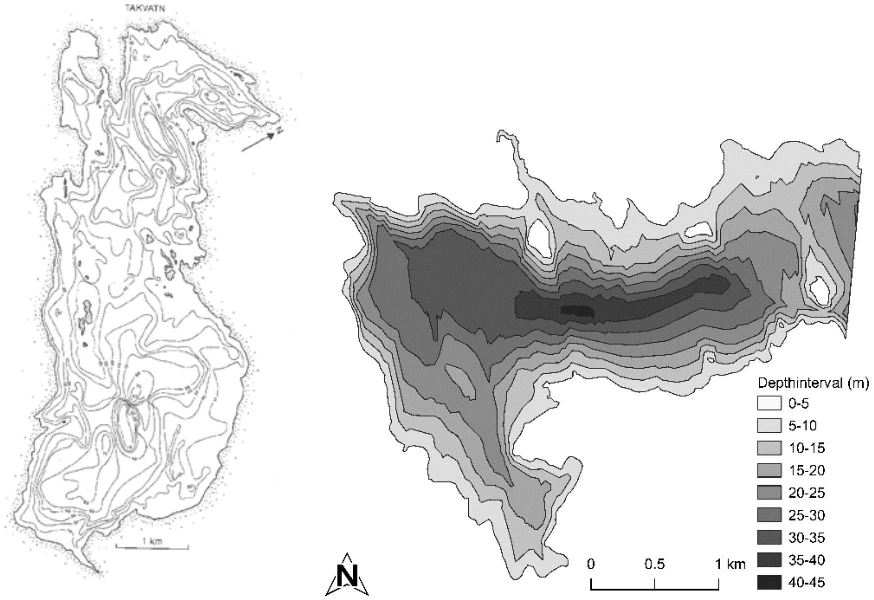


Figure E10. Bathymetric map of Lake Takvatn (left) and Lake Skrukkebukta (right).

Table E1. Locality characteristics of Lake Skrukkebukta and Lake Takvatn.

Parameter	*Lake Skrukkebukta*	*Lake Takvatn*
Latitude (˚N)	69°33′	69°07′
Longitude (˚E)	30°07′	19°05′
Surface Area (km^2)	7	15
Altitude (m.a.s.l)	21	214
Max depth (m)	38	80
Secchi depth (m)	4-5.5	14
pH	6.9	6.9-7.4
ToT P (µg l^{-1})	7	<6
ToT N (µg l^{-1})	156	110

Source: Dahl-Hansen 1995, Primicerio 2000, Kaihlainen et al. 2011.

References:

Dahl-Hansen, G. A. (1995). Long-term changes in crustacean zooplankton—the effects of a mass removal of Arctic chan, Salvelinus alpinus (L.), from an oligotrophic lake. *Journal of Plankton Research, 17,* 1819-1833.

Deslauriers, D., S.R. Chipps, J.E. Breck, J.A. Rice & Madenjian, C.P. (2017). Fish Bioenergetics 4.0: An R-based modeling application. *Fisheries, 42*, 586-596.

Fick, S.E. & Hijmans, R.J. (2017). WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*, 4302-4315.

Hipsey, M.R., Bruce, L.C., & Hamilton, D.P. (2014). GLM – General Lake Model: model overview and user information. *AED Report #26*. University of Western Australia, Perth, Australia, pp. 42.

Kahilainen, K.K., Siwertsson, A., Gjelland, K.Ø., Knudsen, R., Bøhn, T., & Amundsen, P.-A. (2011). The role of gill raker number variability in adaptive radiation of coregonid fish. *Evolutionary Ecology, 25*, 573-588.

Landgren, O.A., & Haugen, J.E. (2016). Updated ranking of GCM-RCM results for five Scandinavian locations. *METreport 7/2016*. Norwegian Meteorological Institute, Oslo, Norway, pp. 14.

Primicerio, R. (2000). Seasonal changes in vertical distribution of zooplankton in an oligotrophic, subarctic lake (Lake Takvatn, Norway). *Limnologica*, *30,* 301-310.

Paper 3

Increase in relative importance of cool-water fish at high latitudes emerges from individual level responses to climate warming.

Aslak Smalås[1], Raul Primicerio[1], Kimmo K. Kahilainen[2], Petr M. Terentyev[3], Nikolay A. Kashulin[3], Elena M. Zubova[3] and Per-Arne Amundsen[1]

[1]Faculty of Bioscience, Fisheries and Economy, UiT – The Arctic University of Norway.

[2]Lammi Biological Station, University of Helsinki, Finland.

[3]Institute of the Industrial Ecology Problems of the North (INEP) KSC RAS, Russia.

Corresponding author: Aslak Smalås, e-mail: aslak.smalas@uit.no

Abstract

High latitude ecosystems are experiencing the most rapid warming on earth, expected to trigger a diverse array of ecological responses. Climate warming effects on the ecophysiology of cool-water adapted fish close to their northern range edge, i.e., at the cold end of their thermal distribution, will promote somatic growth, which in turn affects maturation schedules, reproduction and survival, boosting their population growth. At high latitudes, cool-water adapted perch, a spring-spawning species, is expected to benefit from increasing temperatures and a prolonged productive season driven by warming, thereby increasing in abundance relative to cold-water fish living in the same lakes. We studied 11 perch populations at the northern range edge of the species to investigate if their relative importance has increased during the recent period of rapid warming. Ten of the studied populations displayed a marked increase in their numerical importance in the benthic fish communities during the recent period of rapid warming. To further investigate the influence of climate warming on the population responses in perch, we focused on two long-term studies spanning 30 years (1991-2020). We show that climate warming affects population level processes via direct and indirect temperature effects on perch individuals. The increase in abundance of perch in high latitude lakes arises from increased survival of 0+ individuals, faster juvenile growth and ensuing earlier maturation, all boosted by climate warming. Given the speed and magnitude of the perch population response to warming, management strategies should focus on limiting future introductions and invasions of cool-water fish in high latitude ecosystems.

Keywords: perch, climate change, thermal guilds, population dynamics, life history, growth, age at maturation, recruitment

Introduction

High latitude regions are experiencing the most rapid warming on Earth, a trend projected to continue towards year 2100 (Parmesan 2006, IPCC 2013). Rapid warming strongly affects freshwater ecosystems (O'Reilly et al. 2015), leading to changes in species abundance, phenology and distribution (Hickling et al. 2006, Comte et al. 2013, Campana et al. 2020). Temperature driven changes in physiological rates of ectotherms are expected to trigger a diverse array of ecological responses (Biro et al. 2007, Arula et al. 2017, Huss et al. 2019, Rezende et al. 2019), with implications for ecosystem structure and function (Dodds et al. 2013, Benateau et al. 2019). Fish are strongly influenced by ambient temperature, with species displaying distinctive thermal niches (Hayden et al. 2014) that provide a basis for classification into thermal guilds (Magnuson et al. 1979). Climate warming tends to favor fish populations currently experiencing the cold end of their species thermal range, typically in proximity of the northern limits of a species distribution (Ficke et al. 2007, Campana et al. 2020). As temperature increases, these populations are likely to outperform competing species of colder temperature guilds (Hein et al. 2014, Hayden et al. 2017). Evidence in support of, or against, these expectations is presently lacking due to a paucity of long-term ecological studies of freshwater fish communities in the rapidly warming Arctic (Amundsen et al. 2019, Zubova et al. 2020).

The impact of increasing temperatures on fish populations is mediated by direct ecophysiological effects and indirect life history responses that ultimately affect survival and reproduction. In ectotherms, temperature limits biological rates, affecting for instance food intake and metabolism and their balance determining the net energy gain of an organism (Jobling 2002). Growth rate will therefore depend on ambient temperature, with maximum growth being reached at an intermediate, optimum temperature within the thermal niche of a species (Magnuson et al. 1979, Gvoždík 2018). The growth rate of individuals living at temperatures below their optimum might increase with climate warming, given sufficient food availability (Huss et al. 2019, Smalås et al. 2020, Smalås et al. MS in prep.). Higher juvenile growth rates lead to larger size at age and earlier maturation. Larger size at age might increase survival, especially during early life stages, because mortality in fish is largely size-dependent (Elliott 1993, Hurst 2007, Perez & Munch 2010). Spring-spawning fish tend to benefit from climate warming as an extended growth season helps to gain a sufficient size for successful overwintering (Hurst 2007, Rolls et al. 2017). Thus, faster growth increases the probability of reaching maturity, which is further enhanced by earlier maturation, overall resulting in higher transition rates to the adult, reproductive stage. Recruitment rates can be further enhanced by faster somatic growth as young adult females become larger, thereby producing larger clutches. Furthermore, fecundity has been demonstrated to be higher in fish living closer to their thermal optima (Pörtner et al. 2001), and thus climate warming is likely to enhance population fecundity (Heibo et al. 2005). In addition, some life stages, in particular the egg and larvae, often have a narrower temperature range for survival and successful development than other life stages (Dahlke et al. 2020). These critical life stages are classified as bottlenecks and might therefore be pivotal in determining individual fitness and population recruitment. Populations living close to the northern end of their distribution, might in colder years suffer from temperatures that are too low for successful development, especially in critical periods such as survival over the first winter, and should therefore benefit from climate warming (Reist et al. 2006, Hurst 2007, Shuter et al. 2012, Dahlke et al. 2020).

The effects of climate warming on high latitude lakes go beyond increasing water temperatures, and predicted changes in the aquatic environment such as increased productivity, decreased dissolved oxygen levels and altered seasonality, are likely to favor cool-water species more than the dominant cold-water salmonids (Klapper 1991, Ficke et al. 2007, Kundzewicz et al. 2008, Finstad et al. 2016, Rolls et al. 2017, van Dorst et al. 2019). Increase in temperature and productivity will expectedly first favor percids, and later cyprinids, over salmonids (Persson et al. 1991, Hayden et al. 2017). Furthermore, shorter duration of ice cover, more rapid warming of the epilimnion and decreasing oxygen levels in the hypolimnion will limit the habitat availability of cold-water adapted salmonids in contrast to cool- and warm-water adapted species (Lehtonen 1996, Ficke et al. 2007, Rolls et al. 2017). These cool-water species have been shown to redistribute northwards and to higher altitudes over the last few decades of rapid warming (Comte et al. 2013, Hayden et al. 2014, Rolls et al. 2017). One such cool-water species, the European perch (*Perca fluviatilis*), hereafter perch, (Hayden et al. 2014), has its northern range edge in subarctic regions of Eurasia around 70°N, but with its wide temperature range for growth, between 5-33°C, and an optimum between 16-27 °C (Hokanson 1977, Willemsen 1977, Craig 1978, Karås 1987, Karås 1990), it has a wide distribution, reaching about 40°N in the south. In high latitude lakes, perch thrives in benthic areas, mostly in the littoral zone of lakes, but in warmer systems perch also uses the pelagic habitat extensively (Hayden et al. 2019). Perch is an ontogenetic generalist, feeding on zooplankton as larvae, and shifting to a diet of zoobenthos, and later fish, as it grows larger (Persson 1988, Hjelm et al. 2001, Amundsen et al. 2003; Hayden et al. 2014) (more detailed information in material and methods).

Here, we address the effects of climate warming on perch populations at the northern end of the species distribution, using long-term surveys of high latitude freshwater fish communities (68-70°N). As a cool-water adapted species, we expect perch to benefit from increasing temperatures and a prolonged productive season, leading to increased abundance and numerical importance relative to cold-water adapted fish co-inhabiting the sampled lakes. Several mechanisms underlie our expectation of an increase in the relative importance of perch following the recent rapid warming. Specifically, we focus on the life history and ecological implications of temperature-induced increase in somatic growth rate, anticipating that higher growth rates i) reduce the duration of critical life stages, ii) increase size at age, and iii) anticipate maturation age; overall improving survival and increasing recruitment rates and total population fecundity (see Fig. 1).

Material and Methods

Study area and model species

The study area is concentrated in northern Fennoscandia, with lakes situated in Norway, Finland and Russia. All lakes are located north of the Arctic Circle, towards the northern end of the distribution of cool-water fish species (> 68˚N) (Fig. 2). To assess the relative importance of Eurasian perch, we compiled data from 11 lakes sampled on multiple occasions over the last 30 years. The eleven study lakes were sampled between 2 and 26 times, with time series ranging from 8 to 32 years (Appendix Table S1). Two study sites, Lake Vaggatem and Lake Skrukkebukta, were selected for an in depth analysis because these two lakes were sampled almost annually for 30 years, while also including daily data on water temperature for most of the long-term series (see more details below).

The Eurasian perch is distributed throughout northern Eurasia, ranging from 40°N to 70°N. The species is common and widespread in lakes, ponds and slow-running rivers. It is a generalist that has a size-dependent ontogenetic dietary niche-shift, where larvae and small juveniles are pelagic zooplankton feeders, before they shift to feeding on benthic macroinvertebrates at intermediate sizes, and larger individuals feed on fish (Persson 1988, Hjelm et al. 2001). It is common in both recreational and subsistence fisheries, with a global catch statistics of around 30 000 tons (FAO 2020). Perch is a cool-water fish (e.g. Shuter et al. 2012, Hayden et al. 2014), with temperature requirements for development and growth that are size and stage dependent (Hokanson 1977, Dahlke et al. 2020). The temperature range for normal egg development is between 7-18 ˚C, and the optimum is estimated to be between 13-

14˚C (Hokanson & Kleiner 1974, Hoestlandt & Devienne 1980, Saat et al. 1996). The reported minimum temperature for growth is between 5-10 ˚C (Karås 1987, Karås 1990, Hokanson & Kleiner 1974) and maximum temperature for growth between 31.4- 33.5 ˚C (Alabaster & Downing 1966, Willemsen 1977). Optimal temperature ranges for growth vary between the different life stages. At the larval stage there is an optimum range between 12-25 ˚C (EIFAC 1969 in Küttel et al. 2002, Karås 1996), whereas for juveniles the reported optimum temperature is 25 ˚C (Kleiner 1974). For adult perch, the reported optimum range is between 16-27 ˚C (Horoszewicz 1973 in Hokanson 1977, Craig 1978), and the range of spawning temperatures falls between 5-19 ˚C (Hokanson 1977) (see Appendix Fig. S11 for relationship between water temperature and somatic growth in perch).

Fish sampling and individual data

The total number of sampled fish across the 11 lakes was nearly 60 000, of which 12 000 were perch, and the littoral catches from this data were used to describe the development in proportion of perch in the 11 lakes (Appendix Table S1). In addition to perch, whitefish (*Coregonus lavaretus*) was present in all lakes except for Lake Shounjavri, and was either the most abundant or the second most abundant fish species, next to perch, in the littoral zone of the different lakes. Besides perch and whitefish, pike (*Esox lucius*), burbot (*Lota lota*), trout (*Salmo trutta*), grayling (*Thymallus thymallus*), ninespined stickleback (*Pungitius pungitius*) and common minnow (*Phoxinus phoxinus*) were present in lower abundances in most lakes. Arctic charr (*Salvelinus alpinus*) was only present in Lake Shounjavri and Lake Stourajavri, while vendace (*Coregonus albula*) was present in a few lakes. Fish were collected using multimesh gill-nets or gill net series in all three sampled habitats (i.e. littoral, pelagic, profundal) of the lakes, but only fish from the littoral zone were included in the analyses because the sampling in the other habitats was more scattered in both time and space. The fish communities were usually sampled between July and September, with the majority of the sampling being conducted in September. Benthic multi-mesh gillnets with mesh-size ranging from 8 to 60 mm and mono-mesh gillnets with one mesh-size throughout the net were used, these nets are 1.5-1.8 m deep and 25-40 m long. The gillnets were put out in the evening and taken up in the morning, giving approximately 12 hours of soaking time.

We used individual data from the two lakes most frequently and intensively sampled (Lake Vaggatem and Lake Skrukkebukta), to assess changes in life history parameters over time in the perch populations. These two lakes were selected because of their long time series (~1991-2020) with mostly annual sampling, and detailed individual data collected from year 2003 to 2020. A total of 2960 individual perch from Lake Vaggatem (n=38-608 per year) and Lake Skrukkebukta (n=30-130) were sampled and inspected using the following procedure between 2003 and 2020: fork length was measured to nearest mm, weight was measured to nearest gram, sex and maturation status were determined visually, the latter as either immature or mature, and age was determined from cleaned and intact operculum bones under preparation microscope using magnification 2x-20x. Age estimation for each fish individual was performed independently by a minimum of two different persons. For summary information on mean body length (cm), mean body weight (g), sex ratio, proportion of 1 year olds within the perch population, average Fulton’s condition factor (K) (calculated as: $K = 100 \cdot \text{weight}/\text{length}^3$) (Froese 2006), and von Bertalanffy`s growth parameters, asymptotic length $L_\infty$ and initial growth, $g$ (Mooij et al. 1999), see Tables S2 & S3 in the Appendix. The estimation of the von Bertalanffy`s growth parameters are described below. Mean body size and the estimated average condition factor (K) did not change significantly over time or with the different explanatory variables tested here.

Temperature

For the two main study systems, Lake Skrukkebukta and Lake Vaggatem, daily water temperature measurements were available from an automated datalogger at the Skogfoss hydropower plant situated 25 km upstream from Lake Skrukkebukta and 23 km downstream from Lake Vaggatem. We calculated annual mean water temperature, mean summer temperature (Jun-Jul-Aug) and mean autumn temperature (Sep-Oct-Nov) from the logger data. Mean annual water temperature has increased significantly by 0.3°C per decade ($p<0.01$, $F=9.361_{1,25}$, adj-R^2= 0.243, Appendix Table S4), mean autumn temperature (September-November) has also increased significantly by 0.4 °C per decade ($p<0.01$, $F=11.26_{1,26}$, adj-R^2= 0.275, Appendix Table S5), and mean summer water temperature (June-August) by 0.4 °C per decade (Fig. 3) ($p=0.037$, $F=4.87_{1,25}$, adj-R^2= 0.13, Appendix Table S6).

Statistical analysis

The proportion of perch in the fish community was calculated as the number of perch caught relative to the total number of fish caught in the littoral zone of the different lakes. To estimate how the proportion of perch in the catches changed over time we used a Linear Mixed Effect model (LME) with location (lakes) as random effect, using the nlme-package in R. The response variable was log(x+1) transformed. Relative density of fish in terms of Catch-Per-Unit-Effort (CPUE) was readily available for the two main study systems, Lake Skrukkebukta and Lake Vaggatem. The CPUE was calculated as the number of fish caught per 100 m^2 per night (or 12 hours). To investigate the change in relative density over time, we estimated separate linear models for the two lakes, with log(CPUE+1) as the response and year as the predictor. To estimate the relationship of relative density and water temperature, we again used CPUE on a natural logarithmic scale with annual mean water temperature as predictor in a linear regression model. We transformed the predictor to a weighted-moving-average over the last two years with more weighting given to the latest year, to better reflect any long-term effects of temperature on relative density of perch. To investigate recruitment in the perch population, we used the proportion of one-year-old individuals within the perch population as a measure of the number of individuals surviving the first winter, which is suggested to be dependent on both water temperature and food availability (or density of competitors), but also density of predators their first growth season (Heermann et al. 2009). We used linear regression with summer water temperature the preceding year and a simple moving average of the density of perch over the last two years to predict the proportion of one-year-old individuals in the perch populations. In the statistical analyses, we combined both lakes as the number of sampling points were too low to treat them separately.

To compare somatic growth in the perch population over time and between the different populations we used, in addition to a back-calculation routine (described below), a modified version of the von Bertalanffy growth model for every sampling year in Lake Skrukkebukta and Lake Vaggatem (results are shown in Appendix Table S7-S8 and Appendix Fig. S1-S2):

$$L(t) = L_\infty - (L_\infty - L_0)\, e^{[-(gL_\infty{}^{-1})t]} \qquad (1)$$

where $L(t)$ is the mean length at age (t), L_∞ is the asymptotic length as age approaches infinity, L_0 is the length at hatching, g is the absolute initial growth rate (length·year^{-1}) which represent the maximum growth rate, occurring early in life according to the von Bertalanffy growth model (Sandlund et al. 2013). The advantage of using the modified version of the von Bertalanffy growth model is that we are not dependent on the unit-less coefficient k, which is hard to interpret and is not independent of L_∞. In addition, g has the unit length·year^{-1} which is very interpretable biologically (Mooij et al. 1999, Sandlund et al. 2013). L_∞ and g were estimated using non-linear least-square regression based on length at age data for the different years and populations. Perch hatching size is around 5 mm (Olin et al. 2012) L_0 were therefore set to 5 mm. To investigate the development in initial growth (g, length·year^{-1}), we used the summer water temperature (°C) the preceding year and relative density of perch (CPUE) the preceding year (because of the lack of 0+ perch in the data set, we had to relate initial growth to 1 year old fish and used the temperature when these fish were 0 year old) in a multiple linear model with an interaction term between the predictors.

Back-calculated length at age and length increment

The back-calculated length increment was estimated for a sub-sample of perch from Lake Vaggatem and Lake Skrukkebukta. On the opercular bones of individual perch, we measured the width of annual growth increments as the distance between the opaque zones. We used these measurements in addition to the total opercular length and the body length of the individual perch to estimate length-at-age with the nonlinear body-proportional hypothesis method. This method is commonly used for perch (Thoresson 1996) and assumes that the deviation in body size from the expected body size given by the operculum size does not change through life (Thoresson 1996, Tarkan et al. 2006),

$$L_a = L_A(\frac{O_a}{O_A})^{\beta_1}, \qquad (2)$$

where L_a is the back-calculated length-at-age a, O_a the measured operculum radius at age a, O_A the observed operculum size at time of capture, and L_A the observed fish length at time of capture. β_1 is the linear regression slope coefficient estimated from the log-log relationship between the body length and operculum length at capture. A total of 1646 perch were used in the back-calculation procedure. We back-calculated length increment (mm·year^{-1}) for juvenile fish in the age group of 1-4 years with individual perch ranging from age 2 to 10 years, giving us length increment data from year 1995 to year 2018. We did not asses growth during the sampling year, because those estimates would be dependent on sampling time within the year, which was not exactly the same every year. A comparison between back-calculated length at final winter before capture and length at capture revealed a good fit of the back-calculation model ($p<0.001$, $F= 2501$ on 1 and 1644 df, adj-$R^2=0.94$) (Appendix Fig. S3 & Table S9). Back-calculated length increment ($mm \cdot year^{-1}$) for 1, 2, 3 and 4 years old perch were related to summer water temperature and relative density in a Linear Mixed Effect model (LME) with sampling year and age at capture as random effects, with the nlme-package in R. In addition, we estimated cohort-mean (year class) length increment from age 1 to 4, which was related to mean summer water temperature (°C) and mean relative density (CPUE) for the same time period (three-year moving-average) with linear regression.

Age at maturity

We estimated age at maturity (A_{50}, age at 50% probability of the individuals have reached maturation age) for each cohort (year-class) with sufficient data in the time series for perch in both Lake Vaggatem ($n_{cohorts}= 12$) and Lake Skrukkebukta ($n_{cohorts}= 4$) (Appendix Fig. S10) using logistic regression,

We related the estimated cohort-specific A_{50} to the estimated total cohort-specific length increment (age 1 to age 4 year old) using linear regression. We estimated cohort-specific A_{50} to address how environmental variables (water temperature and relative density) indirectly affected age at maturity mediated through individual juvenile growth. In addition, we estimated maturation age separately for males and females to explore if it differed between the sexes. This was, however, only done for each sampling year and not for each cohort as the amount of data was not sufficient to separate into the different sexes in the cohort analysis.

Age at maturation is assumed to be plastic and depending on a probabilistic maturation reaction norm (PMRN) describing the length- and age-specific probabilities of maturation (Heino et al. 2002, Dieckmann & Heino 2007). To illustrate how age at maturity changes with differing individual growth rate and to highlight the population response to altered individual growth rate, we calculated the PMRN from the long-term data on perch in the Pasvik watercourse. We calculated the PMRN by the demographic method assuming a linear reaction norm (Barot et al. 2004). We implemented a model that involves both age and size, and assumed that these two variables have independent and linear effects, following Heino et al. (2002),

$$P_{\mathrm{m}} = 1/\left\{1 + \exp\left(-\frac{L-(a+as)}{d}\right)\right\}, \tag{3}$$

where L is the length of fish, i is the PMRN intercept, a is the age of fish, s is the PMRN slope, and d is the PMRN width.

To investigate causal relationship between environmental variables and age at maturation (A_{50}) we used structural equation modelling (SEM) with the “piecewiseSEM” package in R. We constructed the SEM to assess direct and indirect effects of summer water temperature and relative density on age at maturation (A_{50}) mediated through mean length increment ($\mathrm{mm \cdot year^{-1}}$) from age 1 to age 4 year old perch. Summer water temperature and relative density of perch were modelled as exogenous random variables, influencing other variables, but not themselves being influenced by other variables. The biotic variable length increment (from age 1 to age 4, $\mathrm{mm \cdot year^{-1}}$) was included as endogenous variable influenced by others and itself also influencing other variables. Finally, age at maturity (A_{50}) was set as a response endogenous variable, influenced by all other variables, but not influencing other variables. All variables were standardized prior to the analysis. Figures and maps were created by using the ggplot-package in R or BioRender.com, and tables were made using the Sjplot-package in R.

Results

The proportion of perch is increasing in high latitude lakes

The proportion of perch in the littoral zone of the sampled lakes substantially increased over the study period (Fig. 4a). All lakes with more than two sampling points showed an overall increase in proportion of perch with time. The overall mean trend reveals that the proportion of perch increased exponentially over time ($p<0.01$, mar-$R^2=0.356$, Table S10), from under 10% in the early 1990ies to above 70% in most lakes during the last decade, however with large variation between lakes (Fig. 4a). The relative density (CPUE) data in Lake Skrukkebukta and Lake Vaggatem shows a similar trend as the overall proportion data (Fig. 4b), with a substantial increase in relative density of perch in the littoral zone of both lakes (Skrukkebukta: $t=8.014$ on 22 d.f., $p<0.01$, adj-$R^2= 0.73$. Vaggatem: $t=4.042$ on 24 d.f., $p<0.01$, adj-$R^2= 0.38$, Appendix Table S11 & S12). This was related to an increase in water temperature where relative density of perch increased with annual mean water temperature (Weighted-Moving-Average over the last two years) in both Lake Skrukkebukta and Lake Vaggatem (Fig. 4c). In Lake Skrukkebukta the relative density has increased with 1.83 ln-CPUE$\cdot$°C^{-1} of temperature increase ($t=3.788$ on 20 d.f., $p<0.01$, adj-$R^2=0.389$, Appendix Table S13), while in Lake Vaggatem, the increase was weaker, but significant with an increase of 0.89 ln-CPUE$\cdot$°C^{-1} of temperature increase ($t=3.788$ on 20 d.f., $p=0.048$, adj-$R^2=0.141$, Appendix Table S14).

Survival of juveniles increases with temperature and decreases with perch density

We used the proportion of 1-year olds in the perch population in Lake Vaggatem and Lake Skrukkebukta as a proxy for number of individuals surviving the first critical winter. The proportion of one year old perch increased with mean summer water temperature (Jun-Aug) the preceding year and decreased with relative density of perch in the littoral zone (Fig. 5). The proportion of one year old perch was significantly related to temperature and density ($p<0.001$, adj-$R^2=0.62$), increasing by 9.7 % per degree centigrade increment in preceding year summer water temperature (°C) ($t=4.950$ on 17 d.f., $p<0.001$), and decreasing by 4.5% per 10-CPUE increase in relative density of the perch population ($t=-2.731$ on 17 d.f., $p=0.014$). In addition, there was a significant interaction term between the two predictors in the linear model ($t=-2.541$ on 17 d.f., $p=0.021$, Appendix Table S15).

Faster juvenile growth with higher summer water temperature

The overall trend for the juvenile perch was that annual length increment increased with summer water temperature and decreased with relative density of perch in both Lake Vaggatem and Lake Skrukkebukta (Fig. 6, Appendix Fig. S4-7). The combined length increment ($mm\cdot year^{-1}$) from age 1 to age 4 year old perch increased substantially with increasing 3-year-mean summer water temperature and decreased similarly with an increase in 3-year-mean relative density (Fig. 7a & 7b). The combined length increment (age 1 to 4 year) for Lake Vaggatem and Lake Skrukkebukta perch was significantly related to temperature and density in a linear regression model ($p=0.004$, adj-$R^2=0.28$), increasing by 8.5 mm per degree centigrade of temperature increment ($t=2.481$ on 31 d.f., $p=0.019$) and decreased by 6.8 mm per 10 CPUE increment ($t=-3.806$ on 31 d.f., $p=0.001$) (Appendix Table S16). In addition, there was a difference in intercept between the lakes, where the length increment was larger in Lake Vaggatem compared to Lake Skrukkebukt (Appendix Table S16). However, for the individual age groups, the effect of water temperature and relative density on length increment varied.

For the youngest age group (1 year old) there was no significant change in length increment ($mm\cdot year^{-1}$) with either increasing summer water temperature or relative density of perch (Fig. 6, Appendix: Fig. S4, Table S17 & S18). For all the other juvenile age groups (2 to

4 year old), length increment (mm·year^{-1}) increased significantly with increasing summer water temperature in both lakes, whereas only in Lake Vaggatem length increment decreased significantly with relative density of perch (Fig. 6, Appendix: Fig. S5-S7, Table S19-S24). Length increment (mm·year^{-1}) for 2 year old perch increased by 2.21 mm·°C^{-1} (Lmme: CI=0.19-3.99, p<0.001, mar-R=0.117) and 3.08 mm (Lmme: CI=1.6-4.58, p<0.001, mar-R=0.085) per degree centigrade of water temperature increment in Lake Vaggatem and Lake Skrukkebukta, respectively (Fig. 6, Appendix Fig. S5, Table S19 & S20). For 2 year old perch, length increment decreased by 1.5 mm·10-CPUE^{-1} with relative density (CI=-2.89- -0.04, p<0.001, mar-R=0.117) in Lake Vaggatem, whereas no significant change was apparent with relative density in Lake Skrukkebukta (Fig. 6, Appendix Fig. S5, Table S19 & S20).

Length increment (mm·year^{-1}) for 3 year old perch increased by 1.59 mm·°C^{-1} (Lmme: CI=0.21-2.98, p=0.025, mar-R=0.07) and 1.21 mm·°C^{-1} (Lmme: CI=0.24-2.2, p=0.031, mar-R=0.022) in water temperature increase in Lake Vaggatem and Lake Skrukkebukta, respectively (Fig. 6, Appendix Fig. S6, Table S21 & S22). For 3 year old perch, length increment decreased by 1.1 mm per 10-CPUE increment in relative density (CI=-1.93- -0.16, p=0.021, mar-R=0.07) in Lake Vaggatem, whereas no significant change was apparent with relative density in Lake Skrukkebukta (Fig. 6, Appendix Fig. S6, Table S21 & S22). Length increment (mm·year^{-1}) for 4 year old perch increased by 2.24 mm (Lmme: CI=1.03-3.21, p<0.001, mar-R=0.09) and 1.82 mm (Lmme: CI=0.65-3.51, p=0.005, mar-R=0.097) per degree centigrade increment in water temperature in Lake Vaggatem and Lake Skrukkebukta, respectively (Fig. 6, Appendix Fig. S7, Table S23 & S24). For 4 year old perch, length increment did not significantly change with relative density (Fig. 6, Appendix Fig. S7, Table S23 & S24).

The absolute initial growth (g) derived from population estimates of the von Bertalanffy growth model from Lake Skrukkebukta and Lake Vaggatem varied between 4.2 and 9.4

(cm·year^{-1}) over the study period. In a simple linear regression pooling data for both lakes, the initial growth increased with 6 mm per degree centigrade increment in summer water temperature the preceding year (t=2.653 on 18 d.f., p=0.016, adj-R^2=0.24, Appendix Table S7, Fig. S1).

Earlier maturation age with faster growth

Age at maturation (A_{50}) differed between males and females in the perch populations in Lake Vaggatem and Lake Skrukkebukta; males matured on average at an age of 4.1 years whereas females matured on average at an age of 7.5 years (Appendix Fig. S8). The difference in age at maturity between the sexes did not change over time (t=-0.767 on 12 d.f., p=0.45) (Appendix Fig. S9). The observed increase in combined length increment (mm·1-4years^{-1}) substantially affected the cohort specific age at maturation (A_{50}) negatively (Fig. 7c), with -0.8 years reduction per cm increase in length increment (t=-3.783 on 14 d.f., p=0.002, adj-R^2=0.47) (Appendix Table S25 & Fig. S10). The effect of summer water temperature and relative density on age at maturity was mediated through growth (length increment) for perch in Lake Vaggatem and Lake Skrukkebukta, as illustrated by the structural equation model (SEM) results (Fig 8a). We found a positive effect of cohort-specific (age 1 to age 4 year old) mean summer water temperature and a negative effect of relative density of perch in the same time period on length increment of perch from age 1 to age 4 year, which further affected age at maturity (A_{50}) negatively (Fig. 8a). Figure 8b illustrates these relationships theoretically, where individuals with higher growth rate, due to temperature increase or reduced density, will reach maturation age earlier than populations experiencing lower growth rates according to the estimated PMRN from the perch populations in Lake Vaggatem and Lake Skrukkebukta.

Discussion

We find that the numerical importance of Eurasian perch in fish communities at the northern edge of its distribution increased substantially during the last two decades of rapid warming. The positive trend was registered in ten out of the eleven lakes investigated. For our main two study lakes, Lake Vaggatem and Lake Skrukkebukta, the trend was driven by an increment in perch density associated with the increase in water temperature. These two perch populations showed higher recruitment with warming, with the proportion of 1 year old fish in catches increasing by almost 10 % per degree increment of mean summer water temperature. The demographic responses to warming were concomitant with individual level effects on somatic growth, which increased with temperature across young age classes, resulting in earlier maturation. The latter is an indirect effect of warming mediated by increased temperature-dependent growth rate of juveniles, an eco-physiological response, and phenotypic plasticity in maturation schedules, a life history adaptation. The resulting earlier maturation and larger size at age of juveniles help explain the increased recruitment rates promoting perch population density at higher temperatures. Both somatic growth and recruitment (assessed as proportion of 1 year olds in the perch population) displayed negative density-dependence, which may mask individual and demographic responses to warming in field studies. Considering that perch is a generalist species engaging in many direct and indirect ecological interactions, its increasing importance is likely to have a pervasive, food-web mediated impact on high latitude lake communities.

Increase in temperature-dependent growth

During the recent period of warming, the increased numerical importance of perch was accompanied by positive temperature effects on juvenile growth in our two reference lakes. The yearly mean growth significantly increased with temperature across all investigated juvenile age classes, with the exception of the 1 year old age group. The cohort mean cumulative length increment from age 1 to 4 years increased by 8.5 mm (~12%) per degree centigrade increment in summer water temperature. Individual perch growth displayed substantial negative density-dependence, decreasing by 6.8 mm per 10 CPUE units increase in relative density, in line with earlier findings for this species (Byström & García-Berthou 1999, Horppila et al. 2010, Olin et al. 2017). The observed positive effect of temperature on perch somatic growth was expected considering that in our lakes mean summer water temperature varied between 10-14 °C, which, although within the species temperature tolerance range (Kleiner 1974, Karås & Thoresson 1992), is well below the optimum temperature for perch growth, estimated to be within 16-27°C (Hokanson 1977). Positive effects of higher summer water temperatures on perch growth rates have been described in regions where temperature variability is within the thermal tolerance range of the species (Jeppesen et al. 2012, van Dorst et al. 2019, Huss et al. 2019), where the increased size at age was maintained also in adult age classes owing to faster growth in young stages (Huss et al. 2019, Gårdmark et al. 2020). Projected lake water temperatures, forced by climate model outcomes under RCP-scenarios 4.5 and 8.5 (Smalås et al. MS in prep.), suggest that in the coming decades warming should continue to promote growth in perch populations from our study area, assuming that species composition is similar in the future (see appendix figure S9 for relationship between water temperature and growth in perch). The higher ambient temperatures will increase metabolic demands (Huey & Kingsolver 2019), but at high latitudes, lake productivity mediated by catchment greening is expected to increase with warming (Schindler et al. 2005, O'Beirne et al. 2017), and should ensure sufficient food availability to support growth (Kao et al. 2015). The documented and projected positive effects of warming on growth of perch living at its northern range edge affect its life history, demography, and ecological interactions.

Life history and demographic implications of faster growth

The faster growth induced by warming resulted in earlier maturation of perch. The latter is an indirect effect of warmer temperatures mediated by adaptive plasticity in perch maturation schedules. The indirect effect of warming, estimated and summarized via a structural equation model, is substantial, with maturation age (A_{50}) decreasing by 0.8 years per cm increase in juvenile length increment (from age 1 to 4 years). The adaptive plastic response in maturation age is dependent on the eco-physiological process of somatic growth, which in turn is affected by the ambient temperature and food availability (Ward et al. 2017). In our perch populations, the orientation of the estimated maturation reaction norm is such that faster growth will lead to earlier maturation. A reduction in maturation age as a consequence of increased growth has been documented repeatedly in fish (Reznick 1993, Haugen 2000). Furthermore, an increase in juvenile growth rate has been associated with a subsequent increase in reproductive output in fish (Ward et al. 2017), and an increase in reproductive output is seen as a direct effect of an increase in water temperature for perch (Heibo et al. 2005). The climate driven increase in temperature-dependent growth thus results in larger size at age and earlier maturation, increasing the perch populations reproductive output and recruitment, thus promoting population growth, as seen in other stocks (Denney et al. 2002, Ottersen et al. 2006, Ward et al. 2017).

Survival of individuals during different life stages is a process which could be directly affected by ambient temperature either through temperature-specific developmental rates, temperature-dependent mortality rates or time spent in different life stages mediated by individual somatic growth (Sponaugle et al. 2006, Mirth et al. 2021). We show that the proportion of 1 year olds in the populations increased with summer water temperature during their 0+ summer, but decreased with perch density. Increasing summer water temperatures has been shown to increase recruitment in other perch populations (Lappalainen et al. 1996, Kokkonen et al. 2019), whereas it is suggested that cannibalism is an important factor reducing recruitment when the density of perch is high (Persson et al. 2000). The effect of increased summer temperature is usually related to larger body size and condition in autumn that subsequently lower the winter mortality (Hurst 2007, Shuter et al. 2012, Estlander et al. 2017). Developmental rates increase with water temperature in ectotherms. For instance, mortality and the duration of the perch egg-stage are decreasing with temperature, with normal development of eggs occurring in the temperature range of 7-18 °C (Saat et al. 1996, Küttel et al. 2002). Therefore, an increase in summer water temperature might increase the number of surviving hatchlings as more eggs might develop normally and the shorter duration of the egg-stage might decrease the predation risk at this life stage. Embryos and hatchlings are defined as critical life stages with a narrow thermal range (Dahlke et al. 2020), and at the northern edge of perch distribution an increase in spring and summer water temperature might have been pivotal for an increase in recruitment and subsequent increase in density and relative importance of the perch populations.

How warming increases importance of cool-water species at high latitudes

Considering the rapid warming experienced in the study area during the last three decades, an increased numerical importance of a cool-water species could be expected (Ficke et al. 2007, Heino et al. 2009, Rolls et al. 2017). However, the speed and magnitude of the observed increase in perch abundance and importance across the investigated lake communities was surprising. The population process outlined above helps explain the sudden response to climate warming, and suggests that similar responses should be expected in other populations of cool-water species at their northern range edge, unless kept in check by negative ecological interactions. However, many of the lakes near the northern range edge of perch are salmonid dominated systems, with little resistance capacity against percid fish at higher temperatures (Hayden et al. 2013, 2014). Shifts in dominance from cold-water fish to more cool- or warm-water fish have been documented in other freshwater systems (Jeppesen et al. 2012, Hansen et al. 2017). One candidate mechanism for the increased dominance of cool-water fish in high latitude lakes that is also supported by this study, is the increased recruitment with temperature often observed for spring-spawning cool-water fish (Rolls et al. 2017). Furthermore, an increase in somatic growth reduces time in critical life stages, which thus improves survival and promotes a faster transition between ontogenetic dietary stages which may further improve growth and individual performance (Heibo et al. 2005).

Implications of warming for ecological interactions and freshwater communities

Climate change impact on high latitude freshwater ecosystems is predicted to further increase as warming favours resident and invasive cool-water species, potentially displacing native cold-water salmonids from these ecosystems (Hayden et al. 2017, van Zuiden et al. 2016, Hansen et al. 2017, Campana et al. 2020). Perch is a generalist fish that has high capacity as a resource competitor in littoral habitats, and subsequently also as a predator, for native cold-water species such as whitefish (Hayden et al. 2014). Such ecological interactions with resident cold water species mediate higher order effects of climate change, which may change in character and outcome under warming. For instance, the activity and aggression level of perch will increase (Jacobsen et al. 2002, Nakayama et al. 2016), and a more rapid body growth will enhance the rate of ontogenetic transition towards piscivory (Heibo et al. 2005), and reduce the period perch is vulnerable for predators (Rudolf & Ramen 2018), which thus may change the strength and character of both intra- and interspecific interactions. Warming and increased productivity will change food webs towards pelagic-driven energy sources that will likely boost growth of small planktivorous perch and lower the size at shift to piscivory via the pelagic prey resources (Hayden et al. 2019). Climate induced changes in size-structured interactions may have cascading effects within the food web, and the outcome is dependent on thermal niche, population size structure and the existing ecological interactions within the ecosystem (Gårdmark et al. 2020). Cold-water sympatric species will be more vulnerable as perch increase in competitive and predatory capacity with warming, possibly causing major alterations within fish communities in high latitude lakes. In a wider perspective, cool-water perch dominance may eventually shift towards warm-water cyprinid (roach, bleak) fish dominance along increasing temperature and productivity in lakes where cyprinids are present or able to immigrate (Hayden et al. 2017).

Conclusion

Our study documents rapid cool-water fish responses to warming at their northern range edge, a finding render possible by the available long-term surveys. The causal links between individual and population effects of warming considered in this study help to account for the speed and magnitude of the population responses. The magnitude of these responses is such that dominance is shifting from salmonids to percids, warning of an ongoing reorganization of high latitude fish communities. Evidently, water-temperature increase from climate change has already favoured cool-water fish at high latitudes, and future projected climate warming will accentuate this development, potentially at the further expense of cold-water salmonids. Climate adaptation strategies must therefore focus on limiting the ecological impact of warmer water fish in high latitude ecosystems, given that successful establishment and rapid increase in population size of cool- and warm-water fish is likely as climate continuous to warm.

Author contribution

A.S., R.P., and P.-A.A. conceived the ideas and planned the paper. A.S., P.-A.A., K.K., P.M.T., N.A.K., and E.M.Z. collected the data and did the preliminary data processing. A.S. and R.P.

analysed the data with substantial input from all co-authors. A.S. led the writing. All authors contributed significantly to the drafts and approved the paper.

Acknowledgements

Thanks are due to the Freshwater Ecology group at the UiT-The Arctic University of Norway, for collecting and sharing their long-term time series. A.S. and R.P. acknowledge funding by the EU-H2020 project ClimeFish (project id 677039). P.-A.A acknowledge funding by the Norwegian research council (project no. 183984). K.K. thank people helping in the field and lab work as well as funding from Finnish Ministry of Agriculture and Forestry, Inari County, and Academy of Finland (projects 140903, 1268566). P.M.T., N.A.K., and E.M.Z. acknowledge funding by RFBR (grant 18-05-60125 Arctic).

Data availability statement

Summary data on both population level properties and individual data will be available upon acceptance of the MS.

References

Alabaster, J. S. & Downing, A. L. 1966. A field and laboratory investigation of the effect of heated effluents on fish. *Fisheries Investigation Series, London, 6.*

Amundsen, P.-A., Bøhn, T., Popova, O. A., Staldvik, F. J., Reshetnikov, Y. S., Kashulin, N. A., & Lukin, A. A. 2003. Ontogenetic niche shifts and resource partitioning in a subarctic piscivore fish guild. *Hydrobiologia, 497,* 109-119.

Amundsen, P. A., Primicerio, R., Smalås, A., Henriksen, E. H., Knudsen, R., Kristoffersen, R., & Klemetsen, A. 2019. Long-term ecological studies in northern lakes—challenges, experiences, and accomplishments. *Limnology and Oceanography, 64,* 11-21.

Arula, T., Shpilev, H., Raid, T., Vetemaa, M., & Albert, A. 2017. Maturation at a young age and small size of European smelt (*Osmerus eperlanus*): A consequence of population overexploitation or climate change? *Helgoland Marine Research, 71,* 7. https://doi.org/10.1186/s10152-017-0487-x

Barot, S., Heino, M., O`Brien, L., & Dieckmann, U. 2004. Estimating reaction norms for age and size at maturation when age at first reproduction is unknown. *Evolutionary Ecology Research, 6,* 659–678.

Benateau, S., Gaudard, A., Stamm, C., & Altermatt, F. 2019. Climate change and freshwater ecosystems: *Impacts on water quality and ecological status,* pp. 110.

Biro, P. A., Post, J. R., & Booth, D. J. 2007. Mechanisms for climate-induced mortality of fish populations in whole-lake experiments. *Proceedings of the National Academy of Sciences, 104,* 9715–9719.

Byström, P., & García-Berthou, E. 1999. Density dependent growth and size specific competitive interactions in young fish. *Oikos, 86,* 217-232.

Campana, S., Casselman, J., Jones, C., Black, G., Barker, O., Evans, M., Guzzo, M., Kilada, R., Muir, A., & Perry, R. 2020. Arctic freshwater fish productivity and colonization increase with climate warming. *Nature Climate Change, 10,* 428-433. https://www.nature.com/articles/s41558-020-0744-x

Comte, L., Buisson, L., Daufresne, M., & Grenouillet, G. 2013. Climate-induced changes in the distribution of freshwater fish: observed and predicted trends. *Freshwater Biology, 58*, 625–639. https://doi.org/10.1111/fwb.12081

Craig, J. F. 1978. A study of the food and feeding of perch, *Perca fluviatilis* L., in Windemere. *Freshwater Biology 8,* 59-68.

Dahlke, F. T., Wohlrab, S., Butzin, M., & Pörtner, H. O. 2020. Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science, 369,* 65–70. https://doi.org/10.1126/science.aaz3658

Denney, N. H., Jennings, S., & Reynolds, J. D. 2002. Life–history correlates of maximum population growth rates in marine fishes. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 269,* 2229-2237.

Dieckmann, U., & Heino, M. 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. *Marine Ecology Progress Series, 335,* 253–269. https://doi.org/DOI 10.3354/meps335253

Dodds, W. K., Perkin, J. S., & Gerken, J. E. 2013. Human impact on freshwater ecosystem services: a global perspective. *Environmental Science & Technology, 47,* 9061–9068.

van Dorst, R. M., Gardmark, A., Svanback, R., Beier, U., Weyhenmeyer, G. A., & Huss, M. 2019. Warmer and browner waters decrease fish biomass production. *Global Change Biology, 25,* 1395–1408. https://doi.org/10.1111/gcb.14551

Elliott, J. M. 1993. The pattern of natural mortality throughout the life cycle in contrasting populations of brown trout, *Salmo trutta* L. *Fisheries Research, 17,* 123–136. https://doi.org/10.1016/0165-7836(93)90012-v

Estlander, S., Kahilainen, K. K., Horppila, J., Olin, M., Rask, M., Kubečka, J., Peterka, J., Říha, M., Huuskonen, H., & Nurminen, L. 2017. Latitudinal variation in sexual dimorphism in life-history traits of a freshwater fish. *Ecology and evolution, 7,* 665-673.

FAO. 2020. Species fact sheet: *Perca fluivitalis*. *Food and Agriculture Organization of the United Nations*. http://www.fao.org/fishery/species/2298/en

Ficke, A. D., Myrick, C. A., & Hansen, L. J. 2007. Potential impacts of global climate change on freshwater fisheries. *Reviews in Fish Biology and Fisheries, 17,* 581–613. https://doi.org/10.1007/s11160-007-9059-5

Finstad, A. G., Andersen, T., Larsen, S., Tominaga, K., Blumentrath, S., De Wit, H. A., Tømmervik, H., & Hessen, D. O. 2016. From greening to browning: Catchment vegetation development and reduced S-deposition promote organic carbon load on decadal time scales in Nordic lakes. *Scientific Reports, 6,* 1–8. https://doi.org/10.1038/srep31944

Froese, R. 2006. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *Journal of applied ichthyology, 22,* 241-253.

Gvoždík, L. 2018. Just what is the thermal niche? *Oikos, 127,* 1701-1710.

Gårdmark, A., & Huss, M. 2020. Individual variation and interactions explain food web responses to global warming. *Philosophical Transactions of the Royal Society B, 375,* 0190449. http://dx.doi.org/10.1098/rstb.2019.0449

Hansen, G. J., Read, J. S., Hansen, J. F., & Winslow, L. A. 2017. Projected shifts in fish species dominance in Wisconsin lakes under climate change. Global change biology, 23, 1463-1476.

Haugen, T. O. 2000. Growth and survival effects on maturation pattern in populations of grayling with recent common ancestors. *Oikos, 90,* 107– 118.

Hayden, B., Holopainen, T., Amundsen, P. A., Eloranta, A. P., Knudsen, R., Præbel, K., & Kahilainen, K. K. 2013. Interactions between invading benthivorous fish and native whitefish in subarctic lakes. *Freshwater Biology, 58,* 1234–1250. https://doi.org/10.1111/fwb.12123

Hayden, B., Harrod, C., & Kahilainen, K. K. 2014. Lake morphometry and resource polymorphism determine niche segregation between cool- and cold-water-adapted fish. *Ecology, 95,* 538–552. https://doi.org/10.1890/13-0264.1

Hayden, B., Myllykangas, J. P., Rolls, R. J., & Kahilainen, K. K. 2017. Climate and productivity shape fish and invertebrate community structure in subarctic lakes. *Freshwater Biology, 62,* 990-1003. https://doi.org/10.1111/fwb.12919

Hayden, B., Harrod, C., Thomas, S. M., Eloranta, A. P., Myllykangas, J. P., Siwertsson, A., Præbel, K., Knudsen, R., Amundsen, P-.A., & Kahilainen, K. K. 2019. From clear lakes to murky waters–tracing the functional response of high-latitude lake communities to concurrent ‘greening’and ‘browning’. *Ecology letters, 22,* 807-816.

Heermann, L., Eriksson, L.-O., Magnhagen, C., & Borcherding, J. 2009. Size-dependent energy storage and winter mortality of perch. *Ecology of Freshwater Fish, 18,* 560–571. https://doi.org/10.1111/j.1600-0633.2009.00371.x

Heibo, E., Magnhagen, C., & Vøllestad, L. A. 2005. Latitudinal variation in life-history traits in Eurasian perch. *Ecology, 86,* 3377-3386.

Hein, C. L., Öhlund, G., & Englund, G. 2014. Fish introductions reveal the temperature dependence of species interactions. *Proceedings of the Royal Society B-Biological Sciences, 281,* pp. 7. https://doi.org/Artn 20132641 10.1098/Rspb.2013.2641

Heino, M., Dieckmann, U., & Godo, O. R. 2002. Measuring probabilistic reaction norms for age and size at maturation. *Evolution, 56,* 669–678. https://doi.org/DOI 10.1111/j.0014-3820.2002.tb01378.x

Heino, J., Virkkala, R., & Toivonen, H. 2009. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews, 84,* 39–54. https://doi.org/10.1111/j.1469-185X.2008.00060.x

Hickling, R., Roy, D. B., Hill, J. K., Fox, R., & Thomas, C. D. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology, 12,* 450–455. https://doi.org/10.1111/j.1365-2486.2006.01116.x

Hjelm, J., Svanbäck, R., Byström, P., Persson, L., & Wahlström, E. 2001. Diet-dependent body morphology and ontogenetic reaction norms in Eurasian perch. *Oikos, 95,* 311–323. https://doi.org/10.1034/j.1600-0706.2001.950213.x

Hoestlandt, H., & Devienne, A. 1980. A more precise statement of the relation between incubation time and temperature in the teleosteen fish, *Perca fluviatilis* L. *Comptes Rendus Hebdomadaires des Seances de l'Academie des Sciences. Serie D (France), 290,* 1123-1125.

Hokanson, K. E. F., & Kleiner, C. F. 1974. Effects of constant and rising temperatures on survival and developmental rates of embryonic and larval yellow perch, *Perca flavescens* (Mitchill). In *The early life history of fish,* pp. 437-448. Springer, Berlin, Heidelberg.

Hokanson, K. E. F., 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. *Journal of Fisheries Research, 34,* 1524–1550.

Horppila, J., Olin, M., Vinni, M., Estlander, S., Nurminen, L., Rask, M., Ruuhijärvi, J., & Lehtonen, H. 2010. Perch production in forest lakes: the contribution of abiotic and biotic factors. *Ecology of Freshwater Fish, 19,* 257-266.

Horoszewicz, L. 1973. Lethal temperatures of roach fry (*Rutilus rutilus* L.) from lakes with normal and artificially elevated temperature. *Polskie Archiwum Hydrobiologii, 18,* 69-79.

Huey, R. B., & Kingsolver, J. G. 2019. Climate warming, resource availability, and the metabolic meltdown of ectotherms. *The American Naturalist, 194,* 140-150. https://doi.org/10.1086/705679

Hurst, T. P. 2007. Causes and consequences of winter mortality in fishes. *Journal of Fish Biology, 71,* 315-345.

Huss, M., Lindmark, M., Jacobson, P., van Dorst, R. M., & Gardmark, A. 2019. Experimental evidence of gradual size-dependent shifts in body size and growth of fish in response to warming. *Global Change Biology, 25,* 2285–2295. https://doi.org/10.1111/gcb.14637

IPCC. 2013. Climate change 2013: the physical science basis. *Working Group I contribution to the Fifth assessment report of the Intergovernmental Panel on Climate Change.* (T. Stocker (ed.)). Cambridge University Press.

Jacobsen, L., Berg, S., Broberg, M., Jepsen, N., & Skov, C. 2002. Activity and food choice of piscivorous perch (*Perca fluviatilis*) in a eutrophic shallow lake: a radio-telemetry study. *Freshwater Biology, 47,* 2370-2379.

Jeppesen, E., Mehner, T., Winfield, I. J., Kangur, K., Sarvala, J., Gerdeaux, D., Rask, M., Malmquist, H. J., Holmgren, K., Volta, P., Romo, S., Eckmann, R., Sandstrom, A., Blanco, S., Kangur, A., Stabo, H. R., Tarvainen, M., Ventela, A. M., Sondergaard, M., Lauridsen, T. L., & Meerhoff, M. 2012. Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. *Hydrobiologia, 694,* 1–39. https://doi.org/10.1007/s10750-012-1182-1

Jobling, M. 2002. Environmental factors and rates of development and growth. In P. J. B. Hart & J. D. Reynolds (Eds.). *Handbook of fish biology and fisheries, 2,* 97–122. Wiley-Blackwell.

Karås, P. 1987. Food consumption, growth and recruitment in perch (*Perca fluviatilis* L.). Ph.D. thesis, Uppsala University, Uppsala, Sweden. pp. 129.

Karås, P. 1990. Seasonal changes in growth and standard metabolic rate of juvenile perch, *Perca fluviatilis* L. *Journal of Fish Biology, 37,* 913– 920.

Karås, P., & Thoresson, G. 1992. An application of a bioenergetics model to Eurasian perch (*Perca fluviatilis* L.). *Journal of fish biology, 41,* 217-230.

Karås, P. 1996. Basic abiotic conditions for production of perch (*Perca fluviatilis* L.) young-of-the-year in the Gulf of Bothnia. *Annales Zoologici Fennici, 33,* 371-381.

Kao, Y. C., Madenjian, C. P., Bunnell, D. B., Lofgren, B. M., & Perroud, M. 2015. Potential effects of climate change on the growth of fishes from different thermal guilds in Lakes Michigan and Huron. *Journal of Great Lakes Research, 41,* 423–435. https://doi.org/10.1016/j.jglr.2015.03.012

Klapper, H. 1991. *Control of eutrophication in inland waters*. Ellis Horwood Ltd.

Kokkonen, E., Heikinheimo, O., Pekcan-Hekim, Z., & Vainikka, A. 2019. Effects of water temperature and pikeperch (*Sander lucioperca*) abundance on the stock–recruitment relationship of Eurasian perch (*Perca fluviatilis*) in the northern Baltic Sea. *Hydrobiologia, 841,* 79-94.

Kundzewicz, Z. W., Mata, L. J., Arnell, N. W., Döll, P., Jimenez, B., Miller, K., Oki, T., Şen, Z., & Shiklomanov, I. 2008. The implications of projected climate change for freshwater resources and their management. *Hydrological sciences journal, 53,* 3-10.

Küttel, S., Peter, A., & Wüest A. 2002. Temperaturpräferenzen und-limiten von Fischarten Schweizerischer Fliessgewässer. *Rhône Revitalisierung, 1,* pp. 41.

Lappalainen, J., Lehtonen, H., Böhling, P., & Erm, V. 1996. Covariation in year-class strength of perch, *Perca fluviatilis* L. and pikeperch, *Stizostedion lucioperca* (L.). *Annales Zoologici Fennici, 33,* 421-426.

Lehtonen, H. 1996. Potential effects of global warming on northern European freshwater fish and fisheries. *Fisheries Management and Ecology, 3,* 59-71.

Magnuson, J. J., Crowder, L. B., & Medvick, P. A. 1979. Temperature as an ecological resource. *American Zoologist, 19,* 331-343.

Mirth, C. K., Saunders, T. E., & Amourda, C. 2021. Growing up in a changing world: Environmental regulation of development in insects. *Annual Review of Entomology, 66,* 81-99.

Mooij, W. M., Van Rooij, J. M., & Wijnhoven, S. 1999. Analysis and comparison of fish growth from small samples of length-at-age data: Detection of sexual dimorphism in

Eurasian perch as an example. *Transactions of the American Fisheries Society, 128,* 483–490. https://doi.org/10.1577/1548-8659(1999)128<0483:aacofg>2.0.co;2

Nakayama, S., Laskowski, K. L., Klefoth, T., & Arlinghaus, R. 2016. Between-and within-individual variation in activity increases with water temperature in wild perch. *Behavioral Ecology, 27,* 1676-1683.

O'Beirne, M. D., Werne, J. P., Hecky, R. E., Johnson, T. C., Katsev, S., & Reavie, E. D. 2017. Anthropogenic climate change has altered primary productivity in Lake Superior. *Nature communications, 8,* 1-8.

Olin, M., Jutila, J., Lehtonen, H., Vinni, M., Ruuhijärvi, J., Estlander, S., Rask, M., Kuparinen, A., & Lappalainen, J. 2012. Importance of maternal size on the reproductive success of perch, *Perca fluviatilis*, in small forest lakes: implications for fisheries management. *Fisheries Management and Ecology, 19,* 363–374. https://doi.org/10.1111/j.1365-2400.2012.00845.x

Olin, M., Tiainen, J., Rask, M., Vinni, M., Nyberg, K., & Lehtonen, H. 2017. Effects of non-selective and size-selective fishing on perch populations in a small lake. *Boreal Environment Research, 22,* 137-155.

Ottersen, G., Hjermann, D. Ø., & Stenseth, N. C. 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fisheries oceanography, 15,* 230-243.

O'Reilly, C. M., Sharma, S., Gray, D. K., Hampton, S. E., Read, J. S., Rowley, R. J., Schneider, P., Lenters, J. D., McIntyre, P. B., Kraemer, B. M., Weyhenmeyer, G. A., Straile, D., Dong, B., Adrian, R., Allan, M. G., Anneville, O., Arvola, L., Austin, J., Bailey, J. L., … & Zhang, G. Q. 2015. Rapid and highly variable warming of lake surface waters around the globe. *Geophysical Research Letters, 42,* 10773–10781. https://doi.org/10.1002/2015gl066235

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics, 37,* 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Perez, K. O., & Munch, S. B. 2010. Extreme selection on size in the early lives of fish. *Evolution: International Journal of Organic Evolution, 64,* 2450-2457.

Persson, L. 1988. Asymmetries in competitive and predatory interactions in fish populations. *Size-structured populations*, pp. 203-218. Springer, Berlin, Heidelberg.

Persson, L., Diehl, S., Johansson, L., Andersson, G., & Hamrin, S. F. 1991. Shifts in fish communities along the productivity gradient of temperate lakes-patterns and the importance of size-structured interactions. *Journal of Fish Biology, 38,* 281–293. https://doi.org/10.1111/j.1095-8649.1991.tb03114.x

Persson, L., Byström, P., & Wahlström, E. 2000. Cannibalism and competition in Eurasian perch: population dynamics of an ontogenetic omnivore. *Ecology, 81,* 1058-1071.

Pörtner, H. O., Berdal, B., Blust, R., Brix, O., Colosimo, A., De Wachter, B., Giuliani, A., Johansen, T., Fischer, T., Knust, R., Lannig, G., Naevdal, G., Nedenes, A., Nyhammer, G., Sartoris, F. J., Serendero, I., Sirabella, P., Thorkildsen, S., & Zakhartsev, M. 2001. Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod

(*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Continental Shelf Research, 21,* 1975–1997. https://doi.org/Doi 10.1016/S0278-4343(01)00038-3

Reist, J. D., Wrona, F. J., Prowse, T. D., Power, M., Dempson, J. B., King, J. R., & Beamish, R. J. 2006. An overview of effects of climate change on selected Arctic freshwater and anadromous fishes. *Ambio, 35,* 381–387. https://doi.org/Doi 10.1579/0044-7447(2006)35[381:Aooeoc]2.0.Co;2

Rezende, E. L., & Bozinovic, F. 2019. Thermal performance across levels of biological organization. *Philosophical Transactions of the Royal Society B: Biological Sciences, 374,* 20180549. https://doi.org/10.1098/rstb.2018.0549

Reznick, D. N. 1993. Norms of reaction in fishes. Pages 72– 90 *in* T. K. Stokes, J. M. McGlade, and R. Law, editors. The exploitation of evolving resources. Springer-Verlag, Heidelberg, Germany.

Rolls, R. J., Hayden, B., & Kahilainen, K. K. 2017. Conceptualising the interactive effects of climate change and biological invasions on subarctic freshwater fish. *Ecology and Evolution, 7,* 4109–4128. https://doi.org/10.1002/ece3.2982

Rudolf, V., & Roman, A. 2018. Trophic structure alters consequences of environmental warming. *Oikos, 127,* 1646–1656. doi:10.1111/oik.05535

Saat, T. A., Saat, V., & Veersalu, T. 1996. The rate of early development in perch *Perca fluviatilis* L. and ruffe *Gymnocephalus cernuus* (L.) at different temperatures. *Annales Zoologici Fennici, 33,* 693-698.

Sandlund, O. T., Gjelland, K. O., Bohn, T., Knudsen, R., & Amundsen, P. A. 2013. Contrasting population and life history responses of a young morph-pair of European whitefish to the invasion of a specialised coregonid competitor, vendace. *Plos One, 8,* pp. 13. https://doi.org/ARTN e68156 10.1371/journal.pone.0068156

Schindler, D. E., Rogers, D. E., Scheuerell, M. D., & Abrey, C. A. 2005. Effects of changing climate on zooplankton and juvenile sockeye salmon growth in southwestern Alaska. *Ecology, 86,* 198-209.

Shuter, B. J., Finstad, A. G., Helland, I. P., Zweimüller, I., & Hölker, F. 2012. The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. *Aquatic Sciences, 74,* 637-657.

Smalås, A., Strøm, J. F., Amundsen, P., Dieckmann, U., & Primicerio, R. 2020. Climate warming is predicted to enhance the negative effects of harvesting on high-latitude lake fish. *Journal of Applied Ecology, 57,* 270–282. https://doi.org/10.1111/1365-2664.13535

Smalås, A., Primicerio, R., Dieckmann, U., Strøm, J. F., & Amundsen, P.-A. (MS in prep.). Temperature affinities and life history determines vulnerability of freshwater fish to multiple stressors in a warming Arctic.

Sponaugle, S., Grorud-Colvert, K., & Pinkard, D. 2006. Temperature-mediated variation in early life history traits and recruitment success of the coral reef fish *Thalassoma bifasciatum* in the Florida Keys. *Marine Ecology Progress Series, 308,* 1-15.

Tarkan, A. S., Gaygusuz, O., Acipinar, H., & Gursoy, C. 2006. Validation of different back-calculation methods by using scales, opercula and cleithra of three co-existing cyprinid species. *Journal of Fisheries and Aquatic Science, 1,* 54–63.

Thoresson, G. 1996. Guidelines for coastal fish monitoring. http://www.slu.se//Documents/externwebben/akvatiskare-surser/publikationer/FIV/KLAB/PM087-eng%20hand%201996-2.pdf

Ward, H. G., Post, J. R., Lester, N. P., Askey, P. J., & Godin, T. 2017. Empirical evidence of plasticity in life-history characteristics across climatic and fish density gradients. *Canadian Journal of Fisheries and Aquatic Sciences, 74,* 464-474.

Willemsen, J., 1977. Population dynamics of percids in Lake Issel and some smaller lakes in the Netherlands. *Journal of Fisheries Research, 34,* 1710–1719.

van Zuiden, T. M., Chen, M. M., Stefanoff, S., Lopez, L., & Sharma, S. 2016. Projected impacts of climate change on three freshwater fishes and potential novel competitive interactions. *Diversity and Distributions, 22,* 603–614. https://doi.org/10.1111/ddi.12422

Zubova, E. M., Kashulin, N. A., Dauvalter, V. A., Denisov, D. B., Valkova, S. A., Vandysh, O. I., Slukovskii, Z. I., Terentyev, P. M., & Cherepanov, A. A. 2020. Long-term environmental monitoring in an Arctic lake polluted by metals under climate change. *Environments, 7,* pp. 23.

Figure legends

Figure 1. Schematic representation of how the life cycle of the Eurasian perch might be affected by increased water temperatures in high latitude populations.

Figure 2. Map of northern Europe with the box depicting the study area (left panel), and the location of the sampled lakes within the study area (right panel).

Figure 3. Water temperature in the Pasvik watercourse from year 1992 to 2020. Annual mean temperature (blue circles). Mean autumn temperature (Sep-Nov) (green triangles). Mean summer temperature (Jun-Aug) (orange squares). Temperature data is missing from January 1998-July 1999.

Figure 4. Development of perch populations in the littoral zone of study lakes from year 1990 to year 2020. a) Proprtion of perch in the study lakes, the black line shows the overall trend given by the Linear-mixed-effect model (Appendix Table S11). b) Relative density (ln-CPUE, no. of fish per 100m^2 per 12h) of perch in the littoral zone of Lake Vaggatem (green) and Lake Skrukkebukta (blue) from year 1990 to year 2020. c) Relative density (ln-CPUE) of perch dependent on annual mean water-temperature (Weighted-Moving-Average, WMA, over the last two years) in Lake Skrukkebukta (blue) and Lake Vaggatem (green) in the Pasvik watercourse.

Figure 5. Proportion of one-year-old individuals in Lake Skrukkebukta (blue) and Lake Vaggatem (green) perch populations related to a) the preceding summer water temperature (°C) and b) two-year-simple-moving-average (SMA) of the relative density (CPUE, (100m^2/12h)$^{-1}$)

of perch. Trend lines depict the linear regression model results with the shading illustrating the standard error of the line.

Figure 6. Back-calculated length increment (mm·year^{-1}) for age 1 year (top left), 2 years (top right), 3 years (bottom left) and 4 years (bottom right) perch from Lake Vaggatem (green) and Lake Skrukkebukta (blue) in the Pasvik watercourse dependent on summer water temperature (°C). Points represent the mean, whiskers represent the bootstrapped 95 % confidence interval of the mean, trend line with shading represent linear regression with standard error.

Figure 7. Relationship between the average length increment from age one to four years (mm·1-4 years^{-1}) for the different cohorts of perch and a) summer water temperature (three-year moving-average, SMA), b) relative density (three-year moving-average, CPUE) with solid lines representing the multiple linear regression model results (predictors centred and scaled). c) The relationship between age at maturation (A50, given by logistic regression) and average length increment from age one to four years for the different perch cohorts from 1998-2013, with the solid line representing the linear regression model and shaded area depicting the standard error of the model. NB. Lakes were pooled in the linear regressions because no significant difference in the slope between lakes were detected.

Figure 8. a) Structural equation model showing the relationship between predictor variables affecting length increment (combined from age 1 year to age 4 year olds) and the effect of increasing length increment on age at maturation in the perch populations in Lake Vaggatem and Lake Skrukkebukta. Arrows represent causal pathways, highlighted black lines represent significant relationships and grey lines represent non-significant relationship within the model.

Numbers in boxes denote the effect size of standardized coefficients and R^2 is shown for each endogenous variable. b) Relationship between somatic growth and maturation in perch in the Pasvik watercourse illustrated by the maturation reaction norm, length at age for perch in the Pasvik watercourse (grey dots) with blue dotted line representing a slow growth rate, i.e. “cold and high density situation” (10th percentile) and orange dotted line representing a fast growth rate, i.e. “warm and low density situation” (90th tercentile). The population estimated probabilistic maturation reaction norm (PMRN) midpoint (solid line), the 25th and 75th percentile (dashed lines).

Figures

Figure 1.

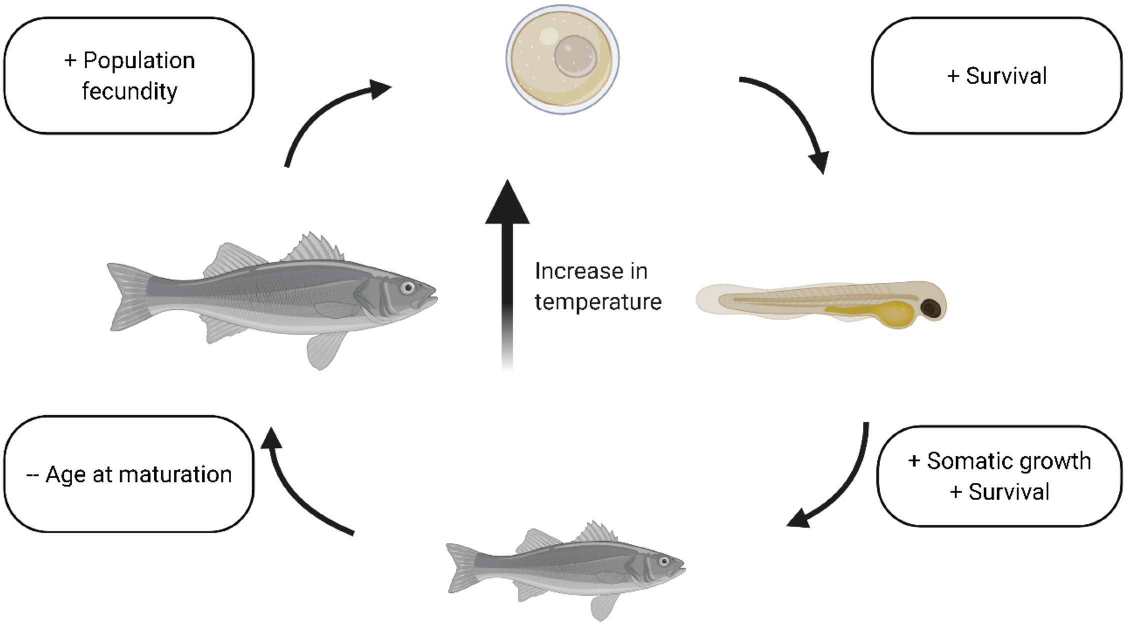


Figure 2.

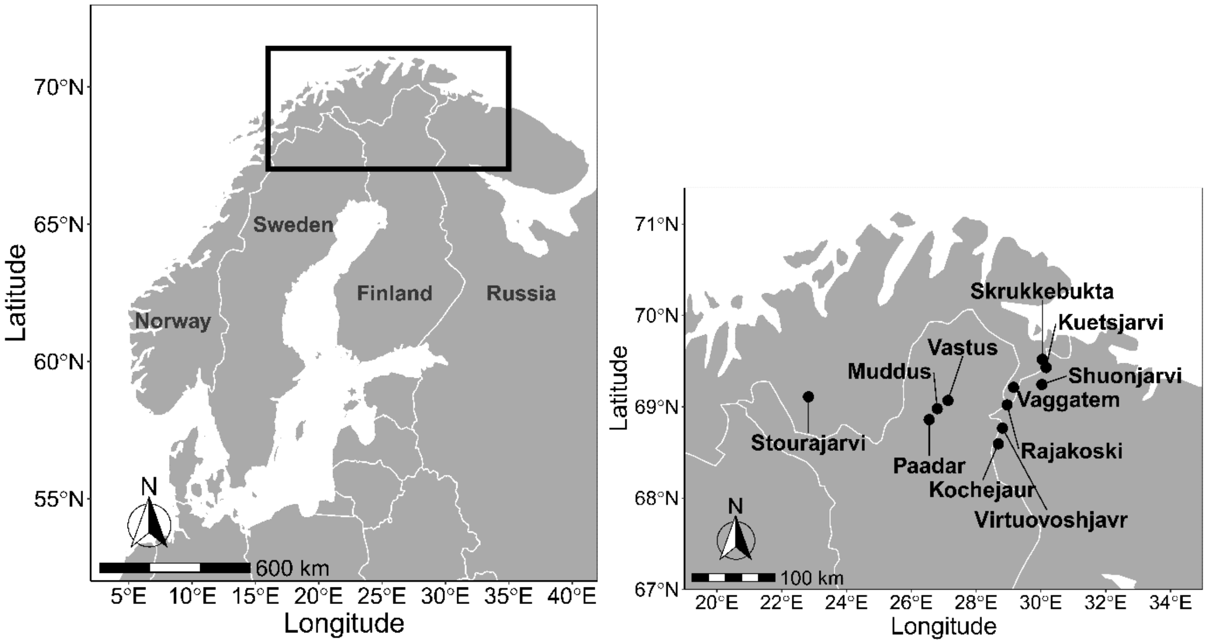

70°N
65°N
60°N
55°N
Latitude
Sweden
Norway
Finland
Russia
N
600 km
5°E
10°E
15°E
20°E
25°E
30°E
35°E
40°E
Longitude
71°N
70°N
69°N
68°N
67°N
Latitude
Skrukkebukta
Kuetsjarvi
Vastus
Muddus
Shuonjarvi
Vaggatem
Stourajarvi
Rajakoski
Paadar
Kochejaur
Virtuovoshjavr
N
100 km
20°E
22°E
24°E
26°E
28°E
30°E
32°E
34°E
Longitude

Figure 3.

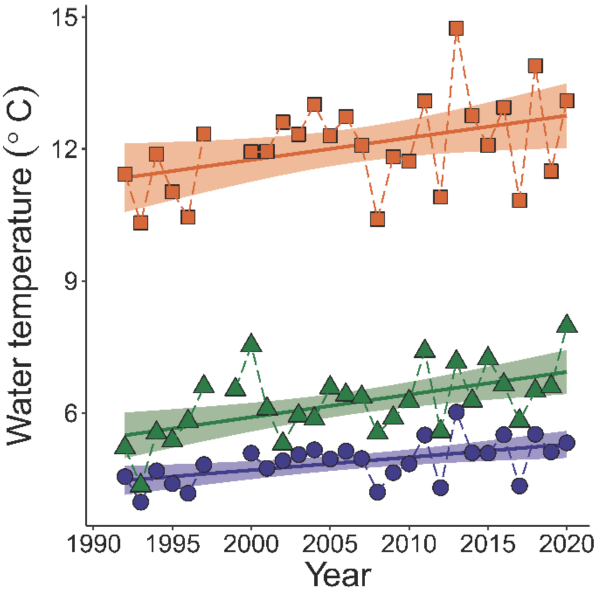

15
12
9
6
Water temperature (° C)
1990
1995
2000
2005
2010
2015
2020
Year

Figure 4.

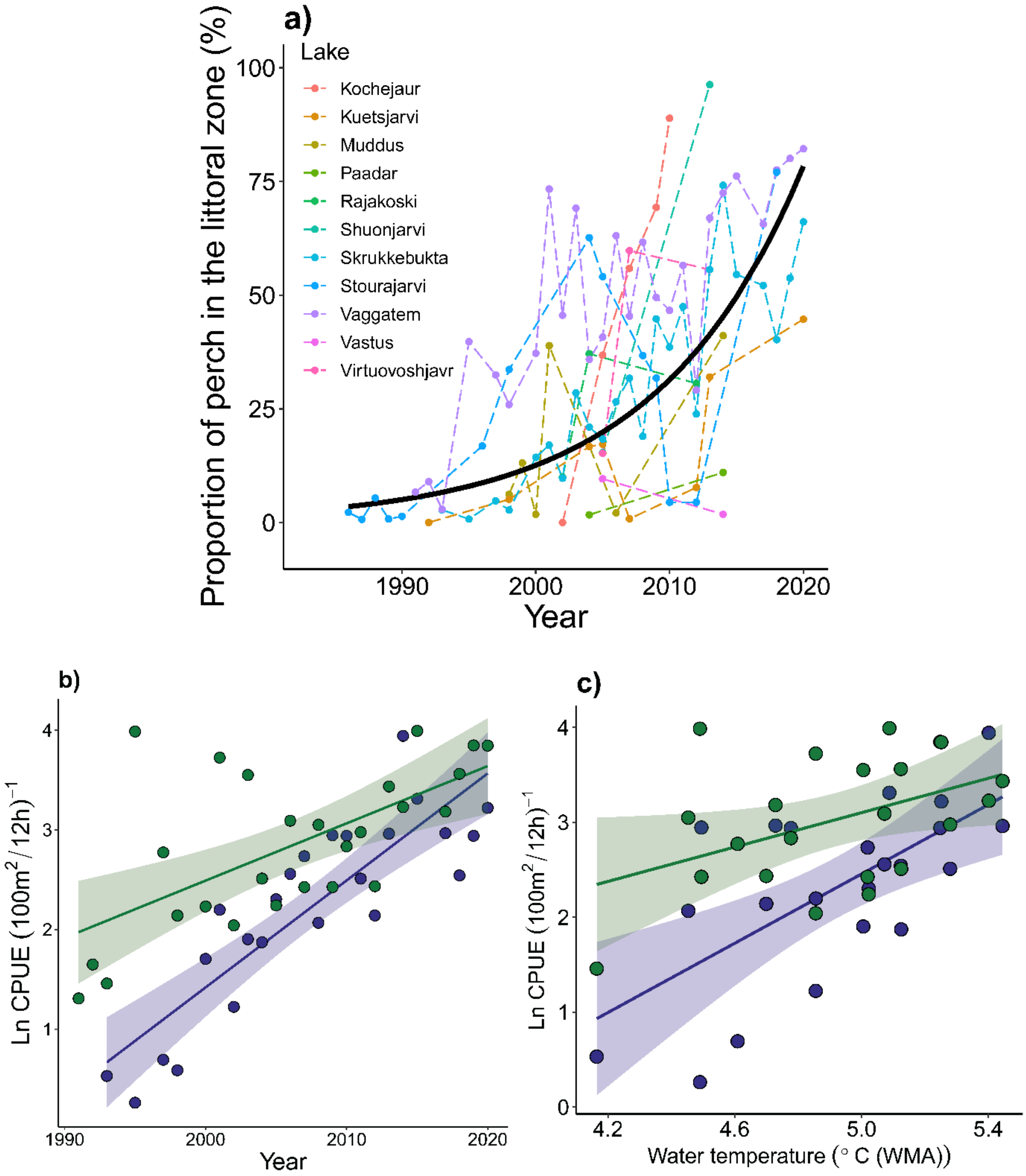
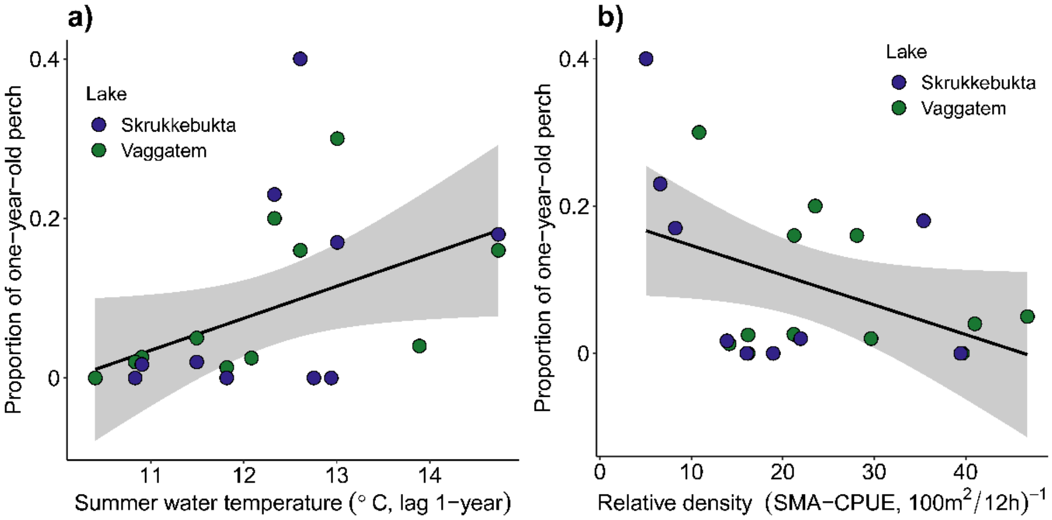

a)
Lake
Kochejaur
Kuetsjarvi
Muddus
Paadar
Rajakoski
Shuonjarvi
Skrukkebukta
Stourajarvi
Vaggatem
Vastus
Virtuovoshjavr
Proportion of perch in the littoral zone (%)
100
75
50
25
0
1990
2000
2010
2020
Year
b)
Ln CPUE (100m2 / 12h)-1
4
3
2
1
1990
2000
2010
2020
Year
c)
Ln CPUE (100m2 / 12h)-1
4
3
2
1
0
4.2
4.6
5.0
5.4
Water temperature (° C (WMA))

Figure 5.



a)
Proportion of one−year−old perch
0.4
0.2
0
Lake
Skrukkebukta
Vaggatem
11
12
13
14
Summer water temperature (° C, lag 1−year)
b)
Proportion of one−year−old perch
0.4
0.2
0
Lake
Skrukkebukta
Vaggatem
0
10
20
30
40
Relative density (SMA−CPUE, 100m^2/12h)$^{-1}$

Figure 6.

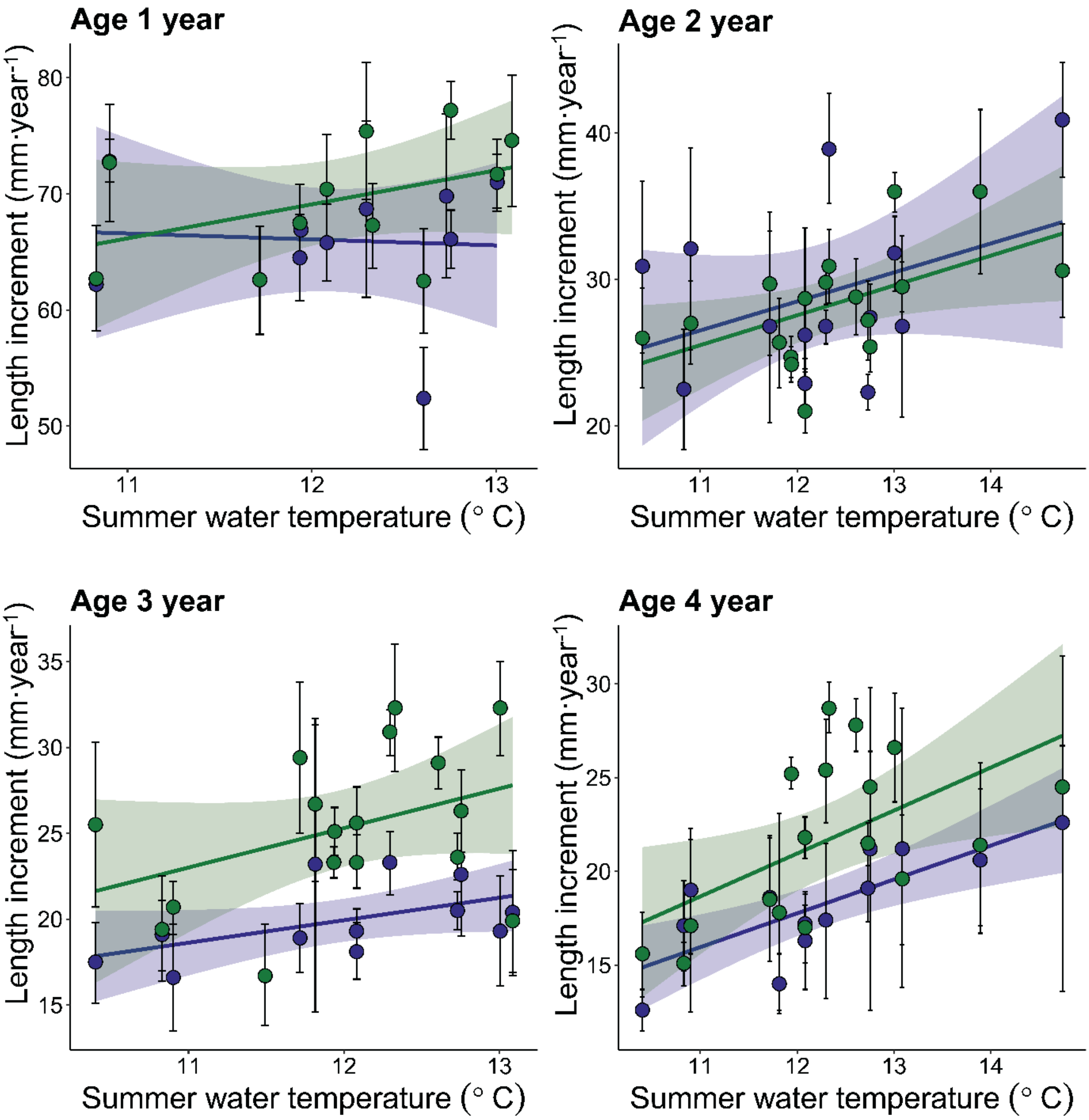

Age 1 year
Length increment (mm·year⁻¹)
80
70
60
50
11
12
13
Summer water temperature (° C)
Age 2 year
Length increment (mm·year⁻¹)
40
30
20
11
12
13
14
Summer water temperature (° C)
Age 3 year
Length increment (mm·year⁻¹)
35
30
25
20
15
11
12
13
Summer water temperature (° C)
Age 4 year
Length increment (mm·year⁻¹)
30
25
20
15
11
12
13
14
Summer water temperature (° C)

Figure 7.

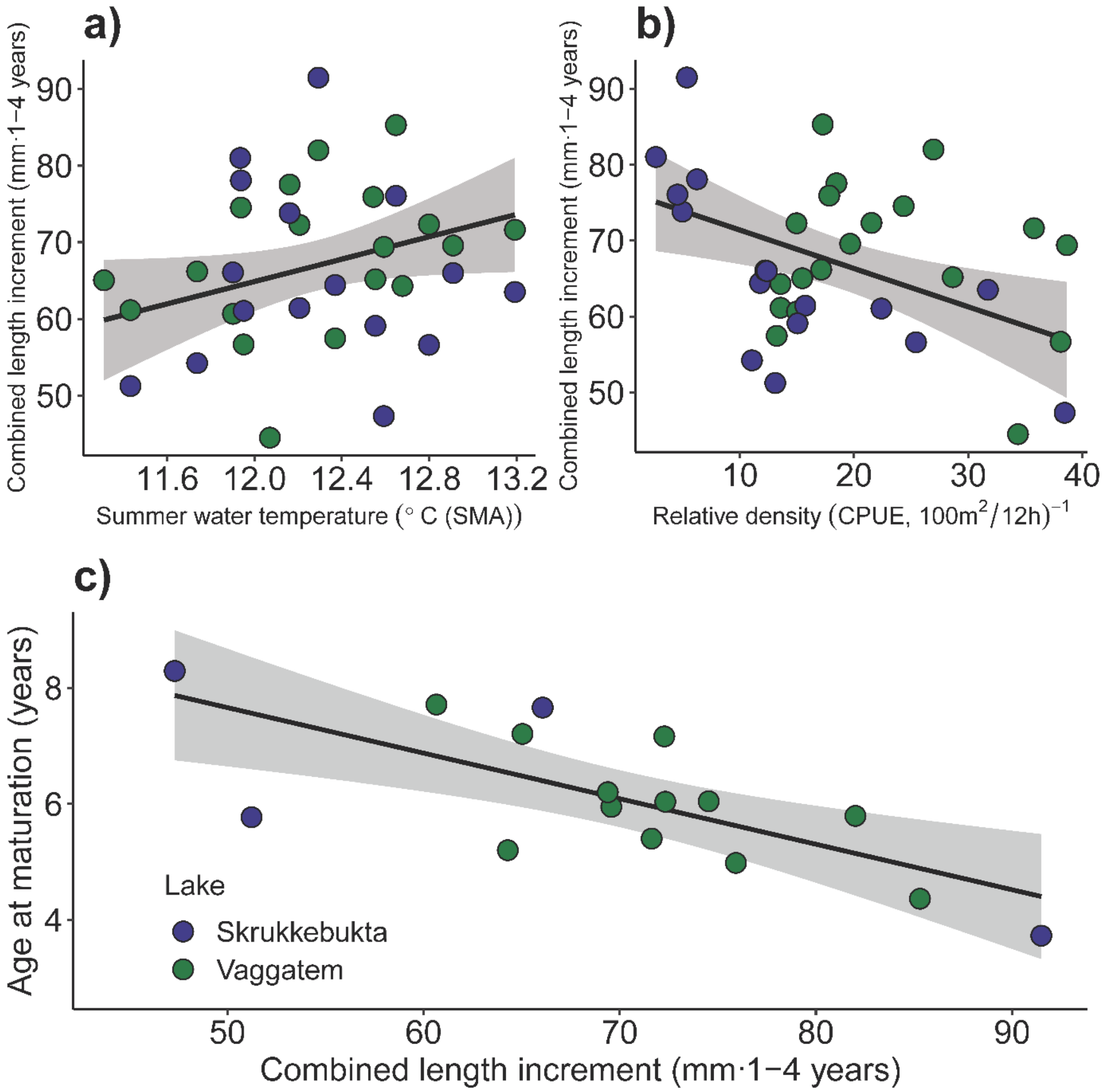
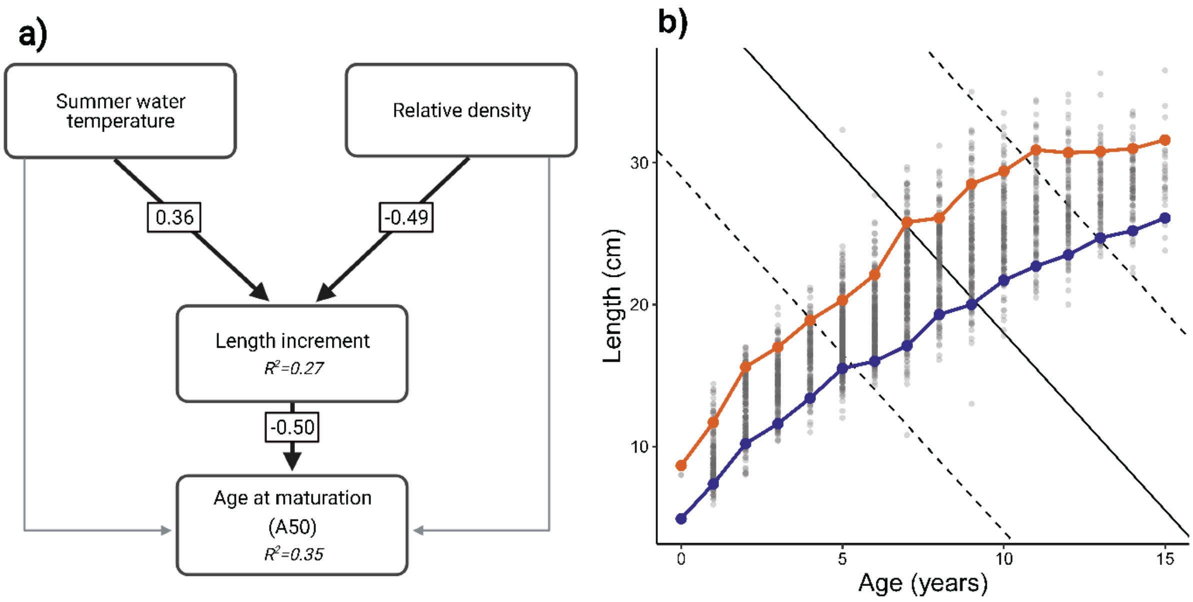

a)
Combined length increment (mm·1−4 years)
90
80
70
60
50
11.6
12.0
12.4
12.8
13.2
Summer water temperature (° C (SMA))
b)
Combined length increment (mm·1−4 years)
90
80
70
60
50
10
20
30
40
Relative density (CPUE, 100m^2/12h)$^{-1}$
c)
Age at maturation (years)
8
6
4
50
60
70
80
90
Combined length increment (mm·1−4 years)
Lake
Skrukkebukta
Vaggatem

Figure 8.


a)
Summer water temperature
Relative density
0.36
-0.49
Length increment
R²=0.27
-0.50
Age at maturation (A50)
R²=0.35
b)
Length (cm)
10
20
30
0
5
10
15
Age (years)

Supplementary information

Appendix 1: Lake characteristics and summary data of the sampled material

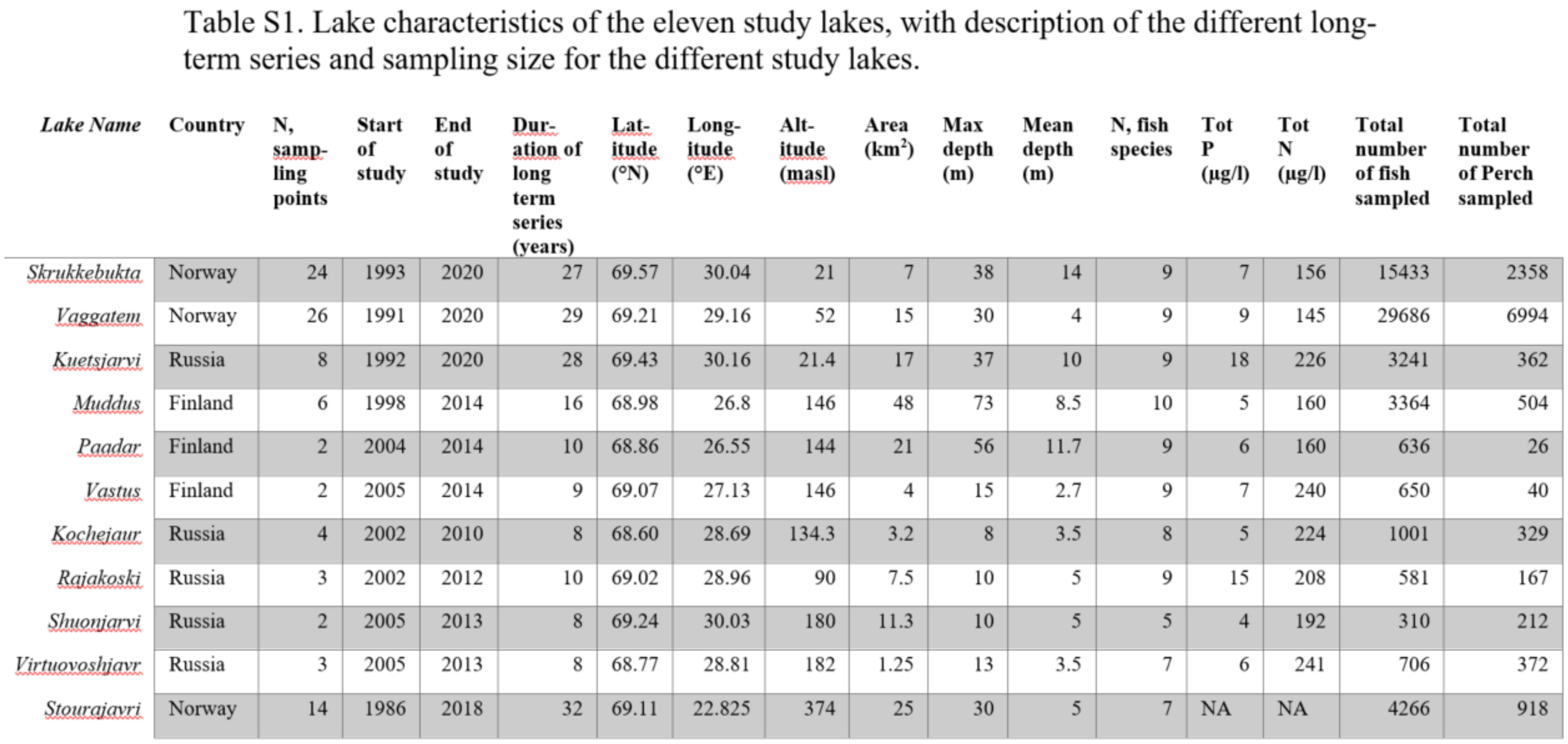


Table S1. Lake characteristics of the eleven study lakes, with description of the different long-term series and sampling size for the different study lakes.

Lake Name	**Country**	**N, samp-ling points**	**Start of study**	**End of study**	**Dur-ation of long term series (years)**	**Lat-itude (°N)**	**Long-itude (°E)**	**Alt-itude (masl)**	**Area (km^2)**	**Max depth (m)**	**Mean depth (m)**	**N, fish species**	**Tot P (µg/l)**	**Tot N (µg/l)**	**Total number of fish sampled**	**Total number of Perch sampled**
Skrukkebukta	Norway	24	1993	2020	27	69.57	30.04	21	7	38	14	9	7	156	15433	2358
Vaggatem	Norway	26	1991	2020	29	69.21	29.16	52	15	30	4	9	9	145	29686	6994
Kuetsjarvi	Russia	8	1992	2020	28	69.43	30.16	21.4	17	37	10	9	18	226	3241	362
Muddus	Finland	6	1998	2014	16	68.98	26.8	146	48	73	8.5	10	5	160	3364	504
Paadar	Finland	2	2004	2014	10	68.86	26.55	144	21	56	11.7	9	6	160	636	26
Vastus	Finland	2	2005	2014	9	69.07	27.13	146	4	15	2.7	9	7	240	650	40
Kochejaur	Russia	4	2002	2010	8	68.60	28.69	134.3	3.2	8	3.5	8	5	224	1001	329
Rajakoski	Russia	3	2002	2012	10	69.02	28.96	90	7.5	10	5	9	15	208	581	167
Shuonjarvi	Russia	2	2005	2013	8	69.24	30.03	180	11.3	10	5	5	4	192	310	212
Virtuovoshjavr	Russia	3	2005	2013	8	68.77	28.81	182	1.25	13	3.5	7	6	241	706	372
Stourajavri	Norway	14	1986	2018	32	69.11	22.825	374	25	30	5	7	NA	NA	4266	918

Table S2. Summary data per sampling year for perch in Lake Vaggatem including total number of perch (n), mean body length (cm), mean body weight (g), proportion of female perch in the dataset, mean condition factor and the von Bertalannffy`s growth variables L_∞ and initial growth, g. NA describes missing data.

	Number of fish	**Mean body length (cm)**	**Mean body weight (g)**	**Proportion female perch**	**Proportion of one-year olds**	**Mean Condition factor**	**Asymptotic length, L_∞**	**Initial growth, g (cm·year^{-1})**
2003	608	19.7	139.8	0.56	0.16	1.32	31.47	6.0255
2004	55	18.1	98.8	0.6	0.20	1.26	26.47	8.059
2005	132	21.1	165.1	0.67	0.30	1.33	26.89	8.67
2006	NA	NA	NA	NA	NA	NA	NA	NA
2007	NA	NA	NA	NA	NA	NA	NA	NA
2008	110	19.5	110.8	0.58	0.025	1.25	25.62	6.31
2009	109	23.4	202.7	0.63	0	1.39	36.22	5.13
2010	86	21.1	134.6	0.65	0.013	1.31	29.03	5.257
2011	NA	NA	NA	NA	NA	NA	NA	NA
2012	NA	NA	NA	NA	NA	NA	NA	NA
2013	38	22.5	192.9	0.68	0.026	1.37	30.35	6.02
2014	165	19.7	142.7	0.64	0.16	1.29	27.86	5.99
2015	121	20.6	153.4	0.69	0	1.32	30.77	5.64
2016	NA	NA	NA	NA	NA	NA	NA	NA
2017	181	20.6	132.1	0.65	0	1.26	27.44	6.83
2018	100	20.5	139.0	0.65	0.02	1.31	29.9	4.92
2019	158	19.5	118.2	0.54	0.04	1.29	30.57	4.58
2020	172	18.6	103.4	0.54	0.05	1.28	26.95	5.32

Table S3. Summary data per sampling year for perch in Lake Skrukkebukta including total number of perch (n), mean body length (cm), mean body weight (g), proportion of female perch in the dataset, mean condition factor and the von Bertalanffy`s growth variables L_∞ and initial growth, g. NA describes missing data. NA* describes data which were not good enough to estimate the different variables.

	Number of fish	**Mean body length (cm)**	**Mean body weight (g)**	**Proportion female perch**	**Proportion of one-year olds**	**Mean Condition factor (K)**	**Asymptotic length, L_∞**	**Initial growth, g (cm·year^{-1})**
2003	30	16.0	63.6	0.53	0.40	1.20	NA*	NA*
2004	50	15.6	57.8	0.62	0.23	1.20	NA*	NA*
2005	73	15.0	50.1	0.53	0.17	1.17	NA*	NA*
2006	NA	NA	NA	NA	NA	NA	NA	NA
2007	NA	NA	NA	NA	NA	NA	NA	NA
2008	NA	NA	NA	NA	NA	NA	NA	NA
2009	NA	NA	NA	NA	NA	NA	NA	NA
2010	67	17.1	63.4	0.70	0	1.18	22.59649	5.55072

2011	NA	NA	NA	NA	NA	NA	NA	NA
2012	NA	NA	NA	NA	NA	NA	NA	NA
2013	59	23.2	197.4	0.66	0.02	1.33	37.84762	4.326264
2014	130	19.2	121.1	0.62	0.18	1.20	24.26648	9.368055
2015	47	19.2	136.2	0.57	0	1.15	36.95272	4.695531
2016	NA	NA	NA	NA	NA	NA	NA	NA
2017	78	20.4	148.3	0.54	0	1.20	29.62441	6.796229
2018	81	21.2	164.7	0.64	0	1.24	33.10267	4.713568
2019	111	20.4	133.8	0.52	0	1.17	37.64752	4.2
2020	100	19.8	119.3	0.59	0.02	1.22	31.75967	4.725684

Appendix 2: Water temperature data

Table S4. Summary results for the linear model of the development of mean annual water temperature over the sampling period (year 1990 to year 2020).

	Mean Annual Water temperature		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	4.42	4.07 – 4.78	**<0.001**
year	0.03	0.01 – 0.05	**0.005**
Observations	27		
R^2 / R^2 adjusted	0.272 / 0.243		

Table S5. Summary results for the linear model of the development of mean summer water temperature over the sampling period (year 1990 to year 2020).

	Mean Summer Water temperature		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	11.27	10.42 – 12.12	**<0.001**
year	0.05	0.00 – 0.09	**0.037**
Observations	27		
R^2 / R^2adjusted	0.163 / 0.130		

Table S6. Summary results for the linear model of the development of mean autumn water temperature over the sampling period (year 1990 to year 2020).

	Mean Autumn Water temperature		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	5.41	4.85 – 5.97	**<0.001**
year	0.05	0.02 – 0.08	**0.002**
Observations	28		

R^2 / R^2 adjusted	0.302 / 0.275

Appendix 3: Population level estimates of somatic growth

The absolute initial growth (*g*) derived from population estimates of the von Bertalanffy growth model from Lake Skrukkebukta and Lake Vaggatem varied between 4.2 and 9.4 (cm·year^{-1}) over the study period (Fig. S1). In a simple linear regression combined for both lakes the initial growth is increasing with 0.6 cm·year^{-1} per degree of increasing summer water temperature the preceding year (t=2.653 on 18 d.f., adj-R^2=0.24, p=0.016, Appendix Table S7) (Fig. S1). In a multiple regression model with the preceding summer water temperature (scaled and standardized) and relative density (CPUE) of perch (scaled and standardized) there was a large effect of temperature on initial growth rate (*g*) (1.07 cm·year^{-1} per standard deviation of temperature increase) (t=4.397 on 14 d.f., p<0.001, adj-R^2=0.51), no significant effect of relative density (t=-1.024 on 14 d.f., p=0.32), but a substantial negative effect of the interaction between the two predictors (-1.02 decrease per increase in standard deviation of relative density) (t=-2.940 on 14 d.f., p=0.011 Appendix Table S8).

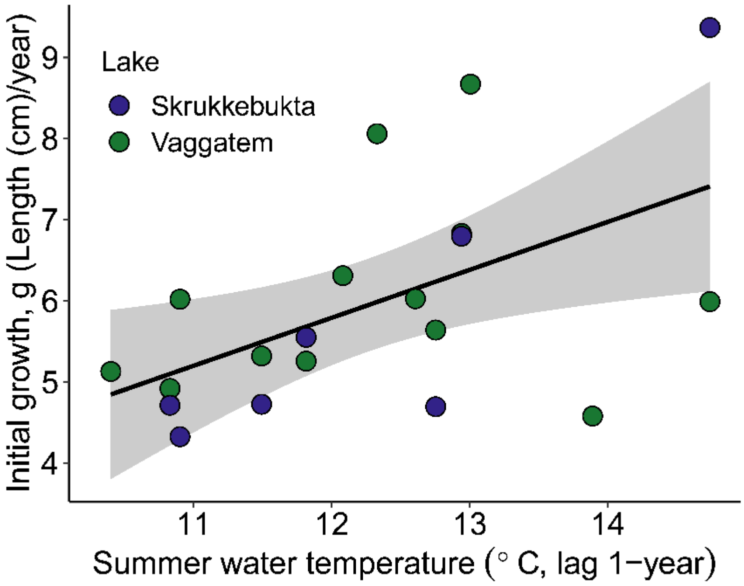


Figure S1. Initial growth (g) given by the modified von Bertalanffy growth model for perch in Lake Skrukkebukta (blue) and Lake Vaggatem (green) dependent on summer water temperature (°C) from the preceding year with a linear regression (solid line) and standard error of the linear regression (shaded area).

Table S7. Initial growth (g) (length, cm/year) given by the modified von Bertalanffy growth model in Lake Skrukkebukta and Lake Vaggatem perch populations dependent on mean summer-water-temperature (°C, Jun-Aug) the preceding year in linear regression model.

	Initial growth (g)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-1.30	-7.07 – 4.47	0.809
Preceding year, mean summer-water-	0.59	0.12 – 1.06	**0.016**

temperature (°C, Jun-Aug) (lag-SWT)	
Observations	20
Degrees of freedom	18
R^2 / R^2 adjusted	0.281 / 0.241

Table S8. Initial growth (g) (length, cm/year) given by the modified von Bertalanffy growth model in Lake Skrukkebukta and Lake Vaggatem perch populations dependent on mean summer-water-temperature (°C, Jun-Aug) and relative density (CPUE) the preceding year in a linear model with an interaction term of the predictors (standardized and scaled).

	Initial growth (g)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	6.12	5.55 – 6.69	**<0.001**
Preceding year, mean summer-water-temperature (°C, Jun-Aug) (lag-SWT)	1.07	0.55 – 1.60	**0.001**
Lag-$CPUE_{perch}$ (lag=1, $(100m^2/12h)^{-1}$)	-0.30	-0.93 – 0.33	0.323
Lag-SWT * Lag-$CPUE_{perch}$	-1.02	-1.77 – -0.28	**0.011**
Observations	18		
Degrees of freedom	14		
R^2 / R^2 adjusted	0.595 / 0.508		

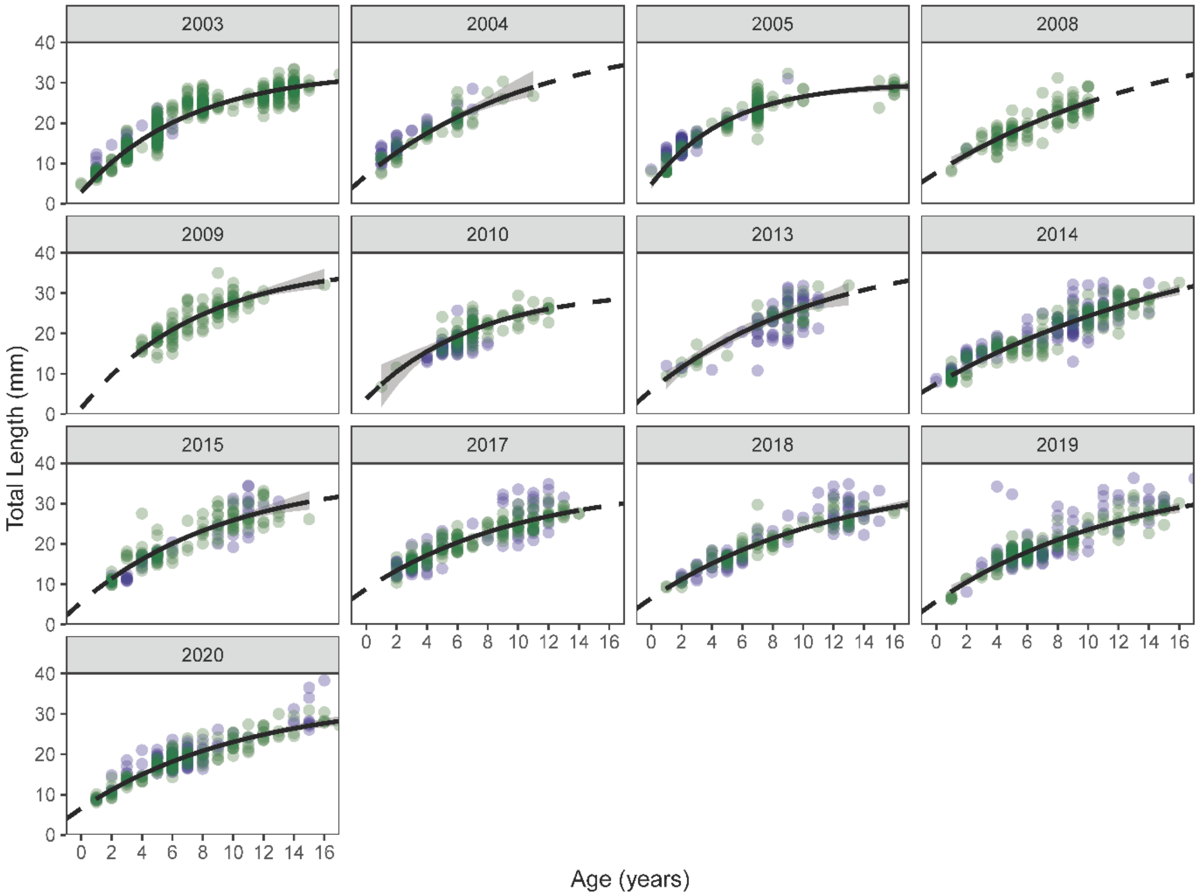


Figure S2. Length at age with von Bertalanffy growth model (stippled and solid line) from year 2003 to year 2020 in Lake Skrukkebukta (blue dots) and Lake Vaggatem (green dots). Shaded area represent the bootstrapped 95 % confidence interval of the line.

Appendix 4: Correlation between back-calculated length and observed length

Table S9. Linear model representing the correlation between back-calculated length (mm) the final winter before capture and observed length (mm) at capture for perch in both Lake Skrukkebukta and Lake Vaggatem.

	Observed length (mm)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-20.60	-23.20 – -18.01	**<0.001**
Back-calculated length (mm)	1.04	1.03 – 1.05	**<0.001**
Observations	1646		
R^2 / R^2 adjusted	0.938 / 0.938		

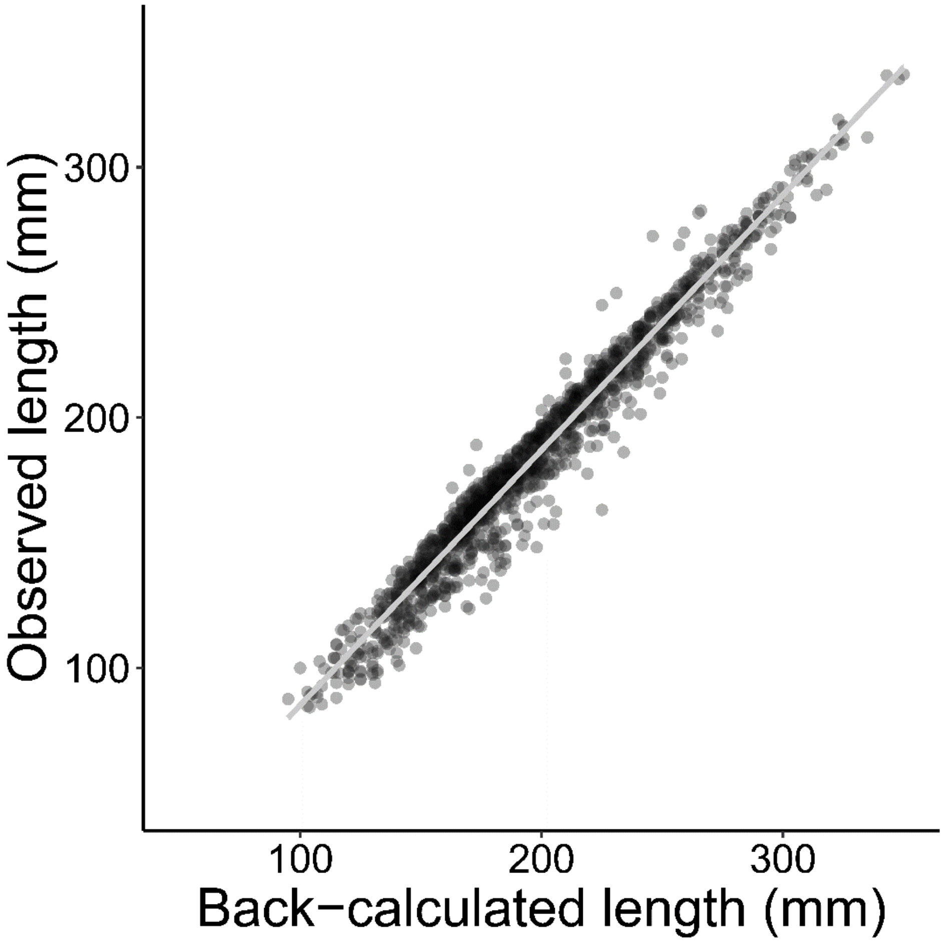


Figure S3. The correlation between back-calculated length (mm) the final winter before capture and observed length (mm) at capture with the solid line (grey) representing the linear regression model.

Appendix 5: Proportion and density of perch in the different study lakes

Table S10. Summary results for the Linear Mixed Effect model (LME) of the development of proportion of Eurasian perch in the littoral zone of 11 high latitude lakes over time. The response is on a natural logarithmic scale.

	ln(Proportion perch+1)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	1.27	0.71 – 1.83	**<0.001**
Sampling year	0.09	0.07 – 0.11	**<0.001**
Random Effects			
σ^2	0.67		
$\tau_{00\ \text{Lakes}}$	0.34		
ICC	0.34		
N_{Lakes}	11		
Observations	95		

Marginal R^2 / Conditional R^2	0.356 / 0.574

Table S11. Summary results for the linear model of the development in relative density (CPUE) of Eurasian perch in the littoral zone of Lake Skrukkebukta over the 30-year sampling period. The response is on a natural logarithmic scale.

	Ln CPUE Perch $(100m^2/12h)^{-1}$			
Predictors	*Estimates*	*CI*	*t-value*	*p*
(Intercept)	0.35	-0.18 – 0.87	1.361	0.187
Sampling year	0.11	0.08 – 0.14	8.014	**<0.001**
Observations	24			
Degrees of freedom	22			
R^2 / R^2 adjusted	0.745 / 0.733			

Table S12. Summary results for the linear model of the development relative density (CPUE) of Eurasian perch in the littoral zone of Lake Vaggatem over the 30-year sampling period. The response is on a natural logarithmic scale.

	Ln CPUE Perch $(100m^2/12h)^{-1}$			
Predictors	*Estimates*	*CI*	*t-value*	*p*
(Intercept)	1.93	1.40 – 2.46	7.520	**<0.001**
Sampling year	0.06	0.03 – 0.08	4.042	**<0.001**
Observations	26			
Degrees of freedom	24			
R^2 / R^2 adjusted	0.405 / 0.380			

Table S13. Relative density of Eurasian perch in Skrukkebukta dependent on water-temperature (Weighted-Moving-Average (WMA) over the last two years) (°C). The response is on a natural logarithmic scale.

	Ln CPUE Perch $(100m^2/12h)^{-1}$			
Predictors	*Estimates*	*CI*	*t-value*	*p*
(Intercept)	-6.67	-11.63 – -1.72	-2.808	**0.011**
Water-temperature (°C) (WMA)	1.83	0.82 – 2.83	3.788	**<0.001**
Observations	22			
Degrees of freedom	20			
R^2 / R^2 adjusted	0.418 / 0.389			

Table S14. Relative density of Eurasian perch in Vaggatem dependent on water-temperature (Weighted-Moving-Average (WMA) over the last two years) (°C). The response is on a natural logarithmic scale.

	Ln CPUE Perch $(100m^2/12h)^{-1}$			
Predictors	*Estimates*	*CI*	*t-value*	*p*
(Intercept)	-1.32	-5.63 – 2.99	-2.808	0.530
Water-temperature (°C) (WMA)	0.89	0.01 – 1.76	3.788	**0.048**
Observations	22			
Degrees of freedom	20			
R^2 / R^2 adjusted	0.182 / 0.141			

Appendix 6: Survival

Table S15. Proportion of one-year-old individuals in Lake Skrukkebukta and Lake Vaggatem perch populations dependent on mean summer-water-temperature (°C, Jun-Aug) (μ=12.06, σ=1.05) the preceding year and a two-year-simple-moving-average (SMA) relative density (when the perch individuals was 0 and 1 year old) (CPUE) (μ=16.64, σ=10.93) in a linear model with an interaction term of the predictors (standardized and scaled).

	Proportion of 1 year old individuals in the perch populations		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	11.57	7.96 – 15.18	**<0.001**
Preceding year, mean summer-water-temperature (°C, Jun-Aug) (lag-SWT)	9.71	5.57 – 13.85	**<0.001**
$CPUE_{perch}$ (SMA, $(100m^2/12h)^{-1}$)	-4.49	-7.96 – -1.02	**0.014**
(lag-SWT) * $CPUE_{perch}$	-4.31	-7.88 – -0.73	**0.021**
Observations	21		
Degrees of freedom	17		
R^2 / R^2 adjusted	0.673 / 0.615		

Appendix 7: Back-calculated length at age

Table S16. The relationship between back-calculated length increment ($mm \cdot year^{-1}$) from age 1-4 year old perch for individual cohorts and the mean summer water temperature (°C, three-year moving-average, 3YA) (μ=12.24, σ=0.49) and the mean relative density (CPUE, three-year moving average, 3YA) (μ=17.51, σ=9.9) in Lake Vaggatem and Lake Skrukkebukta (Centred and scaled predictor variables).

	Length increment (mm·year^{-1}) (age 1-4 years)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	62.83	58.02 – 67.64	**<0.001**
Mean relative density (CPUE, 3YA)	-6.80	-10.44 – -3.16	**0.001**
Mean summer water temperature (°C, 3YA)	4.08	0.73 – 7.44	**0.019**
Lake [Vaggatem]	7.58	0.77 – 14.39	**0.030**
Observations	35		
R^2 / R^{2}adjusted	0.347 / 0.283		

Table S17. Back-calculated length increment for age 1 year old perch (mm·year^{-1}) in Lake Vaggatem dependent on summer water temperature (°C, Jun-Aug) (μ=12.72, σ=0.98) and relative density of perch (CPUE) (μ=23.2, σ=12.22) (centred and scaled predictor variables) in a linear mixed-effect model with sample year and age when caught as random effect.

	Length increment (mm·year^{-1}) in age 1 year old perch		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	69.51	67.27 – 71.75	**<0.001**
Summer water temperature (°C)	0.57	-1.72 – 2.85	0.618
Relative density of perch (CPUE)	-0.15	-2.27 – 1.97	0.887
Random Effects			
N $_{\text{year}}$	18		
N $_{\text{Age}}$	5		
Observations	407		
Degrees of freedom	366 and 34		
Marginal R^2 / Conditional R^2	0.024 / 0.17		

Table S18. Back-calculated length increment for age 1 year old perch (mm·year^{-1}) in Lake Skrukkebukta dependent on summer water temperature (°C, Jun-Aug) (μ=12.31, σ=0.69) and relative density (CPUE) (μ=20.52, σ=18.49) (centred and scaled predictor variables) in a linear mixed-effect model with sample year and age when caught as random effect.

	Length increment (mm·year^{-1}) in age 1 year old perch		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	71.78	68.62 – 74.95	**<0.001**
Summer water temperature (°C)	-0.35	-3.20 – 2.50	0.803
Relative density of perch (CPUE)	0.15	-3.37 – 3.66	0.932
Random Effects			
N $_{year}$	16		
N $_{Age}$	5		
Observations	292		
Degrees of freedom	259 and 26		
Marginal R^2 / Conditional R^2	0.07 / 0.311		

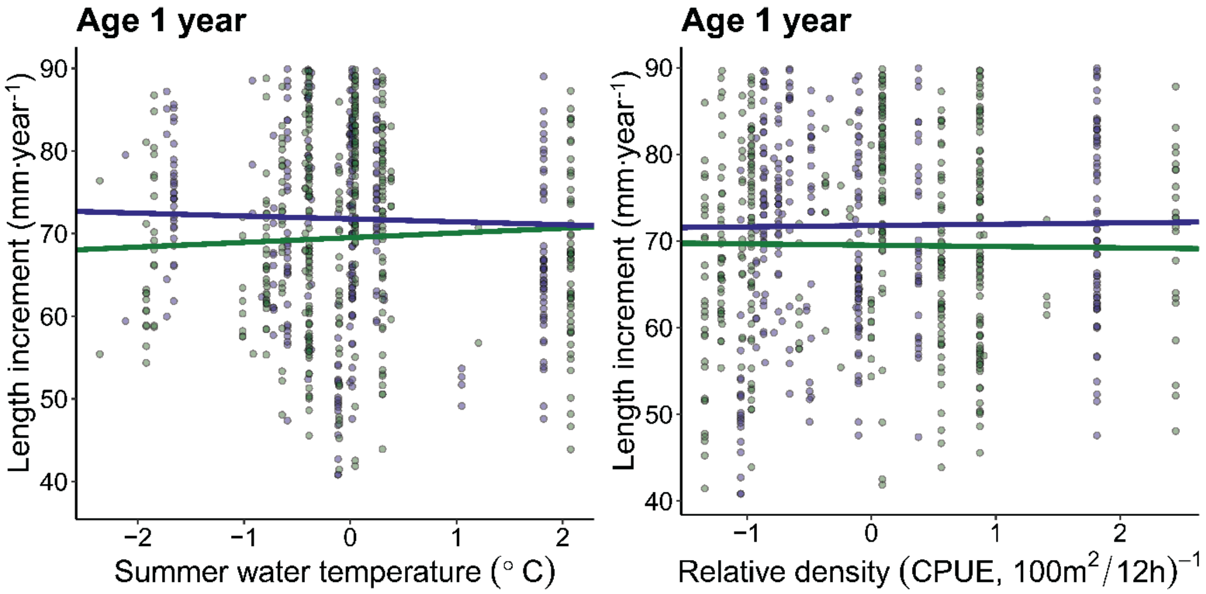


Figure S4. Back-calculated length increment for age 1 year old perch (mm·year^{-1}) in Lake Skrukkebukta (blue dots) and Lake Vaggatem (green dots) dependent on summer water temperature (°C, Jun-Aug) (right) and relative density of perch (CPUE) (left) (centred and scaled). The lines describes the linear mixed-effect model results.

Table S19. Back-calculated length increment for age 2 year old perch (mm·year^{-1}) in Lake Vaggatem dependent on summer water temperature (°C, Jun-Aug) (μ=12.42, σ=0.796) and relative density of perch (CPUE) (μ=22.83, σ=15.06) (centred and scaled predictor variables) in a linear mixed-effect model with sample year and age when caught as random effect.

	Length increment (mm·year^{-1}) in age 2 year old perch

Predictors	*Estimates*	*CI*	*p*
(Intercept)	28.53	26.81 – 30.25	**<0.001**
Summer water temperature (°C)	1.76	0.15 – 3.18	**<0.001**
Relative density of perch (CPUE)	-2.24	-4.35 – -0.06	**<0.001**
Random Effects			
N_{Year}	20		
N_{Age}	13		
Observations	877		
Degrees of freedom	791 and 71		
Marginal R^2 / Conditional R^2	0.117 / 0.264		

Table S20. Back-calculated length increment for age 2 year old perch (mm·year^{-1}) in Lake Skrukkebukta dependent on summer water temperature (°C, Jun-Aug) (μ=12.50, σ=0.84) and relative density (CPUE) (μ=17.7, σ=13.54) (centred and scaled predictor variables) in a linear mixed-effect model with sample year and age when caught as random effect.

	Length increment (mm·year^{-1}) in age 2 year old perch		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	29.22	26.74 – 31.70	**<0.001**
Summer water temperature (°C)	2.59	1.34 – 3.85	**<0.001**
Relative density of perch (CPUE)	-1.00	-2.74 – 0.74	0.252
Random Effects			
N_{Year}	10		
N_{Age}	12		
Observations	580		
Degrees of freedom	515 and 51		
Marginal R^2 / Conditional R^2	0.085 / 0.278		

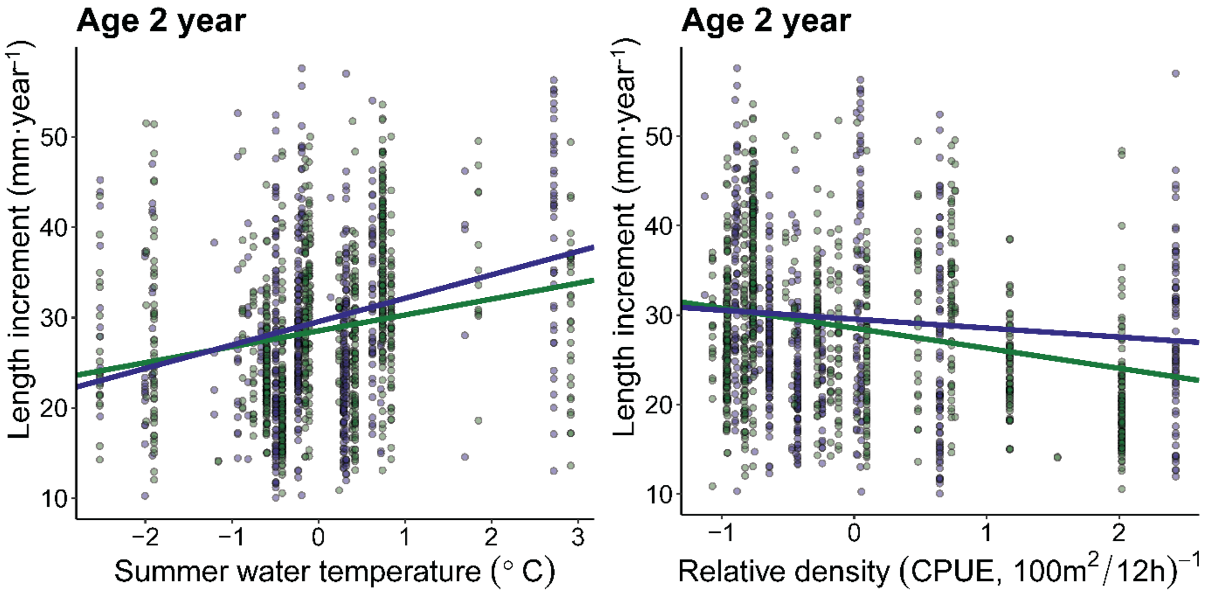


Figure S5. Back-calculated length increment for age 2 year old perch (mm·year^{-1}) in Lake Skrukkebukta (blue dots) and Lake Vaggatem (green dots) dependent on summer water temperature (°C, Jun-Aug) (right) and relative density of perch (CPUE) (left) (centred and scaled). The lines describes the linear mixed-effect model results.

Table S21. Back-calculated length increment for age 3 year old perch (mm·year^{-1}) in Lake Vaggatem dependent on summer water temperature (°C, Jun-Aug) (μ=12.31, σ=0.82) and relative density of perch (CPUE) (μ=20.24, σ=14.72) (centred and scaled predictor variables) in a linear mixed-effect model with sample year and age when caught as random effect.

	Length increment (mm·year^{-1}) in age 3 year old perch		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	26.04	24.88 – 27.20	**<0.001**
Summer water temperature (°C)	1.30	0.17 – 2.44	**0.025**
Relative density of perch (CPUE)	-1.55	-2.85 – -0.24	**0.021**
Random Effects			
N$_{Year}$	11		
N $_{Age}$	11		
Observations	791		
Degrees of freedom	719 and 59		
Marginal R^2 / Conditional R^2	0.069 / 0.363		

Table S22. Back-calculated length increment for age 3 year old perch (mm·year^{-1}) in Lake Skrukkebukta dependent on summer water temperature (°C, Jun-Aug) (μ=12.15, σ=0.85) and relative density of perch (CPUE) (μ=16.05, σ=9.99) (centred and scaled predictor variables) in a linear mixed-effect model with sample year and age when caught as random effect.

	Length increment (mm·year^{-1}) in age 3 year old perch		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	20.35	19.31 – 21.40	**<0.001**
Summer water temperature (°C)	1.03	0.2 – 1.88	**0.031**
Relative density of perch (CPUE)	-0.07	-0.99 – 0.93	0.883
Random Effects			
N $_{Year}$	10		
N $_{Age}$	10		
Observations	503		
Degrees of freedom	439 and 47		
Marginal R^2 / Conditional R^2	0.022/0.193		

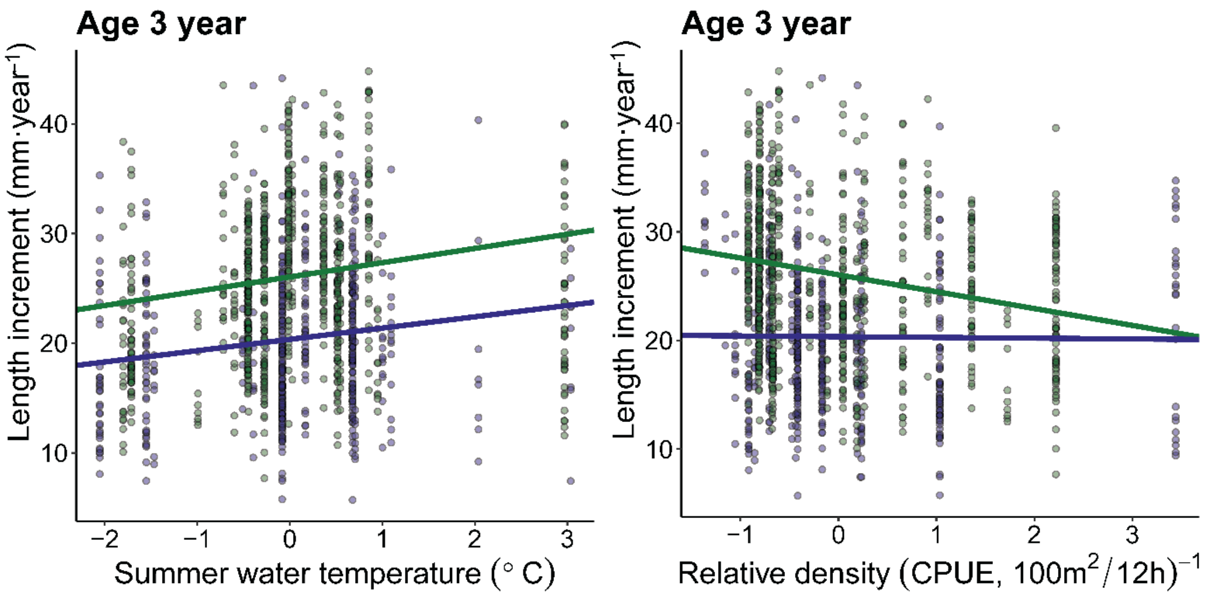


Figure S6. Back-calculated length increment for age 3 year old perch (mm·year^{-1}) in Lake Skrukkebukta (blue dots) and Lake Vaggatem (green dots) dependent on summer water temperature (°C, Jun-Aug) (right) and relative density of perch (CPUE) (left) (centred and scaled). The lines describes the linear mixed-effect model results.

Table S23. Back-calculated length increment for age 4 year old perch (mm·year^{-1}) in Lake Vaggatem dependent on summer water temperature (°C, Jun-Aug) (μ=12.31, σ=0.98) and relative density of perch (CPUE) (μ=23.6, σ=12.25) (centred and scaled predictor variables) in a linear mixed-effect model with sample year and age when caught as random effect.

	Length increment (mm·year^{-1}) in age 4 year old perch

Predictors	*Estimates*	*CI*	*p*
(Intercept)	22.11	20.99 – 23.23	**<0.001**
Summer water temperature (°C)	2.17	1.05 – 3.28	**<0.001**
Relative density of perch (CPUE)	-0.57	-1.67 – 0.53	0.301
Random Effects			
N $_{Year}$	11		
N $_{Age}$	11		
Observations	761		
Degrees of freedom	689 and 59		
Marginal R^2 / Conditional R^2	0.09 / 0.404		

Table S24. Back-calculated length increment for age 4 year old perch (mm·year^{-1}) in Lake Skrukkebukta dependent on summer water temperature (°C, Jun-Aug) (μ=11.87, σ=1.07) and relative density of perch (CPUE) (μ=14.26, σ=7.16) (centred and scaled predictor variables) in a linear mixed-effect model with sample year and age when caught as random effect.

	Length increment (mm·year^{-1}) in age 4 year old perch		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	18.11	16.67 – 19.56	**<0.001**
Summer water temperature (°C)	1.95	0.61 – 3.28	**0.005**
Relative density of perch (CPUE)	-0.19	-1.33 – 0.96	0.745
Random Effects			
N $_{Year}$	10		
N $_{Age}$	10		
Observations	474		
Degrees of freedom	416 and 46		
Marginal R^2 / Conditional R^2	0.097 / 0.296		

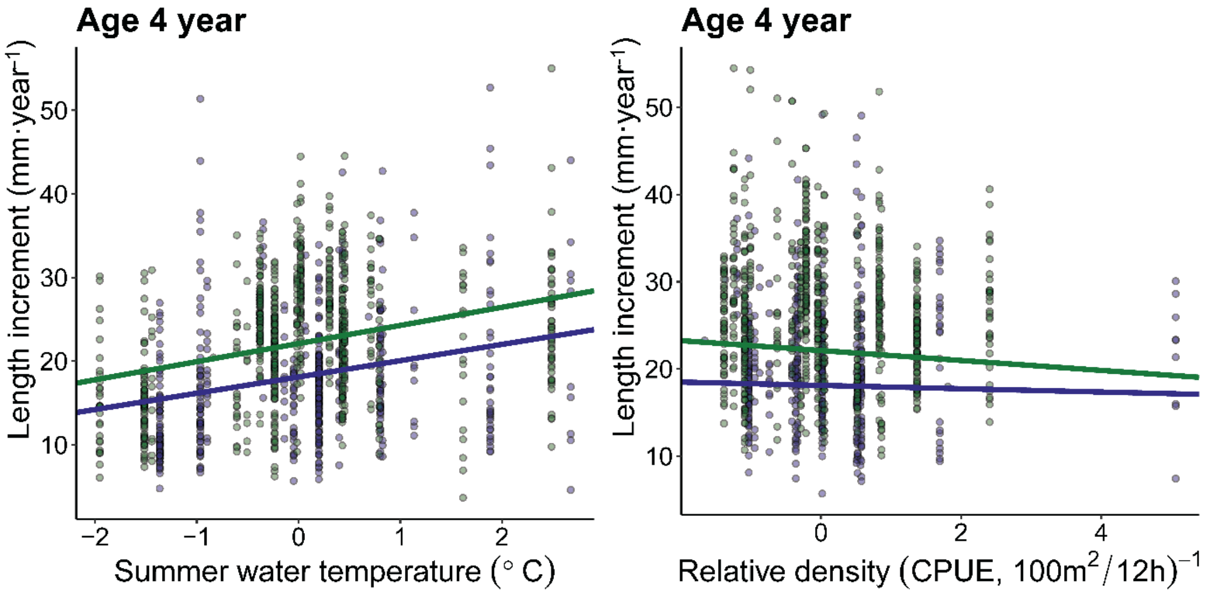


Figure S7. Back-calculated length increment for age 4 year old perch (mm·year^{-1}) in Lake Skrukkebukta (blue dots) and Lake Vaggatem (green dots) dependent on summer water temperature (°C, Jun-Aug) (right) and relative density of perch (CPUE) (left) (centred and scaled). The lines describes the linear mixed-effect model results.

Appendix 8: Age at maturation and sex ratio

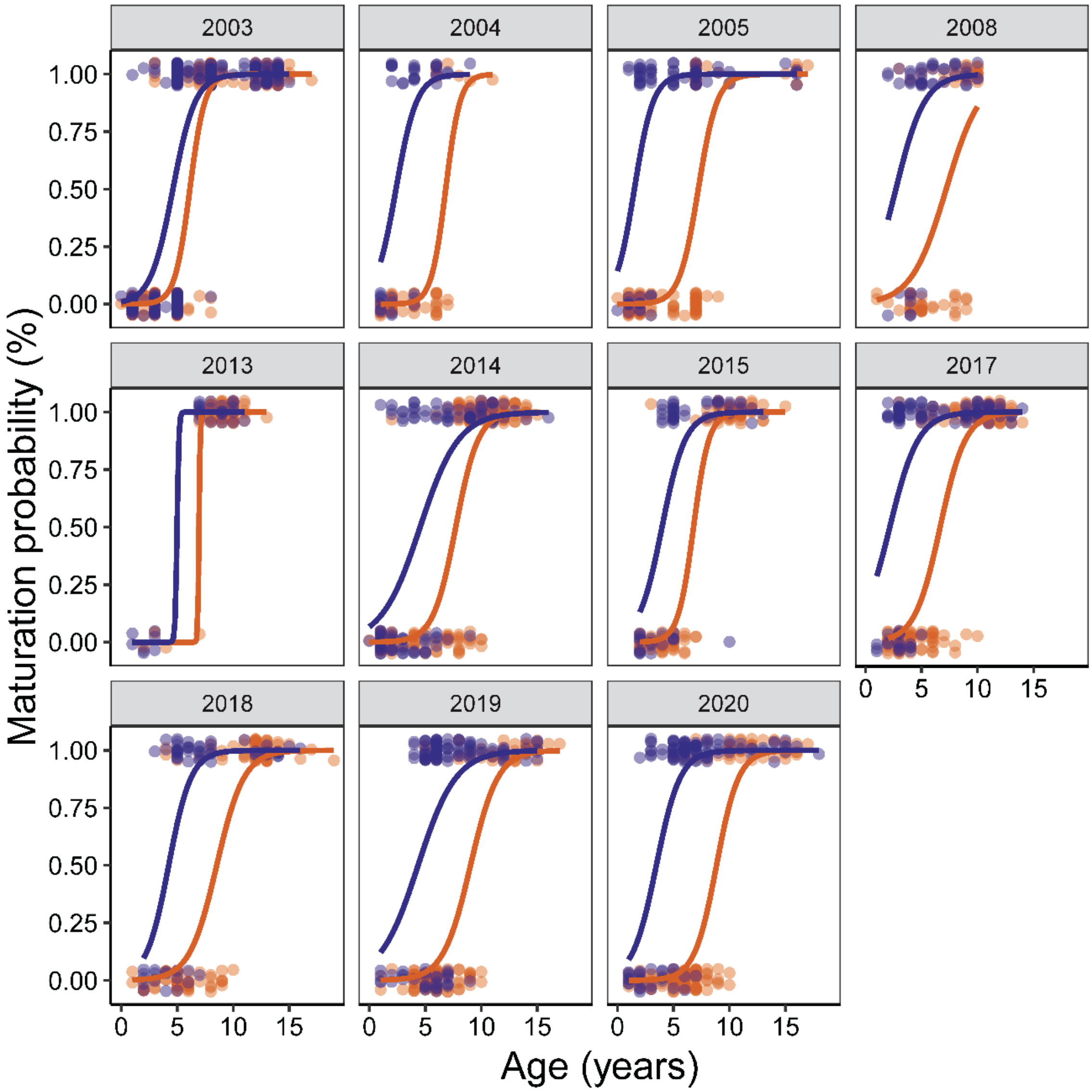


Figure S8. Probability of being mature dependent on age of the perch with logistic regression lines for the individual sampled cohorts. Blue dots and lines depict male individuals. Orange dots and lines depict female individuals.

Cohort-specific age at maturation was not dependent on the difference in sex ratio (proportion of females) for the different cohorts within the perch populations (fig. S9) ($p=0.92$, $t=0.102$ on 15 d.f., adj-$R^2=-0.07$). The sex ratio (proportion of females) was between 0.48-0.72 for the different cohorts, with no change in sex ratio over time ($p=0.21$, $t=-1.31$ on 15 d.f., adj-$R^2=0.04$).

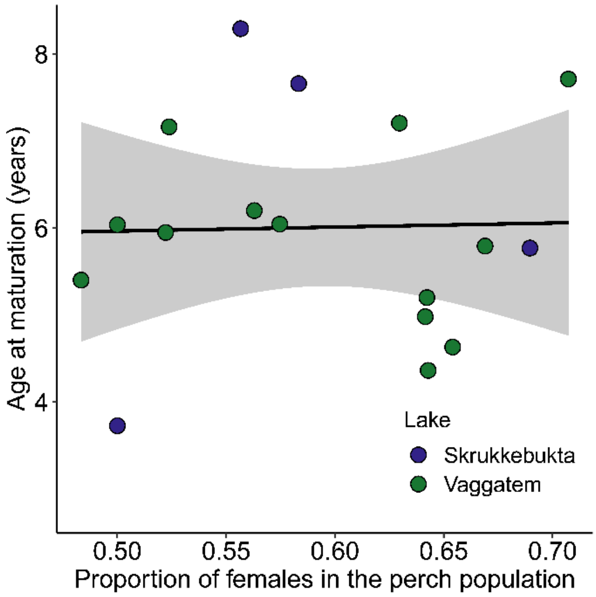


Figure S9. Shows how the difference in proportion of females in the different cohorts affects the age at maturation estimated for the different cohorts. The black line depicts results from the linear model with the shaded area describes the 95% confidence interval.

Table S25. Cohort-specific age at maturation (A_{50}, from logistic regression, fig. S7) dependent on back-calculated length increment ($mm \cdot year^{-1}$) from age 1-4 years.

		A_{50}	
Predictors	*Estimates*	*CI*	*p*
(Intercept)	11.58	8.43 – 14.74	**<0.001**
Length increment (1-4 years)	-0.08	-0.12 – -0.03	**0.002**
Observations	16		
R^2 / R^2adjusted	0.506 / 0.47		

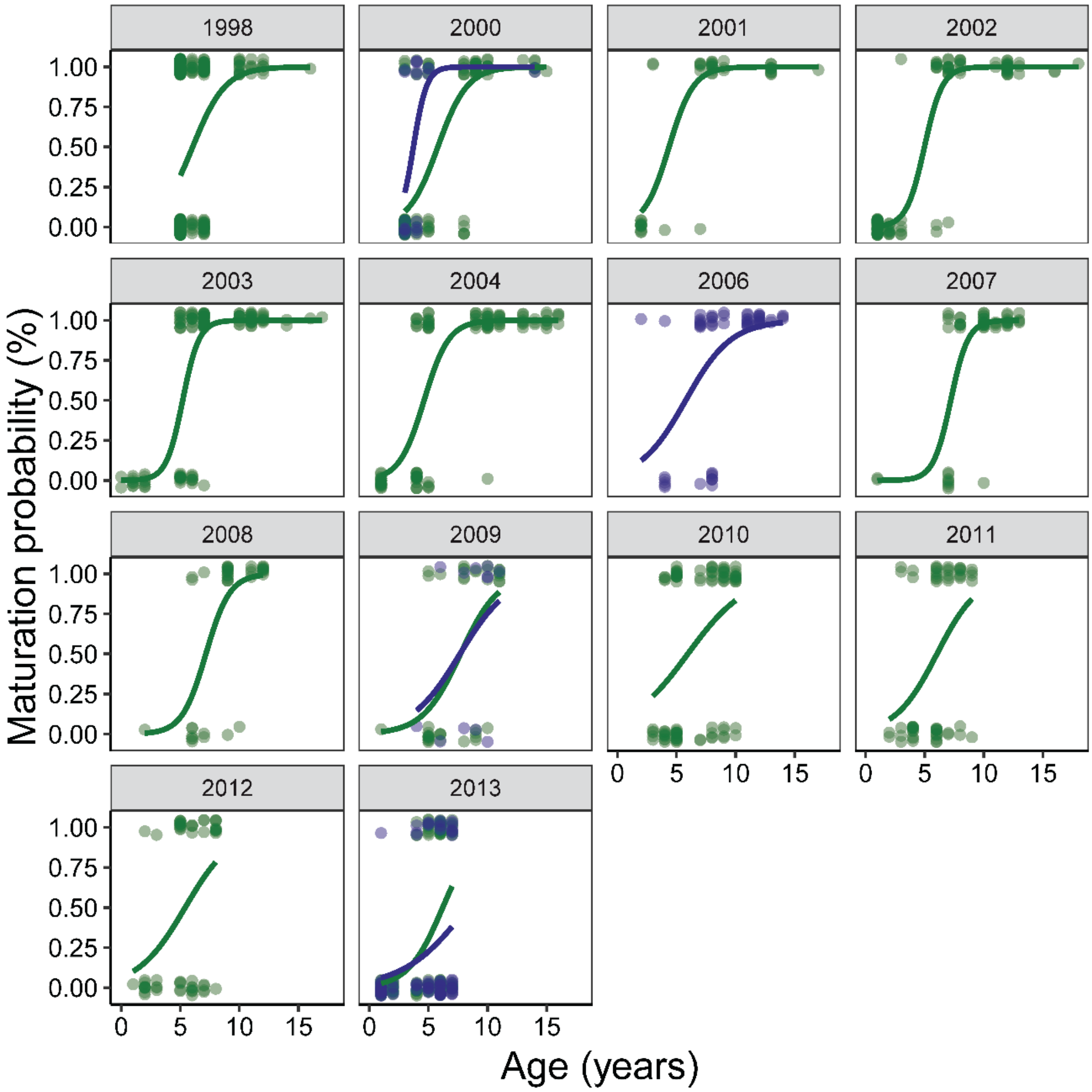


Figure S10. Probability of being mature dependent on age of the perch with logistic regression lines for the individual sampled cohorts. Blue dots and lines depict individuals sampled in Lake Skrukkebukta. Green dots and lines depict individuals sampled in Lake Vaggatem.

Appendix 9: Temperature dependent growth in perch

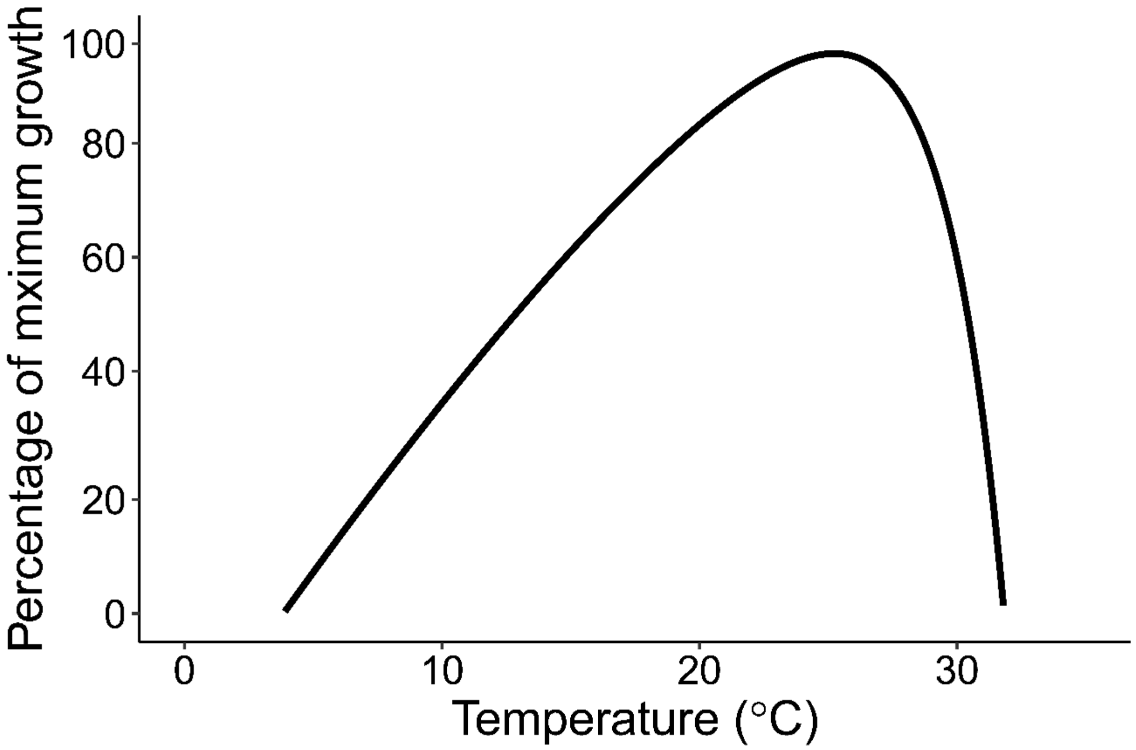


Figure S11. The relationship between growth and water temperature for perch fed on maximum rations from existing literature (see material and methods). Where minimum temperature for growth is 5 °C, optimum temperature for growth is 25 °C and maximum temperature for growth is 32 °C.