RESEARCH ARTICLE

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.

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 ecogenetic 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,

$$M = M_r (L/L_r)^{-c}, \tag{1b}$$

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),

$$\log \left(M_r / \text{year}^{-1} \right) = -z_1 - z_2 \log \left(L_\infty / \text{cm} \right) \\ + z_3 \log \left(K / \text{year}^{-1} \right) + z_4 \log \left(\bar{T} / °C \right), \tag{1c}$$

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 $\bar{T}$ (= 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,

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

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 σ (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,

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

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,

$$f = f_r L^b, \tag{4a}$$

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,

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

where R_t is the total number of recruits, that is surviving offspring, to the population in year t, $f_{tot,t}$ 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 $f_{tot,1/2}$ 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)
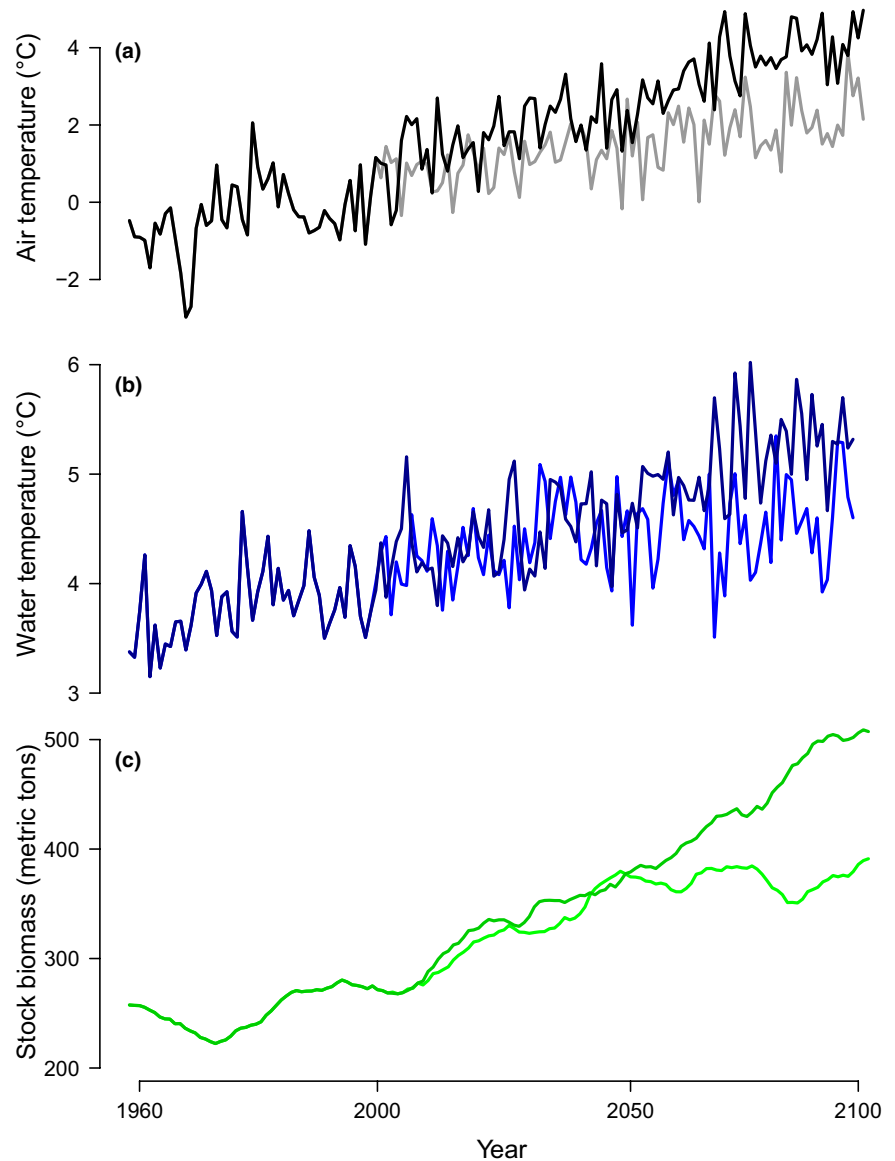
charr populations are often allopatric in high-latitude lakes (Klemetsen et al., 2003).

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 $\overline{B}_{RCP\text{-}8.5}/\overline{B}_{RCP\text{-}4.5} = 1.25$ (comparing RCP-8.5 and RCP-4.5), $F = 0.1$ year^{-1} results in $\overline{B}_{RCP\text{-}8.5}/\overline{B}_{RCP\text{-}4.5} = 1.22$, $F = 0.2$ year^{-1} results in $\overline{B}_{RCP\text{-}8.5}/\overline{B}_{RCP\text{-}4.5} = 1.14$,

$F = 0.3$ year^{-1} results in $\overline{B}_{RCP-8.5}/\overline{B}_{RCP-4.5} = 1.09$, and $F = 0.5$ year^{-1} results in $\overline{B}_{RCP-8.5}/\overline{B}_{RCP-4.5} = 1.03$. 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
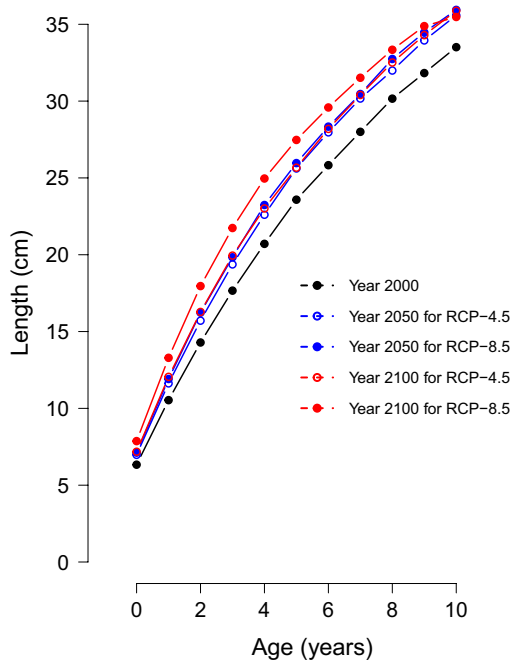

FIGURE 2 Model predictions of lengths at age of Arctic charr in Lake Takvatn for two climate scenarios without harvesting

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}.

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, $W = 49,375$,
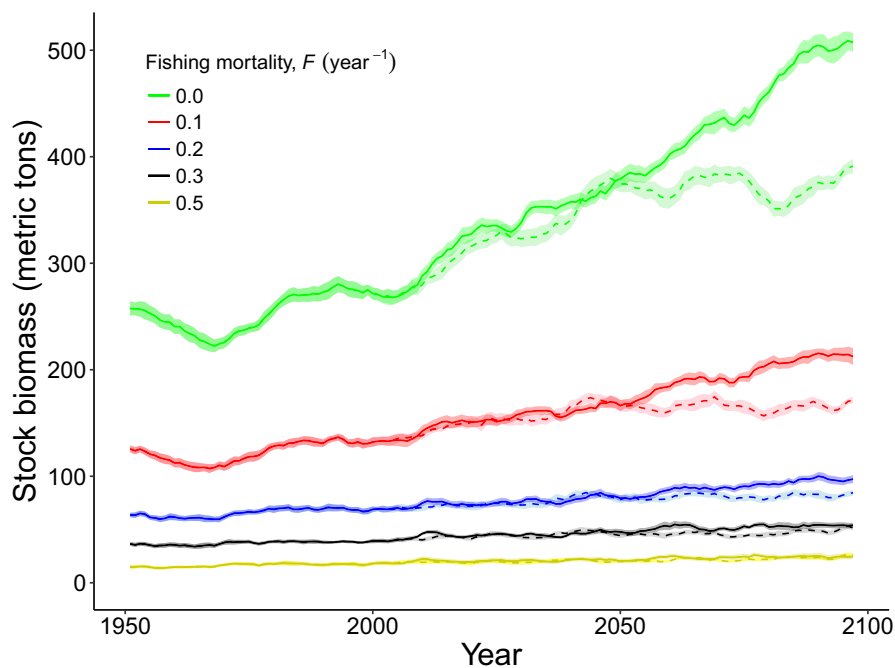
FIGURE 3 Model predictions of stock biomass of Arctic charr in Lake Takvatn for two climate scenarios (dashed lines for RCP-4.5, continuous lines for RCP-8.5) and five fishing mortalities (0.0, 0.1, 0.2, 0.3 and 0.5 year^{-1}) from 1953 to 2005 (hindcasted) and from 2006 to 2100 (forecasted) with 95% confidence intervals indicated by shading
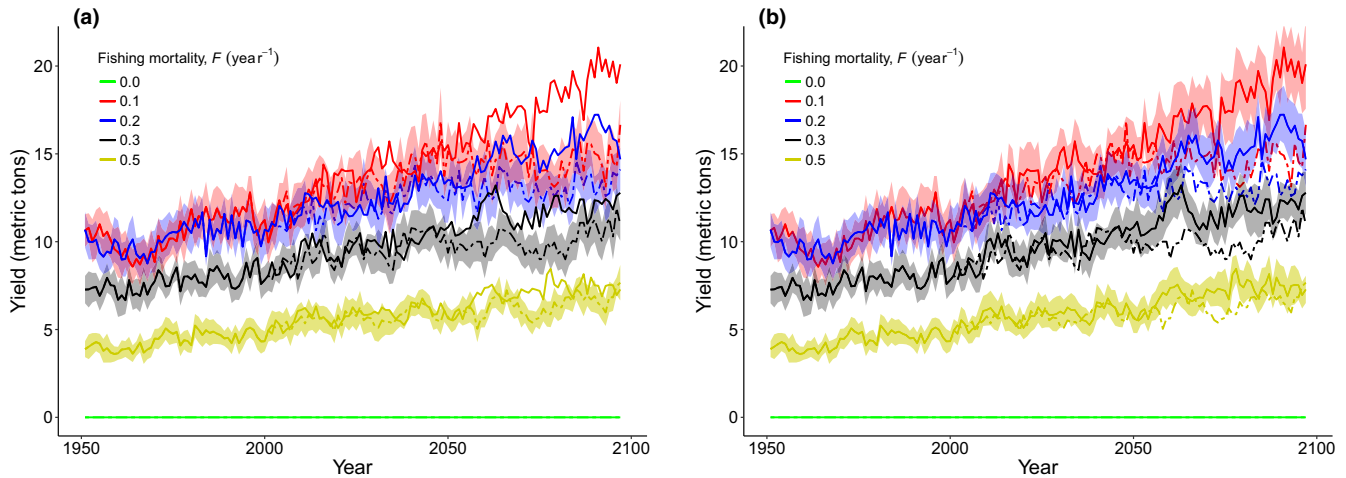
FIGURE 4 Model predictions of yield of Arctic charr in Lake Takvatn for two climate scenarios (dashed lines for RCP-4.5, continuous lines for RCP-8.5) and five fishing mortalities (0.0, 0.1, 0.2, 0.3 and 0.5 year^{-1}) from 1953 to 2005 (hindcasted) and from 2006 to 2100 (forecasted). (a) Focus on RCP-4.5 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
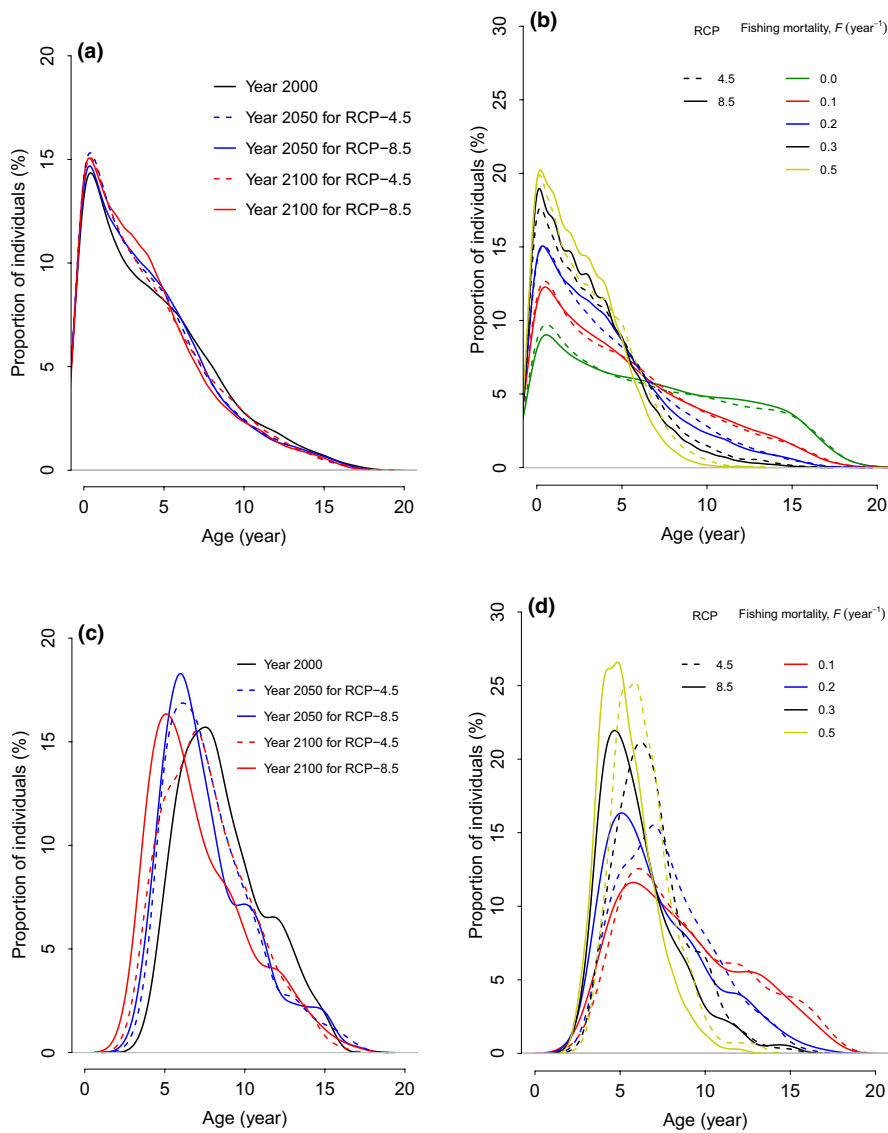
biomass. Higher growth rates and production have been suggested to be a consequence of climate warming for freshwater fish populations living in high-latitude lakes (Brander, 2007; Reist et al., 2006). There are few studies testing the impact of climate warming on somatic growth in salmonids; however, 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 ($F < 0.2$ 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
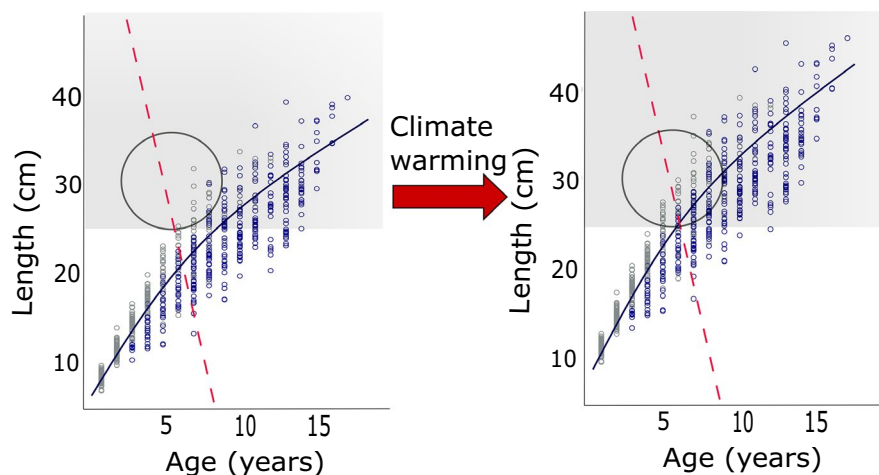
FIGURE 6 Conceptual illustration of the demographic changes caused by the combination of climate warming and size-dependent harvesting. The grey shading shows the size range of the fishery, the dashed red line shows the age-dependent probabilistic maturation reaction norm (PMRN) midpoints, and the blue 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.

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.