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Climate change and Arctic charr (*Salvelinus alpinus*) in North America: modelling possible changes in range with different climate scenarios and interspecific interactions

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Abstract

One of the greatest challenges for researchers today is understanding climate-change impacts on fish populations, particularly in vulnerable and understudied ecosystems such as the Canadian Arctic. Among other impacts, northern fishes will undergo thermal stress as atmospheric and sea surface temperatures are projected to rise globally. Models that consider how both environmental factors such as temperature and potential species interactions will impact population extirpation and species' range contraction can help project the future distribution of a species in the face of a warming climate. Here, we investigate the climate-change impacts of rising temperatures and the potential northward distributional shift of brook charr (*Salvelinus fontinalis*) on Arctic charr (*Salvelinus alpinus*), Canada's northernmost freshwater fish species. Specifically, we used a logistic regression model to establish baseline relationships between the current distribution of Arctic charr and the variables, degree-days (a key climate variable), geographical location, and brook charr occurrence. We developed the model applying the expected changes in degree-days to 2050 (25–50% increase from the average of 1976–2005) and 2080 (50–100% increase) while incorporating the historical distribution of Arctic charr to estimate the change in Arctic charr distribution over that time. We found that growing degree-days, longitude, latitude, and brook charr occurrences correctly classified 93% of Arctic charr historical occurrences in Canada. We estimate that in a high-carbon scenario, where degree-days are expected to increase by 50 to 100%, Arctic charr range is projected to decrease by 18% in Canada by 2051–2080 and decrease even further by 3% with the presence of brook charr. The Canadian high Arctic may provide refuge for Arctic charr, likely maintaining temperatures optimal for species persistence. Regardless, management that considers the climate stresses on Arctic charr populations will be important to preserve this highly valued resource that is pivotal for food security and traditional ways of life for northerners.

Keywords Climate change · Arctic charr · Models · Ecosystem · Growth · Diet

Introduction

Climate change has a significant and pronounced impact on the Canadian Arctic, with consequences for the environment, communities, and ecosystems in the region. The key ways in which climate change affects the Canadian Arctic are complex, diverse and multifaceted. First, the Canadian Arctic is warming at about four times the global average rate (van Wijngaarden 2015; Rantanen et al. 2022). Warmer temperatures lead to various changes, including the thawing of permafrost and the reduction of sea ice. Permafrost contains vast amounts of stored carbon, and as it thaws, it releases greenhouse gases such as carbon dioxide and methane, further contributing to global warming. Second, land erosion is

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expected to increase drastically with Arctic climate change (Schuur et al. 2015). As temperatures rise, permafrost thaws at an accelerating rate (Schuur et al. 2015). This has several consequences, including infrastructure damage (buildings, roads, pipelines) as the ground becomes unstable, and the release of greenhouse gases trapped in the permafrost, exacerbating climate change (Murton 2021). Rapid temperature increases associated with climate change are expected to directly affect the Arctic through changes in water levels and river flow, increases in water temperatures, fluctuating nutrient supply, and changes in water quality (Ficke et al. 2007; Van Vliet et al. 2013). The Arctic Sea ice extent is also decreasing and has far-reaching implications for the region (Post et al. 2013). Less sea ice means less habitat for ice-dependent species such as polar bears and seals. It also affects the traditional practices of Indigenous communities, such as hunting and travelling across frozen waters. The melting of sea ice has also made the Arctic more accessible for shipping and resource extraction. While this may bring economic opportunities, it also poses risks to the environment and Indigenous communities if not managed sustainably. With less sea ice to protect the shoreline, coastal erosion is also accelerating in many parts of the Canadian Arctic. This threatens infrastructure, homes, and cultural sites, impacting the livelihoods and safety of local communities (Manrique et al. 2018).

As temperatures rise, the distribution of plant and animal species continues to shift. New species are moving into the region, while others are facing challenges in adapting to changing conditions (Post et al 2013). This can disrupt traditional subsistence hunting and gathering practices of the Indigenous peoples. Furthermore, as the Arctic Ocean absorbs more carbon dioxide from the atmosphere, it becomes more acidic, which can harm marine life, particularly species with calcium carbonate shells or skeletons like shellfish and some plankton species (Lam et al. 2016). These changes affect Indigenous peoples in the Canadian Arctic who are particularly vulnerable to the impacts of climate change, as their traditional ways of life are closely tied to the environment (Vogel and Bullock 2021). Rapid environmental changes can affect food security, housing, and cultural practices, leading to significant social and economic challenges (Crépin et al. 2017). Overall, the effects of climate change in the Canadian Arctic are complex and interconnected, and they require a multifaceted response that addresses both environmental and social aspects. Adaptation and mitigation efforts, as well as collaboration between governments, Indigenous communities, and international organizations, are essential to address the challenges posed by climate change in this region (Tallman et al. 2019).

Management strategies aimed at mitigating or reducing climate-change impacts must consider the sustainability and adaptability of fish stocks. Understanding the climatic effects on fish behaviour and population dynamics has been challenging and this is especially true within Arctic ecosystems that are relatively understudied (Ulvan et al. 2011). An improved understanding of climate-change impacts on northern fishes is relevant for conserving Arctic biodiversity and promoting ecosystem health and food security (Van Vliet et al. 2013). The Intergovernmental Panel on Climate Change (IPCC) has reported that many parts of the world are already experiencing the negative consequences of global warming through increased climate events such as increases in sea surface temperatures and rising sea levels (IPCC 2022). Indeed, climate warming and subsequent changes in environmental factors associated with anthropogenic climate change is affecting the livelihoods of communities in the Arctic (Pearce et al. 2015; Falardeau et al. 2022). The IPCC has reported that, if anthropogenic-driven global warming continues at the current rate, temperatures are anticipated to increase ~1.5°C between 2030 and 2052, with the Arctic experiencing increases two to three times faster than the global average (Falardeau et al. 2022; IPCC 2022). The Arctic has the highest proportion of species potentially threatened with thermal stress, which may cause local extinctions, northward shifts of species ranges, and forced adaptation (Rouse et al. 1998; Van Vliet et al. 2013).

A group of fishes, which are primarily cold water adapted and sensitive to extreme warming, within the genus *Salvelinus* (charrs), are used as models to study the impacts of climate change in northern aquatic taxa (Johnson 1980; Meisner 1990; Coad and Reist 2017; Lehnherr et al. 2018). Within this group of fishes, the Arctic charr (*Salvelinus alpinus*) is restricted to cold water environments and can survive at temperatures as low as 1°C, making them the most cold-adapted salmonid species in the world (Brännäs 1992; Gerdeaux 2011). Therefore, it is especially vulnerable to increasing water temperatures (Gilbert et al. 2020). The optimal temperature for Arctic charr growth and development is surprisingly high and lies between 12°C and 17°C (Larsson et al. 2005; Gunnarsson et al. 2011). The optimum temperature for growth of the Arctic charr is reduced as the fish grow larger and growth may occur best at lower temperatures (Gunnarsson et al. 2011; Imsland et al. 2020; Árnason et al 2022). In fact, in marine environments, Arctic charr atypically occupy temperatures between 5 and 8°C which is assumed to be optimal for physiological functioning (Harris et al. 2020). In wild Arctic charr, temperatures ~16°C become detrimental for this species and charr typically become arrhythmic at ~21°C (Gilbert et al. 2020). Brook charr (*Salvelinus fontinalis*), a close relative of Arctic charr endemic to North America, is also considered a cold-adapted species (Scott and Crossman 1973; Chadwick and McCormick 2017). The native range of brook charr spans the temperate northeastern parts of North America and southeastern parts of Canada (Scott and Crossman 1973). As a habitat generalist found in lakes and streams, they thrive in northern latitudes and can be occasionally anadromous (Lenormand et al. 2004). Brook charr optimal growth and feeding temperature are from 11 to 18°C with the best growth and food consumption at 13°C (Baldwin 1957; Mullan 1958). It overlaps with optimum temperature ranges for Arctic charr, although Arctic charr is a bit more stenothermic. It should be noted that even though brook charr and other temperate species can survive at winter temperatures, they simply do not exist within a large part of the range of Arctic charr. We presume that this is because the biology of Arctic charr makes it better adapted to sustained cold temperatures and the Arctic environment. Brook and Arctic charr spawning can vary with latitude and temperature typically occurring in late summer or fall (Scott and Crossman 1973).

Arctic charr and brook charr both recolonized eastern Canada post-glacially from multiple refugia (Moore et al. 2015; Dupont Cyr et al. 2018). They have similar morphological characteristics in terms of mouth size, body shape, and fin size and shape suitable for salmonids occupying a wide range of habitats from streams, lake, and ocean (Scott and Crossman 1973; Hammer et al. 1991), and can exhibit both benthic and pelagic morphotypes (Scott and Crossman 1973; Dupont Cyr et al. 2018). In coastal areas, Arctic charr and brook charr can exist as freshwater residents, where they have access to marine environments, but remain in freshwater throughout their lives, landlocked, where they have no access to marine environments; or, anadromous, where they make seasonal migrations between lakes and marine environments (Stewart and Watkinson 2004; Dupont Cyr et al. 2018). They both use anadromy as a strategy for energetic and opportunistic marine feeding advantages to prepare for reproduction in freshwater habitats (Skúlason and Smith 1995; Gunn and Snucins 2010). All of the above suggested that brook charr and Arctic charr are likely to have competitive interactions in sympatry. While both species are cold adapted, Arctic charr typically occurs in water temperatures ranging 5–19°C and brook charr 8–20°C (Dupont Cyr et al. 2018). Arctic charr is known to have the northernmost distribution in North America (Wilson et al. 1996), occupying freshwater lakes and streams up to 84°N at Ellesmere Island, Canada (Christiansen and Reist 2013). Arctic charr southern range is not limited by temperature. It is considered that Arctic charr are inhibited from extending their range south because they are less behaviourally competitive compared to other species such as brook charr (Reist et al. 2013; Bommersbach 2023).

Growing degree-days (GDD) are the accumulation of daily mean temperatures (including the minimum and maximum daily temperatures) above a specified threshold base temperature (Neuheimer and Christopher 2007; Climate Atlas of Canada 2022). The base temperature is considered the threshold temperature, where the minimum development threshold must be for significant metabolic activity, allowing the fish to grow, move, feed, and do other activities beyond torpor to occur (Neuheimer and Christopher 2007; Climate Atlas of Canada 2022). While most descriptions of climate focus on absolute temperature change, the important effect is warmth which results in metabolic activity and how long suitable temperatures are maintained. In other words, a ten degree change in average winter temperature from -30°C to -20°C, for example, will have no impact as growth is still inhibited at these temperatures, whereas a longer and warmer growing season will matter impacting growth and physiological functioning. Therefore, GDD are a measure of the biologically relevant aspect of climate change. Neuheimer and Christopher (2007) explained that GDD is a metric providing greater explanatory power than solely using annual mean temperature data because it is a physiologically relevant measure of temperature and considers the timing of a season (i.e. seasonal temperature responses of fish maturity; size-at-age recruitment). Explaining or predicting growth, development, and survival in fishes is often essential to population dynamics and ecosystem studies on topics such as food-web relationships or determining fishing practices suitable for sustaining a fishery (Neuheimer and Christopher 2007; Falardeau et al. 2022).

The distribution of Arctic charr has undoubtedly been affected by the glacial events over the last 20,000 years when most of Canada was covered by an ice sheet. The recession of the ice sheet from the last glacial maximum proceeded in a northeasterly direction. Even today, the distribution of plants and animals reflects the process of recolonization and the timing of the land becoming ice free. Therefore, we expect that latitude and longitude may be relevant in predicting the likelihood of occurrence of Arctic charr as well as other aspects of their ecology, because some populations will have had many more generations to adapt than others.

Finally, Arctic charr possess rather unique behavioural characteristics that may be related to spending long periods of the year under the ice in relatively close quarters. Compared to other salmonids, Arctic charr lack the interspecific agonistic behaviour characteristic of the taxon. Their success may lie in the ability to rapidly re-colonize areas post-glaciation where there are no aggressive competitors. The lack of aggressiveness may be required for the group to survive throughout the long winter. As climate warming occurs, it may allow temperate zone species heretofore not present to expand northward and come into contact with Arctic charr. In particular, congeneric species, with similar ecologies, such as brook charr, may present a problem for Arctic charr.

Comte et al. (2013) provided an extensive review of the papers on species distribution and climate change. They categorized studies into three forms: physiological, distributional, and empirical. The most common study was based on physiological parameters such as maximum temperature tolerance. Our work is focused on the distributional approach and, while not unique, does use information heretofore not available to categorize climate change and Arctic charr distribution. We have also accounted for the glacial history, which for field workers such as ourselves is readily apparent when travelling in the Canadian Arctic. For example, trees grow in the western Arctic Coast, whereas the treeline occurs much further south in the east. As well, by focusing on degree-days we relate the outcome to fish growth which will be more directly translatable to assessing changes in stock productivity in the assessment of fisheries in the north (Boyce et al. 2021).

Predicting how species may respond to climate warming, especially those in the vulnerable Arctic Region, is a challenge for biologists. Yet, such predictions will be essential to guide resource managers and decision-makers. Few studies, however, have considered the growing season in a quantitative fashion. As well, the question of brook charr influence on Arctic charr distribution has not been examined mathematically. As such, we used GDD, latitude, longitude, and knowledge of brook charr distribution to predict the future distribution of Arctic charr based on two future climate scenarios. We expected that the increase in GDD and the presence of brook charr would be associated with a reduced likelihood of Arctic charr occurrence and establishment. To verify this, we developed two logistic regression models to understand the current distribution of Arctic charr and its future distribution under climate change. These models describe Arctic charr distribution for the time period of 1976–2005 in Canada related to GDD and brook charr occurrence to predict changes to Arctic charr distribution as a result of expected increases in temperature associated with climate changes to the year 2080. The results of our model will have important implications for the management of vital resource for the Inuit and First Nations of the Canadian north.

Materials and methods

To simulate the change in growing season expected with a warming climate, we used GDD to quantify the expected effect of climate warming. As noted earlier, GDD provide many advantages in biological realism compared to simple temperature measurements. The technical description of GDD is the annual sum of the number of degrees Celsius that each day's mean temperature is above a specified base temperature (Climate Atlas of Canada 2022; Eq. 1):

$$\left[(Max\,daily\,temp + min\,daily\,temp)/2\right] - base\,temp = GDD. \quad (1)$$

To determine the future climate, we used the information in the Climate Atlas of Canada (https://climateatlas.ca/), an online software that operates as a standard grid square (Bommersbach 2023). The squares on the Atlas are 100×100 km. The Climate Atlas of Canada uses the Pacific Climate Impacts Consortium (PCIC's) climate data (Constructed Analogues and Quantile mapping, Version 2; BCCAQv2), which originates from global climate models (Climate Atlas of Canada 2022). The Climate Atlas of Canada projects two carbon emission scenarios at varying time periods: 1) a low-carbon scenario, defined as where the rate of greenhouse gas emissions slows, peaks at mid-century, and then drops rapidly, leading to lower emissions that cause less severe warming. This scenario assumes that greenhouse gas emissions increase until about 2050 and then rapidly decline; 2) a high-carbon scenario that assumes that world greenhouse gas emissions continue to increase at the current rates through the end of the century. This is the "business as usual" scenario and the large amount of greenhouse gas emissions results in more severe global warming (Climate Atlas of Canada 2022).

For the model to describe the relative effects of brook charr presence, growing season, latitude, and longitude on the likelihood of Arctic charr occurrence, we used a database developed by the University of Toronto Mandrak lab for Arctic charr and brook charr distribution for the period 1976–2005. We converted the raw data into a format that would match it with the Climate Atlas of Canada data for GDD based on Cartesian geographical coordinates. A multivariate logistic regression model with predictor variables of brook charr occurrence, GDD, and geographical location was developed as a baseline model.

The complete dataset equated to 832 cells within Canada based on the Climate Atlas of Canada and included climate variables of growing degree-days (GDD, base 4°C) and annual mean temperature (°C) for the time period 1976–2005. We assumed close correspondence between air temperature and water temperature (Livingstone and Lotter 1998). It should be acknowledged, however, that air temperature model outputs and scenarios are likely to be less precise than the ones based on water temperatures. Within small systems, such as many of the Nunavut Arctic charr environments, Stefan and Preud'homme (1993) noted smaller deviations between air and water temperatures than large systems. Many studies have developed models to convert air temperatures to water temperatures (Piccolroaz et al. 2013). However, water temperature models and scenarios for the Canadian Arctic and sub-Arctic do not exist. We used the lowest temperature with available data, 4°C, as the base temperature (Jobling et al. 1993; Climate Atlas of Canada 2022). This temperature is also the most likely minimum for development and physiological activity in Arctic and brook charr (Jobling et al. 1993; Koops and Tallman 2004).

To determine the occurrence of brook and Arctic charr, we used the continuous range distributions of Arctic charr and brook charr across Canada based on information from the literature and data collected by the Mandrak lab (unpublished data). The distributional maps reflect broad areas where Arctic charr and brook charr occur over landscapes and water bodies. The distributional maps for Arctic charr and brook charr were acquired from the Mandrak lab database (Fig. 1). Only native occurrences of Arctic charr and brook charr were included in the dataset. The dataset was manually created where 832 cells within Canada reflected the presence (*presence* = 1) or absence (*absence* = 0) of Arctic charr and brook charr.

A generalized linear model function (glm) in R version 3.6.1 (R Development Core Team 2019) was used to create the regression model.

The binomial logistic regression model equation is:

$$Ln[P/(1-P)] = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_k X_k, \quad (2)$$

where $Ln[P/(1-P)]$ is the natural log odds (native Arctic charr occurring in a region) against various predictor variables (X_i) and their corresponding coefficients (β_i). β_0 and

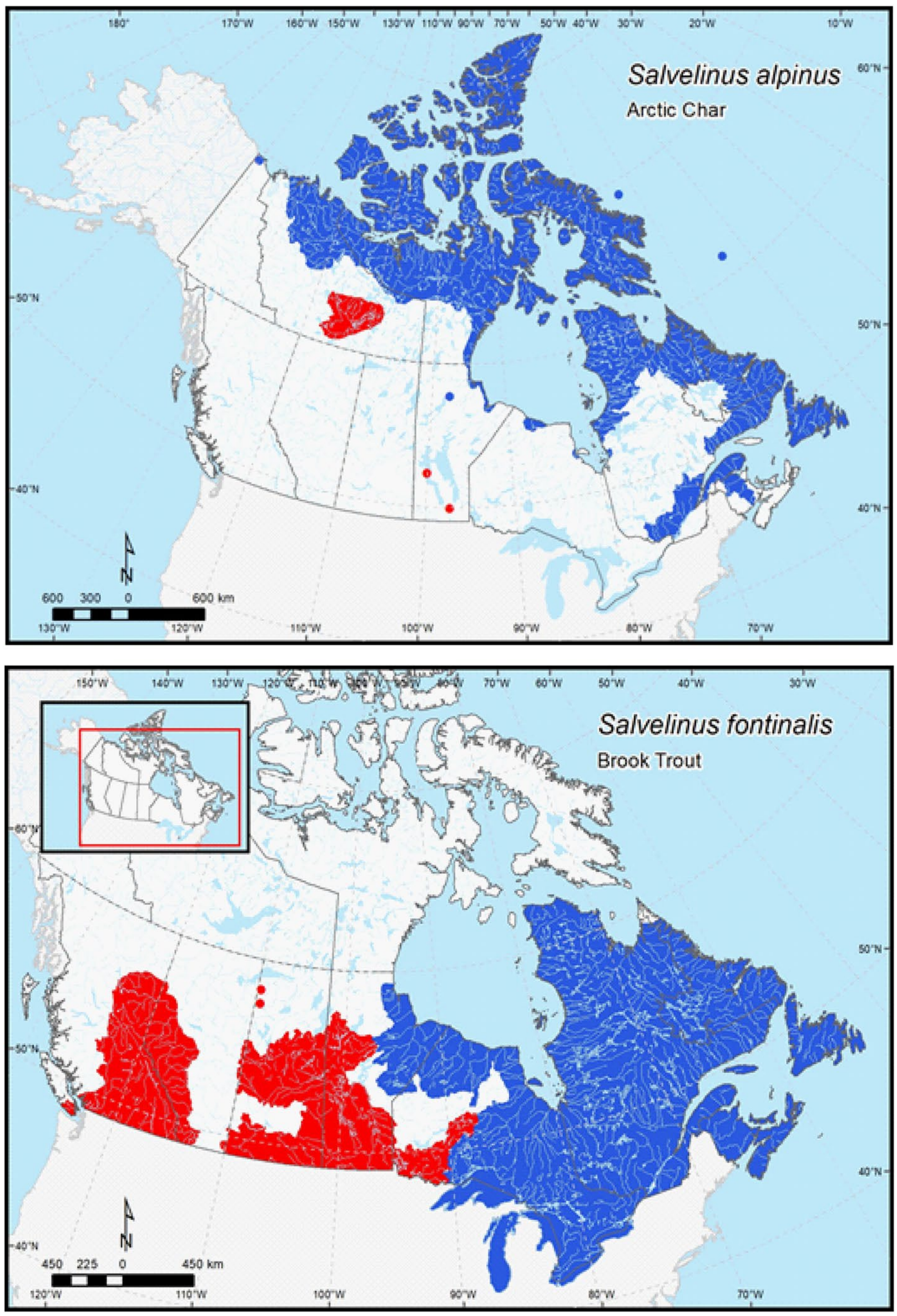

Fig. 1 Continuous distributional range of Arctic charr and brook char in Canada. Distributions highlighted in blue are known native occurrences and distributions highlighted in red are known introduction occurrences (Bommersbach 2023 after figures supplied by N. Mandrak)

$\beta_1 \ldots \beta_k$ are parameters to be estimated (Quinn and Keough 2002).

The baseline time period ranged from 1976 to 2005 at the low-carbon scenario. Models were specified with a binomial distribution and a logistic link function. The full dataset was randomly divided by Arctic charr occurrence data into a training dataset (321 presences, 345 absences) and a testing dataset (80 presences, 86 absences; Bommersbach 2023). The training dataset fit the logistic regression model, and the testing dataset was used to evaluate model performance. A correlation matrix including all variables was performed to determine the degree of correlation between variables and check that they were independent (Table 1). As a measure of sensitivity, we calculated the detection probability, which is defined as the likelihood of detecting or predicting the positive outcome based on the logistic regression model (Hein et al. 2012).

The training dataset developed a model suite (Table 2), which involved variations of the parameters chosen to predict the Arctic charr present within their distributional range: GDD (base 4°C, 1976–2005); annual mean temperature (°C 1976–2005); longitude (-); latitude (+); presence (1) or absence (0) of brook charr.

We used the Akaike's information criterion (AIC) to find the best predictor model:

$$AIC = 2K - 2Ln(L), \quad (3)$$

where K is the number of parameters in the model and $Ln(L)$ is the likelihood (natural log-likelihood) evaluated at the maximum likelihood estimates to determine which model performed best (Burnham and Anderson 2002; Hein et al. 2012).

The future (2021–2050 and 2051–2080) distributions of Arctic charr looked at the distributional continuous range of natural log odds of the occurrences. Predictions for future distributions of brook charr were not found; therefore, brook charr inputs were kept constant based on their range of occurrences.

Table 2 Akaike's information criterion (AIC) and difference in AIC (AICi - AICmin, ΔAIC) for candidate models predicting the presence of Arctic charr. The full model included the following predictor variables: growing degree-days (*D*), longitude (*H*), latitude (*V*), and brook charr (*B*). The model in bold is the chosen model used to predict the future distribution of Arctic charr in Canada

MODEL	AIC	ΔAIC
D + H + V + B + D × H + H × V	232.33	0
D + H + V + B + H × V	**235.99**	**3.67**
D + H + V + B + D × B + H × V	236.78	4.46
D + H + V + B + D × H	236.82	4.49
D + H + V + B + D × B + H × B + V × B	259.47	27.15
D + H + V + B + D × B	266.12	33.8
D + H + V + B	285.22	52.9

Results

For the baseline time period (1976–2005), the annual mean temperature across all cells was: mean = -5.7°C, range = -22.6–9.4°C. GDD for the period were: mean = 826.85, range = 7.8–2,591. Within Canada, there were 401 presences and 431 absences for Arctic charr, and 266 presences and 566 absences for brook charr across all cells within the Climate Atlas of Canada. Arctic charr and brook charr co-occurred in 113 cells. Arctic charr occurred in 248 cells without brook charr, whereas 153 cells contained brook charr but not Arctic charr. Arctic charr and brook charr were not present in 318 cells.

The chosen logistic regression model predicted Arctic charr distributions for the baseline time period of 1976–2005. The baseline time period model was used for the projected Arctic charr distributions for two future 30-year time periods of 2021–2050 and 2051–2080. GDD values were compiled for two emissions scenarios (Climate Atlas of Canada 2022).

The baseline regression model determined was:

$$O = 59.51 - 0.0051(D) + 0.73(H) - 0.72(V) - 0.28(B) - 0.010(H \times V), \quad (4)$$

Table 1 Correlation matrix of mean climate data (growing degree-days and temperature), species interactions of Arctic charr and brook charr, and spatial data of latitude and longitude for Canada measured from 1976 to 2005. Note the high positive correlation between GDD and AMT

	Latitude	Longitude	AMT	GDD	Arctic charr	Brook charr
Latitude		-0.24	-0.95	-0.86	0.50	-0.50
Longitude			0.042	-0.014	0.46	0.74
AMT				0.92	-0.61	0.36
GDD					-0.68	0.24

GDD growing degree-days, *AMT* annual mean temperature where O is the predicted Arctic charr occurrences (1), D is the growing degree-days (base 4°C), H is the longitude, V is the latitude, and B is the occurrence of brook charr (1 = present) to project the distributions of Arctic charr for two future time periods (2021–2050 and 2051–2080) within Canada under high- or low-carbon scenarios and the presence or absence of brook charr.

The baseline time period (1976–2005) model is interpreted as: *59.5*: the constant term; *(D)*: its coefficient is -0.0051 [note the negative value; keeping all other variables constant, for each unit increase in GDD, the odds of Arctic charr occurrence decreased by a factor = exp(-0.005)]; *(H)*: its coefficient is 0.73. Note the positive value is not truly a positive value relationship. For this model, longitude values were imputed as negative values (i.e. Churchill, Manitoba: latitude = 58.77072 and longitude = -94.16928). Therefore, keeping all other variables constant, for each unit decrease in longitude, the odds of Arctic charr occurrence increased by a factor = exp(0.73). (*V*): its coefficient is -0.72.

The logistic regression model with the best score (AIC = 232.33) included four predictor variables (GDD, longitude, latitude, and brook charr) and two interactions (between longitude and latitude; and between GDD and latitude; Table 2). We chose the second best model to predict the current occurrences of Arctic charr, though it had a slightly higher score (AIC = 235.99). This logistic regression model included four predictor variables (GDD, longitude, latitude, and brook charr) and one interaction (between longitude and latitude; bolded in Table 2). Dropping one interaction term (between GDD and latitude) made the model simpler with relatively little change in AIC. The interaction between GDD and longitude, and between longitude and latitude, could be interpreted as having the same meaning. Four main effects coefficients (see equation 4) were significant ($p < 0.05$), except for brook charr ($p > 0.704$).

The training dataset produced a logistic regression model where 80% of the source data were correctly classified as Arctic charr presence or absence, with detection probability $P = 0.93$ (95% confidence interval = 0.91–0.95). The testing dataset had 20% of the source data and correctly classified Arctic charr presence or absence, with detection probability $P = 0.94$ (95% confidence interval = 0.89–0.97).

The probability of the occurrence of Arctic charr decreased in all the future time period scenarios (Table 3). The low-carbon scenario for the time period 2021–2050 decreased the distributional range of Arctic charr by 6% from the baseline time period of 1976–2005. The low-carbon scenario for the time period of 2051–2080 decreased the distribution of Arctic charr by 10% from the baseline time period. The two high-carbon scenarios decreased the distribution of Arctic charr, 7% for 2021–2050 and 18% for 2051–2080 (Table 3). When including the presence of brook charr, the distributional range of Arctic charr is expected to decrease by 21% in the future time period of 2051–2080 at a high-carbon scenario from the baseline time period of 1976–2005 (Table 3). Figure 2 shows an approximation of the change in range to the year 2080 under a high-carbon scenario including brook charr.

Table 3 The projected probability of Arctic charr occurrence in Canada. Future time periods (2021–2050, 2051–2080) were explored at low- and high-carbon scenarios without the brook charr interaction and including the brook charr (*B*) interactions for the time period of 2051–2080

Arctic charr model	Average log odds *(O)*	Probability *(P)*	ΔProbability *(ΔP)*
Baseline Data 1976–2005 W/O B	3.84	0.90	-
Low Carbon 2021–2050 W/O B	3.03	0.84	0.06
Low Carbon 2051–2080 W/O B	2.72	0.80	0.10
High Carbon 2021–2050 W/O B	3.04	0.83	0.069
High Carbon 2051–2080 W/O B	1.98	0.73	0.18
Baseline Data 1976–2005 W/B	3.74	0.90	-
High Carbon 2051–2080 W/B	**1.69**	**0.70**	**0.21**

W/O B Without brook charr, *W/B* with brook charr

Discussion

Climate change is an ever-pressing global concern that has far-reaching implications for ecosystems and biodiversity across the planet. Among the many ecosystems affected, aquatic environments stand out as particularly vulnerable to the impacts of rising temperatures and changing climatic patterns. In recent decades, the world's fish populations have been thrust into the spotlight as they face unprecedented challenges posed by a rapidly warming climate. Scientific research and studies from various sources have shed light on the complex interplay between fish and climate change. These sources highlight the multifaceted consequences of warming waters, altered ocean currents, and shifting marine ecosystems on fish species worldwide. The effects ripple through marine and freshwater ecosystems, affecting not only fish populations, but also the communities and economies that rely on them.

This paper delves into the intricate relationship between fish and climate change, drawing upon a range of scientific findings and expert assessments to provide a comprehensive understanding how warming might affect growth, productivity, and Arctic charr distribution. From the impact of

Fig. 2 Expected change in Arctic charr distribution to 2080 under the high-carbon scenario

rising temperatures on fish habitats to the challenges posed by ocean acidification, this exploration seeks to underscore the urgency of addressing climate change to ensure the resilience and sustainability of our aquatic ecosystems and the fisheries that sustain human populations. These studies offer valuable insights into the impacts of climate change on various fish species and their habitats. Researchers have been diligently studying these effects to better understand and mitigate the challenges posed by climate change to freshwater ecosystems and their inhabitants. The review by Comte et al. (2013) underscores the importance of monitoring and understanding how climate change is altering the distribution patterns of freshwater fish, particularly cold water species. This comprehensive review highlights the observed and predicted trends in response to changing climatic conditions. Additionally, the subsequent studies delve into specific cases, such as the changes in Arctic charr distributions in response to climate change (Winfield et al. 2010; Svenning et al. 2022), potential habitat fragmentation for charrs in Japan due to warming (Nakano et al. 1996), and the anticipated effects of climate warming on bull trout habitats in the interior Columbia River basin (Rieman et al. 2007). These studies provide in-depth analyses of the impacts on various charr species and other trout populations. Furthermore, Bell et al. (2021) shed light on the broader implications of climate change and invasive species on native trout in the northern Rocky Mountains, emphasizing the need for conservation measures to address the widespread declines observed in several native trout species. Collectively, these studies underscore the urgency of addressing climate change and its consequences for freshwater fish species and their ecosystems. They contribute valuable data and insights that inform conservation efforts and highlight the interconnectedness of climate change, habitat alteration, and fish population dynamics in freshwater environments.

Widespread warming in Canada will likely result in environmental changes in aquatic ecosystems including annual temperature increases, shorter ice-covered seasons, increased nutrient availability, rising sea levels, and longer growing seasons (Budy and Luecke 2014; Government of Canada 2021; Dunmall et al. 2022; IPCC 2022). Longer summers will likely result in more days for optimal growth in many temperate and Arctic fish species, but also may increase thermal stress after a certain level. Arctic-adapted species could decline because they will be more likely to be exposed to temperatures above their threshold tolerance (Reist et al. 2013). To cope with these potential changes, some temperate species may be able to expand their range northward, thereby coming into contact with previously undisturbed Arctic fishes. Here, we examine the effects of increased growing seasons and possible competitive overlap with brook charr on the future distribution of Arctic charr. Our logistic regression model showed that for low-carbon scenarios, the range of Arctic charr is estimated to decrease by 6% by 2050 and 10% by 2080 from the baseline time period of 1976–2005. For the high-carbon scenarios, the distribution was estimated to decrease by 7% by 2050 and 18% by 2080. The additional presence of brook charr as a variable decreased the Arctic charr distribution by 21% by 2080 under the high-carbon scenario. While the brook charr influence is small, we speculate that it may reflect a degree of competition among the species (Alofs et al. 2013).

In the face of climate change, Reist et al. (2006) noted that several temperate fish species such as Atlantic salmon (*Salmo salar*), brook charr, and introduced brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) will likely expand their ranges northward as they track preferred or optimal temperatures as waters continue to warm (Reist et al. 2006). In particular, brook charr is a species limited in its northernmost distribution by temperature (Reist et al. 2006). Prime brook charr feeding water temperatures are between 7 and 18°C (Reist et al. 2006). While both species are cold adapted, Arctic charr typically occurs in water temperatures ranging 5–19°C and brook charr 8–20°C (Dupont Cyr et al. 2018). While it has no northern limit, the southern limit of Arctic charr is likely a function of temperature and/or the presence of potential fish competitors such as brook charr (Reist et al. 2006).

Indeed, the distributions of some temperate fish species are already expanding northward to Canada's high Arctic regions. Pacific salmon (*Oncorhynchus* spp.) are now commonly found in the Canadian high Arctic waters where they were previously rarely documented (Dunmall et al. 2022). The continuous long-term impacts of climate change results in reduced sea ice cover and longer open water seasons in the Arctic, which may allow Pacific salmon to establish self-sustaining reproductive populations (Dunmall et al. 2022). Other species such as capelin and sand lance (Ammodytidae) have also shown steady progression northward from temperate to Arctic regions (Ogloff et al. 2020; Florko et al. 2021).

It is difficult to predict if sympatry will automatically result in competition to the detriment of Arctic charr as we assume in our model. Dunham et al. (2002) reviewed brook charr invasions in the western United States and Canada, and their impacts on native cutthroat trout (*Oncorhynchus clarkii*) populations. Brook charr establishment in the western United States was the result of stocking; they were introduced as a game fish in 35 states (Dunham et al. 2002). Since then, brook charr has increased and dispersed, while native cutthroat trout populations have rapidly declined (Dunham et al. 2002; Peterson and Fausch 2003). It is hypothesized that brook charr behaviourally dominated, displacing cutthroat trout from preferred feeding and spawning habitats (Dunham et al. 2002). This highlights that brook charr is an effective competitor with endemic salmonids.

However, it should be noted that Arctic charr and brook charr co-occurred in 113 locations. It is not known if they were in the same water bodies and if so were they in direct contact. It is possible that they can co-exist and competition would not occur. We note that the overlap (unsurprisingly) occurs in the more southerly range of Arctic charr where it is less likely that they are forced into extremely limited overwintering habitat together. Possibly, the Arctic charr are more aggressive in these localities. Testing the hypothesis that brook charr would displace Arctic charr directly via competition, for example in controlled arena experiments, would be valuable in understanding interactions between both species where they occur in sympatry or are predicted to overlap in distribution and habitat use the future.

It would be beneficial to explore the climate-driven brook charr invasion theory through the development of a brook charr distribution model, where brook charr is the dependent variable. Warmer water temperatures are known to bring new species that seek out thermally preferred habitats and may also force species to leave their natural ranges. Chu et al. (2005), employing a statistical modelling approach, suggested a 49% decrease of brook charr by the year 2050 in the southeastern region of Quebec and Labrador, Canada. They concluded that an expansion of the range northward was unlikely because brook charr was limited as a freshwater-only species and therefore could not disperse along coastal marine habitats. Others, however, have strongly suggested that brook charr is likely to expand its range northward in response to climate change (Reist et al. 2006). It has been suggested that brook charr populations could migrate northward from the Arctic coastline of Quebec to Baffin Island or along Hudson Bay, colonizing brackish water systems as temperatures rise. The latter seems more likely given the ability of brook charr to occupy brackish systems (Doucett et al. 1999).

Climate change may have a number of cumulative effects on Arctic charr. With range expansion northward by other species, Arctic charr might be exposed to competition and new pathogens (Lehtonen 1996; Falardeau et al. 2022). If temperatures in excess of the thermal range persist over the long term, physiological impairment or behavioural changes in habitat use will likely occur (Gilbert et al. 2020; Falardeau et al. 2022). As water temperatures rise in lake habitats, Arctic charr will likely avoid warm littoral zones and move to colder, deeper benthic habitats if available (Power et al. 2008; Reist et al. 2013). However, many lakes inhabited by Arctic charr are shallow, without stratification and lack a profundal temperature refugia. Consequently, for landlocked charr there may be no place to go. Additionally, since Arctic charr often migrates upstream in nearly dewatered streams during the high tide such as in Baffin Island, anadromous Arctic charr may find access to freshwater and marine systems challenging due to lowered water levels and changing tides (Reist et al. 2006; Dubos et al. 2023). All told, rising temperatures could impact Arctic charr through exposure to new pathogens, temperature-induced physiological stress, and disruption of migration pathways, in addition to invading competitors.

Alternatively, climate change may be beneficial for some populations of anadromous Arctic charr due to the potential for increased growth with warmer temperatures and access to greater food resources as the marine ice-free season persists longer (Falardeau et al. 2022; Harris et al. 2022). In the short term, climate change may increase productivity by creating longer open water seasons, by advancing spring runoff and delaying the onset of winter (Reist et al. 2006; Falardeau et al. 2022). Warming temperatures should increase productivity, manifesting in an array of readily available food resources for Arctic charr. For example, Atlantic forage species, such as capelin (*Mallotus villosus*), are establishing breeding populations in the Arctic (Ogloff et al. 2020) and Arctic charr have taken advantage of this new prey in some Arctic regions (Ulrich and Tallman 2021). In addition to the potential positive impacts of novel prey species, longer open water seasons may result in anadromous Arctic charr that are in better condition and larger in size given increased foraging opportunities associated with longer ice-free seasons (Grenier and Tallman 2021; Falardeau et al. 2022). Indeed, Falardeau et al. (2022), have suggested that some Inuit fishers are currently meeting commercial quotas of Arctic charr faster than ever before, possibly a result of the increased size of individual Arctic charr. Grenier and Tallman (2021) also determined that the faster-growing juveniles were more likely to become anadromous and coupled with warmer lake habitats will likely lead to a higher proportion of anadromous charr in each system. The population productivity gain would result because anadromous Arctic charr grow larger and live longer than resident charr (Grenier and Tallman 2021).

While climate change is likely to have both positive and negative impacts on Arctic charr, there is also a case that climate change may have little impact on charr as a whole. Arctic charr is considered one of the most phenotypically plastic vertebrates and can inhabit a variety of habitats (Klemetsen 2013). The plasticity of Arctic charr allows it to adapt to seasonal changes in environmental conditions, including variations in water temperatures, salinity, and other environmental variables (Reist et al. 2006; Smith et al. 2022). Over the course of its life cycle, Arctic charr experiences temperatures from 0°C to over 20°C, and salinities from nearly nil to full seawater (Reist et al. 2006; Hein et al. 2012; Campbell et al. 2021). Overall, the flexibility may be positive for Arctic charr potentially allowing for adaptation to new Arctic conditions resulting from climate change. Most recently, Svenning et al. (2024) produced a study of the Arctic charr in Svalbard, one of the few places in Europe that mirrors the Arctic conditions in Canada. This study discussed the potential future positives and negatives for these charr with climate warming. Their results suggested that climate effects from increases in air temperature and snow accumulation will increase the growth in YOY charr in their two Arctic charr populations and, although their study did not consider competitive interactions, it is a perfect complement to our modelling exercise.

In this study, we hypothesized that environmental factors and the occurrence of brook charr would influence the distribution of Arctic charr for two future time periods: 2021–2050 and 2051–2080. We estimated that the change in growing degree-days and the presence of brook charr would be associated with a reduced likelihood of Arctic charr occurrence. Our results show that in response to climate change, the distribution of Arctic charr is estimated to decrease in all the five model scenarios. Overall, the results are important for understanding future challenges to the conservation of Arctic charr based on several combinations of climate change and species interactions that might occur in the future. Our work provides a quantitative estimate of the effect of anthropogenic change on the environment in terms of the geographic range of Arctic charr. It emphasizes the need for future research on physiological, behavioural, and population responses by Arctic charr to Arctic warming and highlights the need for direct studies of competition between Arctic charr and brook charr.

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Declarations

The authors have no relevant financial or non-financial interests to disclose.

Conflicts of interest We declare that we have no conflict of interest.

Ethics approval We declare that all applicable international, national, and/or institutional guidelines for sampling, care, and experimental use of fishes for the study have been followed, and that all necessary approvals have been obtained as per the Nagoya protocol on Access and Benefit Sharing within the Convention on Biological Diversity, and the Convention on International Trade in Endangered Species of Wild Fauna and Flora guidelines, in addition to the national laws of Canada.

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