

Arctic freshwater fish productivity and colonization increase with climate warming

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Climate warming at high latitudes has long been expected to exceed that predicted for tropical and temperate climes, but recent warming in the Arctic has exceeded even those expectations¹. The geophysical consequences of this warming are reasonably well established², but the impacts on freshwater fauna are poorly understood. Here we use a large-scale geospatial analysis of the population dynamics of one of the most abundant north temperate freshwater fish species to forecast increased demographic rates, productivity and colonization range in response to IPCC climate warming scenarios. Geospatial lake morphometry data were used to characterize 481,784 lakes in the Canadian Arctic capable of supporting lake trout (*Salvelinus namaycush*) populations. Lake trout productivity in existing habitat is projected to increase by 20% by 2050 due to climate change, but an expanded habitable zone may result in a 29% increase in harvestable biomass. Although many ecosystems are likely to be negatively impacted by climate warming, the phenotypic plasticity of fish will allow a rapid relaxation of the current environmental constraints on growth in the far north, as well as enhanced colonization of bodies of water in which there are few potential competitors.

Climate change is expected to disrupt biological communities in many parts of the world, with first-order effects on distribution, growth and mortality. The unprecedented melting of sea ice and permafrost in the Arctic could reorganize conditions for population growth as access to potentially suitable habitat increases^{3,4}. The species most likely to be negatively affected would be those with inflexible life history traits such as limited dispersal abilities, slow reproductive rates, specialized habitat and dietary requirements, restricted distribution and narrow physiological tolerances^{5,6}. Yet the response of poikilothermic fishes to warming would be expected to be very different than that of homeothermic birds and mammals, which account for the vast majority of existing animal studies on climate effects⁶. Moreover, many large-scale fish vulnerability studies have focused on marine species, which are not limited by the fragmented landscape characteristic of lakes; although a marine fish population can shift its distribution in response to changing environment⁷, freshwater fish populations often must live or die in a constrained body of water. A unique aspect of Arctic freshwater fish populations is that any polewards range shifts are likely to occur in bodies of water that are occupied by few competing species and thus will be subject mainly to abiotic constraints, unlike some of the

biotic impediments to redistribution seen in the terrestrial or marine environment⁸. By contrast, within-lake changes to fish productivity would be expected to be driven by either abiotic factors alone, or in conjunction with changes in competition and predation⁹.

Quantitative predictions of warming effects on freshwater Arctic fishes are challenging when both the number and physical morphology of Arctic lakes are unknown. In this study, we used geospatial data of the topography surrounding 7.2 million water bodies in Arctic Canada to identify and describe 481,784 lakes (with surface areas greater than 10 ha) capable of supporting cold-water lake trout populations (Fig. 1). Our geospatial Arctic data thus account for 34% of the world's 1.42 million lakes that are greater than 10 ha (ref. ¹⁰). Most of the Arctic lakes are small, shallow and cold, with a median surface area, depth and water temperature of 21 ha, 2.5 m and 1.54 °C, respectively. Lakes with maximum depths less than 2.5 m were excluded from the inventory of lake trout habitat, as ice thickness can reach 2.5 m in January air temperatures, which average −28 °C. Nevertheless, Arctic lakes were estimated to cover 401,885 km² (~10%) of Arctic Canada north of 60° N, highlighting the large potential role of freshwater habitat on Arctic terrestrial ecosystems.

The physical environment limits the survival rates of all organisms, but temperature and habitat are the most influential variables controlling the age-structured population dynamics of poikilotherms, especially for long-lived fishes such as lake trout, which can reach an age of 65 years¹¹. Previous reports of a threefold range in lake trout longevity, growth, mortality and other age-structured population rates are striking¹², but an unknown proportion of the variability is due to the use of outdated and biased ageing methods (such as scales), many of which can greatly underestimate the age of adult fish¹³. The use of transverse otolith sections (Fig. 2) aged in a single laboratory eliminated the bias due to age underestimation, reduced the variance of population rate estimates (perhaps by >50%)¹⁴ and is thus a key advancement of this study. A detailed biological analysis of 55 well-sampled reference lakes indicated that lake trout growth, maturation, mortality and productivity rates were highly correlated with (and could be accurately predicted by) a suite of lake morphology and environmental variables (Supplementary Figs. 1 and 2; Supplementary Note 1); this multivariate suite of lake descriptors was therefore first used to estimate population parameters in the remaining unsampled 481,784 lakes and then to model their responses to climate change.

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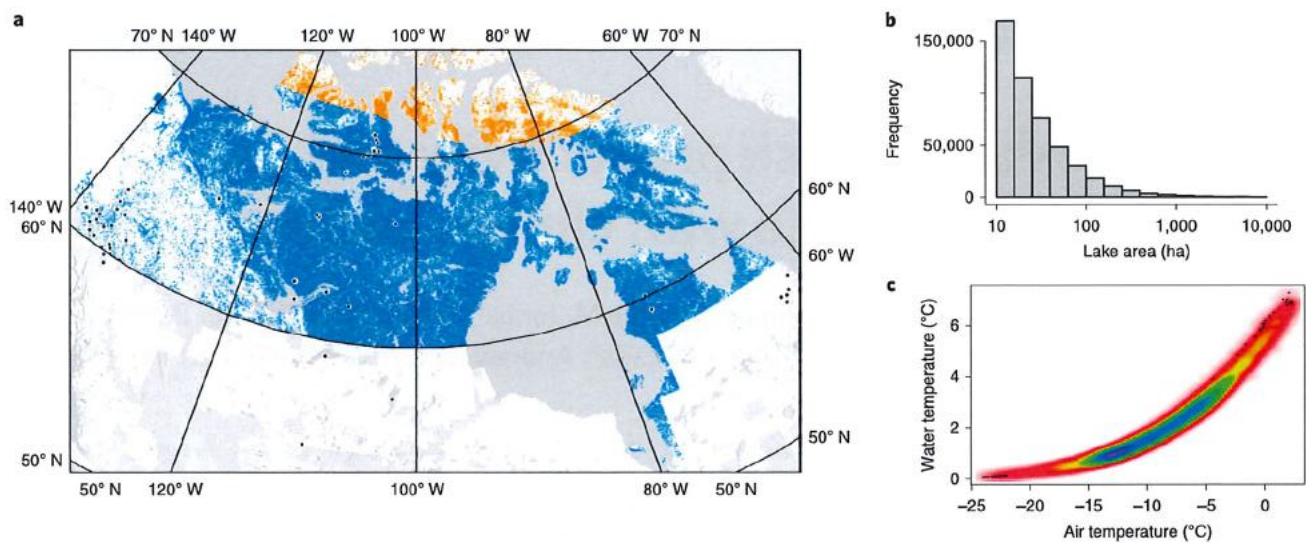


Fig. 1 | Distribution and characteristics of 481,784 lakes with a surface area >10 ha in the Canadian Arctic. **a**, The lakes outlined in blue have been colonized (or are capable of being colonized) by lake trout, whereas those in orange are too cold for colonization. Detailed biological samples were collected from the 55 reference lakes indicated by black circles. **b**, The logarithmic frequency distribution of lake surface areas is shown. The median lake size was 21 ha and 75% were less than 40 ha. **c**, The relationship between the mean annual air temperature and estimated mean annual water temperature for all lakes is shown. The lake number at any given temperature is shown as a smoothed kernel colour density. The mean annual temperature of most lakes was <3 °C.

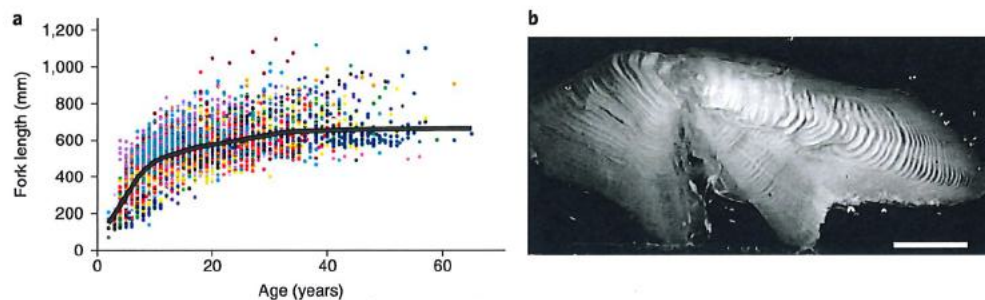


Fig. 2 | Length at age of lake trout. **a**, Length versus age for 4,649 lake trout from 55 reference lakes is shown (the lakes are indicated by coloured symbols). Although all growth parameters were estimated for each lake individually, a loess curve fit to the aggregated data highlights the marked slowdown in growth associated with the onset of sexual maturity. **b**, Lake-specific lake trout age, growth and mortality parameters were based on calibrated, accurate (validated) age interpretations from images of sectioned otoliths that were digitally enhanced to reveal annually repeating pairs of opaque-translucent growth bands. The sectioned otolith shown is from a lake trout 44 years of age with a length of 688 mm. Scale bar, 500 μ m.

There was marked variability in growth trajectories across the Arctic reference lakes, even between those immediately adjacent to each other (Fig. 2). Lake trout grew rapidly to the size of sexual maturity (~480 mm), but the mean annual growth rate of adults was only 23% of that of juveniles (7.55 versus 33.2 mm yr⁻¹). Lake-specific growth parameters estimated from von Bertalanffy models varied by a factor of 20 (growth parameter (K)=0.02–0.47; mean \pm s.e.m.=0.144 \pm 0.014 yr⁻¹) in the 55 reference lakes and were inconsistently correlated with lake area, water temperature, latitude and fish diversity; only fishing effort had a significant effect on both the asymptotic length L_{∞} (decreasing) and K (increasing) (analysis of variance (ANOVA), $P < 0.005$, 42 d.f., $r^2 = 0.21$). In the more northerly lakes, adults grew very little (Fig. 2b) and thus growth was poorly described by traditional growth models¹⁵. All von Bertalanffy growth models were therefore discarded in favour of two-stage growth trajectories defined by linear juvenile (immature) growth and asymptotic adult growth. Differences in lake

morphometry and environment explained much of the variation in juvenile growth rate, which increased by up to 50% with water temperature, lake area and fishing (general linear model (GLM), $P < 0.001$, 51 d.f., $r^2 = 0.53$). By contrast, there was no effect of lake morphometry, latitude, fish diversity or fishing on adult growth (GLM, $P > 0.2$, 38 d.f.). Two-stage growth trajectories have been observed in other long-lived fish species and are characteristic of environments where limited surplus energy is channeled to reproduction¹⁶. Our observation of up to a 25% increase in adult condition factor (relative fatness) with fish diversity ($P < 0.01$, 53 d.f., $r^2 = 0.12$) is consistent with the expectation that the increased prey fields observed in warmer waters leads to a better condition in adult fish and thus greater reproductive capacity.

The predicted occupancy rates of lake trout in Arctic lakes are very high, with 93% of all lakes >10 ha meeting the criteria for a viable population. Ground observations of occupancy ($n = 55$ reference lakes + 11 additional lakes) were 94% consistent with model

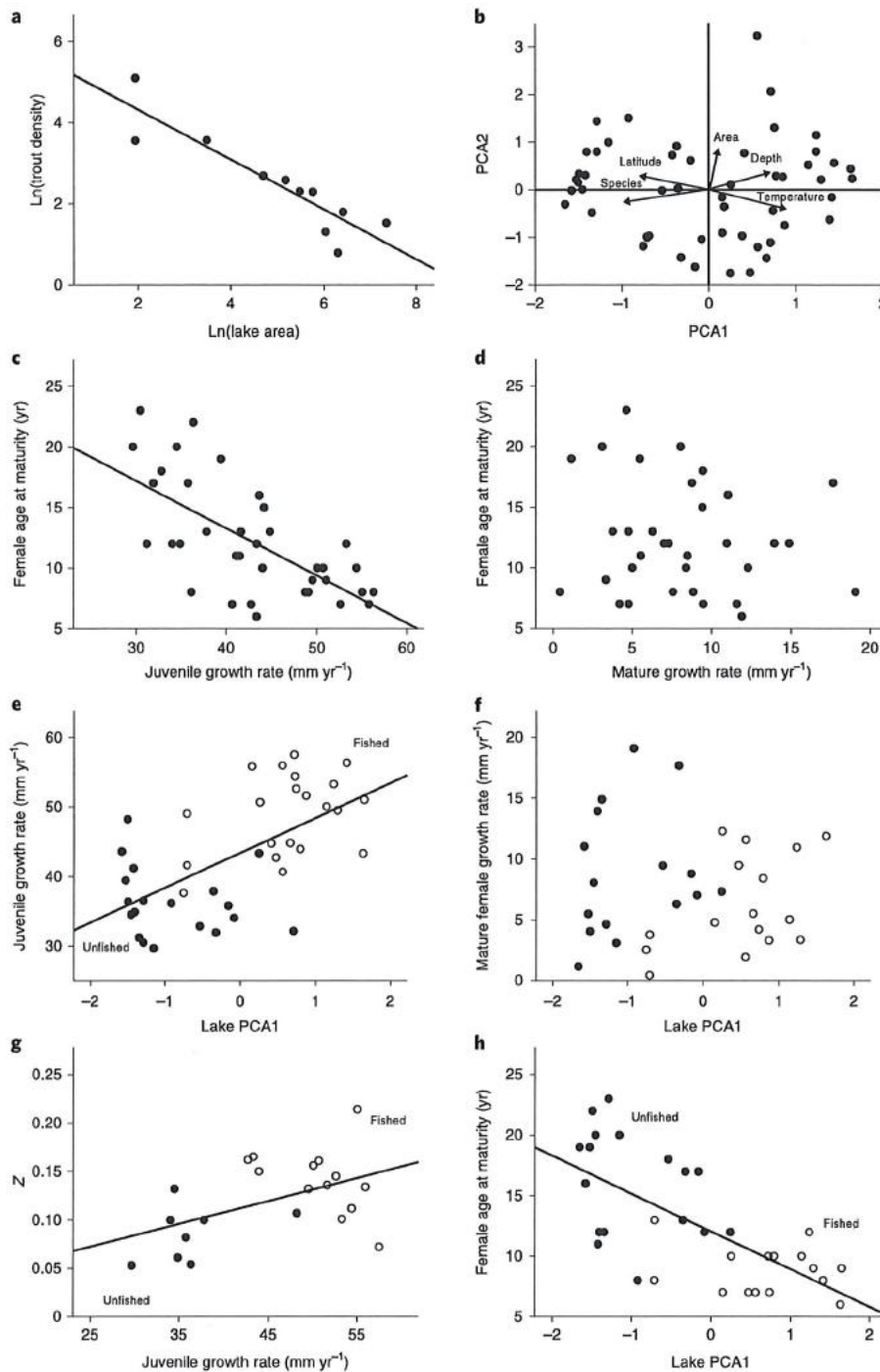


Fig. 3 | Lake trout population dynamics. **a**, Lake trout density and abundance were estimated from the natural logarithm regression of density on the lake area using published data for 11 Arctic lakes^{29–31} of known absolute abundance ($P < 0.001$, $r^2 = 0.80$). **b**, A PCA of 55 reference lakes was used to better visualize correlated lake characteristics; the first two components explained 80% of the variance. Water temperature, latitude, lake depth and the numerical proportion of lake trout in the large-bodied fish community (species) were all strongly correlated with PCA1, whereas the natural-logarithm-transformed lake area was most correlated with PCA2. **c,d**, The relationship between female age at maturity (A_{50}) and the juvenile growth rate in 35 reference lakes with reliable maturity ogives was significant ($P < 0.001$, $r^2 = 0.42$), whereas there was no relationship between A_{50} and the mature female growth rate ($P = 0.43$) (**d**). The juvenile growth rate was the mean to an age of 10 yr, whereas the mature female growth rate was that observed at ages $> A_{50}$. **e,f**, The relationship between the juvenile growth rate and the first principal component of lake morphometry (shown in **b** above) was significant ($P < 0.01$), but was better described with a GLM incorporating fishing as a main effect (see text). The mature female growth rate was not related to PCA1 ($P = 0.76$) nor was it significant in a GLM with both PCA1 and PCA2. **g**, The juvenile growth rate was significantly related to the total instantaneous mortality rate (Z) in the 25 lakes, where Z could be estimated from a Chapman-Robson model. In an unfished lake, Z is equivalent to the instantaneous natural mortality rate, M . **h**, The female age at maturity (A_{50}) was significantly related to the first principal component of lake morphometry (PCA1) ($P < 0.01$), but was better described with a GLM incorporating fishing as a main effect (see text).

predictions based on minimum depths and air degree-days. Almost all of the lakes that lacked trout were predicted to lie north of 69°N, mainly between 69 and 74°N. The factors predicting lake trout occupancy differed from those controlling density (abundance per area), however, with only lake area acting as a significant predictor of density in lakes of known abundance ($P < 0.001$, 10 d.f., $r^2 = 0.80$) (Fig. 3a). The greatest effect of Arctic warming on lake trout abundance should therefore be evident as a northwards colonization rather than changes in within-lake density.

Spatial variation in lake trout population dynamics was far more age-structured than size-structured, typified by a decline in female age at 50% maturity (A_{50}) as the juvenile growth rate increased (Fig. 3; Supplementary Note 2). As several of the environmental variables linked to lake morphology were collinear, a principal component analysis (PCA) explaining 94% of the variance was used to better visualize the relationships (Fig. 3b). There were clear relationships between the PCA components and both juvenile growth rate and female A_{50} in both fished and unfished lakes; the growth and maturation rates in unsampled lakes could therefore be reasonably accurately predicted from lake morphology and environment (Supplementary Note 1). In keeping with an analysis of individual environmental variables, none of the PCA components successfully predicted mature growth rate ($P > 0.2$, 38 d.f.).

We observed a significant positive relationship between mortality and the juvenile growth rate (slope $b = 0.002$, $P = 0.01$, 25 d.f., $r^2 = 0.23$) (Fig. 3g), and an inverse relationship between mortality and A_{50} ($b = -0.006$, $P < 0.001$, 25 d.f., $r^2 = 0.54$; Supplementary Note 2). Productivity losses due to mortality were thus almost exactly counterbalanced by increases due to juvenile growth and were reflected in a strong spatial cline from southeast to northwest (Fig. 4a–c). The strong relationship between juvenile growth and mortality explained the observed high growth rates and low maturity at age estimates for fished lakes throughout the study area, which tended to cluster within 50 km of communities. There was no evidence of a relationship between growth and mortality in adult fish, presumably because of the increased role of predation and competition after maturity.

The IPCC climate projections for the Arctic predict a spatially variable mean increase of 2.8 °C by 2050¹⁷. Temperature fields in the 2006 model starting year were provided at a relatively low spatial resolution and were not expected to exactly mirror current conditions¹⁸. The difference between the AR5 RCP8.5 models in prediction years 2006 and 2050 was added to our existing temperature fields to preserve the detailed spatial resolution of our geospatial temperature data; our population dynamics models were then used to project the changes expected of each of the individual lake trout populations by 2050. The juvenile growth rate is predicted to increase throughout its range by 0–14% (mean of 7.1%), with the largest changes in the southern and western Arctic (Fig. 4c). The mortality rate is projected to increase by 0–21% (mean of 10.4%). The yield per recruit (YPR) is a measure of population productivity adjusting for variation in growth, M , A_{50} and lifespan, as well as the increased turnover associated with a higher mortality rate. A mean increase in lake-specific YPR of 8.4% is expected by 2050, although the increase is not spatially monotonic (Fig. 4d). The most revealing index of fish productivity is a calculation of surplus production (harvestable biomass) at a fishing mortality of $F_{0.1}$, which takes into account both YPR, abundance and recruitment of young. Surplus production in the existing lakes inhabited by lake trout is expected to increase by about 20% by 2050 (Supplementary Note 4), with the most marked increase in the southern Arctic. When the expanded habitable zone is included in the calculation, surplus production is predicted to increase about 29% overall, amounting to an increase in annual surplus production of 1,959 mt. Enhanced fish production in the Arctic could provide welcome food security for the indigenous population¹⁹, but the risk of overfishing and extinction in a

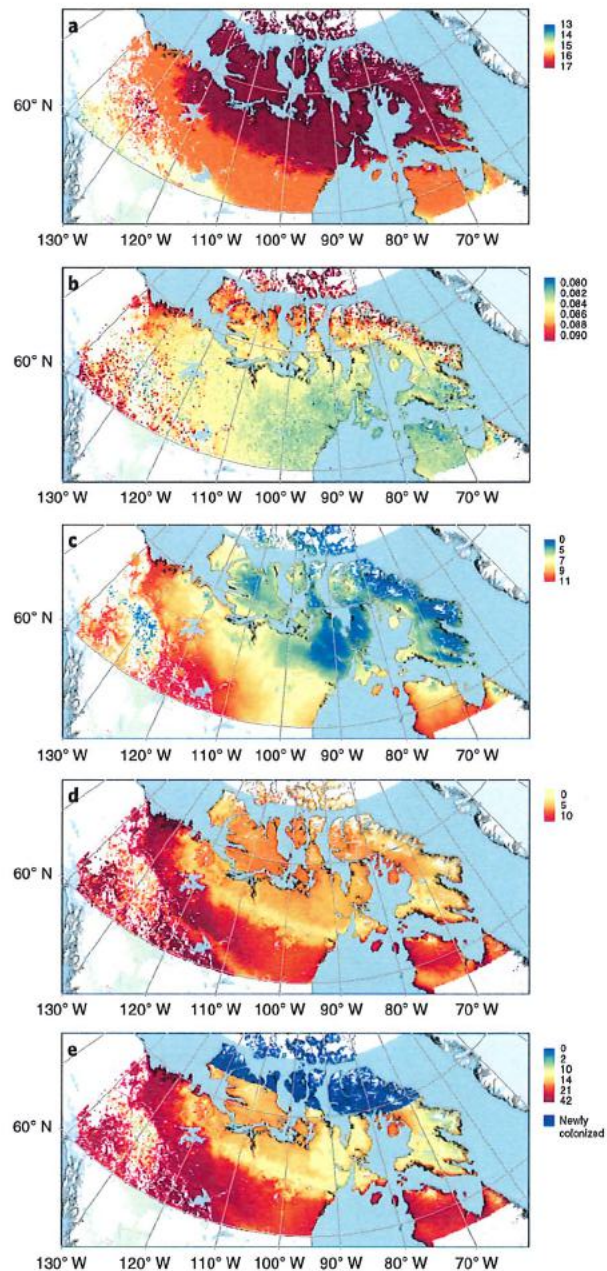


Fig. 4 | Observed spatial patterns in lake trout growth, mortality and productivity, and those predicted under climate change model RCP8.5 to the year 2050. a, b. Current patterns in female age at maturity (A_{50} in years) (a) and M (b). **c.** The percentage increase in the modelled mean juvenile growth rate (to an age of 10 yr) by 2050 relative to the current estimates of juvenile growth rate. **d.** The percentage increase in modelled YPR by the year 2050, where YPR is a measure of individual female productivity accounting for growth, mortality, age at reproduction and lifespan. **e.** The percentage increase in modelled surplus production (harvestable biomass) by the year 2050 while fishing at $F_{0.1}$, which is considered to be a moderate and sustainable fishing mortality. Surplus production was calculated as YPR multiplied by the estimated recruitment. Although the surplus production in the purple zone was calculated in the same manner as those lakes further south, a percentage increase could not be calculated because the 30,832 lakes in that region are predicted to become habitable only under continued climate change. Lakes ($n = 481,784$) have been aggregated at a 10 km grid size. With the exception of **e**, lake-specific values were calculated ignoring lake trout presence/absence.

long-lived and thus unproductive species is high²⁰, making Arctic lake trout a poor candidate for anything beyond a subsistence fishery.

Colonization of new habitats as the environment changes is largely a continuous extension of range in the case of mammals, birds and marine fishes, even if lagged in time²¹; however, an extension of range is necessarily a punctuated process in the case of freshwater fishes, as it often requires colonization of lakes with no apparent physical connectivity. Our study identified 30,832 lakes in the high Arctic that would become habitable for lake trout by 2050, an increase of 6.8% over existing lake numbers. Some of these lakes would be completely depauperate, whereas others would contain resident or anadromous Arctic charr (*Salvelinus alpinus*) (Supplementary Note 3). There was no loss of habitat in our study area (north of 59–60° N), but our study area did not encompass lake trout populations further south in which habitat losses might be expected due to high temperatures. Our sporadic observations of Arctic lakes containing only a single adult fish suggest that colonization of new lakes can occur through passive dispersal of eggs by birds²², or as free embryos transported along dry-bed streams under flood conditions. Climate models predict up to a 50% increase in precipitation in the Arctic in coming years¹⁷, indicating that flood conditions conducive to increased connectivity should increase in frequency. Although the time frame for colonization is unknown, introduction experiments on other species demonstrate that lakes may become colonized in a relatively short time period after they become habitable²³. Lakes on islands would require a different mechanism for colonization. However, strontium–calcium ratios in otoliths indicate that some lake trout are capable of short periods of ocean residency and thus may be capable of colonizing the many lakes present on islands north of the Arctic mainland²⁴.

Climate change in temperate and tropical regions generally restricts available habitat, increases competitive pressure and reduces productivity⁶. By contrast, the pan-Arctic freshwater fish community is likely to experience ecological opportunity due to rapid relaxation of the environmental constraints on growth and expansion into depauperate bodies of water where the only possible resident fish species (Arctic charr) is likely to be a prey item rather than competitor (Supplementary Table 3, Supplementary Fig. 3 and Supplementary Note 3). Changes in demography and colonization, rather than increases in population density, would fuel this population growth. Although climate impacts on temperate and tropical populations may be driven more by altered species interactions than by direct abiotic effects²⁵, our findings indicate that the relatively simple and species-poor Arctic freshwater ecosystem would respond most to abiotic influences, primarily temperature. The phenotypic plasticity of cold-blooded fish relative to homeotherms may be largely responsible for this productivity difference, as demographic traits such as juvenile growth and sexual maturation can respond rapidly to temperature change²⁶. In contrast, Arctic warming has had little effect on the productivity of Arctic terrestrial vertebrates, other than through effects on habitat availability²⁷. The expansion of Arctic freshwater fish into sparsely populated habitat is also likely to occur quickly, although not as quickly as the rapid colonization of the Arctic Ocean by large generalist motile marine species from the south⁷. Although climate is a limiting factor on the range boundaries of most freshwater and terrestrial organisms²⁸, the increased productivity of poikilothermic freshwater fish responding to climate change in the Arctic has little in common with sympatric birds and mammals.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41558-020-0744-x>.

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Methods

Lake morphometry and depth. Geospatial data downloaded from the Canadian Digital Surface Model and Canadian Digital Elevation Model (DEM) (<http://maps.canada.ca/czs/index-en.html>) included most elements of hydrographic morphometry in northern Canada, including the location of the water body, area, shoreline and surrounding topography. The spatial extent of the analysis was north of 60°N, except for northern Quebec, which extended north of 58°. The polygonal and DEM data were loaded into a PostgreSQL database and processed using PostGIS and R to categorize the lakes. Although the distinction between lakes and rivers was usually clear, value judgements were sometimes required to reject river systems but retain long narrow lakes.

Lake depth is not a standard product of geospatial data and has never been measured in most Arctic lakes. The mean and maximum lake depth were therefore estimated by modelling the surface topography DEM using R, along multiple transects across each lake to a distance of about one lake radius on all sides. Splines were fit to the elevation data along each transect to estimate lake depth. Hollister et al.³² used a similar approach to estimate the maximum lake depth, but based their estimates on a single median slope value in the surrounding topography. As neither method offered clear advantages nor improved accuracy over the other, the mean and maximum depth was estimated using both methods and the overall mean adopted. In 17 lakes where the mean depth was measured (range of 1–15 m), there was no bias between the measured and estimated depths and the CV was 40%.

Temperature and climate data. Lake-specific air temperature data were spatially modelled on the basis of daily mean temperatures and degree-days above zero from 881 weather stations across Canada (data downloaded from Environment Canada http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html). Use of climatic means for the period 1981–2010 provided a close correspondence between the temperature time series and the growth history of lake trout. The spatial interpolation of temperatures to the individual lake level was based on the STE kriging model (R package Gstat), after examination of both directional and non-directional variograms. Interpolated temperatures were subsequently adjusted for altitude differences between the target lake and the kriged weather stations (used to generate the air temperature at the lake) by decreasing the estimated temperature by 0.6 degree for each altitude increase of 100 m (ref. 33).

Climate predictions were those published by the IPCC in AR5³⁰. Both the RCP4.5 and RCP8.5 climate predictions were analysed for our study, but the latter is most consistent with current anthropogenic CO₂ trajectories and thus was used here. Predictions used were those to the year 2050 and 2100. To preserve the detailed spatially resolved air temperatures in our kriged weather station data, the difference between the RCP8.5 temperature predictions between the 2006 start point and the 2050 (or 2100) end point at each given lake was added to the altitude-adjusted air temperature value to calculate the predicted air temperature at each lake.

Estimation of water temperature. The water temperature was estimated on the basis of a model of mean annual air temperature (adjusted for altitude), mean lake depth and fetch (as a proxy for depth of the thermocline)³⁴. The maximum thermocline depth was constrained to 25 m and the surface water temperature under ice cover was assumed to be 1.4 °C (as it was in the two lakes we measured, North and Alexie). Model predictions were tested against mean annual water temperatures at 9 m depth in the two Arctic lakes (Supplementary Table 1), which were fitted with temperature-depth recorders; the observed values were about 2.2 °C warmer than those predicted of surface temperatures, which is consistent with expectations that temperatures at 9 m depth should be warmer in winter than those nearer the surface³⁵. Although our predictions of absolute water temperature were reasonably accurate in the two monitored lakes, relative water temperature accuracy is more important than absolute temperature accuracy in our application.

Biological sampling. A suite of 55 lakes (55–71°N) was sampled to characterize the resident lake trout (*Salvelinus namaycush*) populations across a range of lake sizes, depths and locations across northern Canada^{36,37}. The selection of these reference lakes was not intended to be random, but sampled systematically across the usual range of lake trout habitats north of 60° (Supplementary Table 1). The fish community was sampled using overnight sets of bottom gillnets with graded mesh (2.5–16.5 cm mesh) that were suitable for catching most fish >10 cm in length. Three lakes were sampled with rod and reel. Although lake trout were generally the dominant species in the catch, especially at high latitudes, significant numbers of lake whitefish (*Coregonus clupeaformis*), non-anadromous Arctic char (*Salvelinus alpinus*), cisco (*Coregonus artedii*), round whitefish (*Prosopium cylindraceum*) and burbot (*Lota lota*) were sometimes caught. All fish were measured (fork length) and weighed fresh before internal examination for sex, maturity state, gonad condition and weight and stomach contents. Both sagittal otoliths were removed and stored dry for later examination.

Estimation of lake trout abundance. The current distribution limits of lake trout in this study were based on previously recorded observations of a northern limit around 71.3°N, corresponding to a climatic annual mean of about 600 degree-days. Lakes that froze all of the way to the bottom (~2.5 m maximum depth or 1.75 m mean depth) were assumed to be too shallow to support a fish population, whereas

lakes with a surface area of <10 ha were assumed to be too small. The assumed trout distribution under future climate scenarios made similar assumptions about lake depth, area and air temperature, but no assumptions about a latitudinal limit.

Lake-specific occupancy by lake trout was predicted using the above criteria. Observed occupancy was based on our 55 reference lakes, supplemented by sampling efforts in an additional 11 lakes for a total of 66 lakes.

Lake trout density and abundance were based on published mark-recapture, fish-out or lake-draining studies that were reported for 19 Canadian lakes (Supplementary Table 4). Such estimates are rare, as fish surveys seldom provide such estimates of absolute abundance or density. Multiple regression of lake variables on trout density (abundance per unit area) indicated that latitude and lake area predicted trout density, but that lake depth and number of competitor species did not. The effects of latitude (or water temperature) were only significant when southern temperate lakes (~50°N) were included in the analysis, which were slightly offset to lower densities from the parallel exponential area-density relationship for Arctic lakes. Lake trout density in all Arctic lakes was therefore estimated based on the density–lake area relationship using published data from 11 Arctic lakes^{39–41} (Supplementary Table 4). The areas of these 11 lakes (0.07–16 km²) represented the total inventory of Arctic lakes well, particularly the very abundant, small lakes (Supplementary Fig. 1). The following predictive regression was developed:

$$\text{Ln}(\text{density}) = 5.56 - 0.616(\text{Ln area}) \quad P = 0, 10 \text{ d.f.}, r^2 = 0.80 \quad (1)$$

where the density is the number of lake trout (≥ 12 cm) per area (hectare) of lake. Abundance in the lake was calculated as the product of density and lake area. The observed proportion of mature lake trout in the Arctic lakes ranged from 0.33 (ref. 41) to 0.68 (our data); a proportion of 0.5 mature was assumed for unsampled lakes.

Fish diversity in our study was defined as the proportion of lake trout in the overall lake abundance of fish >15 cm length (that is, the predator–competitor species complex) for a given lake, as competition was expected to be the most influential biological effect on lake trout growth. Diversity in the reference lakes was predicted by latitude (energy supply), lake area and water temperature ($P < 0.001$, 30 d.f., $r^2 = 0.42$), similar to published expectations³⁸, albeit without the inclusion of mixing depth. Fish diversity declines markedly north of ~65°N and is often limited to only one or two predatory species—lake trout and Arctic char—with Arctic char often being the only species north of 72°N. Most of the Arctic char caught in the reference lakes were resident (non-anadromous) forms (Supplementary Fig. 3).

Estimation of fishing effort. Quantitative fishing effort data were available for about half of our reference lakes, whereas interviews with fishing charter operators and local residents provided relative fishing effort indicators for most of the remaining lakes. The distance to the nearest community was derived from the Canadian Geographical Names Database of non-abandoned communities. Hierarchical GLM fits (lm function in R) identified latitude and distance to the nearest community (but not their interaction term) as the most important predictors of a binomial categorization of fishing effort (little or no fishing effort; moderately to heavily fished), but a positive latitude parameter for latitude was nonsensical when lakes other than the reference lakes were considered. Lake area was a significant variable in moderately fished areas, but only for lakes closer than 50 km and with areas less than 25 km². The final binomial categorization of relative fishing effort was based on a significant logistic regression of distance to the nearest community ($P < 0.001$, $r^2 = 0.85$), which correctly classified 95% of the reference lakes.

Age, growth, maturity and mortality estimation. A key advantage of the age-based dynamics reported in this study was the use of carefully calibrated fish age determinations using a method of demonstrated accuracy. All otoliths were processed identically for age determination using modern embedding, sectioning and image analysis methods³⁹. Ages were based on counts of annual growth increments that were visible in transverse sections of the sagittal otolith. Ageing accuracy was confirmed with bomb radiocarbon dating⁴¹. More than 80% of the otoliths were aged in the same laboratory and by the same age readers, and the comparability of the remaining ages was ensured using inter-laboratory calibrations. The age, growth and mortality estimates for all of the lakes are thus completely comparable.

Length (L_{∞}) and age (A_{50}) at sexual maturity for each sex were estimated using logistic regression. Growth model parameters were estimated using the von Bertalanffy model:

$$L_t = L_{\infty} \left(1 - e^{-K(t-t_0)} \right)$$

where L_t is the fork length of the fish in millimetres at age t in years, L_{∞} is the asymptotic length, K is a growth coefficient (in units of per year) and t_0 is the age at zero length. The robustness of growth model parameters was confirmed using a robust formulation of the von Bertalanffy model⁴⁰. In three lakes where only mature fish were available for ageing, the traditional three-parameter von Bertalanffy model provided an unrealistic growth trajectory; for those lakes, a two-parameter version of the model (constrained through the origin) was used to predict length at age (Supplementary Table 2).

A two-stage growth trajectory was characteristic of lake trout in all of the reference lakes, whereby growth before sexual maturity was rapid and linear, transitioning quickly to a much slower and asymptotic growth pattern in mature fish^{15,16}. The lake-specific growth rate was therefore estimated as the linear growth rate until the age of 10 yr (immature growth rate), whereby the length at age 10 was that which was predicted by the von Bertalanffy growth model. Immature growth rate estimates until the length or age of sexual maturity were only available for the 38 lakes in which L_{50} or A_{50} could be estimated, but were very similar to those until the age of 10 ($r=0.88$, $p<0.001$, $n=37$). Immature growth rates did not differ between the sexes. A predictive model of immature growth rate included relative fishing effort as a factor; however, spatial patterns in fishing effort were ignored when modelling large-scale patterns in natural mortality, yield and surplus production (see Fig. 4). The change in juvenile growth rate predicted under climate projections considered only a temperature-driven increase of 2.06 mm yr^{-1} , as other physical predictors remained constant. The growth rate of mature lake trout could not be accurately determined from growth model parameters, and thus was empirically defined as the observed lake-specific growth rate (regression slope of length at age) of all mature females in the reference lakes. Subsequent analyses did not identify any good predictors of mature female growth rate (length-based), so the mean observed value of 7.55 mm yr^{-1} was assumed.

The condition factor (relative fatness) of individual adult fish was calculated as the residual from the \ln - \ln regression of weight on length for fish $>400 \text{ mm}$ in length. Z was estimated from age composition data using the Chapman–Robson estimator, which has been shown to be superior to most other traditional catch-curve analyses for small sample sizes⁴¹. In an unfished population like many of those sampled, Z is equal to M . Reliable Z estimates were available for 28 reference lakes (Supplementary Table 2).

PCA of environmental variables. Many of the lake morphometry characteristics that could influence fish growth were collinear. Principal component analysis (using the factor function in IBM SPSS Statistics v.26) was therefore used to reduce the dimensionality of the key variables: latitude, water temperature, depth, natural-logarithm-transformed lake area and fish diversity (Fig. 3b). Shoreline length did not contribute significantly to the PCA. The first three components of a PCA explained 94% of the variance (56%, 24% and 14% for PCA1, PCA2 and PCA3, respectively), with the following factor loadings for the first two components:

PCA	Latitude	Area	Depth	Water_temp	Species
1	-0.270	0.041	0.252	0.337	-0.320
2	0.297	0.737	0.361	-0.247	-0.131

Although the first principal component was interpreted as a proxy for the variables influencing growth (water temperature and lake morphometry), a PCA without water temperature was also highly significant ($P<0.001$, $r^2=0.88$) and strongly correlated with water temperature ($P<0.001$, $r^2=0.60$). Nevertheless, the addition of water temperature to the PCA improved the model fit. The rationale for including a non-physical variable such as fish diversity into the PCA was because of its high correlation with latitude (solar energy input), its strong effect on mature fish growth and a 5% increase in explained variance. However, a PCA with only the above physical variables produced comparable results in all analyses.

Yield. The YPR (using the Thompson–Bell algorithm as implemented in the R package Fishmethods) was used to quantify the fishing yield for each individual lake⁴². Although the YPR is not designed for year-to-year fisheries management, it is a classic measure of fisheries productivity and is well suited to providing a relative index of across-year fish surplus productivity (kg recruit^{-1}) under equilibrium conditions. The input variables for the YPR are weight at age, instantaneous rate of M , partial recruitment at age (= age-specific net selectivity) and maximum fish age. The weight at age vector (W , in grams) was based on the lake-specific growth in L (in millimetres) curve and an exponential length–weight relationship estimated from trout with ages ≥ 5 ($n=4485$) from all of the reference lakes combined ($P<0.001$, $r^2=0.95$):

$$W = 0.0000059L^{3.099}$$

The maximum age was estimated as that which would result from the lake-specific mortality rate (constant across ages) reducing abundance to 1% of its original value. Full recruitment to rod and reel fishing gear is often similar to that of size at maturity⁴³, which is about 480 mm FL for lake trout. Gillnet selectivity would be expected to peak at a smaller size, making 480 mm a conservative choice for full recruitment. The age-specific partial recruitment vector was thus calculated as the ratio of length at age to 480.

At the maximum sustainable yield (MSY), F was also estimated by YPR analysis; however, it is widely acknowledged that F_{MSY} is a non-precautionary target fishing mortality. The more conservative estimate of $F_{0.1}$ derived from the YPR analysis was thus adopted as a more plausible and widely implemented estimate of sustainable fishing mortality⁴⁴.

A relative measure of surplus production (annual sustainable harvest) was calculated as the product of YPR at $F_{0.1}$ and annual recruitment of new individuals

to the fished segment of the population for all lakes predicted to support occupancy. Assuming temporal equilibrium, annual recruitment to maturity can be calculated as the number of mature fish in the lake multiplied by the annual mortality rate in that lake, where the number of mature fish is calculated as 50% of the total abundance generated from equation (1).

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this Article.

Data availability

The geospatial data (Canadian Digital Surface Model and Canadian Digital Elevation Model) are available from <http://maps.canada.ca/czs/index-en.html>. Air temperature data from 881 weather stations across Canada are available from http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html. Other data that support the findings of this study have been archived at Knowledge Network for Biocomplexity <https://doi.org/10.5063/F1ZP44F1> and <https://doi.org/10.5063/F1TX3CPV>.

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Author contributions

The study was conceived and designed by S.C., J.C. and C.J., and coordinated by S.C. All authors contributed to fieldwork, data collection and/or data interpretation. G.B. (now retired) prepared and analysed the geospatial data. S.C. drafted the paper with contributions from all authors.

Competing interests

The authors declare no competing interests.

Additional information

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