


Temporal changes in the relative abundance of anadromous Arctic charr, brown trout, and Atlantic salmon in northern Europe: Do they reflect changing climates?

Martin-A. Svenning¹  | Morten Falkegård¹ | J. Brian Dempson² | Michael Power³ | Bård-Jørgen Bårdsen¹ | Gudni Guðbergsson⁴ | Per Fauchald¹

¹Norwegian Institute for Nature Research (NINA), Tromsø, Norway

²Fisheries & Oceans Canada, St John's, NL, Canada

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

⁴Marine and Freshwater Research Institute, Reykjavik, Iceland

Correspondence

Martin-A. Svenning, Department of Arctic Ecology, Norwegian Institute for Nature Research, Fram Center, Tromsø N-9296, Norway.

Email: martin.svenning@nina.no

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Abstract

1. Warming temperatures resulting from climate change may alter the distribution and abundance of many freshwater fish species, especially those in northern latitudes. Owing to interspecific differences in temperature adaptations and tolerances, warming may lead to changes in the fish community as a result of shifts in the abundance of co-existing species.
2. We investigated how increased temperatures have potentially affected the abundance and catch composition of anadromous salmonids in northern Europe. We used national angling catch statistics over a period of several decades (1993–2018) as a proxy of relative annual abundance of adult Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and Arctic charr (*Salvelinus alpinus*) in water courses in Iceland and in northern Norway. These are the only locations in the world where the three species coexist naturally as anadromous forms, and where they are distributed across latitudinal gradients characterised by varying temperatures.
3. Interpolated data on average annual air temperatures proximate to the study rivers increased 1–1.7°C in northern Norway and 1.0–1.5°C in Iceland during the 26-year study period.
4. While the overall total number of fish caught has remained relatively stable during the period of study, gradual climate warming has been accompanied by a marked change in the catch composition of the three species in both countries. Increased temperatures were related to a decreased proportion of Arctic charr and an increased proportion of brown trout, while no temperature effect was found for Atlantic salmon. Controlling for the difference between fluvial and lacustrine systems, brown trout has begun to replace Arctic charr in all regions, whereas the relative catch of Atlantic salmon has been stable.
5. Interpretation of angling data can facilitate understanding of longer-term trends in catch data and provide insights into possible underlying changes in fish species and alert managers to shifts in abundance that might be mitigated by management actions. However, care must be taken to avoid the confounding effects that

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changes in fisheries management measures, angler preferences, and effort might have on the metrics of relative change used to make inferences about long-term trends.

KEYWORDS

catch statistics, climate change, salmonids, temperature, thermal change

1 | INTRODUCTION

Anadromous Atlantic salmon, *Salmo salar*, brown trout (sea trout), *Salmo trutta*, and Arctic charr, *Salvelinus alpinus*, are important species in commercial, recreational, and subsistence fisheries, particularly in the northern regions predicted to be most affected by climate change (Reist et al., 2006). They have wide but differing natural distributions that overlap in some areas (Elliott & Elliott, 2010; Klemetsen et al., 2003). Northern Norway and Iceland, and some minor parts of north-west Russia, are the only locations in the world where the three species coexist naturally as anadromous forms. In northern Norway, Atlantic salmon, brown trout, and Arctic charr are reported from c. 200, 350, and 100 watercourses, respectively (Svenning et al., 2012). Most watercourses with Atlantic salmon are typically riverine systems, while brown trout and especially Arctic charr are more commonly found where lacustrine (lake) habitat is available, but all three can coexist in riverine dominated systems (Svenning et al., 2012). In Iceland, Atlantic salmon, brown trout, and Arctic charr are reported from c. 120, 75, and 95 watercourses, respectively. Most watercourses in Iceland include two, sometimes all three species, and in most instances they occur in rivers that flow directly into the sea (i.e. in typical riverine systems) (Guðbergsson, 2014).

A growing body of literature suggests that all three species are likely to be affected by climate change (e.g. Elliott & Elliott, 2010; Finstad & Hein, 2012; Jonsson & Jonsson, 2009, 2011; Todd et al., 2011), although the more cold-adapted Arctic charr is probably the most vulnerable. Based on studies in Great Britain, Winfield et al. (2010) claimed that global warming would threaten the existence of Arctic charr in large parts of its current distribution. Hein et al. (2012) have similarly predicted Arctic charr abundance will decline in northern areas due to climate change, while Finstad & Hein (2012) have noted that higher temperatures may reduce anadromy in Arctic charr, a prediction also reported by Reist et al. (2006) and Reist et al. (2013). From an analysis of catch reports, at least from some of the southernmost water courses in northern Norway and Iceland, anadromous Arctic charr appear to have declined in recent decades relative to catches of Atlantic salmon (Guðbergsson, 2014; Svenning et al., 2012). One explanation based on a recent study in the Veidnes River system in northern Norway is that juvenile Atlantic salmon may benefit from a warmer climate through faster growth, at the expense of the more cold-water-adapted Arctic charr (Svenning et al., 2016).

The latitudinal variation in rivers systems from southern to northern Iceland (63–67°N) and southern to north-eastern northern

Norway (65–71°N) represent the entire distribution area where the three migratory salmonid species coexist. The area displays wide variation in monthly mid-summer (June–July) average air temperatures, ranging from 15°C in the southern areas to 5°C in the northeast. Accordingly, northern Norway and Iceland, where there is coincident significant temperature variation by latitude (Hanssen-Bauer et al., 2017), represent suitable areas to investigate how climate-driven changes in air temperature may potentially affect the relative abundance and diversity of anadromous salmonids. Since 1993, separate reports of the three species have been provided in official catch statistics from more than 400 watercourses in Iceland and northern Norway. The data, therefore, provide a unique opportunity to investigate temporal changes in the relative catch proportions of the three species over a period of several decades (1993–2018).

Fishers from both countries claim Arctic charr have become less abundant during the last 30 years by comparison with brown trout and Atlantic salmon (Guðbergsson, 2014; Svenning et al., 2012). Although relative catches of Arctic charr may have decreased compared to Atlantic salmon and brown trout, we hypothesised that the dominance of Arctic charr would become more pronounced with increasing latitude where temperatures are cooler, whereas the relative catch of Atlantic salmon and brown trout would be positively correlated with historical increases in temperature. Since Arctic charr most often spawn and overwinter in lakes, while Atlantic salmon and brown trout use rivers as their nursery areas, we also hypothesised that the catch of Arctic charr would be relatively higher in lake-based than river-based systems.

2 | METHODS

2.1 | Catch data

In Norway, a systematic collection of catch data (rod and line) for salmonids was started in 1876, but focused only on Atlantic salmon until 1968 (Anon., 2017). Since 1969, fishers have been required to report all three species individually, but in the official data kept by Statistics Norway (Statistisk sentralbyrå; <http://www.ssb.no>), the Atlantic salmon, brown trout and Arctic charr are presented individually only from 1993 (Anon., 2017). Prior to 1993, Atlantic salmon were partitioned into two size groups, whereas from 1993 Atlantic salmon were divided into three size groups, under 3 kg, between 3 and 6.9 kg, and 7 kg and over. The three size groups are assumed

to represent one- (1SW; < 3 kg), two- (2SW; 3–7 kg), and multi-sea-winter fish (MSW i.e. ≥ 3 SW; ≥ 7 kg), respectively (Anon., 2017). Another important amendment introduced in 1992/1993 was the *preservation regulation*, stating that all fishing for salmonids was prohibited in all rivers, unless it was official and individually opened through Norwegian legislation (Anon., 2017). Other requirements regarding catch reports also changed in 1992, and Statistics Norway has declared that it would be difficult to compare the statistics before 1993 and after 1992 owing to the changes in reporting methodology (Anon., 2017). Thus, the historical catch data for north-Norwegian river systems in this study are based on the official national rod catch statistics for the period 1993–2018. The data summarise information obtained from 369 river systems (Figure 1), with 218 rivers from Nordland, 70 from Troms, and 81 systems from the Finnmark county. These three counties form a southwest–northeast gradient, with Nordland in the southwest, Troms in the middle and Finnmark in the northeast. Catchment areas vary considerably (river + lake), with drainage areas varying from 0.005 ha (i.e. 5×10^{-5} km²) to 5200 ha (52.2 km²). Total annual catches (all three species) also vary widely, ranging from less than 10 to more than 35,000 fish. Beginning in 2009 catch and release statistics were reported for the first time in some of the rivers (Anon., 2017).

In Iceland, the river catches of anadromous salmonids are based on angler's log-book records of individual fish caught by rod and line. The records consist of fish length measured to the nearest cm, weight (to 100 g), and the date of capture. The log-book system was introduced in 1946. A limited number of rods are allowed in each salmon river and determined based on an average catch of one fish

per rod per day. A logbook scheme was introduced for brown trout and Arctic charr in the late 1980s. Catch and release was initiated on a voluntary basis for anglers in the early 1990s. Since 1998 systematic records of catch and release have been part of the log-book system.

A study including several Icelandic rivers with fish counters installed indicated that Atlantic salmon catches correlated well ($r^2 = 0.78$) with abundance information obtained via fish counters (Jónsson et al., 2008), a result dependent on the stability of fishing effort over time. Provided effort and harvest regulations remain relatively stable over time, catch data can be used to infer changes in the relative abundance of species (see Crozier & Kennedy, 2001; Otero et al., 2017). Thus, if we assume effort and regulation combined do not affect the relative difference in catchability, one can use the observed changes in the proportion of the species in the catch as a proxy for changes in relative species abundance.

The Atlantic salmon catch is typically divided into grilse (1SW) or Atlantic salmon (2SW), based on the weight distribution where males up to 4 kg and females up to 3.5 kg are classified as 1SW and larger fish are classified as 2SW Atlantic salmon. The separation by sea age has been confirmed from scale pattern analyses, with relatively little overlap in the weight distribution noted. Atlantic salmon that have spent more than 2SW (MSW) are very rare in Iceland and the frequency of repeat spawners has been relatively low for the last 2 decades (Guðbergsson, 2014). The numbers of fish caught and released in the rod fishery have been increasing in Iceland, and in a few rivers catch and release is the only fishing method now allowed. Many rivers have fly fishing only, and mandatory release of 2SW

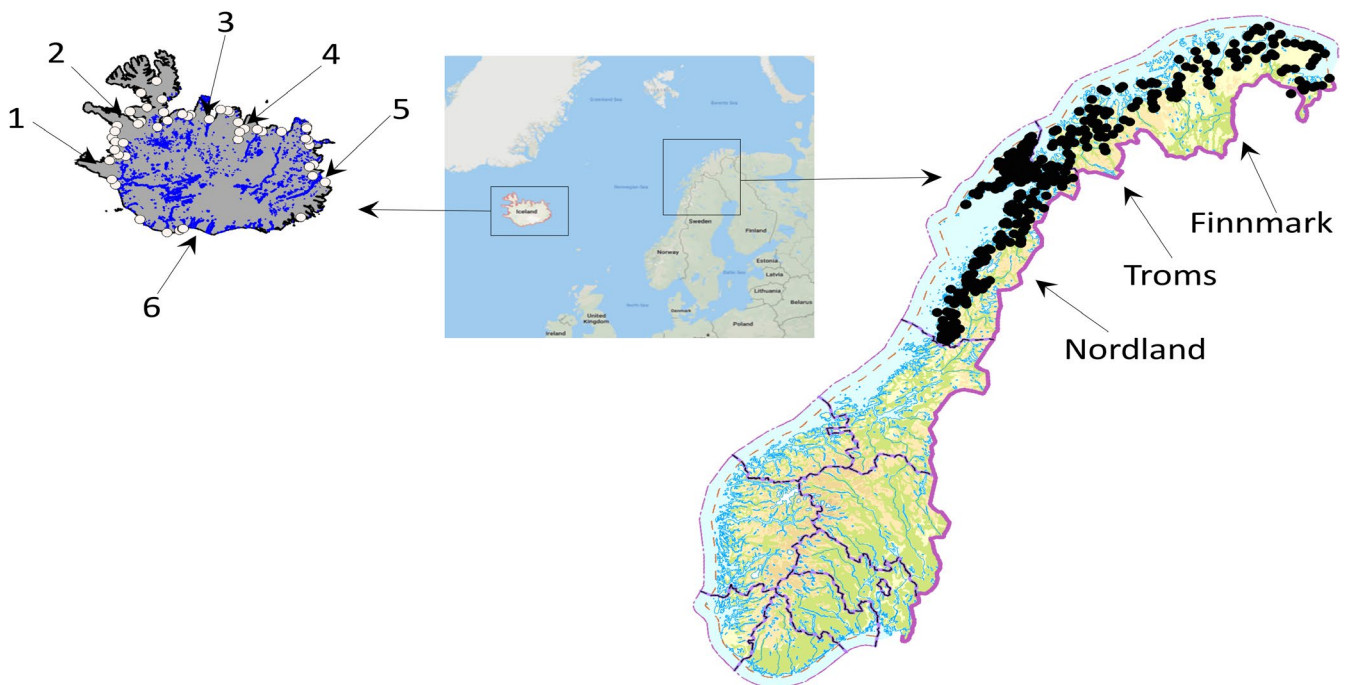


FIGURE 1 Watercourses in Iceland (white circles, $n = 63$) and northern Norway (black circles, $n = 369$) included in this study, and the six meteorological stations in Iceland; Reykjavik (1), Stykkishólmur (2), Bergstaðir (3), Akureyri (4), Dalatangi (5), and Vatnsskarð (6), used to estimate monthly average air temperatures for neighbouring rivers. For north-Norwegian rivers, monthly average air temperatures from each county (Nordland, Troms, and Finnmark) were based on gridded data estimated at the mouth of each study river

Atlantic salmon (fish larger than 69 cm). In a few rivers, a minimum length is set for retaining brown trout and Arctic charr and anglers must release smaller individuals.

A total of 61 rivers are included in the official Icelandic catch reports for the period 1993–2018. The catches in all rivers were larger than zero in at least 20 of the 26 years, plus a total of at least 1,800 fish were caught in each river system during the study period. The 61 rivers included are located in four main geographical areas within Iceland: southern (11 rivers), western (21 rivers), northern (24 rivers), and eastern (5 rivers) areas (Figure 1).

The catch statistics provide information on the total catch by number, including catch and release, but since the majority of released fish are caught only once we have used total catch (catch + released) to describe the annual riverine catch in as well Icelandic as in North Norwegian watercourses. The majority of rivers in both countries are dominated by 1SW Atlantic salmon. Hence, we did not split MSW further into its constituent sea age-classes. Rather we included 2SW fish into the MSW group, because it is common to use the groupings 1SW and MSW in the salmon literature. Further, such disaggregated analysis for Atlantic salmon would have resulted in an unbalanced treatment of the species because Arctic charr and brown trout data (in the catch statistics) are not disaggregated by age or size. Thus, catches of Arctic charr and brown trout contain both first time and repeat migrants, and catches of Atlantic salmon contain both 1SW and MSW fish.

2.2 | Lake and river area and temperature data

Arctic charr most often utilise lentic areas for spawning, while brown trout and Atlantic salmon only spawn in lotic habitats, which makes a comparison between catchments with and without lakes potentially important. When removing water courses with no catch reports, the remaining catchments ($n = 175$) were categorised as: (1) *rivers* (> 80% of wetted area was river; $n = 62$); (2) *lakes* (< 20% of wetted area was river; $n = 82$); and (3) *river/lake* (the rest of the catchments; $n = 31$). Nearly all river systems in Iceland are dominated by lotic areas (Jónsson et al., 2008): i.e. 54 and 7 catchments were categorised as rivers and river/lake, respectively.

For watercourses in Troms and Finnmark counties, lake and river areas were partly based on data provided by the Norwegian Environment Agency and partly on our own estimates derived using *Norgeskart* (<https://www.norgeskart.no/#!?project=norgeskart&layers=1002&zoom=4&lat=7197864.00&lon=396722.00>). For Nordland county, surface area calculations were determined from maps provided by the County Governor of Nordland (<http://fylkesmannen.maps.arcgis.com/apps/webappviewer/index.html?id=5153465451874f10a97f406e9ef8e9ee¢er=18,67&level=5>) and by *Lakseregisteret* at the Norwegian Environment Agency (<http://lakseregisteret.fylkesmannen.no/>). For Iceland, water courses were categorised using data provided by the Marine and Freshwater Research Institute (<https://www.hafogvatn.is>).

Air temperature data used were obtained from the Norwegian Climate Service Center (<https://klimaservicesenter.no>) and the Icelandic Meteorological Office (<https://en.vedur.is/>) as monthly averages for the period of study.

2.3 | Statistical analysis

Since fishing effort is unknown, angling catch data may show a high degree of spatiotemporal variability, and thus the use of catch data to make inferences with respect to population dynamics could be problematic. If we assume that the relative difference in catchability between the three different species is constant, we can use the observed changes in the proportion of the three species in the catches as a proxy for changes in species composition. Accordingly, the analyses are based on catch proportions.

Our aim was to analyse how the proportion of the three species in the catch was related to temperature while accounting for characteristics pertaining to the different regions, watercourses, and years. The response variable is multinomial with three outcomes: Arctic charr, brown trout, or Atlantic salmon. To simplify the analyses, we decided to analyse the proportion of each species separately using logistic (binomial) regressions. To account for the correlation between observations within watercourses and year, we included a nested random structure consisting of Year within River within Region (1|Region|RiverId|Year). In other words, we let the intercept of the model vary for years within rivers within regions. Year within river systems account for year-to-year variation (e.g. in fishing and regulation practices or environmental features affecting catch proportions). River within regions and regions account for river and region-specific variation, respectively. Note that this random structure gives each observation a unique random effect level and is therefore similar to an observation-level random effect, which is often added to models to account for overdispersion (Harrison, 2015). For the present dataset, models with a simplified random structure (e.g. removing year from the random component) gave highly overdispersed models. We therefore decided to keep the nested random structure in all models. Because the random factor includes year as a level, the effects of temporal autocorrelation were accounted for by the models. Similarly, the effects of spatial autocorrelation were accounted for by the river and region factors. Finally, because the random structure represents an observation-level random effect, the models also accounted for overdispersion (Harrison, 2015). To assess the difference in catch between fluvial and lacustrine systems, we defined a *WaterSystem* variable with three levels: River (>80% of river area), River/Lake (between 80 and 20% river area), and Lake (<20% river area). Note that all catchments in Iceland were defined as either river or river/lake. *WaterSystem* and annual temperature were included as fixed effects in the models. For each species, we analysed the proportion of that species in the catch (e.g. number of Arctic charr vs. number of Atlantic salmon vs. brown trout) in a binomial model with a logit-link. We used the *glmer* function with

a Laplace approximation in the lme4 library (Bates et al., 2015) in R (R Core Team (2020)).

We first compared models with and without the two fixed factors. We used Akaike's information criteria and the Bayesian information criterion to compare the models, and likelihood ratio tests were used to test the difference between the selected model and alternative models. Finally, to investigate how the response to temperature varied among regions, we ran separate models for each region.

3 | RESULTS

3.1 | Air temperature trends

Mean annual air temperature data in the three counties in northern Norway and at the six weather stations in Iceland showed an increase ranging from 1–1.7°C and 1.0–1.5°C, respectively, over the 26-year period from 1993 to 2018 (Table 1). The coast line in northern Norway from southern Nordland (65°N) to north-eastern Finnmark (71°N) extends over a distance of approximately 1,000 km and the annual average summer air temperatures (May–September) during the study period (1993–2018) in southern Nordland exceed those in north-eastern Finnmark, being now as much as 4–5°C higher (<https://klimaservicesenter.no>). Similarly,

TABLE 1 Linear regression of air temperature from six meteorological stations in Iceland from 1993 to 2018 (see Figure 1), and for Nordland, Troms, and Finnmark counties in northern Norway. Average air temperatures for the three counties in Norway are based on gridded data estimated at the mouth of each study river. Adjusted square multiple r^2 , standard error (SE) and first order autocorrelation (FOA) and Durbin–Watson D-statistic (DW) are given

Area	Equation	r^2	SE	FOA/ DW
Akureyri (NE)	$y = -89.97 + 0.047 \times \text{TempYear}$	0.349	0.005	0.01/2.0
Bergssta (NW)	$y = -90.60 + 0.047 \times \text{TempYear}$	0.319	0.004	0.24/1.4
Dalatangi (E)	$y = -117.36 + 0.061 \times \text{TempYear}$	0.587	0.004	0.09/2.1
Reykjavik (W)	$y = -87.408 + 0.046 \times \text{TempYear}$	0.322	0.003	0.01/2.1
Stykkisál	$y = -105.14 + 0.055 \times \text{TempYear}$	0.400	0.007	0.11/2.2
Vatnskar (S)	$y = -70.56 + 0.038 \times \text{TempYear}$	0.281	0.004	0.21/2.3
Nordland	$y = -73.09 + 0.039 \times \text{TempYear}$	0.206	0.001	0.22/1.4
Troms	$y = -96.24 + 0.049 \times \text{TempYear}$	0.331	0.003	0.19/1.6
Finnmark	$y = -134.92 + 0.068 \times \text{TempYear}$	0.484	0.003	0.15/1.6

the air temperatures are 2–3°C higher in southern versus northern Iceland (<https://en.vedur.is/>).

3.2 | Relative catches

In western Iceland rivers, Atlantic salmon dominated the catches over the entire period, accounting for 90–95% of the total catch in recent years. In contrast, brown trout dominated catches in southern rivers, accounting for nearly 70% of the total catch during the past 15–20 years (Figure 2). Relative catches of Arctic charr were low in both southern and western streams, decreasing from around 20% in the 1990s to less than 5% in recent years. While catches of Arctic charr have generally been higher in northern and eastern rivers, they have similarly declined over time (Figure 2).

Catch records from river-based systems in northern Norway show that Atlantic salmon dominated the catch across the entire 26-year period, especially in the northernmost rivers (Finnmark) where in recent years they have accounted for close to 80% of the catch years (Figure 2). Further south, in Nordland and Troms rivers, catches of brown trout were more or less equal to those reported for Atlantic salmon, with each species contributing between 40–50% to the total catch (Figure 2). Relative catches of Arctic charr, however, decreased during the 26 year period in riverine systems in northern Norway, and were nearly zero in Nordland rivers (Figure 2).

In lake-based systems, brown trout dominated the catches, especially in Nordland and Troms, amounting to about 60% of the catch during the past 10 years. The catch proportion of Atlantic salmon showed a decreasing trend in Nordland and Troms and a slight increasing trend in Finnmark (Figure 2). Catches of Arctic charr have been low in Nordland, and showed decreasing trends in both Troms (from 40 to 20%) and Finnmark (from 50 to 25%; Figure 2). In all three counties, the catch proportion of Arctic charr was lower in river-based than lake-based systems (Figure 2).

3.3 | Analysis of time series

The selected models for Arctic charr and brown trout included annual temperature and catchment type (WaterSystem) as explanatory variables (Table 2). The alternative models were all significantly different from the selected model. The selected model for Atlantic salmon included catchment type only as an explanatory variable. The parameter estimates from the selected models (Table 3) indicated a strong negative relationship between the catch proportion of Arctic charr and temperature, with the odds of catching Arctic charr compared to the two other species decreasing by 35.7% (95% confidence interval 31.1–39.9%) for each degree (°C) increase in temperature. Similarly, the odds of catching brown trout compared to the two other species increased by 37.9% (95% confidence interval 31.5–44.6%) for each degree increase in temperature. We found no evidence for a relationship between the catch proportion of Atlantic salmon and temperature

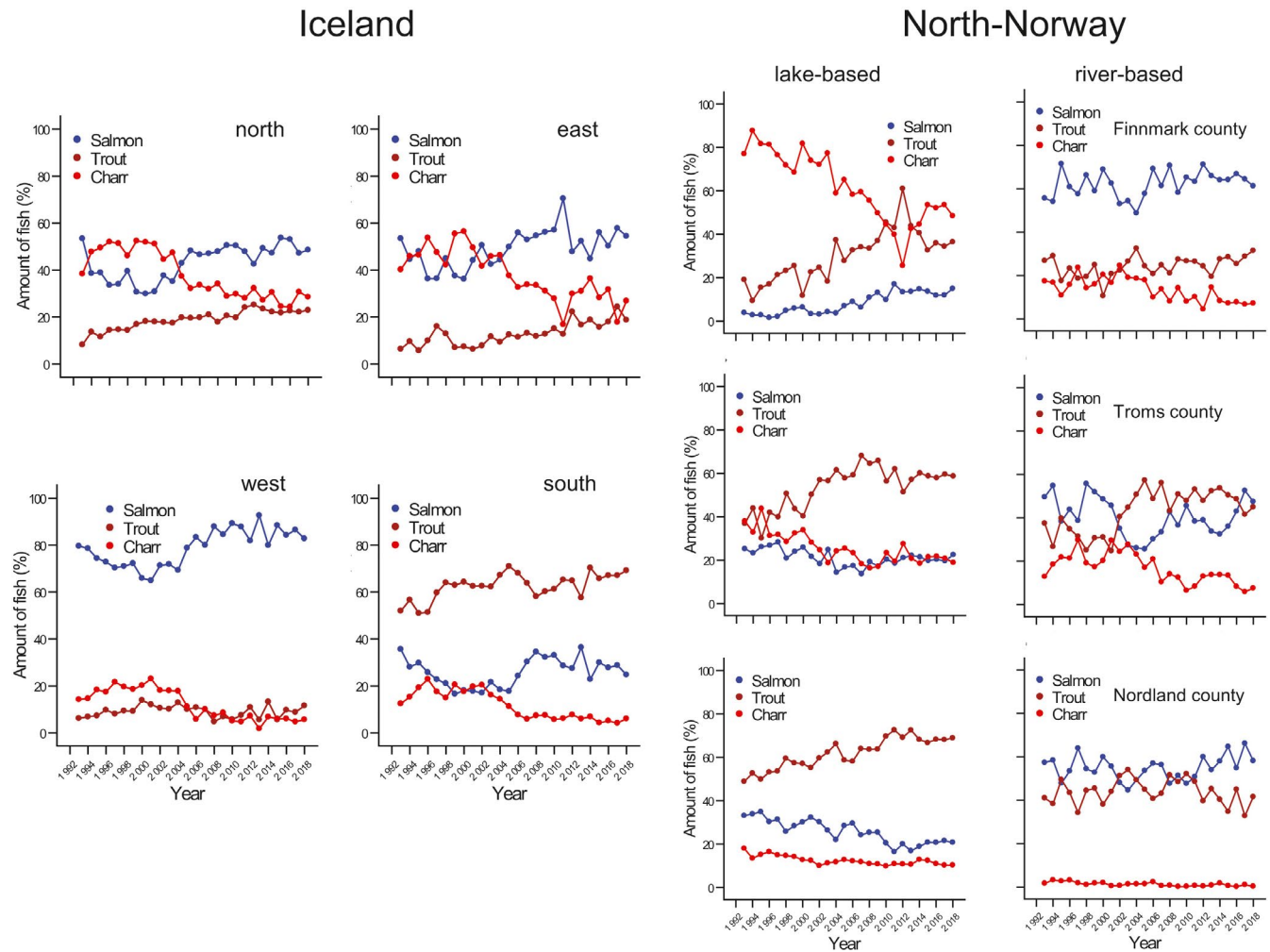


FIGURE 2 Temporal changes in the annual catch (%) of Atlantic salmon, brown trout, and anadromous Arctic charr in Icelandic and north-Norwegian rivers from 1993 to 2018, showing results from west, north, east, and south Iceland (left figure), and in north Norway (right figure) associated with lake-based and river-based water courses extending from Finnmark, Troms, and Nordland county. Lake-based systems are those that are dominated (> 80%) by lacustrine habitat (see section 2.3)

(Table 2). Thus, increased temperature was mainly related to a change in the catch proportions of Arctic charr to brown trout (Figures 3 and 4). Moreover, we found that the catch proportion of brown trout and Arctic charr was higher in lacustrine catchments, while a high catch proportion of Atlantic salmon was associated with fluvial systems (Table 3).

To investigate the relationship between the catch proportions of Arctic charr and brown trout further, we conducted regional analyses using the Arctic charr and brown trout catch ratio as a response variable, annual temperature, and catchment type as fixed factors and year nested within river as a random factor (see Appendix 1 for model results). The parameter estimates for the regional responses to temperature expressed as a percentage change in odds are shown in Figure 3. In all regions, we found significant negative effects of temperature, indicating that the catch ratio of Arctic charr to brown trout decreased with increasing temperature in all regions investigated. The strongest response was found in Iceland (c. 50% decrease in the odds for each degree increase in temperature), while the weakest response was found in

Nordland (25% decrease in the odds for each degree increase in temperature).

4 | DISCUSSION

Our results indicate that a gradual warming in recent decades has been accompanied by a marked change in the composition of anadromous fishes in the freshwater ecosystems in Iceland and northern Norway. Specifically, brown trout is replacing Arctic charr in all regions, while the proportions of Atlantic salmon caught have remained stable. Thus, the recent changes in climate may have altered the relative abundance of salmonids, initially favouring the *Salmo* species, especially brown trout, that have higher temperature tolerances (Elliott & Elliott, 2010), with the increases in catch proportions for *Salmo* species coming at the expense of the more cold-water-adapted Arctic charr (Svenning et al., 2016, and references therein). In Iceland, Atlantic salmon dominated the moderately warmer western rivers while brown trout dominated in the

TABLE 2 Model selection of logistic models relating the proportion of: Arctic charr, brown trout, and Atlantic salmon in the catch to annual temperature and type of catchment (WaterSystem). Year nested within river nested within region were included as random factors in all models. The selected model in terms of Akaike's information criteria (AIC) and the Bayesian information criterion (BIC) for each response variable is indicated. Log likelihood tests were used to compare the selected model with alternative models

Model formula	df	ΔAIC	ΔBIC	logLik	P
Arctic charr / (brown trout + Atlantic salmon)					
~ Temperature + WaterSystem + (1 Region/RiverId/Year)*	7	0	0	-20640	
~ Temperature + (1 Region/RiverId/Year)	5	22	9	-20653	<0.0001
~ WaterSystem + (1 Region/RiverId/Year)	6	154	147	-20718	<0.0001
~ 1 + (1 Region/RiverId/Year)	4	172	152	-20729	<0.0001
Brown trout / (Arctic charr + Atlantic salmon)					
~ Temperature + WaterSystem + (1 Region/RiverId/Year) ^a	7	0	0	-25893	
~ Temperature + (1 Region/RiverId/Year)	5	8	-5	-25899	0.002
~ WaterSystem + (1 Region/RiverId/Year)	6	177	171	-25983	<0.0001
~ 1 + (1 Region/RiverId/Year)	4	188	168	-25990	<0.0001
Atlantic salmon / (Arctic charr + brown trout)					
~ WaterSystem + (1 Region/RiverId/Year)*	6	0	0	-25858	
~ Temperature + WaterSystem + (1 Region/RiverId/Year)	7	2	9	-25858	0.904
~ 1 + (1 Region/RiverId/Year)	4	42	29	-25881	<0.0001
~ Temperature + (1 Region/RiverId/Year)	5	44	37	-25881	<0.0001

^aSelected model.

warmest southernmost rivers. Temperature increases were also associated with reduced relative catches of Arctic charr across all regions. Similarly, in northern Norway, Arctic charr appear to have been the most affected, particularly in some Nordland rivers where they are now nearly extirpated and where air temperatures have been consistently higher. In contrast, the *Salmo* species have been less dramatically affected, with Atlantic salmon dominating river-based systems in the north, i.e. in Finnmark county, and catches of brown trout having increased relative to Arctic charr, especially in many Troms rivers.

The lack of a temperature effect for Atlantic salmon may relate to their known use of thermoregulatory behaviours to maintain preferred body temperatures (Jonsson & Jonsson, 2011; Oppedal et al., 2011), which may include selectively occupying preferred thermal habitats and feeding in deeper ocean waters (Minke-Martin et al., 2015). Indeed, the comparative constancy in the 3.9–9.7°C range of reported temperature use by Atlantic salmon across time and space noted in the literature (e.g. Hanson et al., 2013; Holm et al., 2006; Minke-Martin et al., 2015; Reddin & Friedland, 1993) and the opportunities to shift both geographic position and depth suggest that to date adult Atlantic salmon have been able to offset the effects of temperature observed in more coastal dwelling and freshwater dependent brown trout and Arctic charr.

Numerous studies have concluded that changing climate, particularly warming, will potentially result in pervasive effects on northern

fish populations, including salmonids (e.g. Bilous & Dunmall, 2020; Martins et al., 2012; Pörtner & Peck, 2010; Schindler, 2001; Svenning et al., 2016). These effects may alter the distribution (Jonsson & Jonsson, 2009; McCarthy & Houlihan, 1997), demography and growth (Fjørtoft et al., 2014; Jonsson & Jonsson, 2009; Kovach et al., 2016; McCarthy & Houlihan, 1997; Todd et al., 2008, 2012), phenology (Dempson et al., 2017; Jonsson & Jonsson, 2009; Otero et al., 2014; Todd et al., 2012), and physiology of many species (e.g. Ficke et al., 2007; McCormick et al., 2009). Several studies have also indicated that Atlantic salmon growth and survival of fry and parr would probably increase, while smolt age would decrease resulting in higher smolt production (Hedger et al., 2013; Jonsson & Jonsson, 2011), particularly at more northerly latitudes (Power & Power, 1994). In addition to changes in run timing, i.e. earlier migration to sea and back to fresh water, shifts in marine survival may have significant consequences for overall Atlantic salmon production (Beaugrand & Reid, 2003; Jonsson & Jonsson, 2011; Mills et al., 2013; Todd et al., 2008), with warming waters influencing key vital rates such as age-at-maturity that hold direct consequences for abundance (Condrón et al., 2005; Otero et al., 2012; Todd et al., 2011). Warming conditions have also been linked with declines in Atlantic salmon abundance in the Northeast Atlantic (Beaugrand & Reid, 2012; Todd et al., 2008), particularly in southern areas (e.g. Nicola et al., 2018).

Results as noted here accord well with expected changes in the relative abundance and catch predictable on the basis of the existing

TABLE 3 Parameter estimates from selected logistic models relating the proportion of: Arctic charr, brown trout, and Atlantic salmon in the catch to annual temperature and type of catchment (WaterSystem: River, River/Lake, Lake). Year nested within river nested within region were included as random factors

Arctic charr / (brown trout + Atlantic salmon)~ Temperature + WaterSystem + (1 Region/RiverId/Year)				
Fixed factors	Estimate	SE	z-value	P
Intercept (Lake)	0.559	0.876	0.64	0.524
River	-2.311	0.440	-5.25	<0.0001
River/Lake	-1.956	0.544	-3.59	0.0003
Annual temperature	-0.441	0.034	-12.97	<0.0001
Random factors	SD			
Year:(RiverId:Region)	1.45			
RiverId:Region	2.89			
Region	1.98			
Brown trout / (Arctic charr + Atlantic salmon)~ Temperature + WaterSystem + (1 Region/RiverId/Year)				
Intercept (Lake)	-1.827	0.666	-2.74	0.0061
River	-1.296	0.366	-3.54	0.0004
River/Lake	-0.708	0.458	-1.55	0.122
Annual temperature	0.321	0.024	13.60	<0.0001
Random factors	SD			
Year:(RiverId:Region)	1.08			
RiverId:Region	2.45			
Region	1.47			
Atlantic salmon / (Arctic charr + brown trout)~ WaterSystem + (1 Region/RiverId/Year)				
Intercept (Lake)	-3.028	0.594	-5.10	<0.0001
River	2.790	0.406	6.87	<0.0001
River/Lake	2.390	0.513	4.66	<0.0001
Random factors	SD			
Year:(RiverId:Region)	1.16			
RiverId:Region	2.76			
Region	1.20			

life stage-specific thermal tolerances for the study species. Across all life-stages, but particularly at the egg stage, Arctic charr exhibit lower upper thermal tolerances than either brown trout or Atlantic salmon (Elliott & Elliott, 2010; Jonsson & Jonsson, 2009) and cease feeding at juvenile stages between 21 and 22°C as compared to 19–26°C for brown trout and 22–28°C for Atlantic salmon. A pattern of consistently increasing temperatures, therefore, would be expected to decrease the relative abundance of Arctic charr as was noted here, particularly as Arctic charr is a cold-adapted species (Bilous & Dunmall, 2020; Svenning & Gullestad, 2002).

Several studies have also documented differences among the three salmonid species in regards to optimal temperatures for growth or food conversion, as well as temperature preferences (Elliott & Elliott, 2010; Larsson, 2005; Svenning et al., 2016 and references therein). For most fishes, for instance brown trout, the

optimal temperature for growth and the preferred temperature are closely matched (see Ojanguren et al., 2001 and references therein). Larsson (2005), however, showed a 4–5°C lower preferred temperature for Arctic charr as compared to the laboratory reported optimal temperature for growth, suggesting Arctic charr and brown trout differ in their thermoregulatory behaviour (Larsson, 2005). Consequently, Arctic charr is most likely to exist and persist in the coldest environments (Svenning et al., 2007) and from a climate warming perspective, the more aggressive brown trout (see Jonsson & Jonsson, 2011) may benefit from warmer climates at the expense of the more cold-water-adapted Arctic charr.

Thermal tolerance data for Atlantic salmon suggest that they are also likely to maintain an important competitive feeding advantage over brown trout and Arctic charr that will have positive consequences for growth, survival, and, ultimately, increased abundance at the expense of the other two species, at least in the freshwater stage (see Heggenes et al., 1999; Heggenes & Saltveit, 2007; Svenning et al., 2016). Considerations of ration are important for understanding and predicting actual responses to changes in temperature given that optimum temperatures vary with energy intake (Elliott, 1994; Elliott & Hurley, 2000). Threshold responses may further affect the pattern of observed responses over time, with abundance affected when temperatures surpass critical thresholds. For example, Ayllon et al. (2013) noted functional relationships between temperature and density for Spanish populations of brown trout that depended at lower temperatures on the degree of anthropogenic disturbance and beyond an estimated breakpoint of 19.4°C displayed accelerated declines in abundance with increasing temperature. However, factors in addition to temperature should be considered when attempting to understand the likely ecological responses of fish to climate change (Harley & Paine, 2009) as focusing solely on thermal tolerance data is likely to provide an incomplete understanding of the adaptive potential of salmonids given their high heritability of phenological traits (Carlson & Seamons, 2008) and their noted short-term adaptive evolutionary capacities (e.g. Hendry et al., 2000; Quinn et al., 2000; Westley et al., 2012).

Differential use of varying habitats may mitigate the effects of temperature. Arctic charr largely spawn and overwinter in lakes, while Atlantic salmon and brown trout use rivers (Klemetsen et al., 2003). Accordingly, we hypothesised that Arctic charr should be more abundant in lake-based versus river-based systems. Although the relative abundance of Arctic charr was higher in lake-based versus river-based systems for all three Norwegian counties, our analyses confirmed that Arctic charr have generally decreased in both systems. Greater reliance on lentic systems for the completion of critical life-stages may have exposed Arctic charr to additional temperature-driven consequences, including eutrophication and stratification impacts predicted to reduce habitat suitability and disrupt food webs (Ficke et al., 2007). Presence-absence data for Arctic charr and brown trout from Norwegian lakes reflecting both temperature and productivity gradients suggest competitive exclusion may also affect the relative distribution of Arctic charr and brown trout, with the

FIGURE 3 Regional responses of the catch ratio of Arctic charr to brown trout to annual temperature. The responses are estimates from region-specific logistic models (see text), and are expressed as the percentage change in the proportion of Arctic charr/brown trout for a 1°C increase in temperature. C.I., denotes confidence interval.

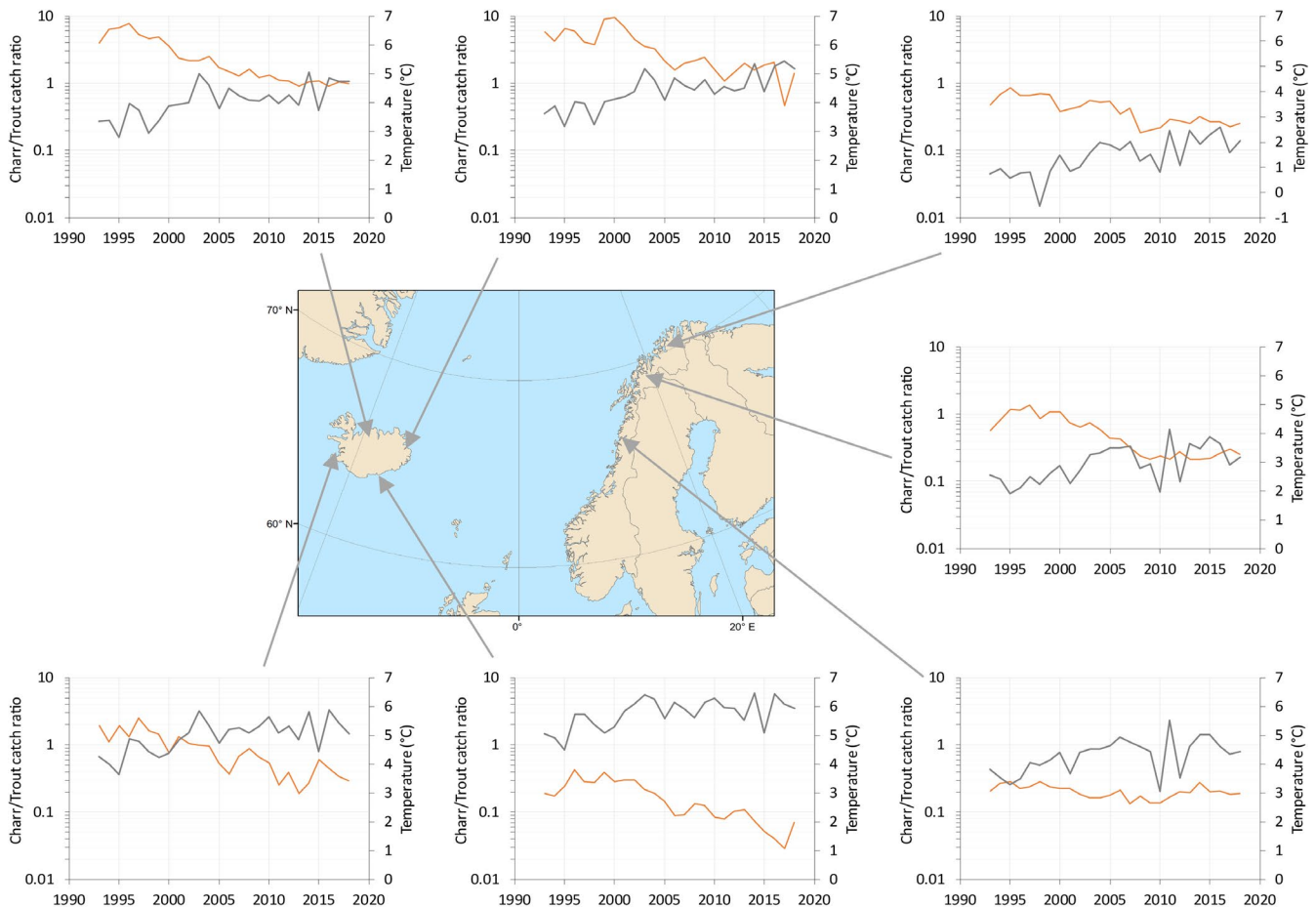
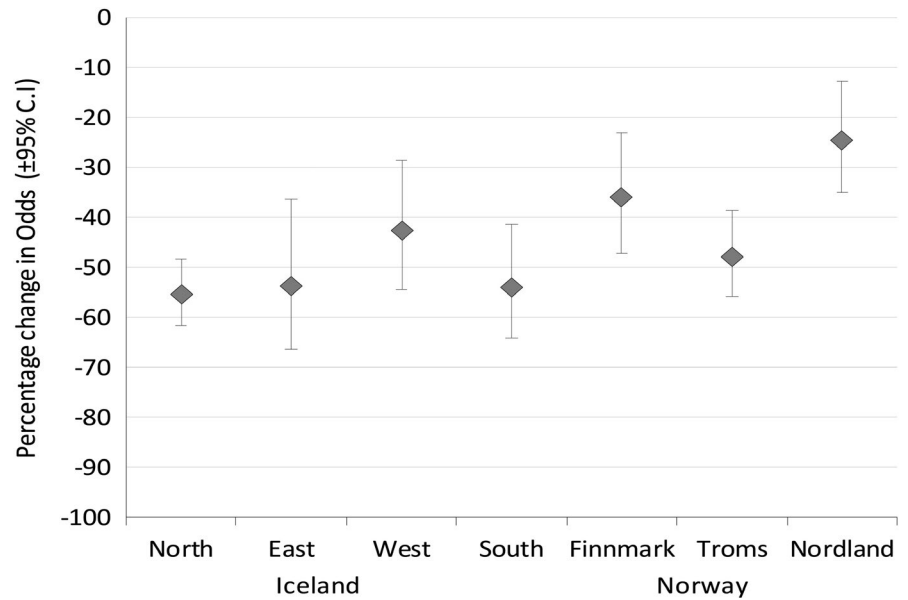


FIGURE 4 Time series of the catch proportion of Arctic charr to brown trout (red solid line) and air temperature (grey hatched line) for seven regions in Norway and Iceland. Note that catch proportions are plotted on a log scale.

combination of productivity, covarying temperature conditions, and aggressive behaviours interacting to determine both the existing geographical distribution of the species and their likely fates

under warming climate scenarios (Finstad et al., 2011). Similarly, Hein et al. (2014) noted that climate change will exacerbate competitive interactions among co-resident species, with co-existence

being context-dependent and relying on factors such as lake area in addition to temperature.

An additional complication may result if non-native species increase in areas where they are currently absent as a result of warming climate. Studies in Ireland have shown that warming temperatures, in conjunction with the presence of non-native fish species, has negative effects on Arctic charr (Morrissey-McCaffrey et al., 2019). With continued warming, it may be necessary for Arctic charr to further avail themselves of deep thermal refugia to continue to co-exist with brown trout in northern Norway or Iceland, similar to situations that Arctic charr face in Irish systems (Morrissey-McCaffrey et al., 2019).

In contrast with lentic habitats, precipitation will also alter the hydrologic regimes of lotic systems and the availability groundwater may critically affect the quality of fish habitats and the ability of habitats to support fish production (Ficke et al., 2007). For example, decreased summer flows typically trigger the emigration of salmonid juveniles to deeper pools (Jonsson & Jonsson, 2009), with the availability of such habitats having immediate consequences for survival (Minns et al., 1995; Power & Power, 1994). Thus, Atlantic salmon are known to seek thermal refugia in rivers when water temperatures warm to unacceptable levels (Daigle et al., 2015; Dugdale et al., 2013; Dugdale et al., 2016; Frechette et al., 2018). Climate change has led to more precipitation and thus increased water flow in most watercourses, thereby influencing the accessibility of rivers for ascending fish (Jonsson & Jonsson, 2009). For example, studies have shown a strong correspondence between the total number of adult Atlantic salmon and maximum discharge during the migration period (Mitchell & Cunjak, 2007). Availability of adequate discharge data is, however, limiting for most of the rivers included in this study. Nevertheless, we suggest climate-driven increases in water flow may have similar effects on anadromous brown trout and Arctic charr as have been observed for Atlantic salmon.

Anthropogenic factors, including Atlantic salmon farming and increases in the density of sea lice, negatively affect the survival of anadromous fish (see Costello, 2009; Shephard & Gargan, 2020; Skaala et al., 2014). Skilbrei & Wennevik (2006) noted a population-regulating effect of salmon lice on Atlantic salmon, although Atlantic salmon smolts migrate relatively quickly out of the fjords and coastal areas where the highest concentrations of fish farms are located. Brown trout, and especially Arctic charr, however, undertake shorter migrations and feed mostly in coastal areas during their periods of sea residency (Klemetsen et al. 2003) and may similarly manifest population-regulating effects as a result of the exposure to fish farms. Brown trout are resident in marine waters for longer periods of time than Arctic charr, and thus are more likely to be negatively affected by sea lice (Klemetsen et al., 2003). Our results indicate, however, that brown trout are replacing Arctic charr in all regions, suggesting that the negative impacts of climate related factors on Arctic charr are more pronounced in fresh waters than any anthropogenic factors during the sea residence.

Anadromous migratory behaviour may also be reduced at the lower latitudes where feeding and rearing resources are more available to fish in freshwater (Finstad & Hein, 2012; Hein et al., 2012;

Reist et al., 2006). Arctic charr exhibit a range of biodiversity including variation in life-history characteristics (Power et al., 2008) that can result in both resident and migratory fish within the same watercourses (cf. Klemetsen et al., 2003; Snorrason et al., 1994). Thus, although catches of anadromous Arctic charr in Iceland and northern Norway have decreased, the abundance of resident Arctic charr in the same water courses may have correspondingly increased as a result of shift in life-histories (Jonsson & Jonsson, 2011).

The annual catch proportions observed for the three species may further have been affected by the fisheries management regime. It is possible that a fisheries regulation that positively influences Atlantic salmon could have a negative influence on brown trout and/or Arctic charr. An example of one such regulation is catch and release. Rivers with increasing harvest restrictions have more fish released than those without (Lennox et al., 2016), which leads to lowered exploitation rates and increased spawning stocks. The extent of catch and release was significantly higher for Atlantic salmon compared to the other two species, with more than twice as many Atlantic salmon being released than Arctic charr and brown trout. The stability of the proportion of Atlantic salmon captured relative to brown trout and Arctic charr, therefore, may in part be due to the positive impacts of catch on release regulations on Atlantic salmon.

Catch declines may also be a response to extended regulations. For example, a change was introduced in the northernmost Norwegian rivers before the 2007 season that reduced fishing time in some rivers. This change was implemented as a response to reports regarding the apparent decline of some Arctic charr stocks. The restriction (shortened season) was aimed at decreasing exploitation on Arctic charr. As such, the regulation could have had a slight impact by lowering the catch proportion of Arctic charr relative to brown trout and Atlantic salmon and hence amplified the apparent decrease in the catch of Arctic charr compared to the actual stock situation. However, while there was a reduction in fishing time, Arctic charr may still have been caught inadvertently, with anglers required to report that such Arctic charr had been released. Thus the overall impact on catch proportions used in this study was probably minimal. Further, if declines in catch proportions were an artefact of changes in fishing regulations alone, comparable declines would not have been observed across all regions or rivers given the localised nature of the changes (i.e. regulation changes were not consistent within Norway or between Norway and Iceland).

In summary, warming climatic conditions across broad latitudinal gradients in Iceland and northern Norway have already influenced the relative abundance, as inferred from catch proportions, of the three dominant salmonid species. While the overall total numbers of fish caught has remained relatively stable, the proportions of Arctic charr caught in lacustrine and fluvial systems have declined with time, with such trends in anadromous Arctic charr predicted previously in the literature (e.g. Finstad & Hein, 2012; Power et al., 2008). In contrast, proportional catches of Atlantic salmon have remained stable while those of brown trout have risen at the expense of Arctic charr in all study regions. This suggests that, in the future, traditional reliance on anadromous Arctic charr as a valued harvest species may be under

threat (e.g. Reist et al., 2006). It is noted that some of the differences reported could be an artefact of the use of proportional catch data rather than reflective of abundances indices inferred from catch per unit effort data. Nevertheless, the methods applied here have been successfully used by others to infer spatial and temporal trends in catches (Otero et al., 2017) and to quantify environmental and anthropogenic effects on the annual variability in catches (Otero et al., 2011). In the absence of detailed catch per unit effort data, the approach used here provides, at minimum, a consistent perspective across both space and time from which inference of likely changes in the relative abundance of co-occurring salmonids in relation to climatic variability might be mitigated by management action.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Martin-A. Svenning  <https://orcid.org/0000-0002-8276-9686>

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APPENDIX 1

Fixed factors	Estimate	SE	z-value	P
a) Iceland, north				
Intercept (River)	5.038	0.616	8.18	<0.0001
River/Lake	-2.059	1.174	-1.75	0.0794
Annual temperature	-0.807	0.074	-10.87	<0.0001
Random factors	SD			
Year:RiverId	0.97			
RiverId	1.94			
b) Iceland, east				
Intercept (River)	5.368	1.117	4.80	<0.0001
Annual temperature	-0.772	0.159	-4.84	<0.0001
Random factors	SD			
Year:RiverId	0.97			
RiverId	1.94			
c) Iceland, west				
Intercept (River)	2.357	1.024	2.30	0.0214
River/Lake	2.791	2.808	0.99	0.3203
Annual temperature	-0.559	0.112	-5.00	<0.0001
Random factors	SD			
Year:RiverId	1.21			
RiverId	3.76			
d) Iceland, south				
Intercept (River)	2.468	0.852	2.90	0.0038
Annual temperature	-0.780	0.124	-6.29	<0.0001
Random factors	SD			
Year:RiverId	1.04			
RiverId	1.54			
e) Norway, Finnmark				
Intercept (Lake)	2.616	1.242	2.11	0.0351
River	-2.902	1.534	-1.89	0.0585
River/Lake	-2.914	1.674	-1.74	0.0818
Annual temperature	-0.449	0.094	-4.79	<0.0001
Random factors	SD			
Year:RiverId	2.03			
RiverId	4.37			
f) Norway, Troms				
Intercept (Lake)	-0.760	0.705	-1.08	0.2810
River	0.073	0.882	0.08	0.9340
River/Lake	1.090	1.300	0.84	0.4020
Annual temperature	-0.652	0.083	-7.82	<0.0001
Random factors	SD			
Year:RiverId	1.58			
RiverId	2.96			
g) Norway, Nordland				
Intercept (Lake)	-3.210	0.493	-6.51	<0.0001
River	-1.734	0.693	-2.50	0.0123

APPENDIX 1 (Continued)

Fixed factors	Estimate	SE	z-value	P
River/Lake	-1.538	0.898	-1.71	0.0867
Annual temperature	-0.284	0.073	-3.89	0.0001
Random factors	SD			
Year:RiverId	1.52			
RiverId	2.99			