

# Among-river pattern in relative abundance of two salmonid fishes reflects temperature-dependent competition

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## Abstract

1. Temperature is a key driver in determining species distribution and abundance across climatic and geographical gradients. This occurs through direct physiological effects of temperature on performance, but may also result from temperature effects on species interactions.
2. In the current study we experimentally test for temperature-dependent competition between juvenile anadromous Atlantic salmon and brown trout and evaluate the role of temperature in shaping the relative abundance of these species across 88 Norwegian rivers.
3. When the two species were reared in allopatry their somatic growth rates were similar across a range of temperatures (4–16°C).
4. When reared in sympatry, the growth of salmon was greatly reduced at the coldest temperature relative to when reared in allopatry, whereas this was not the case for trout. The effect of interspecific competition on growth was more similar for the two species at warmer temperatures. Thus, interspecific competition effects were strongly asymmetric only at the lowest temperature, with trout out-competing salmon.
5. The results from the experiment were reflected in qualitative patterns of relative abundance of salmon and trout in natural populations, which shifted from being trout dominated in rivers with low summer temperatures to being salmon dominated in warmer rivers.
6. These results provide an empirical example of how temperature effects on the relative abundance of species can only be understood in light of information about temperature-dependent species interactions.

## KEYWORDS

condition-specific competition, interspecific competition, *Salmo salar*, *Salmo trutta*, species interactions, temperature

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## 1 | INTRODUCTION

Temperature is a key environmental factor affecting virtually all biological levels from enzymatic reactions and physiological processes to global patterns of species distribution and abundance (Angilletta, 2009; Parmesan & Yohe, 2003; Pörtner, 2002). Through thermal scaling of performance traits such as growth and development, temperature strongly affects the ability of species to sustain viable populations across climatic and geographical gradients. However, the mechanisms underlying the relative abundances of species across thermal gradients are not always clear. In addition to direct temperature effects on physiological performance, temperature may also affect the species success during species interactions (Comeault & Matute, 2021; Dell et al., 2014; Dunson & Travis, 1991). The role of temperature in mediating competition and other ecological interactions has recently received increased attention, as it may be important for understanding the ecological impacts of climate change (Åkesson et al., 2021; Davis et al., 1998; Gilman et al., 2010).

While the integrative role of abiotic factors on interspecific interactions have long been recognised (Connell, 1961; Dunson & Travis, 1991), there are still considerable knowledge gaps in the understanding of how temperature and other abiotic factors affect species interactions and shape performance along environmental gradients. Temperature-dependent species interactions are often considered to arise as a response to differences in thermal performance among the species considered, with the advantage shifting in favour of the species whose thermal optima is closest to the experienced temperature (Dell et al., 2014). Such species interactions are most likely to occur near the range borders, and would typically produce more or less predictable patterns in the outcome of competitive contests (Bestion et al., 2018), with cold adapted species being outperformed by warm adapted species at higher temperatures and vice versa. This may often contribute to explain typical patterns in species distribution such as altitudinal zonation gradients (Taniguchi & Nakano, 2000), and northward expansion of species as a response to warming climate (Milazzo et al., 2013). However, some studies suggest that temperature may have effects on relative species abundances even among species that have similar species-specific thermal performance curves. For example, Arctic char (*Salvelinus alpinus*) appear to be competitively superior to brown trout in cold oligotrophic lakes, whereas brown trout dominate in warmer and more eutrophic lakes, even though thermal growth performance of the two species is similar (Finstad et al., 2011). The documentation of such phenomena is pivotal for understanding how temperature and climate may affect species abundances beyond what can be predicted from species-specific thermal scaling of individual performance traits.

Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) are ideal candidates for testing effects of temperature on competitive relationships; their juveniles occupy similar niches that probably make them strong competitors for available resources (Heggenes et al., 1999), their territorial behaviour results in

strong density-dependent mortality during the early juvenile period (Milner et al., 2003), and they co-occur in rivers and streams across large geographical and latitudinal ranges (Jonsson & Jonsson, 2009). In interspecific competition, brown trout is usually considered to be the most aggressive and found to dominate over salmon juveniles of similar size in territorial contests (Harwood et al., 2002; Skoglund et al., 2012; Stradmeyer et al., 2008). Despite this competitive superiority, the relative abundance of the two species varies considerably among rivers (as will be shown here). Existing models of juvenile growth for the two species indicate that Atlantic salmon have a higher optimum temperature for growth than brown trout, whereas brown trout appears to maintain growth at lower temperatures than salmon (Elliott et al., 1995; Elliott & Hurley, 1997; Forseth et al., 2001). However, the growth performance as a response to temperature may vary among seasons and life stages, and no studies have tested growth performance of both species under similar conditions and life stage including the critical early life stages of the species when they compete for limiting resources for growth.

Although valuable insights have emerged from macroecological observations of abundance of species in time series, experimental approaches can yield better insight to the mechanisms that contribute to such ecological observations. In the present study, we first conducted experiments on growth performance of Atlantic salmon and brown trout in allopatry and sympatry across a wide temperature range to test for temperature dependence in the interspecific competition effects. We then tested for a relationship between river-specific temperature regimes during the main growth season (summer) and the relative abundance of the two species in sports fishery catches across 88 Norwegian rivers. We find that although growth of Atlantic salmon and brown trout responds similarly to temperature in the absence of interspecific competition, a strong competitive effect of trout on salmon is observed at the coldest experimental temperature, and this is mirrored by a shift from trout dominance in rivers with low summer temperatures to salmon dominance in warmer rivers. Thus, this study provides an example of how a change in relative abundance of species in response to a climate variable can only be predicted from experimental data that quantify the effect of the variable on the strength of interspecific competition.

## 2 | MATERIALS AND METHODS

### 2.1 | Allopatric and sympatric growth experiment

The thermal growth performance and effects of temperature on competition were tested by performing allopatric and sympatric growth experiments at the NINA Research Station Ims in southwestern Norway (58°54' N, 5°57' E). Eggs from seven hatchery reared full-sib family groups of both Atlantic salmon and brown trout originating from River Figgjo (58°48' N, 5°32' E) were reared in similar conditions in standard hatchery tanks. To synchronise

ontogeny of the two species the brown trout were incubated at lower temperatures than salmon for 8 days during the alevin stage (i.e. prior to start feeding). While different temperatures during incubation have been found to affect growth performance on later life stages (Finstad & Jonsson, 2012), the growth performance of the two species was similar in allopatric treatments (see Section 3) suggesting this brief adjustment of development did not influence later growth performance in the present case. After complete yolk absorption, the fish were transferred to tanks for start feeding with commercial fish food at a temperature of 8°C. After 13 days of start feeding (30 March), 60 fish were transferred to each of 48 tanks (60×60×60 cm), which had a water level of 20 cm and water flow of 1.5 L/min (16 h L:8 h D light regime), and one of three constant temperatures (i.e. 16 tanks each at 4, 10, and 16°C). The temperatures were chosen to cover the majority of the range of average summer temperatures observed in Norwegian rivers that contain both these species (see Section 3). At each temperature, we had five tanks with allopatric brown trout, five tanks with allopatric salmon, and six tanks with salmon and trout in sympatry (i.e., a substitutive design, Fausch, 1998). The fish were fed ad libitum in the tanks with commercial fish food with automatic feeders distributing food at regular intervals. During 22–23 April, all fish were killed with an overdose of anaesthetics (MS 222), weighed (wet mass, ±0.1 mg), and measured (total length, ±1 mm). Thus, the experiment was conducted during days 14–35 following start feeding, which represents an important period in terms of competition-induced mortality in natural populations of these two species (Einum & Nislow, 2005; Elliott, 1989). In the hatchery, water is heated to speed up development during egg incubation, such that the seasonal timing of this developmental stage does not match that typically seen in natural Norwegian rivers where start feeding for these two species generally occurs in May–July (Jensen et al., 1991). Technical problems with the water supply and automatic feeders resulted in elevated mortality and/or abnormal growth patterns in four tanks (one sympatric tank at 10°C, one allopatric tank at 16°C, and two sympatric tanks at 16°C), these tanks were excluded from further analyses.

As the small body size hampers individual marking of juveniles at this life stage, it was not feasible to obtain accurate individual growth rates. Instead, growth rate was calculated using mean body mass at the beginning of the experiment (mean body mass,  $g \pm SD$ ; brown trout:  $0.150 \pm 0.022$ ; Atlantic salmon:  $0.187 \pm 0.031$ , based on sample of  $n=60$  for each species), and mean body size for each tank at the end of the growth experiment. The standardised mass-specific growth rate ( $\Omega$  %, Ostrovsky, 1995) was calculated from:

$$\Omega = \frac{M_t^b - M_0^b}{b \times t} \times 100$$

where  $M_0$  and  $M_t$  is the mean body mass (wet mass g) at the beginning and end of the experimental period  $t$ , respectively, and  $b$  is the allometric mass exponent for the relationship between growth rate and body size (estimated to be 0.31 for both Atlantic salmon

juveniles and brown trout juveniles, Elliott et al., 1995, Elliott & Hurley, 1997).

## 2.2 | Survey of population abundance across temperature regimes in rivers

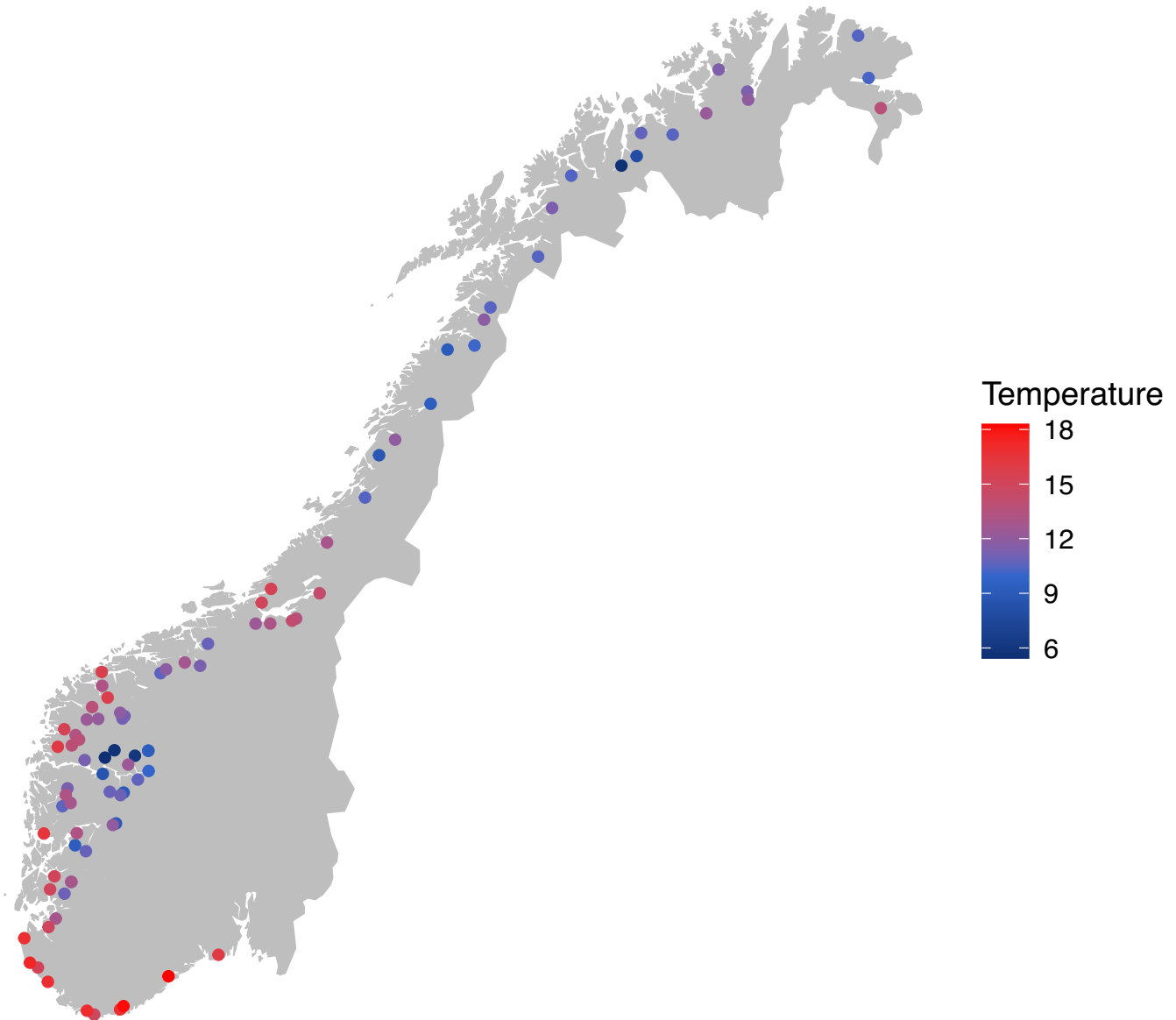
Available data on temperature and population abundance of anadromous Atlantic salmon and brown trout (sea trout) from the period 1980 to 2021 were collected for 88 rivers in Norway, ranging in latitude from 58 to 71°N (Figure 1).

Temperature data series from loggers were provided from the Norwegian water resources and energy directorate, and from collaborating institutions. In rivers where temperature data were available from more than one river section, data from the section inferred to be most important for fish production were used. The average temperature during a 90-day period with highest temperatures (based on mean temperatures across years with available data for each date) was used as a proxy for temperature during the period of the year that are most likely to encompass the most important growth period for juvenile fish in each river (Figure 2).

Official yearly catch statistics time series of number of fish from sport fisheries (both killed and released) of Atlantic salmon and brown trout in rivers in the period 1980–2021 (Statistics Norway, <http://www.ssb.no/>) were used as measures of species-specific population abundances. While the representativity of the two species may be biased in catch statistics due to various river-specific impacts on the fish populations (e.g. river regulation, acidification, hatchery releases, and effects of aquaculture), or fishing regulations over the time period used in this study, it seems unlikely that the magnitude of such bias should depend on temperature, and thus affect the overall conclusion of our study. As the focus of this study is the relative abundance of the two species, the present analyses will be most sensitive to cases when fishing regulations affect one species more than the other. This will be particularly obvious in cases where there has been a fishing moratorium for only one of the species. To limit possible bias due to this reason, data from river-years with missing or zero reported catches for one of the species were removed from the dataset ( $n=681$  of a total of 3,417 river-years from 69 rivers). Data on wetted river area of anadromous river reaches were obtained from the Norwegian Scientific Advisory Committee for Atlantic Salmon (available from Anonymous, 2022).

## 2.3 | Data analyses

All analyses were conducted using the software R (v 4.2.2, R Core Team, 2022). To test for effects of competition on growth at the different temperatures we first calculated the relative growth (mean for tanks) in the sympatric treatment as a proportion of the conspecific mean growth in allopatry at each temperature. Thus, this gives

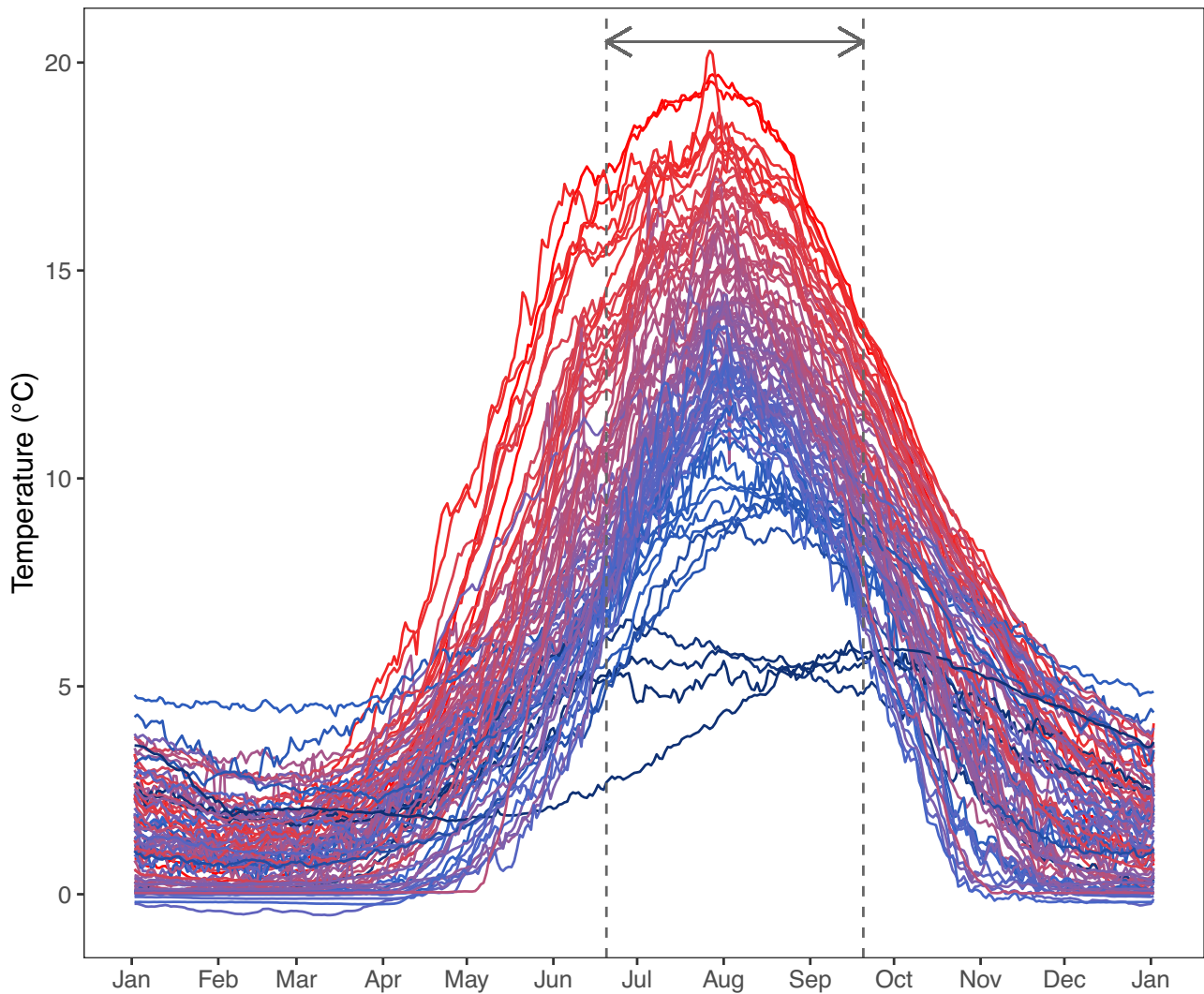


**FIGURE 1** Location of the 88 rivers in Norway with data on temperature and abundance data from catches of both Atlantic salmon and brown trout. The colour displays the average temperature during the summer period.

a measure of how growth responds to interspecific competition. We then fitted a linear model for relative growth as a function of species, temperature, and their interaction. The interaction term in this model represents the temperature-dependent interspecific competition effect on growth. Strength of evidence for temperature-dependent interspecific competition was evaluated by comparing the full model with alternative models without the interaction term, using the corrected Akaike information criterion (AICc).

When analysing abundance of salmon and trout over extended geographical areas, relationships with environmental factors that covary with temperature may arise due to spatial autocorrelation. To account for this, a generalised additive mixed model (GAMM) using the *gamm4* package (Wood & Scheipl, 2020) was fitted to the data using a negative binomial distribution (a Poisson distribution resulted in overdispersion). This model used the number of fish in catches for different river-years as the dependent variable, and included

temperature, species, and their interaction as parametric fixed effects. Latitude and longitude position for the outlet of each river was included as a combined smoother to account for spatial autocorrelation (Pedersen et al., 2019). River and year were specified as random effects, and river area was used as an offset in the model. An offset for river area assumes a proportional relationship between catches and river area, such that deviation from proportionality is included in the random effect of river. This model describes how the number of fish in catches varies across rivers with different temperatures regimes while simultaneously accounting for spatial autocorrelation and river size, and the interaction between species and temperature reveals how this relationship varies for salmon and trout. However, this model does not account for possible spatial autocorrelation in the relative abundance of salmon and trout in different rivers, which is the focus in this study. To test this specifically we fitted a similar GAMM as above, but now with a binomial distribution for the proportion of salmon in the total



**FIGURE 2** Average daily temperatures during the year for 88 Norwegian rivers. The dashed lines and arrow indicate the average start and end of the 90-day period used to calculate mean temperature during the summer, and the colour indicates average summer temperature. Note that the actual time period to calculate average summer temperatures differed among rivers depending on their seasonal dynamics (see text).

catches (i.e. salmon+trout) for each river-year. Temperature was fitted as a parametric fixed effect, latitude and longitude as a combined smoother, and river as a random effect. Model diagnostics using the *testDispersion* function from the *DHARMA* package (Hartig, 2022) suggested that the model was underdispersed (dispersion ratio=0.46), but as underdispersion tends to result in conservative *p*-values the model fit was considered adequate. The prediction from the models were plotted using the *sjPlot* package (Lüdtke, 2022).

### 3 | RESULTS

#### 3.1 | Allopatric and sympatric growth experiments

Growth of Atlantic salmon and brown trout juveniles increased across the three temperature treatments. In allopatry, mean growth was similar for the two species at 10°C, while mean growth of

trout was slightly lower than for salmon at 4°C and higher at 16°C (Figure 3). In sympatry, mean growth was in general lower in both species (except for trout at 4°C, see below).

Comparisons of the linear models for relative growth in sympatry revealed support for the model including the interaction effect between species and temperature (Table 1), demonstrating that the effect of interspecific competition differed across temperatures. The growth of salmon in sympatry with trout was on average 58% relative to growth in allopatry at 4°C, whereas growth of trout in sympatry was slightly higher (102%) than in allopatry (Figure 4, Table 2). At 10 and 16°C, growth of both species was slightly lower than in allopatry (80%–95%) and being poorer for salmon than for trout also at 16°C, but at these temperatures the effect of interspecific competition was more similar for the two species. Thus, interspecific competition effects were strongly asymmetric at the lowest temperature, with trout outcompeting salmon.

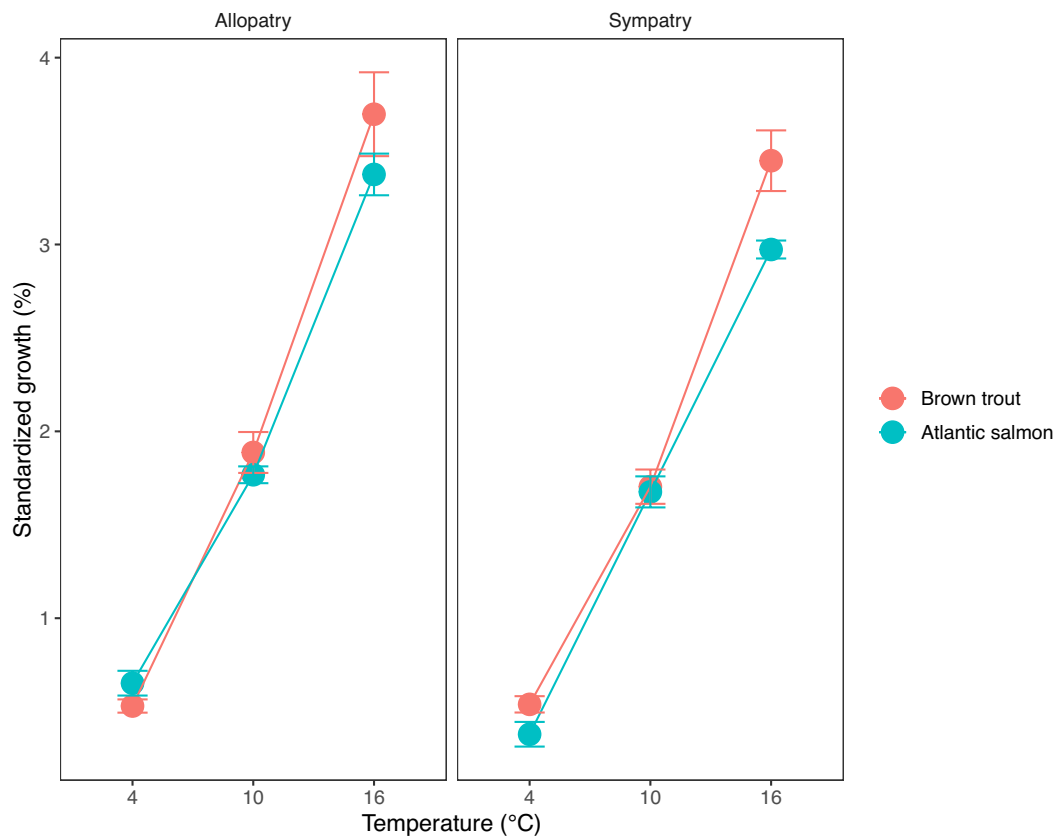


FIGURE 3 Mean standardised growth rates ( $\pm 1$  SE of means from tanks) of brown trout and Atlantic salmon in allopatric and sympatric treatments at the three experimental temperatures.

TABLE 1 Alternative linear models testing the relationship between relative growth rate of Atlantic salmon and brown trout in sympatry at different temperature treatments, sorted by change in corrected Akaike information criterion ( $\Delta$ AICc).

Model	Fixed effects	Df	AICc	$\Delta$ AICc
1	Temperature $\times$ Species	7	-11.7	0.0
2	Species	3	-8.7	3.0
3	Temperature + Species	5	-5.8	6.0
4	Temperature	4	-0.9	10.8

### 3.2 | Abundance across temperature regimes in rivers

The average temperature during the 90-day period with highest temperatures ranged between 5.5 and 18.2°C for the different rivers (mean  $\pm$  SD: 12.2  $\pm$  2.8). The generalised additive mixed model for river catches of salmon and trout in 88 rivers across 41 years, and encompassing 2,736 river-years, revealed that the average temperature in the river during the summer period had significantly different effects on catches of salmon and trout (i.e. species  $\times$  temperature interaction term, Table 3). Exclusion of the interaction term resulted in  $\Delta$ AICc > 100 demonstrating strong evidence for the full model including the interaction term. The prediction from the model

revealed that catches of salmon was lower than trout in rivers with average summer temperatures below c. 12°C, but increased and superseded trout catches in rivers with higher temperatures (Figure 5). Catches of trout, by contrast, were somewhat higher at low temperatures and decreased with increasing temperatures, but strength of the temperature effect was weaker than that observed for salmon. Spatial autocorrelation in these data was weak (Figure S1).

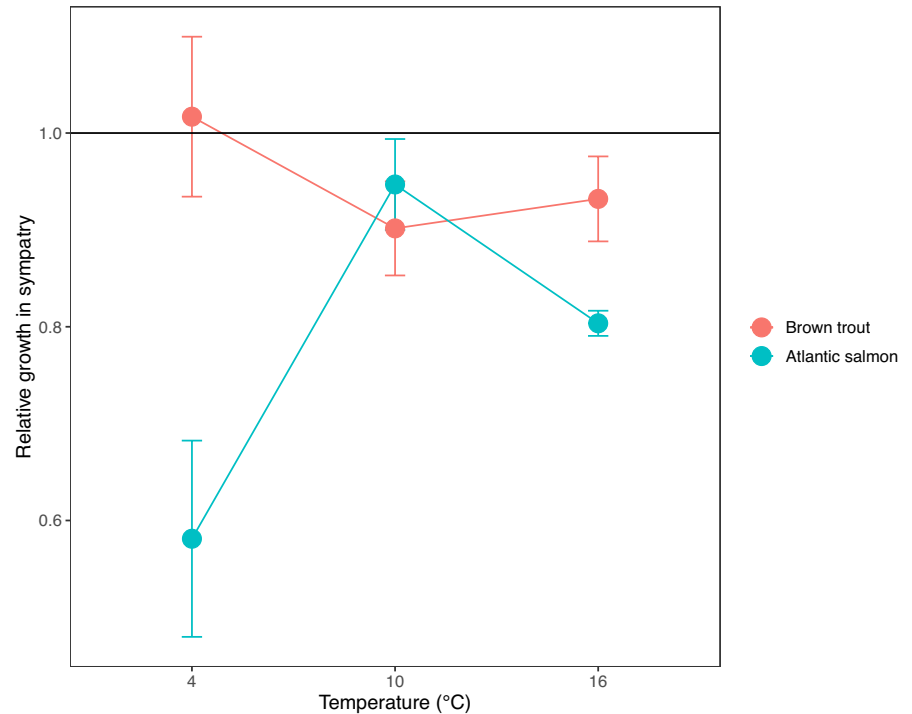
The overall mean proportion of Atlantic salmon in the catches was 0.55 but varied greatly among rivers (range 0.05–0.98, Figure 6). The GAMM revealed that the proportion of salmon in river catches increased with increasing average river-specific summer temperature (Table 4, Figure 6). Model comparison with exclusion of temperature resulted in  $\Delta$ AICc = 12.9, demonstrating strong evidence for the full model including the temperature term. The model also revealed a significant spatial effect on the proportion of salmon in catches, revealing a higher proportion of salmon than expected from the temperature relationship in the northernmost rivers (Table 4, Figure S2).

## 4 | DISCUSSION

Temperature affected the competitive relationship between the closely related and ecologically similar Atlantic salmon and brown trout. Salmon performed relatively poorer than trout when the two



**FIGURE 4** Relative growth (growth/mean growth in allopatry  $\pm 1$  SE of means from tanks) of brown trout and Atlantic salmon in sympatric treatments at the three experimental temperatures. The horizontal line indicates where growth in sympatry is equal to growth in allopatry, and thus intra- and interspecific competition effects are equally strong.



**TABLE 2** Parameter estimates for the linear model best describing the variation in relative growth of Atlantic salmon and brown trout as a response to temperature in sympatric treatments.

Terms	Estimates	SE	t-value	p-value
Intercept [4°C, Trout]	1.02	0.07	<b>1548</b>	<b>&lt;0.001</b>
Species [Salmon]	-0.44	0.09	<b>-4.66</b>	<b>&lt;0.001</b>
Temperature [10°C]	-0.12	0.10	-1.18	0.251
Temperature [16°C]	-0.08	0.10	-0.81	0.425
Temperature [10°C] × Species [Salmon]	0.48	0.14	<b>3.47</b>	<b>0.002</b>
Temperature [16°C] × Species [Salmon]	0.31	0.15	<b>2.08</b>	<b>0.048</b>

Note: Significance differences ( $p < 0.05$ ) are highlighted in bold.

**TABLE 3** Parameter estimates for the negative binomial generalised additive mixed model describing catches of salmon and trout in 88 Norwegian rivers in relation to temperature in the summer period.

Predictors	Incidence rate ratios	Confidence interval	Statistic	p
Intercept [Salmon]	0.00	0.00–0.00	-21.38	<b>&lt;0.001</b>
Species [Trout]	33.47	27.03–41.45	32.19	<b>&lt;0.001</b>
Temperature	1.29	1.19–1.39	6.23	<b>&lt;0.001</b>
Species [Trout] × Temperature	0.74	0.73–0.75	-35.23	<b>&lt;0.001</b>
Smooth term (Lat, Lon)			7.21	0.077

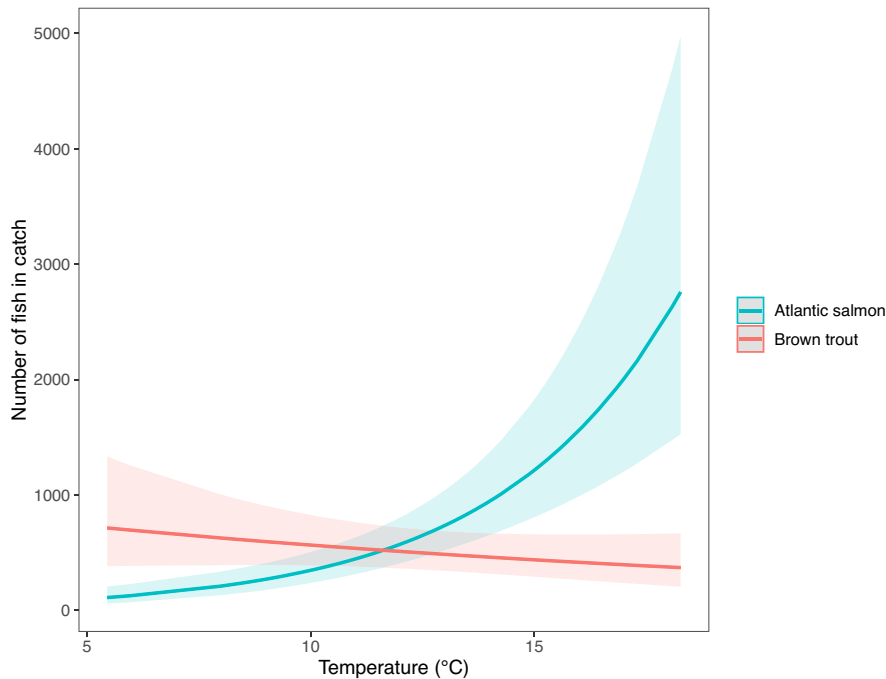
Note: Test statistics are z-values for parametric terms and chi-square values for smooth terms. Significance differences ( $p < 0.05$ ) are highlighted in bold.

species were reared in sympatry at low temperatures under experimental conditions, but less so at the higher temperatures. Thus, the competitive relationship between these two species is shifted in

favour of trout at low temperatures. This pattern was reflected in the macroecological analysis, showing that brown trout is relatively more abundant than Atlantic salmon in rivers that have a low temperature during the main growth season. Importantly, the observed trend of relative abundance of Atlantic salmon and brown trout across temperature regimes could not be explained by differences in physiological thermal growth performance, as the two species were found to have a similar growth response to temperature when reared in allopatry. Thus, the change in relative abundance of species in response to temperature could only be predicted from experimental data that quantified the effect of temperature on the strength of interspecific competition.

Trends in species abundance across thermal gradients are traditionally considered in terms of direct species-specific physiological responses to temperature, but the role of temperature in mediat-

ing species interactions are increasingly recognised in determining species distributions (Gilman et al., 2010). Whereas temperature has been found to affect competitive relationships between species in a



**FIGURE 5** Predictions of the relationship (with 95% confidence interval) between temperature in the summer period and the catches of salmon and trout in 88 rivers in Norway from the generalised additive mixed negative binomial model.

wide range of organisms, such as protists (Jiang & Morin, 2004), phytoplankton (Bestion et al., 2018), insects (Comeault & Matute, 2021), crustaceans (Kordas et al., 2011), and fishes (Milazzo et al., 2013), including salmonid fishes (De Staso III & Rahel, 1994; Taniguchi et al., 1998; Watz et al., 2019), there is still limited knowledge of the ecological mechanisms affecting competitive performance in response to temperature. An implicit assumption in many of the abovementioned studies is that the competitive ability reflects species' differences in thermal reaction norms of fitness related traits such as somatic growth rates (Kordas et al., 2011), with competitive relationships often tested between species with different thermal optima (i.e. warm adapted vs. cold adapted species). In such cases, the shifting competitive ability between species across temperatures typically tend to result in a restriction in realised niches for one or both species and may drive the distribution patterns to shift along altitudinal (Comeault & Matute, 2021; Taniguchi & Nakano, 2000) and latitudinal gradients (Milazzo et al., 2013). However, other traits such as resource acquisition efficiency may also have strong effects on competitive ability, particularly when resources are limited (Tilman et al., 1982). If the ability of a species to use a resource, or monopolise in the case of territorial species, responds differently to temperature than growth rate observed under ad lib conditions (Thomas et al., 2017), the realised thermal niche under competition may differ from the species fundamental niche (Sunday et al., 2024). In the present study, we found temperature to affect the competitive relationship between two coevolved species that exist sympatrically in rivers across most of their natural anadromous distribution range in Europe, and that have very similar thermal somatic growth performance (Jonsson & Jonsson, 2009). Although neither of the two species appear to exclude the other across the temperature range studied here, there was a clear trend in shifting population abundance across the thermal gradient. The existence of temperature dependence in the outcome of interspecific competition despite

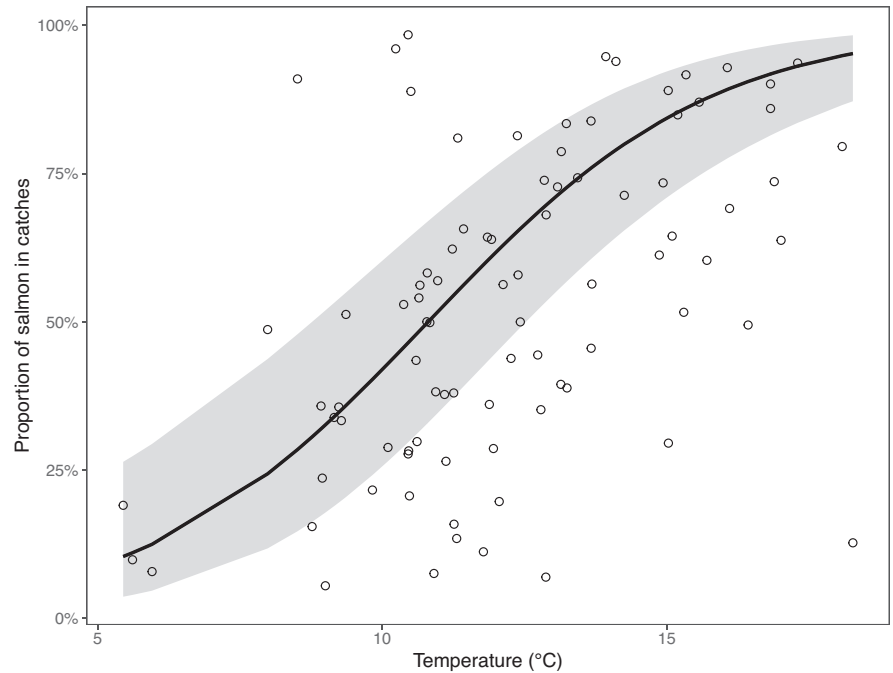
apparent similar thermal performance across temperature gradients is also found in other studies (e.g. Comeault & Matute, 2021; Finstad et al., 2011; Jiang & Morin, 2004). Thus, the current study adds to the growing evidence suggesting that competitive asymmetries across temperature gradients not necessarily reflect species differences in physiological thermal performance curves observed in allopatry.

There are multiple mechanisms by which thermally mediated competition could manifest in the relationship between brown trout and Atlantic salmon. The two species appear to have different strategies with regards to obtaining feeding opportunities under competition, with trout being more aggressive and dominant and are usually found to exclude Atlantic salmon in direct contests for territories (Kalleberg, 1958; Skoglund et al., 2012; Stradmeyer et al., 2008), while Atlantic salmon juveniles appear to be more efficient in intercepting food by adopting a sneaky feeding behaviour in presence of dominant trout (Höjesjö et al., 2005). However, due to slower activity and lower burst swimming capacity (Brett & Glass, 1973), such sneaky behaviour may be more difficult to sustain at cooler temperatures (Metcalf et al., 1997). Moreover, reduced swimming performance at low temperatures may also limit the ability of Atlantic salmon juveniles to take advantage of faster flowing water that are less preferred by brown trout. The two species often occupy different habitats when in sympatry, with salmon with its more streamlined body shape and longer pectoral fins typically predominating in areas with faster water velocities, while trout typically predominate in slower flowing areas near bank margins and in pools (Heggenes et al., 1999). Thus, if the salmon juveniles are forced into more slow-flowing habitat at low temperatures (Vehanen & Huusko, 2002), they are likely to face direct competition with brown trout. More studies are, however, needed to determine the exact mechanisms behind the temperature dependent competition between these two species.

Our experiments demonstrated a competitive advantage for brown trout at the lowest temperature (4°C), while the competition



**FIGURE 6** Relationship between temperature during the summer period and the proportion of Atlantic salmon in catches from 88 Norwegian rivers. The line displays the predicted relationship (with 95% confidence intervals) from the generalised additive mixed binomial model, while the points display the mean proportion of salmon throughout the period for each of the rivers.



**TABLE 4** Parameter estimates for the binomial generalised additive mixed model describing proportion of salmon in sport fisheries catches of 88 Norwegian rivers in relation to temperature in the summer period.

Predictors	Odds ratios	Confidence interval	Statistic	<i>p</i> -value
Intercept	0.01	0.00–0.08	-4.15	<b>&lt;0.001</b>
Temperature	1.49	1.25–1.79	4.42	<b>&lt;0.001</b>
Smooth term (Lat, Lon)			18.64	<b>0.006</b>

Note: Significance differences ( $p < 0.05$ ) are highlighted in bold.

effect at 10 and 16°C was weak or absent. However, in the natural populations, the abundance of Atlantic salmon relative to that of brown trout increased monotonically throughout the complete range of summer temperatures (c. 5–18°C). Thus, it is possible that the temperature effects on competitive relationships established in laboratory settings may manifest differently under more natural conditions. The competitive relationships between species are often context dependent and rely on different environmental conditions that may exacerbate or reduce competition effects in experimental settings (Fausch, 1998), and it is possible that salmon would have displayed a relatively higher competitive ability under other experimental setting (i.e. faster water velocities). Furthermore, while brown trout is the most dominant and often are considered to have a higher competitive impact on salmon than vice versa (Kennedy & Strange, 1986a, 1986b), Hesthagen et al. (2017) found brown trout to decline after recovery of salmon in Norwegian rivers affected by acidification, suggesting that Atlantic salmon also may negatively impact brown trout abundance. However, factors other than competition are also likely to affect the relative abundance of salmon and trout across temperatures. While the

two species show many ecological similarities, they also differ in several respects with regards to life history traits such as timing of spawning, fecundity, and age and size at maturation (Jonsson & Jonsson, 2011), that also may affect their relative productivity across thermal gradients. For example, brown trout typically spawn earlier in the autumn than salmon in rivers where they co-occur (Heggberget et al., 1988), and their juveniles will typically emerge earlier in the spring and obtain a longer growth season during their first year as juveniles. While earlier fry emergence may make the young juveniles more susceptible to unfavourable environmental conditions such as spring floods during the critical early emergence phase (Jensen & Johnsen, 1999; Skoglund et al., 2011), one might speculate that the resulting increase in the duration of the trout's first growth season may be particularly favourable in cold rivers where growth opportunities are restricted. Furthermore, it is also possible that the temperature dependent competitive abilities of the two species differ among populations. Although there still is scant evidence for thermal adaptation in Atlantic salmon (Jonsson et al., 2001) and brown trout (Forseth et al., 2009), significant differences among populations have been found for growth rate (Forseth et al., 2009; Jonsson et al., 2001), suggesting that there also may be differences in underlying factors affecting competitive ability. While we are not able to quantify the relative contribution of competition versus other factors on the abundance patterns of Atlantic salmon and brown trout across temperature gradients, or between populations, it seems reasonable to assume that the pattern in relative abundances is at least partly caused by the observed competitive superiority of trout over salmon at low temperatures.

In the present study we used official fisheries catch statistics from rivers as a measure of population abundance as it provides a standardised, long-term data series that is available for nearly all Norwegian salmon rivers. A limitation with this approach is

that the relative abundance of the two species is evaluated at the adult stage and may thus be affected by local variation in survival during marine feeding migrations. As Atlantic salmon performs extensive ocean migrations it is strongly affected by large-scale oceanographic changes (Vollset et al., 2022), while anadromous brown trout mainly dwell in coastal areas closer to the river of origin and are likely to be more impacted by local environmental effects (Thorstad et al., 2016). Consequently, the catch statistic is likely to introduce spatial trends in the data that may deviate from the freshwater productivity levels. This variation will to some degree be handled by the random effects and spatial structure of our models. Furthermore, we have no reason to believe that these trends will be related to river temperature, and thus affect the overall conclusion of our study.

The ongoing climate change is predicted to have extensive effects on persistence, abundance and distribution of species (Parmesan & Yohe, 2003; Perry et al., 2005; Urban, 2015). Cold-water dwelling freshwater fishes such as salmonids are particularly vulnerable to changing temperature conditions, and declines along the southern latitude ranges are already observed (Donadi et al., 2023; Gallagher et al., 2022). In our data series spanning a 40-year period from 1980 to 2021 the mean river temperature during the summer period has increased by about 1°C (Figure S1). Indirect effects of temperature through altered species interactions are probably a more important driver of climate driven extinctions than direct temperature effects such as physiological temperature limits (Cahill et al., 2013). Our observed pattern of temperature-dependent competition suggests that the relative abundance of salmon is likely to increase to the expense of trout within the geographical range of this study. However, the wide geographical range of coexistence of these two species suggests that salmon is not likely to drive trout extinct by competitive exclusion. For both species, greater impacts are likely to occur due to supra-optimal temperatures causing range loss along the southern distribution boundary, changes in flows due to droughts and floods, and impacts of novel species interactions when species shift their ranges (Alexander et al., 2016; Gilman et al., 2010). The present study suggests that the outcome of species interaction both among present and novel competitors will not necessarily reflect species differences in thermal performance curves obtained under allopatry, but may nevertheless be affected by temperature also for species with closely similar thermal performance curves.

#### AUTHOR CONTRIBUTIONS

Conceptualisation: H.S., S.E., T.F. Developing methods: H.S., S.E., T.F. Conducting the research, data analysis and preparation of figures and tables: H.S. Data interpretation and writing: H.S., S.E., T.F.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

#### DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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