


BRIEF COMMUNICATION

High summer temperatures are associated with poorer performance of underyearling Atlantic salmon (*Salmo salar*) in upland streams

Fionn R. Bernthal¹  | Ben W. Seaman² | Edward Rush² | John D. Armstrong³ | Darryl McLennan¹ | Keith H. Nislow⁴ | Neil B. Metcalfe¹

¹School of Biodiversity, One Health & Veterinary Medicine, University of Glasgow, Glasgow, UK

²Cromarty Firth Fishery Trust, Inverness, UK

³Marine Scotland – Science, Freshwater Fisheries Laboratory, Pitlochry, UK

⁴USDA Forest Service Northern Research Station, Amherst, Massachusetts, USA

Correspondence

Fionn R. Bernthal, School of Biodiversity, One Health & Veterinary Medicine, Graham Kerr Building, University of Glasgow, Glasgow, G12 8QQ, UK.

Email: fbernthal@icloud.com

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Abstract

Future warming scenarios are predicted to result in an increased frequency of high, and potentially stressful, temperatures in aquatic ecosystems. Here we examined whether the performance of wild underyearling Atlantic salmon (*Salmo salar*) in Scottish streams stocked with identical egg densities was influenced by thermal stress. Biomass and density declined with degree hours exceeding 23°C, indicating apparent mortality or emigration as a possible result of exposure to high temperatures. These results strengthen the need for further action such as riparian tree planting to reduce stream summer temperatures.

KEYWORDS

climate change, density, *Salmo salar*, temperature, warming

In aquatic ecosystems, water temperature is one of the most important variables that governs the activity of organisms across multiple levels of biological organization, from cells to populations (Caissie, 2006). As a result of climate change, water temperatures are rising alongside increased precipitation and more variable discharge, and these impacts are expected to be particularly pronounced in northerly latitudes (Schneider *et al.*, 2013). Climate change is thus predicted to disproportionately affect cold-adapted species such as the Atlantic salmon (*Salmo salar*, L. 1758) (Thorstad *et al.*, 2021). The optimal temperatures for growth of juvenile Atlantic salmon are between 16 and 20°C (Jonsson & Jonsson, 2009), whereas temperatures above 23°C are widely recognized to induce heat stress, resulting in the cessation of growth and the initiation of behavioural avoidance strategies (Breau *et al.*, 2011; Lund *et al.*, 2002); the ultimate lethal temperature has been estimated to be between 30 and 33°C (Elliott 1991).

Important Atlantic salmon rivers are already experiencing temperatures that are likely to result in thermal stress to Atlantic salmon (Cunjak *et al.*, 2013) across the species' range: Jackson *et al.* (2021) estimated that in 2018 around 70% of streams in Scotland experienced temperatures stressful to salmon. The impact of high summer temperatures on fish populations is likely to depend on the duration of a hot spell as well as its peak temperature, but there have currently been few attempts to test if this is the case.

Here we test for relationships between the extent of high temperatures and the performance of underyearling Atlantic salmon in neighbouring streams with contrasting temperature regimes. The data for this study were incidentally obtained as part of a set of wider experiments investigating the effects on juvenile Atlantic salmon of manipulating nutrient levels in oligotrophic streams; here we only analyse data from unmanipulated control sites in three adjacent streams

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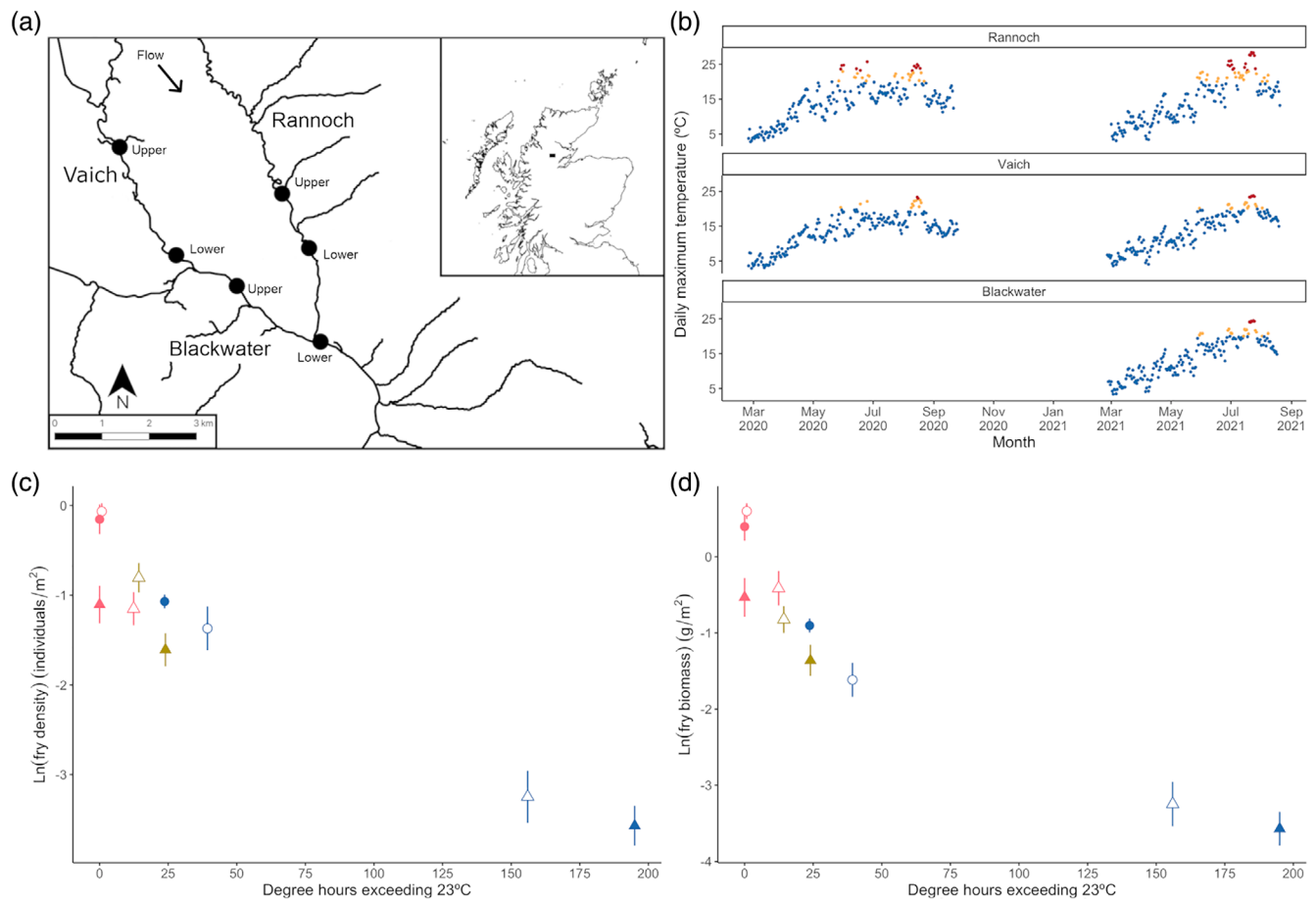


FIGURE 1 (a) Locations of sampling sites (circles) in the river Conon catchment, Northern Scotland. The map depicts the area within the black box in the inset map. (b) Daily maximum temperatures recorded in each stream during the study period (points represent the daily highest temperature for the entire stream, so may be either from the upper or lower sampling sites). Red values indicate temperatures $>23^{\circ}\text{C}$, considered stressful to Atlantic salmon, while yellow values indicate temperatures between 20°C and 23°C , and blue values indicate temperatures $<20^{\circ}\text{C}$. (c) Density and (d) biomass of underyearling Atlantic salmon, *Salmo salar* (both on a natural logarithmic scale, \pm standard error) in relation to duration of peak temperatures (degree hours above 23°C) at sites in the River Conon catchment ($n = 63$ sections sampled across six sites in 2 years, 589 fish). All sites had the same initial density and genetic composition of eggs. Temperature: ● 0–20, ● 20–23, and ● >23 . Year and sampling position: ○ 2020 Downstream, ● 2020 Upstream, △ 2021 Downstream, and ▲ 2021 Upstream. Stream: ● Blackwater, ● Rannoch, and ● Vaich.

that did not receive additional nutrients, allowing the effect of temperature to be investigated independently of any impacts of nutrient supplementation. The streams were two tributaries of the upper reaches of the River Blackwater (Rannoch and Vaich) in northern Scotland, and the section of the Blackwater itself between the junctions of these tributaries (Figure 1a). Owing to the presence of hydro-power dams there is no natural spawning of Atlantic salmon in the Blackwater or its tributaries, but since the 1960s they have been stocked with eggs or first-feeding fry derived from wild parents captured in the same catchment. All three streams contain extensive areas of suitable rearing habitat (in terms of substrate, water depth and flow) for young salmon. The Rannoch runs through moorland and is mostly unshaded, and the Vaich is regulated, being fed from an upstream reservoir, and it is also unshaded and runs through rough grassland. The Blackwater runs through rough grassland and is shaded

in places by riparian trees. The three streams thus have different risks of high summer temperatures despite being at similar elevations and a maximum of only 6 km apart.

Six experimental sites (two per stream, at least 1 km apart) were chosen over the three streams, four of which were used in both 2020 and 2021, with a further two sites (on the Blackwater) added in 2021 (Table S1 in Appendix S1). Each site comprised an approximately 500 m^2 area of suitable habitat. Within each site, 2500 eggs (100 from each of the same 25 families, which differed between years) at the eyed stage of development were planted across three artificial redds. All sites thus started with the same density, number and genetic composition of salmon eggs, despite these being of wild origin. At each site, a temperature logger (-20 to $70 \pm 0.53^{\circ}\text{C}$; HOBO Pendant, Onset Computer Corporation, Bourne, MA, USA) was placed in a plastic lattice box to allow through-flow at the time of egg planting and

TABLE 1 Model coefficients for log density (a) and log biomass (b) with degree hours exceeding 23°C

Predictors	Estimate	s.e.	z value	P
(a) Density model				
Fixed effects				
Intercept	-0.100	0.252	-0.398	0.690
Degree hours >23°C	-0.008	0.001	-5.021	<0.001
Year (2021)	-0.940	0.187	-5.020	<0.001
Stream (Rannoch)	-0.854	0.315	-2.709	<0.01
Stream (Vaich)	-0.019	0.241	-0.082	0.934
Random effects				
	σ^2			
Site	0.000000004904			
Section: site	0.0889310980649			
(b) Biomass model				
Fixed effects				
Intercept	-0.056	0.278	-0.204	0.838
Degree hours >23°C	-0.009	0.001	-4.719	<0.001
Year (2021)	-0.861	0.207	-4.148	<0.001
Stream (Rannoch)	-0.919	0.354	-2.598	<0.01
Stream (Vaich)	0.529	0.269	1.961	<0.05
Random effects				
	σ^2			
Site	0.009			
Section: site	0.071			

Note: The Blackwater river and 2020 are the reference stream and year; bold indicates significance at $P < 0.05$.

Abbreviation: s.e., standard error.

buried in the stream substrate. Loggers were programmed to record water temperatures hourly in 2020 and every 2 h in 2021, and were retrieved at the time of sampling fish by electrofishing in late summer. On three occasions the logger at the site could not be found, and so temperature data from the nearest located logger were used (in each occasion this was for a nutrient addition site, 340–450 m downstream). Temperature profiles confirmed that streams differed in exposure to stressful temperatures (Figure 1b), with the number of degree hours per year exceeding 23°C ranging between 0 and 195 (Table S1 in Appendix S1).

Surviving fry were captured between 21–25 September 2020 and 15–20 August 2021, several weeks after the stream temperatures had last exceeded 23°C, by triple-pass electrofishing (350 V, 60 Hz with a 10% duty cycle; E-fish Ltd, Grange-over-Sands, UK) covering the whole channel width. Each fished area was subdivided using bank-side markers into four to nine sections (dependent on stream width) with a separate tally kept of fish caught per section; surveyed areas contained similar habitats in each stream (see Appendix S1). Fish were lightly anaesthetized (tricaine methanesulfonate, Sigma-Aldrich, Gillingham, UK, 30 mg/l) for measurement of fork length and body mass before being returned to the stream at the site of capture.

All data were analysed using R (v4.2.0). Fish were assigned to the underyearling fry age class based on size frequency distributions within each site. Degree hours exceeding 23°C were quantified for each site by first removing values below 23°C. The remaining values

then had 23°C subtracted, and values were then summed (as Dugdale *et al.*, 2016). Since temperatures were recorded every 2 h in 2021, the values for this year were then multiplied by two (this correction had no effect on the results; see Appendix S1). Calculated degree hours exceeding 23°C for each site were applied to every section within a site. Fish density (individuals/m²) and biomass (g/m²) were calculated by dividing the number or weight of fish caught per section of a site by the section area. The effect of temperature on density and biomass was analysed using separate linear mixed effects models using the package “glmmTMB”. Density and biomass were logged to produce linear relationships after having added 0.02 to each density and biomass value to remove zeroes from the density and biomass data, but this was not applied to the temperature data. Degree hours exceeding 23°C, year and stream were used as fixed effects. Site and section within site were used as random effects to control for the nonindependence of sections within a site. The Blackwater stream was used as the reference level. Moran's I ($P = 0.387$) showed no spatial autocorrelation between sampling sites, and temporal autocorrelation was discounted using visual residual plots and Durbin–Watson tests (for density $P = 0.922$, for biomass $P = 0.926$).

The log density of Atlantic salmon fry differed among streams and was lower in 2021 than 2020, and, after controlling for these effects, was negatively correlated ($P < 0.001$) with degree hours exceeding 23°C (Figure 1c and Table 1a). Similarly, the biomass of

salmon was negatively correlated with degree hours exceeding 23°C independently of the significant differences among streams and years (Figure 1d and Table 1b). These effects were independent of habitat differences among sites (see Appendix S1).

Despite the limitations of this study in addressing areas of variability such as flow regime, potential egg mortality and unknown levels of emigration, the strong negative correlations between related measures of performance or population persistence and temperatures known to induce heat stress suggest that juvenile salmon fry in these northern Scottish streams were experiencing adverse effects of high temperatures. As temperatures in Scottish streams are expected to increase (Hrachowitz *et al.*, 2010), these effects are likely to become more pronounced. Previous work has demonstrated the importance of density, stocking level and discharge on fry production, but showed minimal impacts of temperature (Bal *et al.*, 2011; Glover *et al.*, 2020). In spite of this, the declines in density and biomass seen in the present study may indicate apparent mortality at sites experiencing longer durations of high temperatures. Although factors such as density have been shown to have greater impacts on growth and production than temperature (Bal *et al.*, 2011; Glover *et al.*, 2020), the precise threshold and stress response to high temperature within a population may differ due to natural variability, and thus the impacts of high temperatures may be more pronounced in some populations.

Low densities of juveniles at the warmest sites may be explained by movement of salmon to locate thermal refugia (Dugdale *et al.*, 2016). However, the formation of aggregations of individuals in thermal refugia has been shown to be age-structured, with underyearling fish being much less likely than older cohorts to form such aggregations (Breau *et al.*, 2007). The possibility of juveniles dispersing between sites cannot be discounted, since Atlantic salmon stocked as eggs have been shown to move a mean distance of 403 m both upstream and downstream, with a maximum mean dispersal distance of 1.23 km upstream and 2.14 km downstream (Eisenhauer *et al.*, 2021). In the present study we were unable to separate migration and mortality using the data available, but there was no evidence for sites further downstream having higher densities (Figure 1c), suggesting that any such effect was minimal. The sampling date between years varied, but this was taken into account by including year as a fixed effect in the models used, and the impact of this difference is considered to be negligible.

The adverse effects of temperature on cold-adapted fish show a need for potential mitigation measures. For example, planting riparian vegetation can reduce the impacts of high summer temperatures through increased canopy shading (Imholt *et al.*, 2013), especially in areas of open grassland or moorland (Dugdale *et al.*, 2018; Malcolm *et al.*, 2008), with extensive modelling indicating areas where it may be most effective (Jackson *et al.*, 2018, 2021). Riparian tree planting may help to reduce the effects of high summer temperatures on a species already subject to numerous threats.

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ETHICS STATEMENT

This work was carried out under UK Home Office PPL licences 70/8794 and PP0483054 with approval of the University of Glasgow Animal Welfare & Ethics Review Board.

ORCID

Fionn R. Bernthal  <https://orcid.org/0000-0001-7551-5592>

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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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