

ORIGINAL ARTICLE

Smallmouth bass (*Micropterus dolomieu*) suppress Atlantic salmon (*Salmo salar*) feeding activity and increase aggressive behaviours at warmer temperatures

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Abstract

By 2050, mean temperature in the state of Maine, located in the Northeastern USA, is expected to increase nearly 1°C, which could directly affect native coldwater salmonid behaviour and increase competition with warmwater smallmouth bass. We conducted a microcosm experiment to examine the feeding and agonistic behaviour of endangered juvenile Atlantic Salmon (*Salmo salar*) at two temperatures (18 and 21°C) in the presence and absence of non-native Smallmouth Bass (*Micropterus dolomieu*). By visually reviewing footage of fish competition in our tanks, we quantified feeding and agonistic interactions. We predicted salmon would exhibit lower feeding activity than bass at 21°C and antagonistic interactions between the two species would increase with warming. We found salmon feeding activity was reduced by smallmouth bass presence and this effect was stronger at 21°C. We also found smallmouth bass aggression was strongest at 21°C when salmon were present. Lastly, feeding activity and aggression in both species changed with food availability. These findings illustrate the potential for invasive warmwater species to outcompete native salmonids for resources, especially under the warmer conditions predicted by climate change scenarios.

KEYWORDS

Atlantic salmon, behaviour, competition, feeding, smallmouth bass, temperature

1 | INTRODUCTION

The interactive effects of climate change and competition with non-native organisms threaten native species (Rahel & Olden, 2008). Over the last century, global air temperature has increased approximately 1°C, a warming trend that is expected to continue over the next century (IPCC, 2018). Associated with this warming is an increase in extreme weather events, where heatwaves, flooding and droughts occur more frequently and for prolonged durations than historic norms (IPCC, 2013). Concurrently, non-native species are

increasing within food webs, leading to competition for resources with native species (Carpenter et al., 2011). As a result, freshwaters globally are threatened by climate-driven changes that alter the overall composition and dynamics of freshwater communities (Heino et al., 2009; Perkins et al., 2010; Rahel & Olden, 2008; Woodward et al., 2016).

Environmental temperature affects metabolism, growth and activity of ectotherms (Angilletta et al., 2002). Therefore changes in environmental temperature influences not only an individual's performance and overall fitness (Huey & Kingsolver, 1989), but also

competition outcomes between species that differ in thermal optima and tolerances (Dell et al., 2014; Gilbert et al., 2014, Figure 1a). Temperature-dependent freshwater ectotherms are an ideal model system to test competition between species with differing thermal optima, highlighted by previous work examining temperature-dependent interactions among fishes (Ciepiela et al., 2021; McMahon et al., 2007; Reese & Harvey, 2002; Taniguchi et al., 1998).

Two competing species with similar thermal performance curves (i.e. similar thermal ranges and optimum temperatures) might experience symmetrical, or identical, responses to warming due to climate change. If both species respond similarly to temperature, their interactions may not necessarily change as temperature changes (Figure 1a). However, as seen in freshwater systems, temperature changes have facilitated the spread of invasive, warm-adapted species into previously unsuitable habitat (Bunn & Arthington, 2002; Fausch et al., 2001; Paukert et al., 2016), increasing the potential for interactions between individuals with different thermal physiology. In these cases, an asymmetrical response between two competing species from different thermal guilds may occur, where the warmwater species with a higher temperature tolerance outperforms the coldwater species as temperature increases (Figure 1b). However, empirical evidence for how temperature influences interactions between native coldwater fishes and non-native warmwater fish under

climate-driven warming scenarios is limited. Here, we investigate the temperature dependence of interactions between native Atlantic salmon (*Salmo salar*) and non-native smallmouth bass (*Micropterus dolomieu*) in Maine, USA.

Prior to being listed as a Federally Endangered Species in 2000, Atlantic salmon (ATS) were once abundant in New England's freshwaters. ATS provided sustenance to local populations, supported a commercial fishery in the 1800s, as well as a prominent recreational fishery that saw the largest salmon caught on the opening day of each fishing season being gifted to the President of the United States (Schmitt, 2015). However, multiple anthropogenic stressors, primarily overfishing and habitat degradation from deforestation, damming and pollution, drove ATS declines (Buchsbaum et al., 2005; Saunders et al., 2006; Schmitt, 2015) and now the state of Maine, USA, has the last wild populations of ATS in the United States. ATS spend about 2–3 years as juveniles in Maine streams before smolting, whereby physiological changes prepare them for transition to the marine environment (McCormick et al., 1998).

Despite ongoing conservation and recovery efforts (including dam removals, hatchery programmes and stream habitat restoration), juvenile ATS still face several threats, including warming temperatures and competition with introduced and invasive species, such as SMB (Valois et al., 2009). By 2050, mean air temperatures in

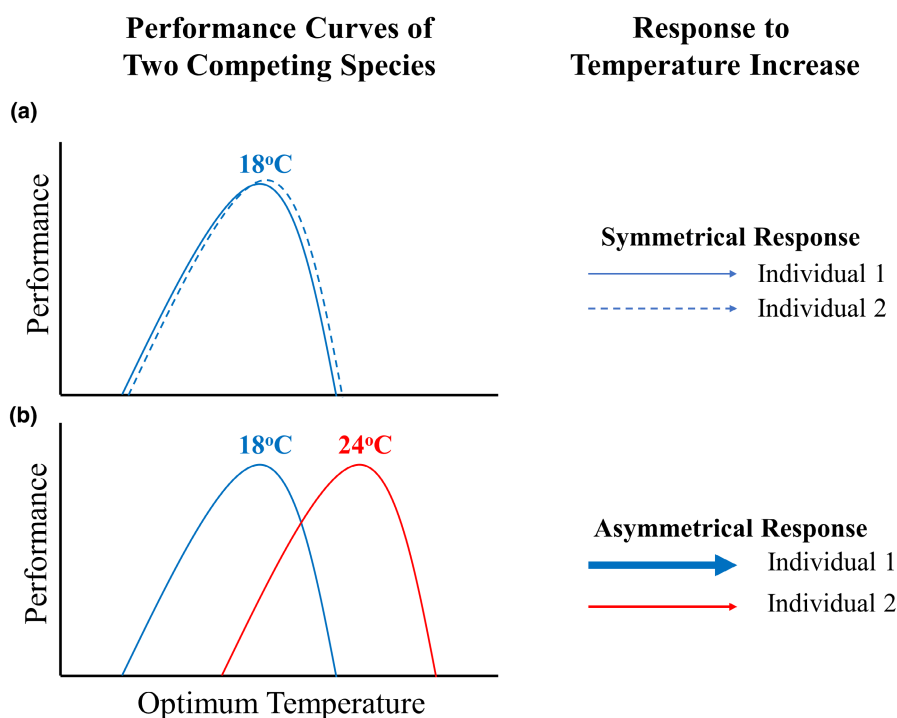


FIGURE 1 Hypothetical performance curves of two interacting species under varying scenarios as temperatures change. (a) demonstrates two interacting species with similar thermal optimums from the same thermal guild before a temperature increase. As temperatures rise these species may experience a symmetrical response to temperature change; indicated by arrows of the same width on the righthand side of the figure. (b) demonstrates two interacting species from different thermal guilds, with different thermal optimums before an increase in temperature. The blue performance curve represents a coldwater species with a thermal optimum of 18°C and the red performance curve indicates a warmwater species with a thermal optimum of 24°C. These species may experience an asymmetrical response as temperatures warm; indicated by arrows with different widths on the righthand side of the figure. Performance curves with varying slopes can also lead to asymmetrical responses of competing species

Maine are expected to increase 1.0–1.7°C and 'hot days' (maximum temperature > 35°C) are expected to triple in occurrence (Fernandez et al., 2015) leading to a predicted increase in stream temperature (Isaak et al., 2012; Swansburg et al., 2002). Warming waters that force fish to perform beyond their thermal optimum often lead to a reduction in feeding and increased metabolic costs. This leads to a reduction in metabolic activity, growth rates, reproduction, and ultimately, fitness (Pörtner & Peck, 2010). Aside from directly affecting the physiology and performance of juvenile ATS, warming waters could both facilitate the range expansion of SMB and alter interactions between ATS and SMB where they already co-occur. SMB are a highly invasive species across North America (Jackson, 2002; MacRae & Jackson, 2001), resulting in detrimental changes such as losses in local biodiversity, shifts in the diet of native species and alterations to existing food web structure (Jackson, 2002; Vander Zanden et al., 1999, 2004). SMB have been present in Maine since they were introduced during the mid-1800s and have since spread prolifically throughout the state (Warner, 2005) with their range predicted to increase due to climate-induced stream temperature warming (Rubenson & Olden, 2020). Understanding the interaction between rising temperatures and increasing ranges of SMB will be crucial to conservation and recovery of ATS.

Our objective was to test how warming influences interactions with an invasive competitor by quantifying the temperature-dependence of feeding behaviour and agonistic interactions between juvenile ATS and SMB in artificial stream channels at 18 and 21°C. ATS are a coldwater fish with a thermal optimum for growth of approximately 18–19°C (Forseth et al., 2001; Murphy, 2004), whereas warmwater SMB have a higher thermal growth optimum of approximately 22–26°C (Horning II & Pearson, 1973; Whitley et al., 2002, 2003). Therefore, we predicted that ATS would feed less at 21°C than at their thermal optimum of 18°C. We also predicted that ATS feeding would be suppressed by the presence of SMB, a known competitive forager (Wuellner et al., 2011) and predicted an interactive effect where the presence of SMB would reduce ATS feeding more at the higher temperature. Aggression in salmonids (Abrams, 2000; Cutts et al., 1998; Keenleyside & Yamamoto, 1962; Nieceza & Metcalfe, 1999; Turnbull et al., 1998) and SMB (Sabo et al., 1996; Wuellner et al., 2011) are both well documented. However, aggression exhibited in SMB juveniles while foraging may provide an advantage when competing with species other than SMB for food (Wuellner et al., 2011). Therefore, we predicted that SMB would exhibit higher levels of intra- and interspecific aggression than ATS in both the 18 and 21°C treatments (Elliott & Elliott, 2010).

2 | METHODS

All experiments took place at the Aquaculture Research Center located at the University of Maine campus (Orono, ME) between 28 August and 20 October 2017. SMB were collected by both backpack

and boat electrofishing in the Kenduskeag and Penobscot Rivers of Maine between June and September 2017 (range of fork length 4.4–7.3 cm, median 6, mean 5.97 ± 0.62 standard deviation (SD)). All SMB were dipped in a 5 ppt saline solution for 2 min before entering the holding tanks to prevent bacterial and/or fungal infections. SMB holding tanks were also treated with preventative measures including continual antifungal treatments (Victorian Green and Kordon® Ridlch Plus Solution) and 600g of salt per 757L of water when needed. Age-0 ATS (East Machias River genetic strain) were hatchery raised and provided by the Downeast Salmon Federation's Aquatic Research Center in East Machias (EM), Maine (range of fork length 4.8–11.9 cm, median 7.1, mean 7.19 ± 1.19 SD). This hatchery relies exclusively on captive broodstock. Age-1 and age-2 parr are collected in the East Machias River and are reared to maturity in freshwater at the US Fish and Wildlife Craig Brook Hatchery (East Orland, Maine). Their progeny are transferred to the East Machias Hatchery and reared to the parr stage as part of a stocked program. Fish used from this source were non selectively taken from a mix of crosses (of approximately 100 families) making direct relationships among fish in a trial unlikely on a given day. This hatchery is fed by water from the adjacent East Machias River and therefore salmon have experienced natural changes in both daily and seasonal temperature, water chemistry and microbial communities. All fish were kept in species-specific holding tanks at a temperature of 18°C for 1 week before use in trials and were machine fed approximately 3 percent body weight in Bio-Oregon pellets and freeze-dried bloodworms (Chironomidae) each day. Fish in holding tanks experienced a 15:9 light/dark (LD) cycle, corresponding to summer months in Maine, with lights on at 0530h and off at 2030h with a 30min sunrise/sunset lamp that gradually lightened and darkened the laboratory.

Experimental arenas consisted of six flow-through stream channels created by placing a standpipe (diameter = 22 cm) in the centre of a cylindrical tank (88 cm diameter × 45.5 cm deep) filled to a depth of approximately 30 cm. Gravel (2 cm diameter) and two half-bricks without masonry holes were provided for substrate and shelter. Flow was generated using a Taam Rio⁺ 1000, Rio®, powerhead pump (1026 L/h) and all velocities were calibrated manually with a flow meter. In all trials, velocity did not exceed 0.07 m/s (mean 0.043 ± 0.003 standard error (SE), range of tank means 0.04–0.06). Water temperature was manipulated using a combination of Fluval 100 watt submersible heaters and adjusting inflow rates of cool ground water (approximately 9–11°C) in each tank. Each tank was also equipped with a digital thermometer and a Hobo Data logger that recorded tank temperature every 5 s for the duration of the trial.

Each trial consisted of 24 fish assigned randomly to a 3 × 2 factorial design with three combinations of fish: four ATS alone, four SMB alone and two ATS with two SMB, crossed by high (range of tank means 20.6–21.2) vs. low (mean $18^\circ\text{C} \pm 0.004$ SE, range of tank means 17.9–18.3) water temperature. As a constraint of manipulating tank temperatures, tanks were designated as low or high

temperature tanks for the duration of all trials. There were six replicate trials; each with the three species combinations at two temperatures. An additional six replicates of the ATS only treatments were conducted due to having more ATS than SMB. All fish were only used once.

Each trial lasted a total of 72 h (see Figure 2 for timeline of specific events). The first 48 h served as an acclimation period during which the water temperature in tanks designated in the high temperature treatment was gradually elevated from 18 to 21°C whereas low temperature tanks remained at 18°C. During the acclimation period, all tanks were covered with screening and only briefly opened when food was manually added to each tank. After 48 h, screening was removed and curtains surrounding the tanks were erected, which minimised potential disturbance from human activity in the room. Fish were fed 1.5 percent of the tank body weight with pre-weighed freeze-dried bloodworms. Food was manually distributed in each tank 4 times per day (0530, 1030, 1530 and 2030 h Eastern Standard Time). All fish were sacrificed at the conclusion of each trial with a lethal dose of buffered MS-222 (250 mg/L in an aerated tank) because they could not be stocked or returned to the hatchery. This work was conducted under the University of Maine Institutional Animal Care and Use Committee (IACUC) protocols.

Fish activity for the final 24 h of the trial was recorded on video cameras fixed ~95 cm above each tank, (Swann Surveillance System; 77-degree field of view). Video files were manually reviewed on a minute-by-minute basis for the 10 min preceding food addition to the tanks (*Pre-Feeding*) and the 10 min following food addition to the tanks (*Post-Feeding*). Thus, we could assess fish behaviour when food was limited and when food was abundant. We recorded feeding behaviour when a fish broke the surface in an attempt to consume the floating food items as well as aggressive behaviours (i.e. chases, charges as described by Keenleyside & Yamamoto, 1962). The top-down perspective of our cameras did permit us to accurately

observe and report nipping behaviour described by Keenleyside and Yamamoto (1962).

2.1 | Data analysis

Mean feeding and aggressive encounters were visually assessed during one-minute intervals to identify overall patterns in feeding activity and aggression by species. Since we were not able to identify specific individuals when recording fish activity, behaviours were averaged across individuals of a given species. Generalised linear models (GLM's) were used to examine the main and interactive effects of temperature (low and high treatments) and competition (presence and absence of each species) on ATS and SMB feeding both pre- and post-feeding. Feeding observations were averaged for both the 10-min pre-feeding period and 10-min post-feeding period and mean per capita feeding observations per species were calculated by dividing total feeding rates by species abundance in each tank. All feeding data were log_e transformed to meet assumptions of normality. Observations of aggression were also grouped for the 10 min pre-feeding and 10 min post-feeding. Aggressions occurred less frequently than feeding, and it was common for no aggressions to be observed in a given species-replicate combination. Thus, we used a zero-inflated Poisson model (Desmarais & Harden, 2013; Lambert, 1992) to examine the main and interactive effects of temperature (low and high treatments) and competition (presence and absence of each species) on ATS and SMB aggression both pre- and post-feeding. Because zero-inflated models require integer data, we calculated an adjusted aggression observation based on number of individuals of each species in each tank by multiplying our aggression observations by the number of fish in each tank and dividing by the abundance of each species:

$$\left[\text{Number of Aggressive Encounters} * \frac{\text{Number of Fish in Each Tank (4)}}{\text{Abundance of Each Species}} \right]$$

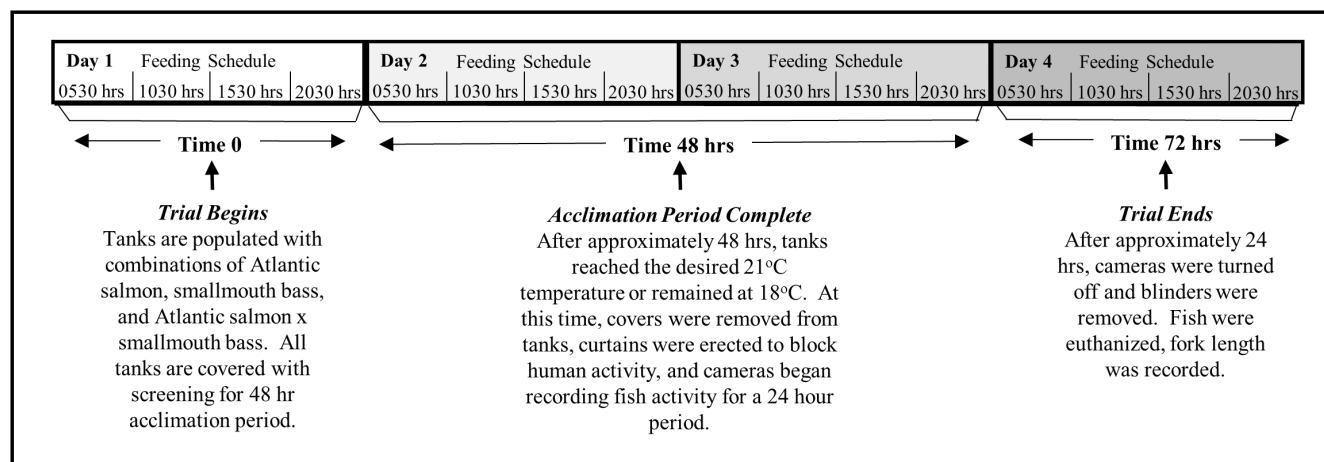


FIGURE 2 Timeline outlining the standard events of a typical trial during the microcosm experiment. Each trial lasts for a total of 72 h, allowing for 48 h of acclimation to the experimental arena and 24 h for recording fish activity. Arrows surrounding the 'Time' increments indicate that a trial can begin at any time on the first day of a trial and subsequent 48 and 72 h intervals will occur with respect to the initial starting time

These methods allowed us to assess per-capita counts of fish behaviours at two temperatures. However, since we did not conduct a density-controlled experiment, we were unable to explicitly separate the effects of interspecific competition from intraspecific density.

3 | RESULTS

3.1 | Feeding behaviour

During the pre-feeding period, observations of feeding level behaviours remained low for both species in both temperature treatments. However, post-feeding, SMB fed more on average than ATS

in both temperature treatments (Figure 3). Prior to feeding, ATS exhibited feeding behaviours less frequently in the higher temperature treatment when SMB were present, but more frequently when bass were absent (Table 1A and Figure 4a), indicating a strong interactive effect of both temperature and competition on ATS feeding behaviour when food is limited (temperature \times competition interaction: $F_{1,32} = 2.14$, $p < .001$). In the post-feeding period, ATS feeding activity was lower when bass were present (competition effect: $F_{1,32} = 3.02$, $p = .09$; Figure 4b) and did not vary with temperature (Table 1B). Conversely, we found that during the pre-feeding period SMB feeding behaviours increased in the presence of ATS (competition effect: $F_{1,20} = 5.43$, $p = .03$; Figure 4c) and this effect was consistent across both temperatures. However, post-feeding SMB feeding rates were consistently

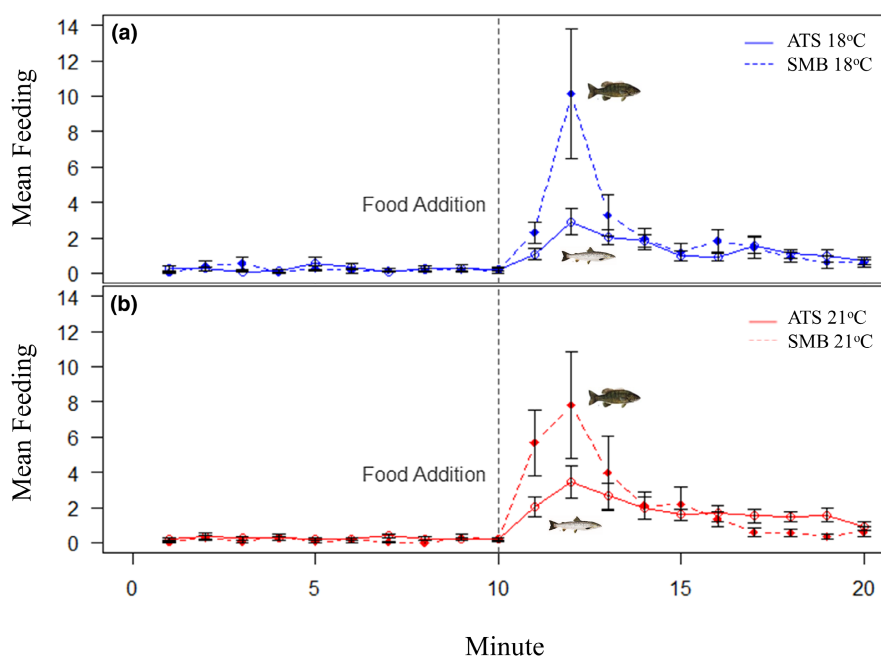


FIGURE 3 Mean feeding per minute for juvenile ATS and SMB over the 10-min period pre- and post-feeding (± 1 SE) for all trials. (a) displays both ATS and SMB feeding in the 18°C treatment. (b) displays salmon and bass feeding in the 21°C treatment

	Timing	Species	Effect	<i>F</i>	Df	<i>p</i>
A.	Pre-feeding	ATS	Comp	2.14	1,32	.15
			Temp	0.03	1,32	.87
			Comp \times Temp	22.5	1,32	<.01
B.	Post-feeding	ATS	Comp	3.02	1,32	.09
			Temp	0.44	1,32	.51
			Comp \times Temp	1.49	1,32	.23
C.	Pre-feeding	SMB	Comp	5.43	1,20	.03
			Temp	0.17	1,20	.68
			Comp \times Temp	0.43	1,20	.52
D.	Post-feeding	SMB	Comp	2.47	1,20	.13
			Temp	0.01	1,20	.91
			Comp \times Temp	0.48	1,20	.5

TABLE 1 Results of generalised linear models (GLM) analysis examining the main and interactive effects of competition and temperature on salmon and bass feeding behaviour before and after food addition to tanks

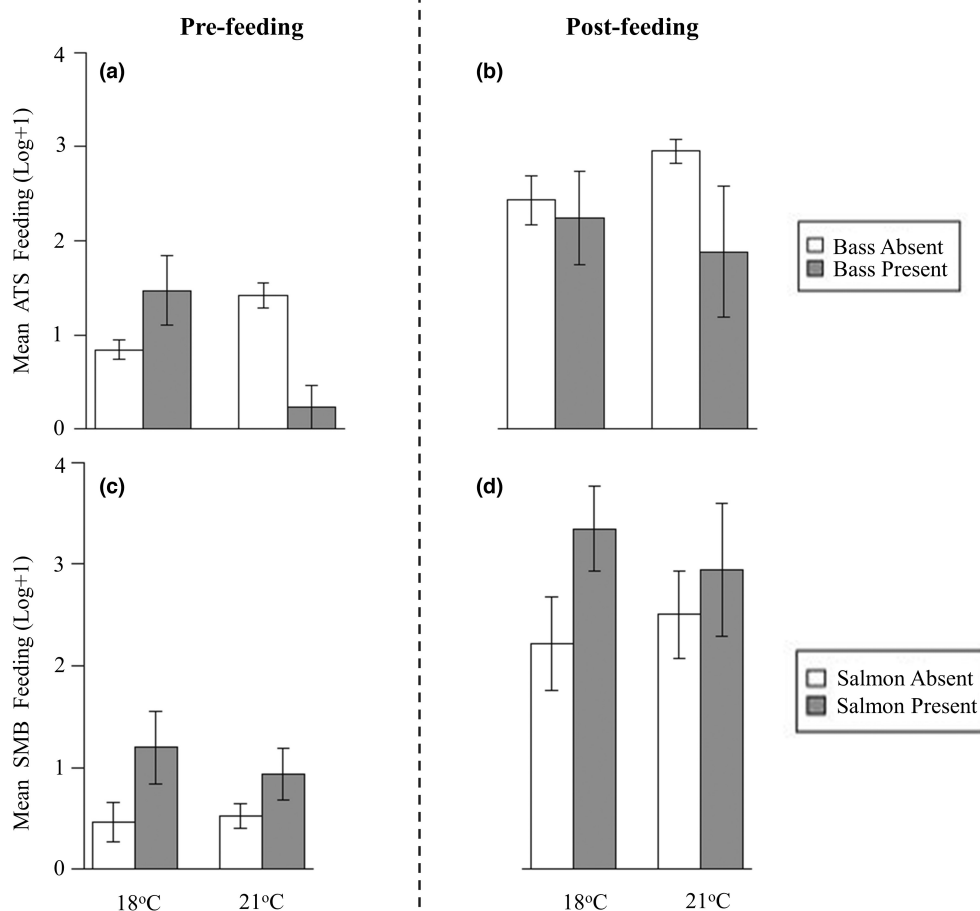


FIGURE 4 Mean feeding ($\pm 1SE$) observations of juvenile ATS (a and b) and SMB (c and d) in the presence and absence of interspecific competitors at 18°C and 21°C prior to (a and c) and after (b and d) food addition

high and did not differ between temperature or competition treatments (Table 1D and Figure 4d).

3.2 | Aggressive behaviour

Overall during the pre-feeding period, ATS showed more aggression compared to SMB in the low temperature treatment. SMB aggression increased immediately after food addition whereas increases in ATS aggression occurred 5 min after food was added to the tank (Figure 5). In the high temperature treatment, SMB had higher levels of aggression compared to ATS in the pre-feeding period. SMB aggression peaked approximately 5 min after food was added to the tanks and ATS aggression increased to levels surpassing that of SMB approximately 8 min after food was added to the tanks (Figure 5). ATS aggression in the 10 min pre-feeding period was reduced when SMB were present (competition effect: $Z = 2.18$, $p = .03$; Figure 6a), but after feeding ATS aggression increased both in the presence of SMB and with temperature (competition effect: $Z = 2.98$, $p = .003$, temperature effect: $Z = -2.13$, $p = .03$; Figure 6b) and these effects were independent (i.e. no significant SMB \times temperature interaction). For SMB we found an effect of competition, where SMB aggression

prior to feeding increased when ATS were present (competition effect: $Z = 4.24$, $p = <.001$; Figure 6c) and we detected a weak interactive effect between competition and temperature (Table 2C), where SMB exhibited less aggression in the higher temperature treatment when ATS were present (Figure 6c). During the post-feeding period we found that aggression in SMB significantly increased when ATS were present and when temperatures were higher (competition effect: $Z = 4.24$, $p = <.001$; Figure 6d). Furthermore, we found interactive effects between competition and temperature, where we observed more SMB aggression when ATS were present at higher temperatures (temperature \times competition interactive effect: $Z = -3.86$, $p = <.001$; Figure 6d).

4 | DISCUSSION

Our research suggests that the combination of increasing temperature and competition from invasive SMB have the potential to affect juvenile ATS behaviours in Maine streams. ATS are a coldwater species with a thermal growth optimum of approximately 18°C (Murphy, 2004) and have a mean upper feeding limit of 22.5°C (Elliott, 1991). Feeding activity in fish typically increases until a

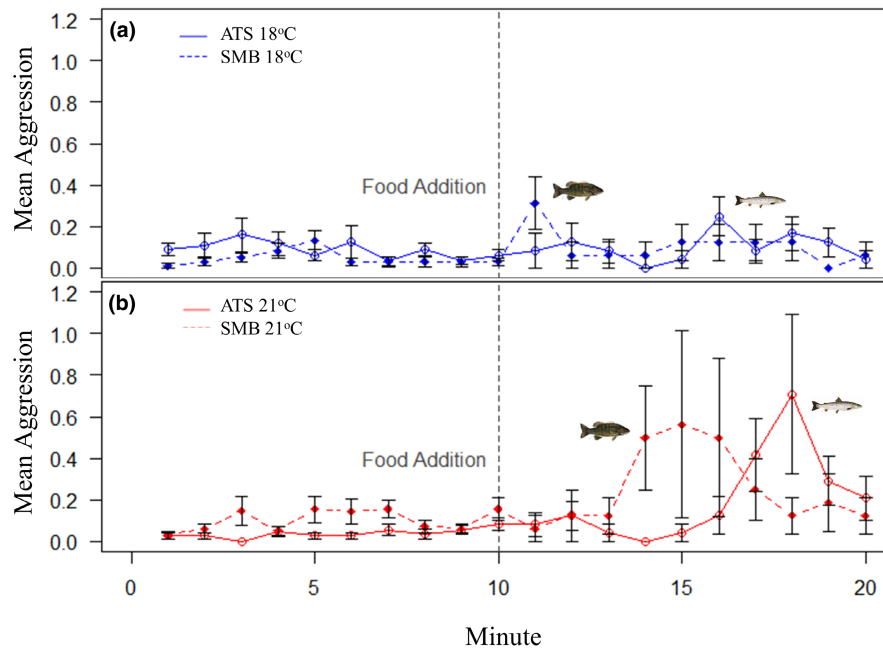


FIGURE 5 Mean aggressive encounters per minute observed for juvenile ATS and SMB over the 10-min period pre- and post-feeding (± 1 SE) for all trials. (a) displays both ATS and SMB aggressive encounters in the 18°C treatment. (b) displays ATS and SMB encounters in the 21°C treatment

thermal optimum is reached, at which point feeding begins to rapidly decline (Brett, 1971; Elliott, 1976). Elliott (1991) found ATS parr had a mean upper feeding limit of 22.5°C, beyond which feeding activity ceased. Interestingly, in our study ATS feeding activity was not suppressed by temperature alone, but instead by the interaction of temperature and competition from SMB when food was scarce prior to feeding (Figure 4a). It is possible that the higher temperatures achieved in our tanks were not thermally stressful for the ATS used in this study, which could be a product of acclimation to temperature fluctuations in the surface water that supplies hatchery tanks during early life stages. Nevertheless, the compounding effects of warmer temperatures and SMB presence indicates the response of ATS to warming is likely contingent on the presence of competitors, especially those with higher thermal tolerance.

Similar to ATS, temperature alone did not influence SMB feeding rates, which is perhaps surprising given that water temperature of 21°C is below the feeding and growth thermal optimum of 22 and 26°C for this species (Horning II & Pearson, 1973; Whitley et al., 2002, 2003). Maximum consumption for sub-adult to adult SMB has been shown to occur at approximately 22°C (Whitley et al., 2003). Studies where juvenile SMB were acclimated to temperatures between 16 and 35°C reported maximal growth occurred at temperatures between 26 and 29°C (Horning II & Pearson, 1973). However, we did find that feeding activity in SMB significantly increased when ATS were present pre-feeding (Figure 4c), although this interaction was not apparent post-feeding. These results parallel the findings of Wuellner et al. (2011), where SMB were quick to feed when in the presence of another species upon food being added into tanks. We also noted that SMB feeding increased immediately

following food addition, at rates much higher than those for ATS. This response to food by SMB could provide a competitive advantage when foraging in the presence of another species such as ATS, potentially resulting in decreases in food intake and growth rates of the competitively inferior species. Moreover, these results further support the conclusion that temperature dependence of foraging behaviours in freshwater fishes is likely contingent on the presence of other species.

In our trials, we found strong effects of temperature and competition on aggressive behaviours in both ATS and SMB. Agonistic interactions among salmonid conspecifics are well documented (Abrams, 2000; Cutts et al., 1998; Keenleyside & Yamamoto, 1962; Nicieza & Metcalfe, 1999; Turnbull et al., 1998) and experiments focused on ATS have observed rates of aggression that increase during periods of feeding (Keenleyside & Yamamoto, 1962; Noble et al., 2007; Slaney & Northcote, 1974; Symons, 1968; Wańkowski & Thorpe, 1979) and with increasing density (Fenderson & Carpenter, 1971; Fenderson et al., 1968). However, temperature-dependent aggressions in salmonids are poorly understood, especially when considering interactions between salmonids and a competitor (Gibson, 2015). Our results indicate temperature and competition modifies aggression, but these outcomes depend on food availability.

Atlantic salmon (ATS) aggression was reduced in the presence of SMB in the pre-feeding period, suggesting a strong effect of competition on aggressive behaviour under food limited conditions (Figure 6a). Gibson (2015) also found that juvenile ATS aggression was suppressed when brown trout, *Salmo trutta* L., were present. Given that SMB are aggressive competitors while foraging, it is not surprising that ATS aggression would be suppressed when competing

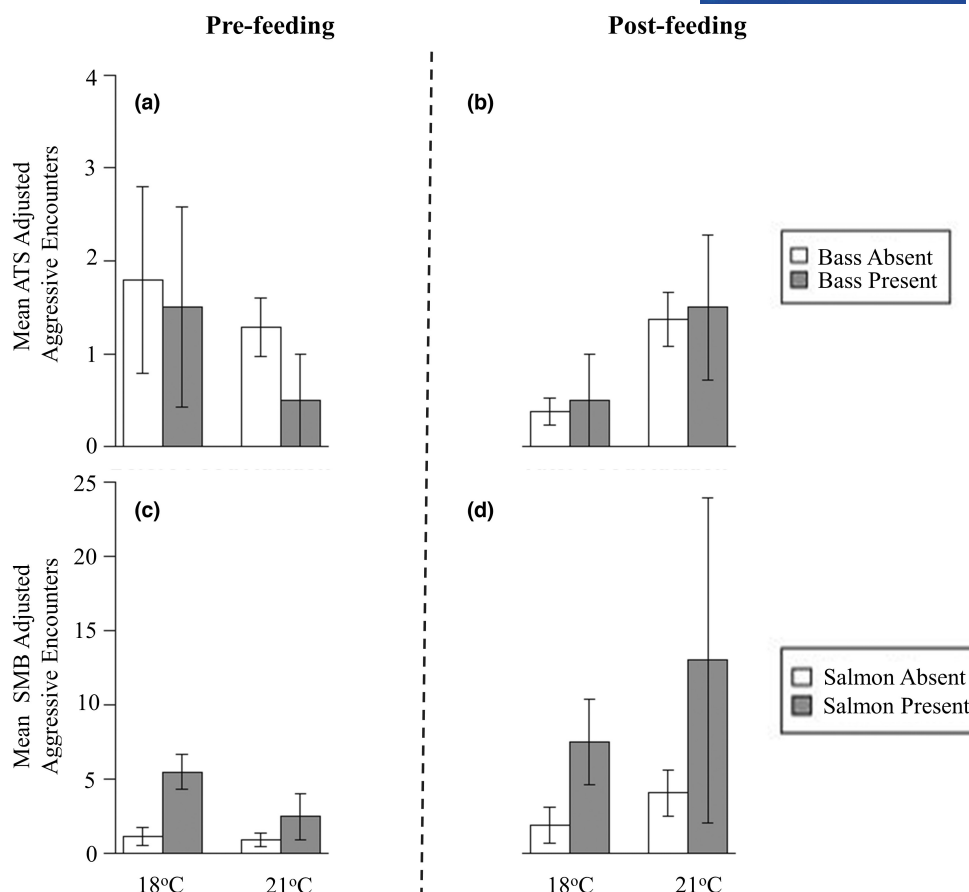


FIGURE 6 Aggressive encounters observed for juvenile ATS (a and b) and SMB (c and d) at 18°C and 21°C both prior to (a and c) and post (c and d) feeding

TABLE 2 Results of zero-inflated Poisson model examining the main and interactive effects of competition and temperature on salmon and bass aggression before and after food addition to tanks

	Timing	Species	Effect	Estimate	Standard error	Z value	p
A.	Pre-feeding	ATS	Comp	1.02	0.47	2.18	.03
			Temp	0.98	0.7	1.4	.16
			Comp × Temp	−0.28	0.55	−0.5	.62
B.	Post-feeding	ATS	Comp	0.9	0.3	2.98	.003
			Temp	−2.11	0.99	−2.13	.03
			Comp × Temp	1.04	0.66	1.6	.11
C.	Pre-feeding	SMB	Comp	1.67	0.39	4.24	<.01
			Temp	1.41	0.93	1.51	.13
			Comp × Temp	−0.86	0.5	−1.71	.09
D.	Post-feeding	SMB	Comp	2.26	0.16	13.76	<.01
			Temp	1.16	0.53	2.2	.03
			Comp × Temp	−1.11	0.29	−3.86	<.01

for limited quantities of ambient food and suspended particles during the pre-feeding period. Indeed, we did find that aggression in SMB increased when ATS were present during the pre-feeding period, especially at low temperatures. Similarly, MacCrimmon and Robbins (1981) reported higher levels of SMB aggression at 10°C compared to elevated temperatures reaching upwards of 30°C,

suggesting elevated temperatures may temper aggression especially when food is unavailable.

Further evidence that food availability alters the effects of temperature and competition on aggression was observed where ATS aggression increased both in the presence of SMB and with increased temperature in the post-feeding period; a pattern opposite to that of

pre-feeding (Figure 6b). Aggression in salmonids occurs most often during periods of feeding (Keenleyside & Yamamoto, 1962; Slaney & Northcote, 1974; Symons, 1968), which is consistent with our observation of higher ATS aggression post-feeding. We also found that SMB aggression post-feeding increased when ATS were present, and this effect was strongest at high temperatures when both species were present (Figure 6b). This temperature dependence of competition on SMB aggression suggests stronger interactions between juvenile ATS and SMB individuals under potential stream temperature warming scenarios stemming from climate change.

Taken together these results suggest that temperature, competition and food availability, play integral roles in shaping the behaviour and performance of juvenile ATS in Maine streams. There are several implications of these results. Most importantly, non-native (invasive) SMB have the potential to outcompete native ATS as Maine's climate changes and stream waters warm. Moreover, these effects may be amplified under food-limited situations, indicating that watershed changes that decrease benthic or terrestrial prey availability for stream fishes likely compound stress associated with water temperature and competition with warmwater fishes. Increasing water temperature, whether rapid or gradually, could force ATS to perform in sub-optimal conditions that impede ATS ability to effectively compete for resources. Warming waters could also further facilitate the range expansion of SMB, a highly invasive species (Jackson, 2002) that has spread prolifically throughout the State of Maine (Warner, 2005).

It is possible that spatial portioning between ATS and non-native species could influence competitive interactions in complex natural streams; however, empirical evidence is limited (Fausch, 1998). Wathen et al. (2012) examined habitat use between ATS and SMB and found that when occupying the same habitat, these species may distribute spatially to prevent high levels of direct competition. Although Wathen et al. (2012) suggests that ATS were inferior competitors, their results offer some potential for these two species to co-exist as juveniles in Maine streams.

Our study is the first to directly test how temperature affects juvenile ATS and SMB interactions where both species are forced to interact with one another. In such situations, our results suggest that SMB presence could significantly affect ATS performance. The information presented here suggests that management decisions for ATS restoration (such as stocking) may be best optimised by considering the presence of SMB and other potential competitors. Nevertheless, in natural streams where interactions occur across a gradient of temperatures and habitat complexity, the results are likely to be more complex, especially if SMB-ATS interactions are mediated by species seeking alternative thermal microhabitats during suboptimal conditions.

Several aspects of the study design need to be considered when interpreting the results. Firstly, we did not control for single species density by including treatments examining behaviour of 2 salmon only and 2 bass only. Thus, the outcome of the interspecific competition effects is potentially influenced by

density-dependent intraspecific competition. Behaviour in fish can be density-dependent, which can influence aggressive interactions among individuals (Ruzzante, 1994) and ultimately affect salmonid growth (Grossman & Simon, 2020). In tanks slightly smaller than ours (0.17 m³), Keenleyside and Yamamoto (1962) found that juvenile salmon aggression increased with density between 2 and 8 individuals, but then decline beyond 14 salmon per tank; where group behaviour was observed and aggression rates were suppressed. Fenderson and Carpenter (1971) also found similar results in similarly sized tanks where salmon aggression increased with a density of up to 8 individuals beyond which aggression plateaued. In comparison, we observed the behaviour of 4 fish in tanks with a volume of approximately 0.26 m³ and therefore our results were unlikely to be obscured by the effects of group behaviour at high densities. Secondly, we observed the behaviours of hatchery ATS competing with wild SMB. Given that ATS are stocked from hatcheries, this resembles the current status of the juvenile ATS population in streams. However, salmon stocked as eggs or fry could acclimate to stream conditions by the parr stage. Hatchery ATS can be more aggressive than wild conspecifics, especially while feeding (Einum & Fleming, 1997; Fenderson et al., 1968) leading to decreased growth rates and reproductive output in wild populations of ATS (Jonsson & Jonsson, 2006). Therefore, given hatchery ATS have the potential to be outcompeted by SMB, then wild ATS could be at a competitive disadvantage as temperatures rise and the potential for competition with SMB increases. Finally, experimental assessment of species interactions can be influenced by the size, structure and heterogeneity of habit patches within the artificial stream channel. For example, the prevalence of deep, slow velocity habitats in our experimental arenas may have favoured SMB and strengthened of competitive interactions with ATS. These caveats should be considered when extrapolating experimental outcomes to streams.

While our results offer new insights regarding temperature-dependent effects of competition on ATS behaviour, the manner in which climate change impacts streams will be much more complex. Changes in temperature often occur simultaneously with changes in stream flow and have the ability to impact multiple species, leading to complex and often uncertain outcomes (Walther, 2010; Woodward et al., 2010, 2016). Conducting future projects over a longer timeframe and including temperature, depth, flow variability and habitat complexity could provide further detail into the consequences of temperature and flow-dependent interactions to both fish behaviour and growth. Overall, the results discussed here pose cause for concern given the threats that juvenile ATS face in Maine streams as an endangered species.

AUTHOR CONTRIBUTIONS

NRP, HG, SC and JZ conceived and designed the experiment and contributed to materials, reagents, and/or analysis tools. NRP, HG and SC performed field and/or laboratory work. NRP, HG, SC and AK analysed the data. NRP, HG, SC, JZ and AK wrote the paper.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Hello, we have a data availability statement in our manuscript. Data are currently held by the authors and are available upon request. Please reach out with any questions.

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