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Responses of Juvenile Atlantic Salmon to Competition and Environmental Change: Implications for Performance in Maine Streams

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RESPONSES OF JUVENILE ATLANTIC SALMON TO COMPETITION AND ENVIRONMENTAL CHANGE: IMPLICATIONS FOR PERFORMANCE IN MAINE STREAMS

By

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A DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of
Doctor of Philosophy
(in Ecology and Environmental Science)

The Graduate School
The University of Maine
August 2020

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By Nicole Ramberg-Pihl

Dissertation Advisor: Dr. Hamish Greig and Dr. Stephen Coghlan

An Abstract of the Dissertation Presented
in Partial Fulfillment of the Requirements for the
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August 2020

New England's climate is changing faster than that of any other region in the continental United States. Over the last century, Maine has experienced an increase in annual temperature of approximately 1.48^{o}C along with a 15 percent increase in annual precipitation. Temperature and precipitation play vital roles in shaping the ecology of freshwater environments. Therefore, changes in regional climate could undermine the structure and stability of Maine's freshwater systems as they currently exist.

Maine currently harbors the last wild populations of Atlantic salmon (*Salmo salar*) in the United States. Atlantic salmon were once abundant in Maine streams, but suffered dramatic declines due to several factors including deforestation, overfishing, and the construction of dams. In 2000, Atlantic salmon were listed as a Federally Endangered species. As juveniles, salmon spend 1 to 3 years in Maine streams before smolting. However, salmon face several threats as juveniles in Maine streams, including changes in climate as well as competition from introduced or invasive species which could outcompete salmon for resources.

This dissertation examines these impacts on juvenile Atlantic salmon (*Salmo salar*) and the stream food webs in which they are embedded by (1.) Using temperature-controlled microcosm experiments to investigate the potential for climate-driven warming to exacerbate the effects of competition between native and invasive species from different thermal guilds. The results suggest that non-native smallmouth bass (*Micropterus dolomeiu*) have the potential to outcompete Atlantic salmon as waters continue to warm. (2.) Running dynamic regression models to analyze the relationship between juvenile Atlantic salmon condition, temperature, and precipitation for 9 streams across 4 drainages over a 16-year period. The results suggest that the impacts of climate change on salmon growth may vary by stream and spatial scale. (3.) Conducting an instream mesocosm experiment to investigate the food-web implications of interactions between omnivorous crayfish and predatory Atlantic Salmon. These results suggest that strong bottom-up processes occur when crayfish are present, whereby increased algal growth could promote the availability of macroinvertebrates important to salmon diet.

DEDICATION

I dedicate this dissertation to my husband and my family, who have always encouraged me to reach for the stars.

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CHAPTER 1

GENERAL INTRODUCTION

Climate Change in Freshwaters and Effects on Biota

With over 100,000 described species (Heino et al. 2009), Earth's freshwater environments demonstrate incredible diversity that promote wonderment in nature and provide important benefits to society (Dudgeon et al. 2006, Heino et al. 2009). However, freshwaters across the globe are threatened by changes in climate that alter the overall composition and dynamics of ecological communities (Rahel and Olden 2008, Heino et al. 2009, Perkins et al. 2010, Woodward et al. 2016). Over the last century, Earth has warmed approximately 1°C, which has been responsible for unprecedented change in our planet's freshwater systems (IPCC 2018). This warming has led to an increase in extreme weather events, where heatwaves along with flooding and drought conditions occur more frequently and for prolonged durations than historic norms. These trends are expected to continue throughout the 21st century and intensify as global temperature continues to rise (IPCC 2013).

On a regional scale, New England's climate is warming faster than any other region in the continental United States (Karmalkar and Bradley 2017). In Maine alone, average annual temperature has increased 1.48°C over the last century, and annual precipitation has increased over 15 percent (Fernandez et al. 2020). By 2050, Fernandez et al (2015) estimates that mean temperature in the state of Maine will increase by 1.1-1.7°C and 'hot days' (when temperatures spike above 35°C) are expected to triple in occurrence; meanwhile rainfall is anticipated to increase another 5-10 percent. While such changes in climate may seem abstract, the effects of changing temperature and precipitation are well documented in New England waters. Later ice-on and earlier ice out dates (Dudley and Hodgkins 2002) as well changes to seasonal variation in stream flow (Hodgkins et al. 2005) have been observed in streams and rivers; which indicate the onset of later winter and earlier spring conditions. Similar trends in ice-on and ice-out dates have also been documented in lakes across New England (Dudley and Hodgkins 2002).

Vulnerability of streams to changes in air temperature and precipitation are due to characteristics of the surrounding physical environment as well as stream morphology (Snelder and Biggs 2002, Allen and Castillo 2007). For instance, topography, tree canopy cover, stream depth, and ground water input produce stream specific responses to changes in climate; resulting in temperature and flow conditions unique to each waterbody (Allen and Castillo 2007). Freshwater organisms are particularly susceptible to climate change because of the dominance of ectothermic species and the fact that their metabolism, growth, and activity is driven by environmental temperature (Angilletta et al. 2002); which ultimately impacts an organism's fitness (Kingsolver and Huey 2008).

Species have minimum and maximum temperature limits, commonly referred to as a thermal range. While metabolic functioning of an organism occurs within these thermal limits, species exhibit an optimum temperature at which their metabolic activity and performance is maximized (Huey and Stevenson 1979, Huey and Kingsolver 1989). In general, cold-adapted species not only exhibit lower thermal optima, but also lower metabolic performance overall compared to warm adapted species (Pörtner et al. 2000, Pörtner 2002). Species also vary in the rate of metabolic response to temperature change within their thermal range (e.g., differ in Q_{10}, Rao and Bullock 1954). Thus overall, temperature is a critical factor controlling the physiology of freshwater organisms.

Energy budgets evaluate the performance and physiology of individuals in relation to their environment according to the amount of net energy gained and lost over time for the whole organism, Equation 1 (Brett and Groves 1979, Pörtner and Peck 2010).

$$Energy\ Consumed\ (C) = Growth\ (G) + Respiration\ \ (R) + Excretion\ (E) + Feces\ Egested\ (F)\ (1)$$

Energy that is not lost via excretion or feces is allocated towards an organism's growth, activity, and metabolism (Warren and Davis 1967). Temperatures that greatly exceed an organism's thermal optimum become problematic because metabolic costs cannot be met by the energetic gains of feeding, resulting in lower net energy gain and reduced fitness (Pörtner and Peck 2010). As temperature changes, consumption rates are affected (Warren and Davis 1967), metabolic rate changes (Clarke and Fraser 2004) as does the amount of energy required for ectothermic species to complete tasks necessary for survival (Spotila and Standora 1985). These include searching for, capturing, consuming, and digesting prey (Ward and Stanford 1982, Anderson et al. 2001, Vucic-Pestic et al. 2011, Dell et al. 2014). These mechanisms mean temperature change can alter outcomes of interactions among species that differ in thermal optima and tolerances (Dell et al. 2014, Gilbert et al. 2014). Since interactions between macroconsumers often drive broadscale multitrophic patterns observed in community composition and basal resources (Carpenter et al. 1985, Rosemond et al. 1998), changes in temperature could have significant consequences on the structure and functioning of food webs (Winder and Schindler 2004, Perkins et al. 2010, Woodward et al. 2016).

While the majority of climate change research has focused on the implications of changing temperature, changes in precipitation that impact the hydrology of freshwater environments can also have severe impacts on freshwater biota. Precipitation regulates hydrological regimes and plays a crucial role in structuring communities (Resh et al. 1988, Poff et al. 1997, Lake 2000, Poff and Zimmerman 2010). Alteration in the timing and magnitude of flooding or drought events is known to alter individual performance, the strength of species interactions, productivity, and diversity in freshwater environments (Townsend and Scarsbrook 1997, Lake 2000, 2003, Poff and Zimmerman 2010, White et al. 2016). Variation in stream flow also acts to facilitate or hinder biological invasions (Moyle and Light 1996, Fausch et al. 2001, Bunn and Arthington 2002). Given that temperature and precipitation play vital roles in shaping the ecology of freshwater systems, abrupt changes in climate with little warning could undermine the structure and stability of Maine's freshwater systems as they currently exist. This thesis examines these impacts by focusing on an iconic species to Maine, Atlantic salmon (*Salmo salar*), and the stream food webs in which they are embedded.

Atlantic Salmon and Threats they Face in Maine

Prior to being listed as a Federally Endangered species, Atlantic salmon were once abundant in New England's freshwaters. Atlantic salmon 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 opening day of each fishing season being gifted to the President of the United States (Schmitt 2015). Now Maine harbors the last wild populations of Atlantic salmon in the United States and their decline was driven by multiple factors including deforestation, overfishing, pollution, and damming (Buchsbaum et al. 2005, Saunders et al. 2006). Juvenile salmon spend about 2-3 years in Maine streams before smolting, where salmon undergo physiological changes that allow them to survive in the marine environment and spend another 1-3 years before returning to freshwater to spawn (McCormick et al. 1998).

Unfortunately, salmon face several threats as juveniles. These include changes in climate as well as competition from introduced and invasive species, such as smallmouth bass (*Micropterus dolomeiu*), which could outcompete salmon for both space and resources (Jonsson and Jonsson 2009, Valois et al. 2009, Hare et al. 2016). Smallmouth bass, were initially introduced into 51 Maine waterbodies as a recreational sport fishery during the period of 1868-1881, but have since spread to hundreds of waterbodies throughout the state (Warner 2005). Across North America, smallmouth bass invasions have demonstrated devastating impacts to fish assemblages in multiple waterbodies (Rahel and Olden 2008). And, with increasing temperatures, suitable habitats for warm-water species, such as smallmouth bass, are increasing while habitat for cold-water species, such as Atlantic salmon, are shrinking (Mohseni et al. 2003).

Atlantic salmon were initially listed as a Federally Endangered species in the year 2000 under the United States of America Endangered Species Act (1973). Since then, salmon recovery action plans, involving both multiple agencies and level of governance have sought to counteract declining Atlantic salmon populations seen in the Gulf of Maine Distinct Population Segment (GOM DPS) (NMFS 2016, U.S. Fish and Wildlife Service and NMFS 2018). These efforts have focused on objectives including removing physical barriers, such as dams, that blocked salmon and other sea run fishes from reaching headwater streams necessary for spawning, replacing traditional culverts with fish-friendly culverts on both public and private properties, and increasing the effectiveness of stocking efforts in Maine streams (U.S. Fish and Wildlife Service and NMFS 2018).

Despite these many efforts, Atlantic salmon are still at risk of extinction. In 2016, Atlantic salmon were included in the National Oceanic and Atmospheric Administration’s (NOAA), ‘Species in the Spotlight’ campaign, which introduced a newly revised 5-year action plan that targeted the most effective strategies moving forward with salmon recovery efforts. These reports highlight the need for continued work in removing barriers from rivers, gaining more insight into Atlantic salmon decline in the marine environment, ensuring Maine’s streams support all life stages, and increasing smolt production in these streams; all in light of a changing climate (NMFS 2016).

The example of continual salmon decline and ongoing recovery efforts, demonstrates the complexity inherent to the salmon situation in Maine, but also highlights both the direct and indirect linkages that exist within the greater coupled human-natural system (Mather et al. 1998). By definition, ecological systems are complex (Bar-Yam 1997); they are comprised of numerous components, as well as multiple levels of hierarchical structure that behave both independently and in concert with one another (Nekola and Brown 2007). Odum (1959) described organization of the biological world as a continuous spectrum ranging from the less complex protoplasm to the inherently more complex biosphere. The study of ecology ranges from the organismal level to that of the biosphere. Each level possesses characteristics unique to only that level and levels are connected to one another in a manner where each level’s existence is dependent upon that of the other levels in the spectrum (Odum 1959).

Factors such as climate change serve as an additional layer of complexity atop the already recognized intricacies of ecological systems. This often leaves ecologists, policymakers, and managers without a clear approach for tackling multifaceted issues surrounding the impacts of climate change on ecological systems (Scheraga and Grambsch 1998, Regier and Meisner 2004). Moreover, multifaceted issues are unlikely to be resolved without collaborative interdisciplinary approaches aimed at informing adaptive management and policy endeavors (Poff et al. 2003, Liu et al. 2007). Fundamental to our attempts at providing solutions, we need to consider the following questions (1.) how does abrupt climate change alter the dynamics of coupled human natural systems? and (2.) how do we inform policy and management to improve environmental security by enhancing resilience and adaptation of coupled human natural systems experiencing abrupt climate change?

Given the ongoing threats Atlantic salmon face in Maine streams, especially concerning climate change and competition from non-native species, I present research that addresses the following questions

(1.) How is the performance of juvenile Atlantic salmon in Maine streams impacted by changes in temperature and competition with non-native smallmouth bass?

Warming waters due to climate change have the ability to directly impact the performance of cold-adapted salmon as well as alter interactions with non-native warmwater competitors such as smallmouth bass. Here I use temperature-controlled microcosm experiments to address a gap in knowledge surrounding the potential for climate-driven warming to exacerbate the effects of competition between native and invasive species from different thermal guilds.

(2.) Is juvenile salmon condition correlated with annual changes in temperature and precipitation at multiple scales over a 16-year period?

Temperature and precipitation play vital roles governing the physiology, performance, and overall condition of Atlantic salmon. While many studies have examined salmon performance in relation to changes in temperature and precipitation, few studies have utilized historical datasets to investigate how salmon condition may be affected by temperature and precipitation across the landscape, especially at multiple scales, as well as through time. Here, I used dynamic regression models to analyze the relationship between juvenile Atlantic salmon condition, temperature, and precipitation for 9 streams across 4 drainages over a 16-year period.

(3.) What is the role of juvenile Atlantic salmon in Maine streams and how does the presence of predatory Atlantic salmon impact invertebrate community structure and basal resources compared to omnivorous crayfish? Within streams, interactions among consumers exert top-down and bottom-up forces in food webs that alter community composition and food-web structure and function. However, little is known about interactions between omnivorous crayfish and predatory Atlantic salmon in Maine streams, how interactions between these two species may impact stream food webs, and the resulting consequences for juvenile Atlantic salmon. Therefore, I used an instream mesocosm experiment to investigate the food-web implications of interactions between omnivorous crayfish and predatory Atlantic salmon.

CHAPTER 2

UNRAVELING THE IMPACTS OF COMPETITION AND WARMING ON JUVELINE ATLANTIC SALMON (*SALMO SALAR*) PERFORMANCE IN MAINE STREAMS

Introduction

The interactive effects of climate warming and competition from non-native organisms threaten native species (Rahel and Olden 2008). Over the last century, temperature has increased approximately 1^{o}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). As a result, freshwaters globally are threatened by climate-driven changes that alter the overall composition and dynamics of freshwater communities (Rahel and Olden 2008, Heino et al. 2009, Perkins et al. 2010, Woodward et al. 2016).

One manner by which freshwater species are impacted by climate change is through thermal impacts on physiological performance that influence the fitness of individuals (Angilletta et al. 2002). The consequences of temperature-dependent interactions are often evident in ectotherms, as their metabolism, growth, and activity are driven by environmental temperature (Angilletta et al. 2002). This also means that environmental temperature influences not only an individual's performance, but also their overall fitness (Huey and Kingsolver 1989). Moreover, temperature change can alter outcomes of interactions among species that differ in thermal optima and tolerances (Dell et al. 2014, Gilbert et al. 2014, Figure 2.1A). However, while we have a firm understanding about the temperature dependence of ectotherms, which comprise the majority of freshwater organisms, our knowledge of how temperature influences interactions among ectotherms is less understood. As temperatures rise, two competing species with similar thermal performance curves (i.e. similar thermal ranges and optimum temperatures) might experience a symmetrical, or identical, response to warming. Given that both species respond similarly, the manner in which these two species interact with one another may not necessarily be impacted (Figure 2.1A).

Climate-induced changes to freshwater systems have also facilitated the spread of invasive, warm adapted species into previously unsuitable habitat (Fausch et al. 2001, Bunn and Arthington 2002, Paukert et al. 2016), increasing the potential for interactions between individuals from thermal guilds that were previously isolated from one another. In contrast to our previous example, we might expect an asymmetrical response between two competing species from different thermal guilds, where ultimately the warmwater species with a higher temperature tolerance outperforms the coldwater species at higher temperatures (Figure 2.1B). This is similar to the situation that juvenile Atlantic Salmon, ATS, (*Salmo salar*) may face in Maine streams, where warming waters have facilitated the spread of Smallmouth Bass, SMB, (*Micropterus dolomieu*) (Rahel and Olden 2008) that likely outcompete juvenile ATS for both space and resources (Valois et al. 2009).

Prior to being listed as a Federally Endangered Species, ATS were once abundant in New England’s freshwaters. 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). Now Maine harbors 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, ATS still face several threats as juveniles, including climate-driven warming that could occur rapidly and unpredictably, along with competition from introduced and invasive species, such as SMB (Valois et al. 2009). By 2050, mean temperatures in Maine are expected to increase 1-1.7^{o}C and 'hot days' (when temperatures spike above 35^{o}C) are expected to triple in occurrence (Fernandez et al. 2015). Aside from directly impacting the physiology and performance of juvenile ATS, warming waters could both facilitate the range expansion of SMB and alter interactions between ATS and SMB that already coexist. SMB are a highly invasive species (Jackson 2002), with invasions documented across North America (MacRae and Jackson 2001), often resulting in detrimental impacts to invaded waterbodies (Zanden et al. 1999, Jackson 2002, Vander Zanden et al. 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).

In order to address the gap in research surrounding the impacts of climate-driven warming and their potential to exacerbate the effects of invasive competitors, we conducted an experiment investigating the temperature-dependence of feeding behavior and agonistic interactions between juvenile ATS and SMB in artificial stream channels at 18^{o}C and 21^{o}C. ATS are a coldwater fish with a thermal optimum for growth of approximately 18-19^{o}C (Forseth et al. 2001, Murphy 2004), whereas warmwater SMB have a higher thermal optimum of approximately 22-26^{o}C (Horning II and Pearson 1973, Whitledge et al. 2002, 2003). Therefore, we predicted that ATS would feed less at 21^{o}C than at their thermal optimum of 18^{o}C. We also predicted that ATS feeding would be suppressed by the presence of SMB a known competitive forager (Wuellner et al. 2011). We also predicted an interactive effect where the presence of SMB would reduce ATS feeding more at higher compared to lower temperatures. Secondly, aggression in salmonids (Keenleyside and Yamamoto 1962, Cutts et al. 1998, Turnbull et al. 1998, Nicieza and Metcalfe 1999, Abrams 2000) and SMB are both well documented. However, aggression in SMB juveniles has been noted from early life stages (Sabo et al. 1996) and may provide an advantage when competing with other species 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^{o}C and 21^{o}C treatments.

Methods

We tested for the temperature-dependence of competition between wild SMB and hatchery-reared ATS juveniles, in a microcosm experiment that investigated how feeding and aggressive behaviors of ATS are impacted by the presence and absence of SMB at two temperatures. All experiments took place at the Aquaculture Research Center located at the University of Maine campus (Orono, ME). Trials occurred 28 August to 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$\underline{+}$0.62 S.D.). All SMB were dipped in a 5ppt saline solution for 2 minutes before entering the holding tanks to prevent bacterial and/or fungal infections. SMB holding tanks were also treated with preventative measures including continual antifungal treatments (Victorian Green and Kordon® RidIch Plus Solution) and 600g of salt per 757 liters of water when needed. Age-0 ATS (F1, East Machias River genetic strain) were hatchery raised and provided by the Aquatic Research Center in East Machias, Maine (range of fork length 4.8 - 11.9 cm, median 7.1, mean 7.19$\underline{+}$ 1.19 S.D.) that is fed by water from the adjacent East Machias River. All fish were kept in species specific holding tanks for one week before use in trials and during this time were provided approximately 3 percent body weight in food each day, fish actively fed on Bio-Oregon pellets and freeze-dried bloodworms (Chironomidae). Fish in holding tanks experienced a 15:9 LD cycle, corresponding to summer months in Maine, with lights on at 0530 hrs and off at 2030 hrs with a 30 min sunrise/sunset lamp that gradually lightened and darkened the laboratory.

The flow-through aquaria simulating stream channels were created by placing a standpipe (diameter = 22 cm) in the center of a cylindrical tank (88 x 45.5 cm) filled with gravel and two half-bricks for shelter. Flow was generated using a Taam Rio$^+$ 1000, Rio©, powerhead pump (1025.85 LPH) and all velocities were calibrated manually with a flow meter. In all trials, velocity did not exceed 0.07 m/s (mean 0.043 $\pm$ 0.003 S.E., 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^{o}C) in each tank.

Each trial consisted of 24 fish assigned randomly to a 3x2 factorial design (three combinations of fish: ATS (n=4), SMB (n=4), and ATS (n=2) x SMB (n=2), and two temperature treatments: low temperature (mean 18^{o}C$\pm$0.004 S.E., range of tank means 17.9-18.3) and high temperature (range of tank means 20.6-21.2) with each of the 6 treatment combinations replicated 6 times by running 6 trials. However, ATS only treatments were replicated 12 times due to having more ATS than SMB. All fish were only used once.

Each trial lasted a total of 72 hours (see Figure 2.2 for timeline of specific events); approximately 48 of these hours were acclimation and also allowed for tanks in the high temperature treatments to reach 21^{o}C. During the acclimation period, all tanks were covered with screening and only briefly opened when food was added to each tank. After 48 hours, screening was removed and curtains surrounding the tanks were erected, which minimized potential disturbance from human activity in the room. Video cameras, Swann Surveillance

System with a field of view of 77 degrees, fixed above each tank recorded fish activity for the final 24 hours of the trial. Fish were fed 1.5 percent of the tank body weight with pre-weighed freeze-dried bloodworms that were manually distributed among tanks 4 times per day (0530 hrs, 1030 hrs, 1530 hrs, and 2030 hrs EST). 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). Fork length measurements of each individual were recorded.

A camera fixed approximately 95 cm above the center of each tank, allowed us to record fish behavior for the duration of each trial. Video files were manually reviewed on a minute by minute basis for the 10 minutes preceding food addition to the tanks (*Pre-Feeding*) and the 10 minutes following food addition to the tanks (*Post-Feeding*). Thus, we could assess fish behavior when food was limited and when food was abundant. We recorded feeding behavior when a fish broke the surface in an attempt to consume the floating food items, as well as aggressive behaviors (i.e. chases, charges as described by Keenleyside and Yamamoto 1962). The top-down perspective of our cameras did not provide the proper vantage point to accurately observe and report nipping behavior described by Keenleyside and Yamamoto (1962).

Data Analysis

Mean feeding and aggressive encounters were visually assessed across one-minute intervals to identify overall patterns in feeding activity and aggression by species. Generalized 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 minute pre-feeding period and 10 minute 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 help meet assumptions of normality. As with our feeding observations, aggression was grouped for the 10 minutes pre-feeding and 10 minutes 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 (Lambert 1992, Desmarais and Harden 2013) 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, in order to account for the number of fish per species in each tank, we calculated an adjusted aggression observation based on number of individuals of each species in each tank. We calculated adjusted aggression by multiplying our aggression observations by the number of fish in each tank and dividing by the abundance of each species $\left[Number\ of\ Aggressive\ Encounters * \frac{Number\ of\ Fish\ in\ Each\ Tank\ (4)}{Abundance\ of\ Each\ Species}\right]$. These methods allowed us to assess per capita fish behavior 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.

Results

Feeding Behavior

Overall, we found that during the pre-feeding period, with only ambient food in the tanks, feeding levels remained low for both species in both temperature treatments. However, post-feeding, SMB fed more on average than ATS in both temperature treatments (Figure 2.3). Pre-feeding, ATS fed less frequently in the higher temperature treatment when SMB were present, but more frequently when bass were absent (Table 2.1A, Figure 2.4A), indicating a strong interactive effect of both temperature and competition on ATS feeding behavior. In the post-feeding period, feeding activity was reduced at high temperatures when bass were present. However, these results indicated only a weak effect of competition when food was abundant (Table 2.1B, Figure 2.4B). Conversely, we found that during the pre-feeding period SMB feeding increased in the presence of ATS (Table 2.1C, Figure 2.4C) and this effect was consistent across both temperatures. However, post-feeding SMB feeding rates were consistently high and did not differ between temperature or competition treatments (Table 2.1 D, Figure 2.4D).

Aggressive Behavior

Overall during the pre-feeding period, ATS showed more aggression compared to SMB in the low temperature treatment, with SMB initially showing increased levels of aggression immediately following food addition to our tanks and ATS aggression only increasing approximately five minutes after food was added to the tank. In the high temperature treatment, SMB showed increased levels of aggression pre-feeding. Post-feeding, SMB aggression peaked approximately five minutes after food was added to the tanks and ATS aggression increased to levels surpassing that of SMB approximately eight minutes after food was added to the tanks (Figure 2.5). ATS aggression in the 10 minute pre-feeding period was reduced when SMB were present (Table 2.2A, Figure 2.6A). Post-feeding, however, we found that ATS aggression increased both in the presence of SMB and with temperature (Table 2.2B, Figure 2.6B), however there was no interactive effect of SMB and temperature. For SMB we found an effect of competition, where SMB aggression increased when ATS were present pre-feeding and we detected a weak interactive effect between competition and temperature, where SMB exhibited less aggression in the higher temperature treatment when ATS were present (Table 2.2C, Figure 2.6C). Post-feeding we found that aggression in SMB significantly increased when ATS were present and when temperatures were higher (Table 2.2D, Figure 2.6D). Furthermore, we found interactive effects between competition and temperature, where we observed more SMB aggression when ATS were present at higher temperatures (Table 2.2D, Figure 2.6D).

Discussion

Our research suggests that increasing temperatures and competition from invasive SMB could negatively impact juvenile ATS performance in Maine streams. As predicted, we found that ATS exhibited less per capita feeding activity in the presence of SMB when temperatures were high, compared to when temperatures were low and SMB were absent (Figure 2.4A). However, this was only observed for the pre-feeding period. In the post-feeding period, we found a marginally significant effect of competition, where ATS fed less per capita when SMB were present (Figure 2.4B).

Interestingly, ATS feeding activity was not reduced by the three degree increase in temperature alone, either pre- or post-feeding. Feeding activity in fish typically increases until a thermal optimum is reached, at which point feeding begins to rapidly decline (Elliott 1976). Optimal temperature for feeding can be a few degrees higher than that for growth (Handeland et al. 2008). ATS are a cold water species with a thermal optimum of approximately 18^{o}C (Murphy 2004). Temperatures exceeding 18^{o}C could become thermally taxing as temperatures surpass that of optimal growth and consumption and approach the upper limits of ATS thermal range, leading to a suppression in feeding behavior. Higher temperatures that exceed an organism’s thermal optimum become problematic because metabolic costs cannot be met by the energetic gains of feeding; resulting in lower net energy gain and reduced fitness (Pörtner and Peck 2010). For example, Elliott (1991) found ATS parr had a mean upper feeding limit of 22.5^{o}C, beyond which feeding activity ceased. Similarly, sockeye salmon *(Oncorynchus nerka*) feeding increased until the optimal temperature of 15^{o}C, and then steadily declined at higher temperatures resulting in decreased growth (Brett 1971).

Comparatively, it was not surprising that SMB feeding appeared to be unaffected by the higher temperatures that individuals were exposed to during our experiment. Water temperature of 21^{o}C is below the thermal optimum of 22^{o}C and 26^{o}C (Horning II and Pearson 1973, Whitledge et al. 2002, 2003). In fact, maximum consumption for sub-adult to adult SMB has been shown to occur at approximately 22^{o}C (Whitledge et al. 2003). And, studies where juvenile SMB were acclimated to temperatures ranging between 16 and 35^{o}C reported maximal growth at temperatures between 26^{o}C and 29^{o}C (Horning II and Pearson 1973). Thus, it is actually surprising that we did not observe less feeding in the low temperature treatment.

We did find, however, that feeding activity in SMB significantly increased when ATS were present pre-feeding (Figure 2.4C); something we did not find 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 to the tanks in magnitudes much higher than that of ATS. It has been suggested that the aggressive nature exhibited by SMB while feeding, could provide a competitive advantage when foraging in the presence of another species (Wuellner et al. 2011).

In our trials, we found strong effects of temperature and competition on aggressive behaviors in both ATS and SMB. Agonistic interactions among salmonid conspecifics are well documented (Keenleyside and Yamasmoto 1962, Cutts et al. 1998, Turnbull 1998, Nicieza and Metcalfe 1999, Abrams 2000) and several studies have examined ATS aggression in relation to feeding (Keenleyside and Yamamoto 1962, Symons 1968, Slaney and Northcote 1974); with many studies reporting aggression to be closely associated with feeding (Wańkowski and Thorpe 1979, Noble et al. 2007) and density (Fenderson and Carpenter 1971). However, temperature-dependent aggression in salmonids is poorly understood, especially when considering interactions between salmonids and a competitor (Gibson 2015).

ATS aggression was reduced in the presence of SMB in the pre-feeding period, suggesting a strong effect of competition on aggressive behavior under food limited conditions (Figure 2.6A). 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 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. We also found that SMB aggression increased at low temperatures when salmon were present. Similarly, previous research by MacCrimmon and Robbins (1981) reported higher levels of SMB aggression at 10^{o}C compared to elevated temperatures reaching upwards of 30^{o}C.

Post-feeding, however, we found the opposite effect of temperature and competition on salmonid aggression, where ATS aggression increased both in the presence of SMB and with increased temperature (Figure 2.6B). Aggression in salmonids occurs most often during periods of feeding (Keenleyside and Yamamoto 1962, Symons 1968, Slaney and Northcote 1974) so it is not surprising that ATS aggression was higher 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 2.6B). This temperature-dependence of competition on SMB aggression suggests stronger interactions between juvenile ATS and SMB individuals as waters warm with climate change.

Taken together these results suggest that temperature, competition, and food availability, play integral roles in shaping the 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 continues to change and waters continue to warm. Rapid changes in temperature, in addition to gradually warming waters could force ATS to perform in sub-optimal conditions that impede their ability to effectively compete for resources. These 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).

Since few studies have examined ATS interactions with non-native species (Fausch 1998), our understanding of how spatial partitioning could influence competitive interactions remains limited. Wathen et al. (2012) examined habitat use between ATS and SMB and found that when occupying the same habitat, these species may partition themselves in a manner that prevents high levels of direct competition. While the results reported by Wathen et al. (2012) suggests that ATS were inferior competitors, it could also offer a level of optimism that these two species may be able to co-exist as juveniles in Maine streams. However, our study is the first of our knowledge to directly test how temperature could impact 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 impact ATS performance. In natural streams where interactions occur across a gradient of temperatures, the results are likely to be more complex. However, since we did not control for density by including treatments examining behavior of 2 salmon only and 2 bass only, we are unable to separate the effects of competition and density in our results. Behavior in fish can be density dependent, which can influence interactions among individuals (Ruzzante 1994) and ultimately affect salmonid growth (Grossman and Simon 2020). In tanks slightly larger than ours with a volume of 1.67cm^3, Keenleyside and Yamamoto (1962) found that juvenile salmon aggression increased with density between 2 and 8 individuals. As density increased above 14 salmon, group behavior was observed and aggression rates were suppressed. In tanks with a volume of 1.93x10^5 cm^3, Fenderson and Carpenter (1971) also found similar results where salmon aggression increased until a density of 8 fish was reached and plateaued through their highest treatment of 16 fish. In comparison, we observed the behavior of 4 fish in tanks with a volume of approximately 1.43x10^5 cm^3 and therefore our results were unlikely to be obscured by the effects of schooling behavior. We also observed the behaviors of hatchery ATS competing with wild SMB. Hatchery ATS can be more aggressive than wild conspecifics, especially while feeding (Einum and Fleming 1997), leading to decreased growth rates and reproductive output in wild populations of ATS (Jonsson and Jonsson 2006). Therefore, if hatchery ATS have the potential to be outcompeted by SMB, as indicated by our results, then wild ATS could face even more dire consequences as temperatures rise and the potential for competition with SMB increases.

While our results offer new insights regarding temperature-dependent effects of competition on ATS behavior, 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 both temperature and flow variability, could provide further detail into the consequences of temperature and flow-dependent interactions to both fish behavior as well as growth. Overall, the results discussed here pose cause for concern given the threats that juvenile ATS face in Maine streams as an endangered species.

Table 2.1 Results of GLM analysis examining the main and interactive effects of competition and temperature on salmon and bass feeding behavior before and after food addition to tanks.

	Timing	**Species**	**Effect**	**F**	**df**	**P**
A.	Pre-feeding	ATS	**Comp**	2.14	1,32	0.15
			Temp	0.03	1,32	0.87
			Comp x Temp	22.5	1,32	<0.001
B.	Post-feeding	ATS	**Comp**	3.02	1,32	0.09
			Temp	0.44	1,32	0.51
			Comp x Temp	1.49	1,32	0.23
C.	Pre-feeding	SMB	**Comp**	5.43	1,20	0.03
			Temp	0.17	1,20	0.68
			Comp x Temp	0.43	1,20	0.52
D.	Post-feeding	SMB	**Comp**	2.47	1,20	0.13
			Temp	0.01	1,20	0.91
			Comp x Temp	0.48	1,20	0.5

Table 2.2 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	0.03
			Temp	0.98	0.7	1.4	0.16
			Comp x Temp	-0.28	0.55	-0.5	0.62
B.	Post-feeding	ATS	**Comp**	0.9	0.3	2.98	0.003
			Temp	-2.11	0.99	-2.13	0.03
			Comp x Temp	1.04	0.66	1.6	0.11
C.	Pre-feeding	SMB	**Comp**	1.67	0.39	4.24	<0.001
			Temp	1.41	0.93	1.51	0.13
			Comp x Temp	-0.86	0.5	-1.71	0.09
D.	Post-feeding	SMB	**Comp**	2.26	0.16	13.76	<0.001
			Temp	1.16	0.53	2.2	0.03
			Comp x Temp	-1.11	0.29	-3.86	<0.001

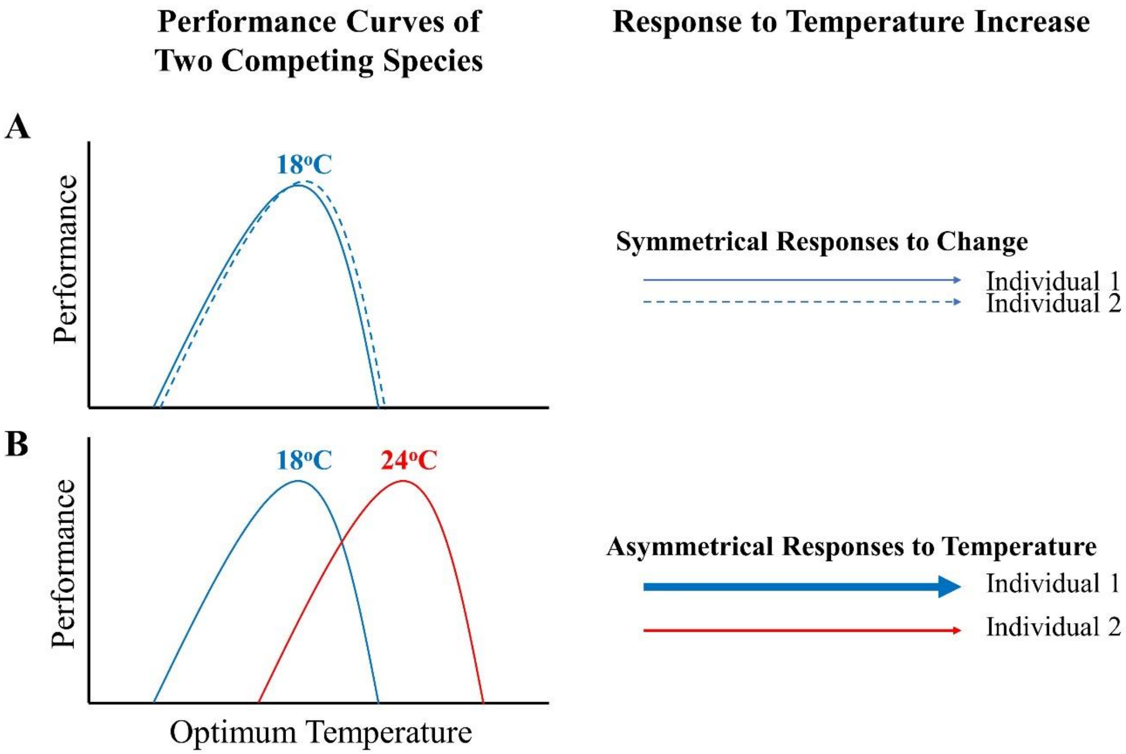
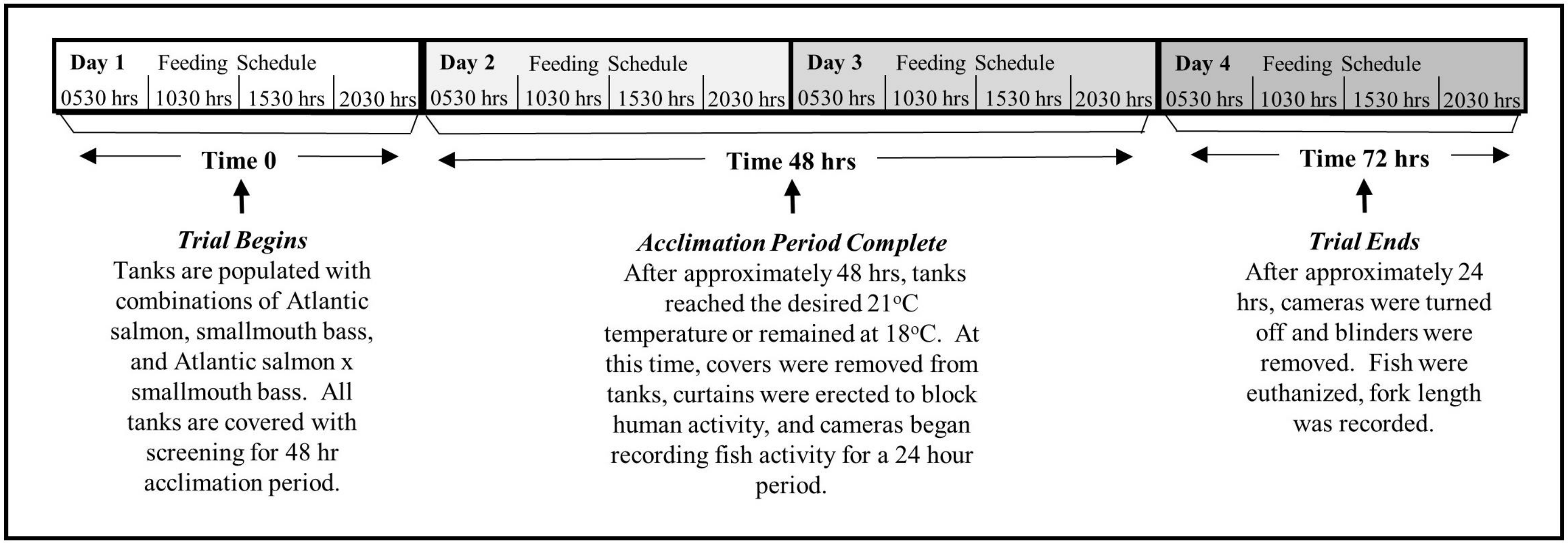


Figure 2.1 Hypothetical performance curves of two interacting species under varying scenarios as temperatures change. *Panel A* demonstrates two interacting species with similar thermal optimums from the same thermal guild before a temperature increase. As temperatures rise these species may experience a symmetrical response to temperature change; indicated by arrows of the same width on the righthand side of the figure. *Panel 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.



Trial Begins

Tanks are populated with combinations of Atlantic salmon, smallmouth bass, and Atlantic salmon x smallmouth bass. All tanks are covered with screening for 48 hr acclimation period.

Acclimation Period Complete

After approximately 48 hrs, tanks reached the desired 21°C temperature or remained at 18°C. At this time, covers were removed from tanks, curtains were erected to block human activity, and cameras began recording fish activity for a 24 hour period.

Trial Ends

After approximately 24 hrs, cameras were turned off and blinders were removed. Fish were euthanized, fork length was recorded.

Figure 2.2 Timeline outlining the standard events of a typical trial during the microcosm experiment. Each trial lasts for a total of 72 hrs, allowing for 48 hrs of acclimation to the experimental arena and 24 hours 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 hr intervals will occur with respect to the initial starting time.

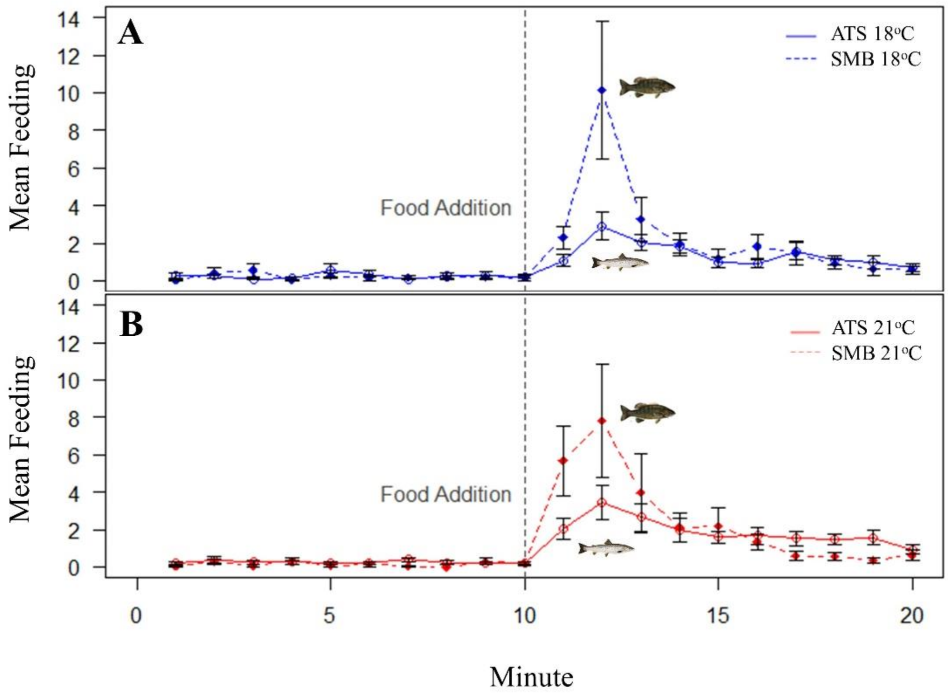


Figure 2.3 Overall mean feeding for juvenile ATS and SMB over the 10 minute period pre- and post-feeding (± 1 Standard Error). *Panel A* displays both ATS and SMB feeding in the 18°C treatment. *Panel B* displays salmon and bass feeding in the 21°C treatment.

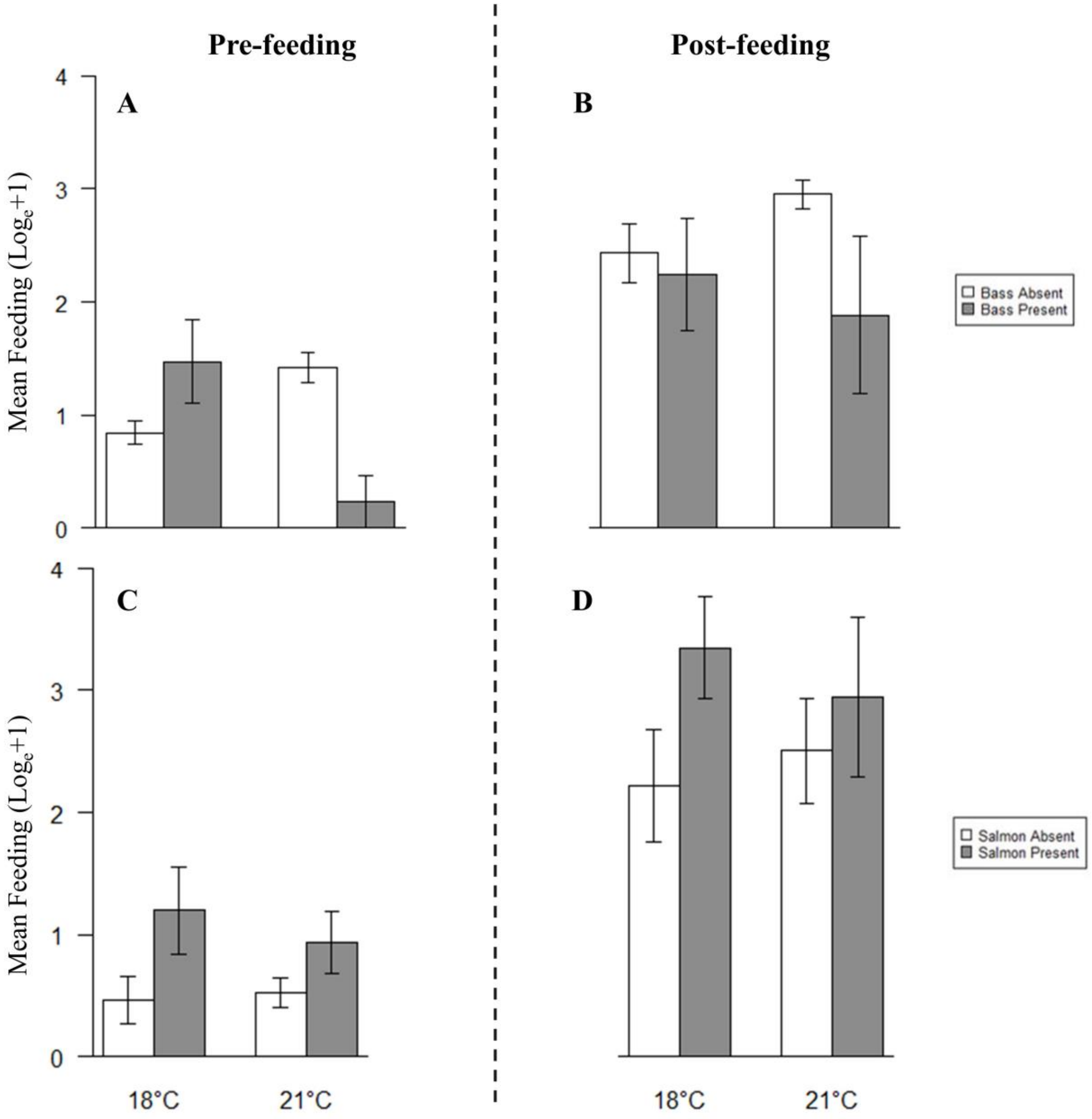


Figure 2.4 Mean feeding (± 1 SE) observations of juvenile ATS and SMB at 18°C and 21°C. *Panel A* Mean ATS feeding during the pre-feeding period in the presence and absence of SMB. *Panel B* Mean ATS feeding during the post-feeding period in the presence and absence of SMB. *Panel C* Mean SMB feeding during the pre-feeding period in the presence and absence of ATS. *Panel D* Mean SMB feeding during the post-feeing period in the presence and absence of ATS.

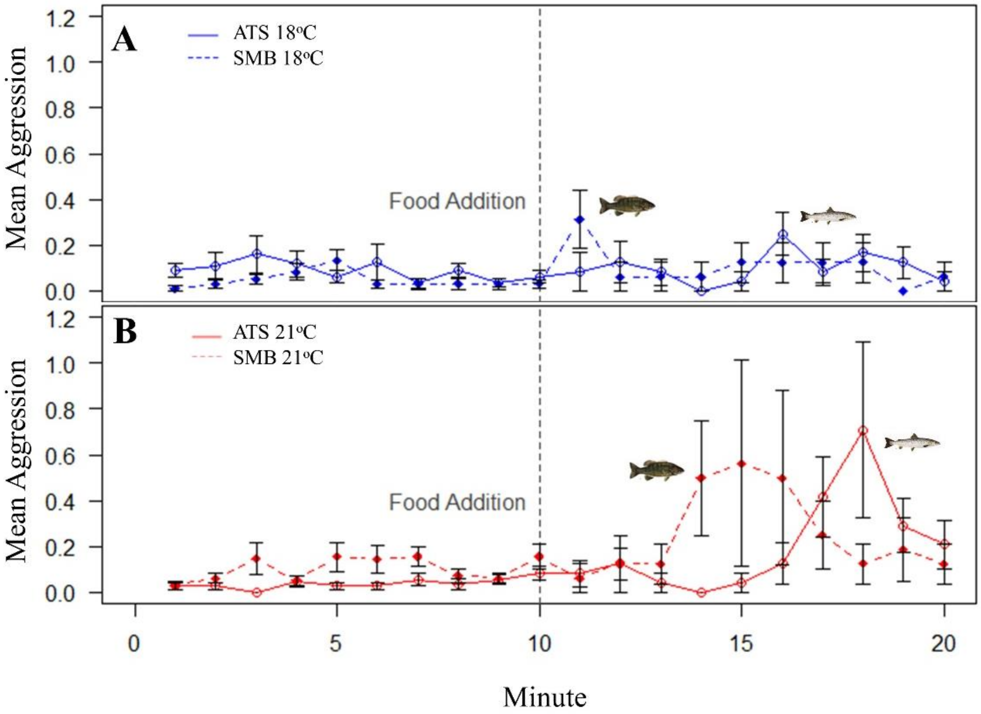


Figure 2.5 Overall mean aggressive enounters observed for juvenile ATS and SMB over the 10 minute period pre- and post-feeding (± 1 Standard Error). *Panel A* displays both ATS and SMB aggressive encounters in the 18ºC treatment. *Panel B* displays ATS and SMB encounters in the 21ºC treatment.

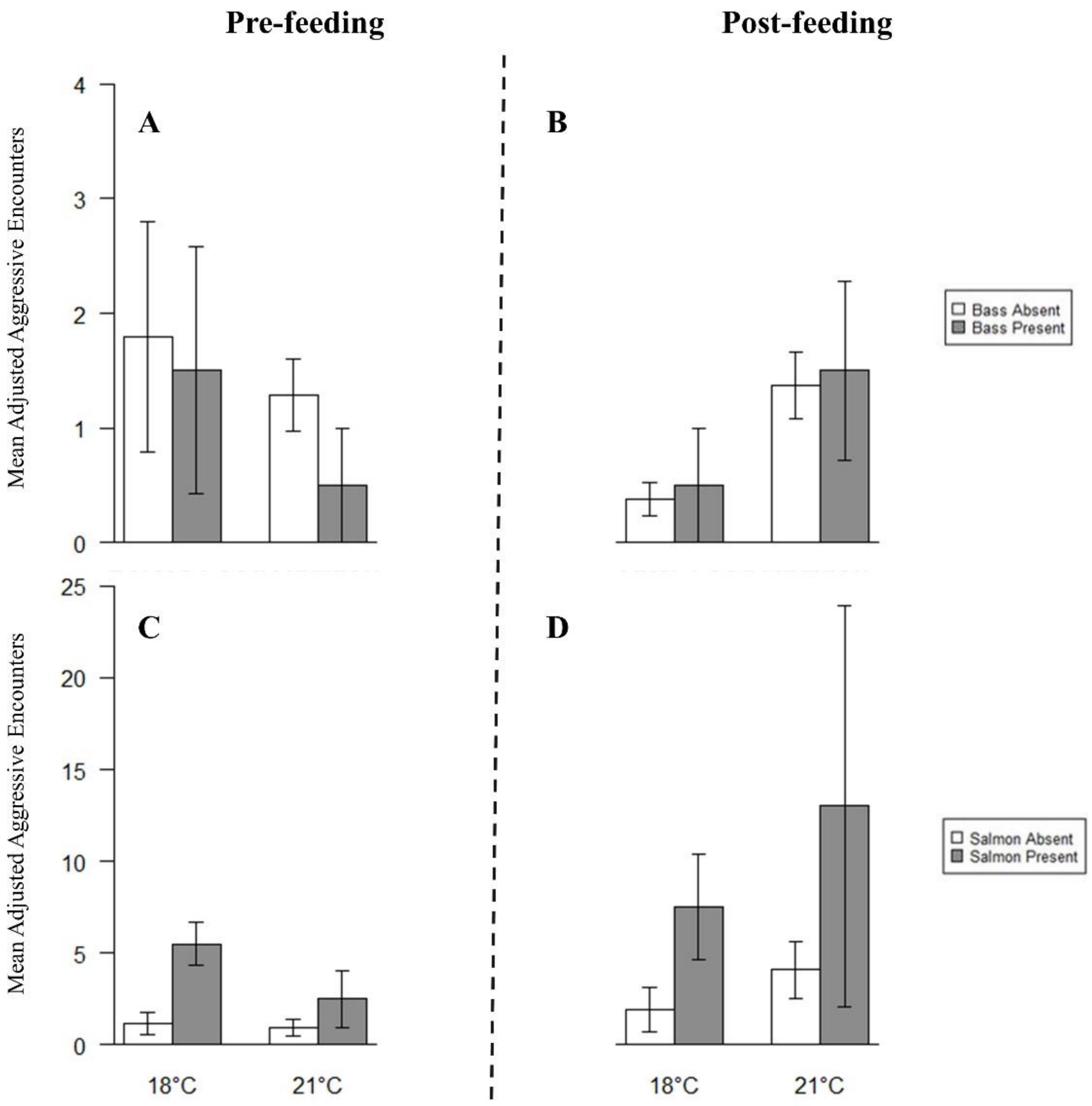


Figure 2.6 Aggressive encounters observed for juvenile ATS and SMB at 18^{o}C and 21^{o}C both pre- and post-feeding. *Panel A* Mean ATS adjusted aggression during the pre-feeding period in the presence and absence of SMB. *Panel B* Mean ATS adjusted aggression during the post-feeding period in the presence and absence of SMB. *Panel C* Mean SMB adjusted aggression during the pre-feeding period in the presence and absence of ATS. *Panel D* Mean SMB adjusted aggression during the post-feeing period in the presence and absence of ATS.

CHAPTER 3

INTERANNUAL VARIABILITY IN TEMPERATURE AND PRECIPITATION HAVE STREAM-SPECIFIC IMPACTS ON JUVENILE ATLANTIC SALMON CONDITION IN MAINE STREAMS.

Introduction

Freshwaters have been detrimentally impacted by changes in climate that alter the suitability of habitat for organisms across the globe. Both warming waters and changes in hydrologic regimes have had broadscale impacts on freshwater systems, including declines in individual performance, facilitation of range shifts and invasions, losses of biological diversity, and species' extinctions (Xenopoulos et al. 2005, Rahel and Olden 2008, Woodward et al. 2010, Hendry et al. 2011). However, the response of freshwater systems to climate change is not uniform across the landscape and varies with temporal and spatial scales as well as species identity (Falke and Fausch 2010). Simultaneous changes in environmental factors lead to uncertain outcomes. For instance, elevated temperatures coupled with periods of drought will likely result in more severe stressors on cold-water species than when elevated temperatures coincide with higher rainfall (Woodward et al. 2016). The effects stemming from changes in environmental variables are also not always immediately apparent, producing effects that manifest at a later period in time (Copeland and Meyer 2011, Comte and Grenouillet 2013, Comte et al. 2013). Given that factors such as temperature and hydrologic regimes are crucial components governing the life histories of freshwater organisms, there has been widespread uncertainty regarding the welfare of freshwater ecosystems and their fisheries across the globe (Ficke et al. 2007).

Stream morphology and characteristics of the surrounding physical environment are linked to a waterbody's vulnerability to changes in air temperature and precipitation (Snelder and

Biggs 2002). For example, vulnerability to warming relates inversely to groundwater input and shading (Allen and Castillo 2007). While the response of freshwater systems to climate change has been well-studied at particular scales or defined periods of time, there is a gap in knowledge regarding how freshwater fish respond to environmental changes at multiple scales across the landscape (Fausch et al. 2002). Fausch et al. (2002) advocated for scale to be included in riverine research in attempts to capture the spatial and temporal trends in fisheries that exist across the landscape; all with the intent to provide a more in-depth understanding of the complexities surrounding freshwater fisheries and better inform management.

In particular, there has been mounting concern for salmonids and their ability to survive as patterns in temperature and precipitation continue to shift (Mangel 1994, Isaak et al. 2012). This includes cold-adapted Atlantic salmon (*Salmo salar*), which have been Federally Endangered since 2000 and are considered highly vulnerable to changes in climate (Hare et al. 2016). Several factors contributed to the dramatic declines of Atlantic salmon observed over the last century, including overfishing, pollution, damming, and habitat degradation (Buchsbaum et al. 2005, Saunders et al. 2006, Schmitt 2015). Currently, Maine harbors the last wild populations of Atlantic salmon in the United States. Salmon have an intimate connection with Maine's freshwater environments, spending 1-3 years in streams as juveniles. However, changes in air temperature that could cause waters to warm and changes in precipitation that could lead to alterations in hydrologic regimes, have the ability to impact the entire stream community as well as directly impact the performance of juvenile Atlantic salmon in Maine waters and threaten their recovery (Jonsonn and Jonsson 2009).

New England's climate is warming faster than that of any other region in the continental United States (Karmalkar and Bradley 2017). In Maine, average annual temperature has increased 1.48°C over the last century and there has been an increase in warmer than average summers, with Maine's coastal region having experienced the largest magnitude of change compared to the rest of the state (Fernandez et al. 2020). Average annual precipitation has also increased over 15 percent in the last 100 years (Fernandez et al. 2020). Observable effects stemming from Maine's changing climate have been documented in decreases in annual snowfall, later ice-on and earlier ice-out dates (Dudley and Hodgkins 2002) along with changes in seasonal variation in stream flow (Hodgkins et al. 2002, 2005), which indicate later onset of the winter season and earlier spring conditions.

Despite ongoing recovery efforts, Atlantic salmon are still at risk of extinction and climate change stands to further exacerbate the serious issues that salmon already face in Maine streams. While multiple studies have examined the impacts of temperature or stream velocity on the performance of juvenile salmon (Arnold et al. 1991, Elliott 1991, Handeland et al. 2008), fewer studies have utilized historical datasets to address whether Atlantic salmon in their natural environment have been impacted by such environmental stressors (Swansburg et al. 2002, Bacon et al. 2009, Mills et al. 2013), even fewer studies include scale as a factor. With access to 40 years of salmon survey data from the Department of Marine Resources (DMR) in Maine, we used dynamic regression models to analyze the relationship between juvenile Atlantic salmon condition, temperature, and precipitation for 9 streams across 4 drainages over a 16-year period.

We predicted that the condition factor for juvenile Atlantic salmon would be associated with changes in environmental variables such as air temperature and precipitation. As temperatures increase, species may be forced to perform in sub-optimal conditions which are thermally taxing; the effects of which manifest through poor performance and mortality (Kingsolver and Huey 2008, Angilletta et al. 2010). For Atlantic salmon which are a coldwater fish with an optimum temperature of approximately 18^{o}C (Murphy 2004), waters that exceed their optimum temperature could force salmon to perform in the upper limits of their thermal range, resulting in declined performance. Since fish condition is a reflection of growth (Nash et al. 2006) and therefore an indicator of fish performance in streams, we predicted that higher temperatures would be associated with a lower condition factor. Salmon performance could also be affected by changes in precipitation that lead to variations in hydrologic regimes. Atlantic Salmon juveniles are adapted to surviving in high flow environments (Arnold et al. 1991) and perform better than potential competitors in these habitats. Furthermore, reduced precipitation can lead to a reduction in freshwater habitat which condenses interaction space among species and amplifies the effects of competition (White et al. 2016). Thus, we expected lower condition values to be associated with decreasing precipitation. We also tested for an interactive effect between temperature and precipitation in relation to salmon condition. Salmonid growth is closely linked with both temperature and stream flow (Hayes et al. 2000), the effects of which cannot always be easily disentangled from one another. We predicted that warm dry years would be associated with poor performance and therefore a lower condition factor. However, the effects of environmental variables are not always immediately realized and may only be observed at a later date (Comte et al. 2013). At early life stages salmonids can be directly impacted by changes in the environment that carryover and impact their growth the following season (Giannico and Hinch 2003, Roussel 2007, Finstad and Jonsson 2012). Salmon could also be impacted indirectly through abiotic conditions or through changes in the community or ecosystem. Therefore, we included a lag of 1-year in our analyses for both temperature and precipitation which allowed us to assess whether salmon condition factor may be impacted, whether it be directly or indirectly, by changes in environmental variables that occurred during the previous year.

Methods

Data Acquisition and Filtering

In order to assess whether juvenile salmon condition was correlated with temperature and precipitation in Maine, we built a set of dynamic regressions which analyzed condition of juvenile salmon in relation to annual temperature and precipitation data. In August and September of each year, the Department of Marine Resources (DMR) conducts electrofishing surveys in streams and rivers across the state of Maine. This dataset contains length and weight measurements of juvenile salmon across 45 streams between 1975-2015. Data associated with each stream was manually assessed for completeness and filtered to remove streams with gaps of two or more consecutive years. Of the 45 streams included in the survey data, only 9 streams contained data suitable for examining salmon condition over multiple consecutive years. The 16-year period between 1999 and 2015 was found to contain the most complete set of data. However, gaps in data and the amount of data available for each year did vary by stream. The final dataset contained length and weight measurements for juvenile salmon from 9 streams belonging to 4 different drainages, spanning the years 1999 to 2015 (see Table 3.1 for list of streams and drainages and Figure 3.1). Extreme outliers beyond the feasibility of body allometry of fish condition (likely data entry errors), were removed from the dataset. Fulton's fish condition (k), was calculated for salmon juveniles using the following formula: $k = \frac{mass(g)}{length\ (cm)^3} * 100$ (Nash et al. 2006). Given that water temperature and stream flow records were either not available for our study streams or not available for all years of our study period, air temperature and precipitation data available at the state level were accessed. It is common practice to utilize air temperature and precipitation when water temperature and stream flow information is not available (Hare et al 2016). Moreover, studies investigating the relationship between water and air temperature have demonstrated that stream temperature often closely tracks air temperature (Swansburg et al. 2002, Isaak et al. 2012). National Oceanic and Atmospheric Administration (NOAA) historical weather station records containing monthly averaged temperature and precipitation data for the state of Maine (Lawrimore et al. 2011) were accessed through Climate Reanalyzer (*Climate Reanalyzer*). Temperature and precipitation were annually averaged to capture environmental conditions throughout the year, such as winter temperatures and precipitation, which can be important to early development in fish (Webb and McLay 1996, Einum and Fleming 2000, Jonsson and Jonsson 2009). We calculated seasonally averaged summer temperatures for June, July, and August, to focus on the period when temperatures tend to be highest throughout the year and could impact the salmon growing season. We tested the appropriateness of state level climate data by comparing temperatures at the state level to regional weather station data from Bangor, Maine with Pearson's correlation. State and local data followed the same trends for both annually (Figure 3.2A, r=0.94) and seasonally averaged (Figure 3.2B, r=0.93) temperatures, indicating the state level data was a useful proxy. Reliable precipitation records at the regional level were not available for comparison.

Dynamic Regression Models

All analyses were conducted in R version 3.4.4. Data for all variables were averaged by year for the study period of 1999 to 2015. Salmon condition was $\log_e$+1 transformed prior to analysis to meet the assumptions of normality and homoscedasticity. Years with missing condition values were interpolated using the 'na.interp()' function from the 'forecast' package in

R. This function utilizes linear interpolation to replace missing values in the dataset with estimated values. In total, 5 of the 9 streams contained interpolated values; 3 streams contained only one interpolated value (Cathance Stream – 2015, East Machias River – 2009, and Narraguagus River – 2012), one stream contained two interpolated values (Dennys River 2013, 2015), and one stream contained three interpolated values (Goud Brook – 1999, 2007, 2012). Data were then formatted as a time series. When working with time series data, it is natural for the mean of the observed variable to change over time, when this occurs data is considered non-stationary. Therefore, detrending techniques are used to obtain a stationary dataset. All variables in our dataset were detrended using regression by testing the variables against year and the residuals were output as the data to be analyzed (Shumway and Stoffer 2017). This allowed us to examine the effects of year to year variation between our variables as opposed to longer term trends over time.

Dynamic regression models allow for time 'lags' to be included as a model parameter which test for latent effects of independent variables on the dependent variable (Shumway and Stoffer 2017). For example, if a time lag of 1 year is included in a model for a variable such as temperature, that means we are testing if temperature in a given year is correlated with condition the following year. In total, we generated 4 dynamic regression models using the 'dynlm' package in R (Table 3.2). Model 1 tested for correlations between salmon condition and temperature. Model 2 tested for correlations between salmon condition and precipitation. Model 3 tested for correlations between salmon condition and temperature + precipitation. Model 4 tested for correlations between salmon condition and temperature + precipitation + temperature:precipitation interaction. For each of the models above, a 1-year lag was included for both temperature and precipitation. All models were run using data belonging to salmon classified as both young-of-year (YOY) and parr by the Department of Marine Resources. Thus, the 1-year lag included in our models reflects both the potential direct effects of temperature and precipitation on age 1+ individuals who experienced the previous season as well as indirect effects which could impact age 0+ individuals during their first year in Maine streams. In addition, we explored the possibility of including salmon CPUE (catch per unit effort) and CPUE of a known competitor, the Smallmouth bass (*Micropterus dolomieu*), as a means to assess how density and competition from conspecifics and non-native species may impact salmon condition. However, CPUE data was only available for the years 2005 to 2015 and when these factors were included, model fits were not reliable.

Models 1 - 4 were run at three spatial scales: the individual stream level represented the finest resolution, the drainage level which often contained multiple streams from the individual level belonging to the same drainage, and all of the streams compiled which represented the coarsest resolution (i.e., Downeast Maine). Models 1-4 were first run using annually averaged and then seasonally averaged summer (June, July, and August) temperature and precipitation values. An information theoretic approach was then used to select the "best" fitting model (Richards 2005) using the 'AICcmodavg' package to calculate Akaike Information Criterion scores corrected for small sample size (AICc) for each model. Change in AICc (Δ AICc) was calculated by finding the difference in AICc between the model with the lowest AICc score and all other models. Models with a difference greater than 4 are considered to have too much information loss to be a "best" fitting model (Burnham et al. 2011). Models 1 – 4 were then ranked by Δ AICc and the "best" fitting model was selected after comparing Δ AICc values and adjusted R^2 values.

Results

Overall juvenile salmon included in our analyses belonged to two life stages, YOY and parr, with the majority of fish, approximately 96 percent, classified as parr by the DMR (Table 3.3). Fish ranged in length from 5.0 to 24.2 cm (Table 3.4, Figure 3.3) and average Atlantic salmon condition factor per stream ranged from 1.13 to 1.21 (Table 3.4). This information suggested the majority of individuals included in our analyses were age 1+ fish. Average annual temperature ranged from 4.69 to 7.02 ^{o}C and average annual precipitation ranged from 6.33 to 13.04 cm. Seasonally averaged summer temperatures ranged from 14.6 to 18.8^{o}C and averaged summer precipitation ranged from 6.5 to 15.6 cm.

Annually Averaged Temperature and Precipitation

At the finest resolution, our analyses detected three streams where condition was significantly correlated with temperature and precipitation: the Dennys River, East Machias River, and Seavey Stream. For Dennys River, Model 1 including temperature and a 1-year temperature lag best predicted salmon condition, whereby salmon condition decreased with warmer temperature (Table 3.5, Figure 3.4) Moreover, temperature was a significant parameter in all models in which it was included (Table 3.5). The second-best model, Model 3 (Δ AICc < 4) provided support for the influence of precipitation where increasing precipitation was associated with a higher salmon condition factor in Denny's river (Table 3.5). For both the East Machias River and the Seavey Stream, an effect precipitation with a 1-year lag was detected. For the East Machias River, precipitation with a 1-year lag best predicted salmon condition in Model 2, where increasing precipitation in a given year was positively associated with condition the following year (Table 3.5, Figure 3.5). Precipitation with a 1-year lag was a significant term in each model in which it was included (Table 3.5). Similarly for Seavey Stream, in Model 2 precipitation with a 1-year lag best predicted salmon condition; whereby higher amounts of precipitation were associated with a higher condition factor (Table 3.5, Figure 3.6).

At the drainage level, our models detected significant relationships between condition, temperature, and precipitation in 2 of the 4 drainages. In the Dennys Drainage, which includes the Dennys River and Cathance Stream, temperature was the best predictor of salmon condition in Model 1; whereby increasing temperature was associated with significantly lower salmon in each model temperature was included. Influence of precipitation was detected in Model 3 (Δ AICc < 4), where precipitation increases, were associated with increases in salmon condition (Table 3.6). The East Machias Drainage includes Beaverdam Stream, the East Machias River, Northern Stream, and Seavey Stream. In Model 2 precipitation with a 1-year lag was the best predictor of salmon condition; where increasing rainfall in a given year was associated with higher condition the following year (Table 3.6). At the coarsest resolution, which combined all of the streams, no relationships between temperature, precipitation, and salmon condition were detected (Table 3.6, Figure 3.7).

Seasonally Averaged Summer Temperature and Precipitation

At the stream level, our analyses detected two streams where salmon condition was correlated with precipitation, Beaverdam Stream and the East Machias River. For both Beaverdam Stream and the East Machias River, Model 2 best predicted salmon condition, whereby salmon condition increased with increasing precipitation (Table 3.7, Figures 3.8 and 3.9, respectively). At the drainage level and at our coarsest resolution with all streams combined, our analyses detected that salmon condition in the East Machias Drainage was correlated with precipitation (Table 3.8). Model 2 best predicted salmon condition at both the drainage level and when all streams were combined, whereby salmon condition increased with increasing precipitation (Table 3.8, Figure 3.10).

Discussion

Our results suggest that changes in temperature and precipitation impact the condition of juvenile salmon in Maine streams, but the relative importance of these factors can vary among streams and drainages. Early life stages are critical in shaping the success of salmonid individuals (Einum and Fleming 2000) whereby changes in environmental variables that affect juvenile salmon performance could have lasting effects that influence growth, maturation, and reproduction (Jonsson and Jonsson 2009). In particular, temperature plays a vital role in the development of salmonids, influencing the timing of spawning, hatching and feeding as well as the bioenergetics that underlie growth (Webb and McLay 1996, Jonsson and Jonsson 2009). While it was therefore not surprising that lower salmon condition was linked with warmer years, it was intriguing that the Dennys River was the sole waterbody where a correlation between salmon condition and annually averaged temperature was detected (Figure 3.4).

Optimal temperature for Atlantic salmon is approximately 18^{o}C (Forseth et al. 2001, Murphy 2004) and the upper critical range spans 22-33^{o}C, with an incipient upper lethal temperature of approximately 27^{o}C (Jonsson and Jonsson 2009). If temperatures approach the upper critical limits of salmonid thermal tolerance, both feeding activity and growth are suppressed (Brett 1971), resulting in a lower condition factor compared to salmon experiencing favorable conditions near their thermal optimum. Temperatures that far exceed the thermal optimum for a species are problematic because metabolic costs cannot be met by the energetic gains of feeding; which ultimately results in reduced fitness (Pörtner and Peck 2010).

Furthermore, changes in temperature likely impact more than individual salmon performance by impacting entire stream communities and their food webs (Woodward et al. 2010). Poff and Huryn (1998) reasoned that changes in climate have the potential to impact invertebrate prey which could impact salmon secondary production. Therefore, we cannot rule out that juvenile salmon may be impacted by changes in prey resources that are affected by change in temperature.

While long term records of water temperature are not available for the Dennys River, data from 2017 (US Fish and Wildlife Service Maine Field Office accessed through the Spatial Hydro-Ecological Decision System - SHEDS) demonstrates that mean water temperature consistently exceeds above 20^{o}C during the summer months, with temperatures reaching upwards of 26^{o}C. Feeding activity in Atlantic salmon parr has been shown to cease beyond 22.5^{o}C (Elliott 1991) and analysis of salmon fork length over an 18-year period in the Mirimachi River, Canada, indicated that smaller parr size was correlated with warmer temperatures (Swansburg et al. 2002). Elliott and Elliott (2010) suggested that temperatures between 22-28^{o}C are likely to be lethal for Atlantic salmon unless individuals find cooler areas of thermal refugia. Dugdale et al. (2016) found that the temperature of 28^{o}C predicted salmon movement out of warm waters in search of thermal refugia.

Since these results were found using annually averaged temperature values, we were not able to differentiate between warm years due to above average winters versus above average summers. However, we tested the relationship between salmon condition and seasonally averaged summer temperature and we did not detect an effect of temperature on salmon condition in any of our streams. This suggests that the effect of temperature detected using annually averaged data could be due to factors beyond summertime means, such as warmer winter, spring, or fall temperatures. For instance, Murphy et al. (2006) found that warm winters with variable temperatures resulted in significant weight loss in Atlantic salmon. Alternatively, extreme temperature events or spikes in temperature that produce abnormally warm conditions can have stronger impacts on ectothermic species compared to elevated mean temperatures (Ledger and Milner 2015, Woodward et al. 2016). It could be that extreme temperature fluctuations have a stronger effect on salmon condition than elevated average summertime temperatures. The impact of such temperature events would not necessarily be captured in our analysis which utilized average monthly temperature values. Regardless, these findings suggest that juvenile Atlantic salmon are experiencing thermal conditions in the Dennys River that may negatively impact their performance and growth.

Stream temperature varies spatially by stream and temporally by season due to regional climate, groundwater input, tree canopy cover, and stream morphology (Allen and Castillo 2007). Thus, the high temperatures observed in Dennys River could be due, in part, to stream morphology and characteristics of the surrounding environment that impact the vulnerability of streams to changing air temperature. For instance, consistent groundwater input can help to regulate stream temperatures (Poole and Berman 2001). While groundwater input information was not available for our streams, habitat information included in the DMR dataset provided some insight into this issue. Dennys River was the widest stream in our dataset with an average width of approximately 19.67m and an average depth of approximately 0.37m (Table 3.1). Furthermore, survey data suggests that approximately only 0-25% of the stream is covered by tree canopy; with very few measurements reaching 75-100% coverage. Canopy cover provides shade in streams and helps to reduce stream temperature (Moore et al. 2005). Therefore, it could be possible that the Dennys River may be more susceptible to changes in air temperature than other streams in our study.

Like temperature, stream flow is intimately linked to salmon performance and growth (Boisclair 2004). Stream flow is, thus, an important component in predicting suitable salmon habitat (Gibson 1993) and behavior (Huntingford et al. 1999, Sykes et al. 2009). Salmon parr are typically found in shallow habitats with high velocities (Arnold et al. 1991, Heggenes and Borgstrøm 1991) such as riffles. Precipitation alone was not found to be a strong predictor of salmon condition when assessing annually averaged precipitation. However, we did find that annually averaged precipitation was the second-best predictor of salmon condition in the Dennys River (Figure 3.4). In comparison, seasonally averaged summer precipitation predicted salmon condition at all three spatial scales spanning Beaverdam Stream (Figure 3.8) and the East Machias River (Figure 3.9), the East Machias Drainage, and all of the streams combined in the Downeast region (Figure 3.10). Given that Beaverdam Stream and the East Machias River were the only streams where precipitation was found to have an effect on salmon condition, it is likely that these streams are driving the effect of precipitation found at the drainage and Downeast region levels. Moreover, for both the East Machias River and Seavey Stream, we found that annually averaged precipitation with a 1-year lag was the best predictor of salmon condition; indicating that variations in precipitation can have latent effects on salmon condition (Figures 3.5 and 3.6).

Precipitation is an important factor in regulating stream flow. Analysis of stream discharge for multiple streams along the Eastern Coast of the United States and Canada revealed that less precipitation translates into reduced stream flows (Allan and Benke 2005). Precipitation and snow melt runoff into streams and filter through soil to recharge groundwater input that helps to maintain stream baseflows throughout the year; even canopy cover from riparian vegetation can influence how much precipitation reaches a stream (Allen and Castillo 2007). Features of the landscape also help determine stream vulnerability to extreme precipitation events such as flooding or drought (Resh et al. 1988). Regional climate, geographic features of the landscape along with vegetation both in and surrounding the waterbody create flow regimes unique to each stream (Poff et al. 1997) that could provide useful proxies for evaluating climate sensitivity of salmonid populations.

In our study, the East Machias River was the second widest river in our study with an average width of approximately 18.21m and average depth of approximately 0.31m. Canopy survey data indicated that the majority of the stream contains 0-25% canopy cover and cover never exceeded 50%. In comparison, Seavey Stream is much smaller with an average width of 6.89m and an average depth of 0.16m. Canopy cover data indicates that the majority of the stream contains 0-25% canopy cover, with very few locations reaching 75-100% coverage. The fact that we found increasing precipitation was associated with increasing salmon condition the following year, suggests that these streams are more susceptible to shifts in precipitation than other streams in our study. The 1-year lag between changes in precipitation and salmon condition could be due to factors such as groundwater recharge. If lack of precipitation prevents groundwater recharge and limits groundwater input into streams (Allen and Castillo 2007), it could result in unfavorable flow conditions for salmon in the future. Therefore, it is possible that even YOY salmon could be indirectly influenced by precipitation patterns that carryover from the previous season.

In comparison to our findings, Nislow et al. (2004) found that Atlantic salmon mass was lowest when streamflow was lowest, and that streamflow impacted salmon growth by also impacting factors such as prey capture rate. Foraging salmonids will compete for the most profitable position in streams, which provides a net energy gain after energetic losses associated with swimming or holding their position are considered (Fausch 1984, Grossman 2014). Changes in streamflow which alter the availability and successful capture of drifting prey (Hughes and Dill 1990) could ultimately impact salmon growth. Since salmon feeding and growth rates can determine individual success over winter and into the following season (Metcalfe et al. 1988), increased precipitation in a given year that results in immediately higher flows could provide salmon parr, like those analyzed here, with favorable conditions that positively impact growth and contribute to their success the following year.

Periods of low flow, especially stemming from drought conditions are dangerous for juvenile salmon for multiple reasons (Elliott and Elliott 2010). Lack of rainfall resulting in a drop in water level can lead to stranding and increase risk of salmon mortality (Saltveit et al. 2001). Drought conditions can also lead to changes in temperatures that quickly warm beyond the upper limits of salmon thermal tolerance. During the summer of 1976 in Wales, over 400 Atlantic salmon died within a 5-day period due to drought conditions in the River Wye (Brooker et al. 1977). A reduction in annual precipitation in 1975 and 1976, coupled with warm temperatures created lethal conditions (Brooker et al. 1977). Coupled interactions between stream flow and temperature can also force salmon to change their foraging strategies. Such a change could force salmon into faster flowing water in attempts to maximize their net energy gain and avoid weight loss (Smith and Li 1983). Since temperature and precipitation can synergistically affect salmon populations, we expected to find a significant interactive effect between these two variables and salmon condition in our models. We anticipated that either cooler, wetter years would be associated with a higher condition factor or that warm, dry years would be associated with a low condition factor. Surprisingly, we did not find any interaction between condition, temperature, and precipitation in any of the streams we analyzed.

The broadest interpretation of our results suggests that scale may be an important factor when examining the relationships between salmon condition, temperature, and precipitation over time. Indeed factors at multiple scales operate simultaneously across the landscape to produce observable effects in fish behavior, ecology, and even metacommunity dynamics (Fausch et al. 2002, Falke and Fausch 2010, White et al. 2014). When analyzing annually averaged temperature and precipitation, our coarsest resolution models which analyzed combined data across 9 locations, detected no significant relationships between condition and the environmental variables tested. At the intermediate scale, the drainage level, the prominent effects of both temperature and the 1-year precipitation lag were detected. Analysis at the stream level demonstrated that salmon responses to temperature and precipitation vary by stream. This suggests that salmon in different streams could be differentially impacted by temperature and precipitation and that even juvenile salmon located within the same drainage may not be impacted by these factors to the same degree.

This could be due to a combination of factors, organized in a hierarchical fashion, that ultimately result in unique responses at the stream level. For instance, higher order factors such as climate, geology, and land cover often operate on a broader scale and watershed level, but feed into characteristics such as landform, that determine stream specific conditions (Snelder and Biggs 2002). Poff and Huryn (1998) suggested that factors such as climate, geology, and land cover determine environmental conditions within streams that then influence the salmon, their invertebrate prey base, and ultimately salmon production. They predicted that salmon production would be highest in streams containing large riffles, open canopy cover, and stream bedrock composed of carbonate (Poff and Huryn 1998). While factoring such characteristics into our analysis was beyond the scope of this study, the varying results that we observed between streams within each drainage and between drainages could be due to attributes of the landscape that produce unique impacts to individual streams and specific responses in salmon to changes in temperature and precipitation. It should be taken into consideration that the number of streams and fish included in our analyses did vary between drainages. Moreover, the fact that we did not detect significant effects of temperature and precipitation on juvenile salmon condition in all streams or at each spatial scale, does not diminish the importance of these two environmental variables when considering salmonid performance and growth.

However, environmental factors alone are not solely responsible for determining the fate of salmon in the wild. Several studies have investigated how factors such as competition and density impact salmon performance (Heggenes and Borgstrøm 1991, Ward et al. 2009). We were interested in including variables such as salmon CPUE into our models that would allow us to capture a more detailed perspective into the many factors influencing salmon growth and thus salmon condition. Moreover, while condition factor is a generalized metric for assessing fish growth and is useful for comparing among multiple populations, Atlantic salmon growth is impacted by several factors including life history events such as maturation and smoltification (Mangel 1994), that can also impact salmon condition in a way that obscures relationships between environmental parameters and salmon performance. Future work which includes environmental variables along with factors such as intraspecific competition or density, which might be indicated by CPUE, that take into account life history events, could address how abiotic and biotic drivers affect salmon populations both spatially and temporally.

Over the last century salmon populations have been impacted considerably by anthropogenic factors such as habitat degradation and overfishing, which have threatened their chances of survival as a species. While salmon recovery efforts have focused on restoring salmon habitat, the anticipated impacts of climate change over the next century threaten salmon recovery. This work serves as an initial step towards understanding the multiple factors that impact salmon condition in Maine streams both spatially and temporally. While multiple factors beyond the scope of this study likely contribute to the overall condition of salmon (i.e. biological interactions among stream dwelling fishes and invertebrates or physical characteristics of the landscape), the results presented here further reinforce that temperature and precipitation are linked to the well-being of juvenile Atlantic Salmon in Maine streams. Perhaps most importantly, our research suggests that not all salmon populations will be uniformly impacted by changes in climate and this is likely due to multiple factors spanning several scales across the riverine landscape in Downeast Maine. This also reinforces that a one-size-fits-all approach to salmon recovery efforts may not always be appropriate. Management practices are as inherently complex as the ecological systems they strive to protect. The decision to implement fine versus broad scale (or patch versus landscape) approaches comes with the consequence that processes from any other scale could be excluded from the potential benefits of management decisions (Lindenmayer et al. 2008). At the very least, multiscale approaches to conservation management attempt to capture processes important to specific species or regions that would otherwise be neglected if only broader scales were considered (Lindenmayer et al. 2008). Targeted management decisions generated on sound science and flexibility that anticipate change in future environmental conditions will be key to managing endangered species (Gregory et al. 2013).

Therefore, it is our hope that this work informs future adaptive management solutions in light of a changing climate.

Table 3.1 The nine streams and four drainages included in our analyses. Average width and depth of each stream were calculated using survey data from the Maine Department of Marine Resources.

Stream	Drainage	Avg. Width	Avg. Depth
Beaverdam Stream	East Machias	7.92	0.38
Cathance Stream	Dennys	10.64	0.18
Dennys River	Dennys	19.67	0.37
East Machias Stream	East Machias	18.22	0.31
Gould Brook	Narraguagus	5.34	0.32
Narraguagus River	Narraguagus	16.45	0.91
Northern Stream	East Machias	6.46	0.17
Old Stream	Machias	11.23	0.27
Seavey Stream	East Machias	6.89	0.17

Table 3.2 Overview of dynamic regression models and the variables included in each model. Models become increasing complex, with Model 4 including an interaction between temperature and precipitation.

Model Name	Model Description
Model 1	Condition ~ Temperature + Temperature Lag 1 Year
Model 2	Condition ~ Precipitation + Precipitation Lag 1 Year
Model 3	Condition ~ Temperature + Temperature Lag 1 Year + Precipitation + Precipitation Lag 1 Year
Model 4	Condition ~ Temperature + Temperature Lag 1 Year + Precipitation + Precipitation Lag 1 Year + Temperature:Precipitation

Table 3.3 Total count of Atlantic salmon individuals included in analyses by stream and life stage.

Stream Name	YOY	Parr	Total Count
Beaverdam Stream	4	384	388
Cathance Stream	10	415	425
Dennys River	18	2283	2301
East Machias River	5	419	424
Gould Brook	18	189	207
Narraguagus River	285	4720	5105
Northern Stream	11	809	820
Old Stream	34	1245	1279
Seavey Stream	2	451	453

Table 3.4 Range of Atlantic salmon length (cm), mass (g), and condition factor by stream.

	Length				Mass				Condition Factor			
Stream	**Min.**	**Max.**	**Median**	**Mean**	**Min.**	**Max.**	**Median**	**Mean**	**Min.**	**Max.**	**Median**	**Mean**
Beaverdam Stream	5	19.2	11.3	11.6	1.3	64.5	16.4	19.5	0.17	1.92	1.16	1.16
Cathance Stream	5.7	20.8	12.9	13	2.3	117	23.4	26.2	0.63	2.51	1.15	1.14
Dennys River	5	24.2	13.7	13.8	1.5	189.5	29	31.8	0.35	3.18	1.16	1.15
East Machias Stream	5.6	22.1	15.3	15.3	2	129.1	43	44.7	0.6	1.79	1.21	1.21
Gould Brook	5.5	16.2	11.4	11.3	1.9	52.8	17.1	18.7	0.55	2.28	1.19	1.19
Narraguagus River	4	23.9	12.5	12.4	0.7	117	22	24.4	0.49	2.08	1.14	1.13
Northern Stream	5.5	20.4	12.55	12.9	2	95.7	23.2	27.6	0.63	2.22	1.19	1.19
Old Stream	5.5	18	11.3	11.6	2.2	64.8	16.7	19.1	0.6	2.4	1.16	1.16
Seavey Stream	5.3	21.7	11.6	12.1	2.3	135.3	17.4	22.7	0.7	3.9	1.14	1.14

Table 3.5 Results of dynamic regression Models 1 – 4 at the stream level, examining the relationship between annually averaged temperature (^{o}C), precipitation (cm), and Atlantic salmon condition (Log_e+1) between 1999 and 2015. Values listed represent p-values unless otherwise stated.

Stream Name	Model	Years Interpolated	Temp	Temp Lag 1 Year	Precip	Precip Lag 1 Year	Temp:Precip	AICc	Change	Adjusted R^2
Beaverdam Stream	Model 2	None			0.43	0.18		-56.188	0	0.05801
	Model 1	None	0.51	0.73				-53.6412	2.54683	-0.1045
	Model 3	None	0.26	0.69	0.43	0.125		-48.5982	7.58981	0.0241
	Model 4	None	0.28	0.7	0.46	0.16	0.94	-41.9421	14.24596	-0.07278
Cathance Stream	Model 1	2015	0.15	0.94				-53.8757	0	0.01893
	Model 2	2015			0.17	0.94		-53.744	0.13161	0.01082
	Model 3	2015	0.12	0.84	0.14	0.74		-47.8698	6.00584	0.07942
	Model 4	2015	0.13	0.79	0.13	0.98	0.35	-42.6597	11.21591	0.03488
Dennys River	Model 1	2013, 2015	0.03	0.4				-70.3222	0	0.241
	Model 2	2013, 2015			0.18	0.94		-66.0342	4.28797	0.007675
	Model 3	2013, 2015	0.03	0.29	0.06	0.46		-66.8813	3.44086	0.3933
	Model 4	2013, 2015	0.02	0.28	0.07	0.64	0.45	-61.1593	9.16285	0.3709
East Machias River	Model 2	2009			0.87	0.04		-65.1324	0	0.1912
	Model 1	2009	0.98	0.63				-59.7401	5.39231	-0.1329
	Model 3	2009	0.59	0.69	0.83	0.05		-56.1459	8.98653	0.08571
	Model 4	2009	0.57	0.74	0.85	0.05	0.53	-50.1385	14.99393	0.03488
Gould Brook	Model 2	1999, 2007, 2012			0.38	0.83		-58.649	0	-0.08308
	Model 1	1999, 2007, 2012	0.52	0.63				-58.4629	0.18608	-0.09575
	Model 4	1999, 2007, 2012	0.57	0.56	0.36	0.79	0.51	-44.0947	5.9364	-0.2575
	Model 3	1999, 2007, 2012	0.53	0.59	0.36	0.94		-50.0311	8.61793	-0.1965

Table 3.5 continued

Stream Name	Model	Years Interpolated	Temp	Temp Lag 1 Year	Precip	Precip Lag 1 Year	Temp:Precip	AICc	Change	Adjusted R2
Narraguagus River	Model 2	2012			0.63	0.49		-67.3362	0	-0.08391
	Model 1	2012	0.99	0.93				-66.3462	0.98996	-0.1531
	Model 3	2012	0.84	0.93	0.66	0.5		-57.7119	9.62423	-0.2752
	Model 4	2012	0.78	0.86	0.68	0.33	0.27	-53.0568	14.27933	-0.237
Northern Stream	Model 2	None			0.98	0.15		-58.3917	0	0.026
	Model 1	None	0.43	0.64				-56.7844	1.60729	-0.07693
	Model 3	None	0.22	0.71	0.94	0.1		-51.2144	7.17736	0.01662
	Model 4	None	0.24	0.72	0.95	0.14	0.99	-44.5478	13.8439	-0.08171
Old Stream	Model 1	None	0.81	0.43				-38.0773	0	-0.09143
	Model 2	None			0.95	0.9		-37.2134	0.86388	-0.152
	Model 3	None	0.8	0.47	0.8	0.9		-28.4423	9.63501	-0.2849
	Model 4	None	0.82	0.48	0.89	0.97	0.8	-21.878	16.19933	-0.4044
Seavey Stream	Model 2	None			0.67	0.07		-54.2809	0	0.1696
	Model 1	None	0.57	0.23				-51.8324	2.44848	-0.02343
	Model 3	None	0.89	0.32	0.78	0.11		-46.1359	8.14493	0.05807
	Model 4	None	0.89	0.33	0.78	0.15	0.86	-39.5183	14.76255	-0.03295

Table 3.6 Results of dynamic regression Models 1 – 4 at the drainage level as well as all stream combined, examining the relationship between annually averaged temperature (°C), precipitation (cm), and Atlantic salmon condition (Log$_e$+1) between 1999 and 2015. Values listed represent p-values unless otherwise stated.

Stream Name	**Model**	**Temp**	**Temp Lag 1 Year**	**Precip**	**Precip Lag 1 Year**	**Temp:Precip**	**AICc**	**Change**	**Adjusted R^2**
DE Drainage *(Dennys River, Cathance Stream)*	Model 1	0.06	0.69				-43.80338	0	0.1386
	Model 2			0.119	0.988		-42.26156	1.54182	0.05148
	Model 3	0.03	0.56	0.06	0.58		-40.17686	3.62652	0.3034
	Model 4	0.04	0.51	0.06	0.82	0.32	-35.1765	8.62688	0.3095
EM Drainage *(Beaverdam Stream, East Machias River, Northern Stream, Seavey Stream)*	Model 2			0.8	0.04		-46.06542	0	0.1959
	Model 1	0.73	0.6				-40.78881	5.27661	-0.1183
	Model 3	0.32	0.65	0.74	0.04		-38.20042	7.865	0.1525
	Model 4	0.35	0.67	0.75	0.05	0.96	-31.53759	14.5278	0.06795
MC Drainge (*Old Stream)*									
NG Drainage *(Narraguagus River, Gould Brook)*	Model 2			0.72	0.56		-51.13151	0	-0.1156
	Model 1	0.65	0.67				-51.09331	0.0382	-0.1182
	Model 4	0.81	0.58	0.66	0.43	0.27	-37.26672	4.65221	0.8259
	Model 3	0.75	0.65	0.69	0.64		-41.91893	9.21258	-0.2791
All Streams Combined	Model 2			0.28	0.21		-34.57138	0	0.08313
	Model 1	0.43	0.81				-31.76809	2.80329	-0.09245
	Model 3	0.2	0.79	0.28	0.13		-27.45834	7.11304	0.07801
	Model 4	0.23	0.81	0.3	0.19	0.83	-20.87267	13.6987	-0.009063

Table 3.7 Results of dynamic regression Models 1 – 4 at the stream level, examining the relationship between seasonally averaged summer temperature (^{o}C), precipitation (cm), and Atlantic salmon condition (Log$_e$+1) between 1999 and 2015. Values listed represent p-values unless otherwise stated.

Stream Name	Model	Years Interpolated	Temp	Temp Lag 1 Year	Precip	Precip Lag 1 Year	Temp:Precip	AICc	Change	Adjusted R^2
Beaverdam Stream	Model 2	None			0.03	0.69		-59.31773	0	0.2254
	Model 1	None	0.89	0.77				-53.22359	6.09414	-0.1337
	Model 3	None	0.97	0.93	0.05	0.70		-49.63388	9.68385	0.08527
	Model 4	None	0.91	0.87	0.05	0.64	0.66	-43.29588	16.0219	0.01426
Cathance Stream	Model 1	2015	0.09	0.66				-55.51109	0	0.1143
	Model 2	2015			0.36	0.83		-52.36885	3.14224	-0.07795
	Model 3	2015	0.12	0.62	0.48	0.97		-46.59085	8.92024	0.002812
	Model 4	2015	0.15	0.65	0.50	0.95	0.90	-39.94863	15.5625	-0.09523
Dennys River	Model 1	2013, 2015	0.17	0.62				-68.48819	0	0.1488
	Model 2	2013, 2015			0.56	0.86		-64.18475	4.30344	-0.1139
	Model 3	2013, 2015	0.21	0.72	0.80	0.89		-58.94824	9.53995	0.00383
	Model 4	2013, 2015	0.15	0.86	0.58	0.92	0.40	-53.47265	15.0155	-0.01718
East Machias River	Model 2	2009			0.07	0.98		-63.98764	0	0.1313
	Model 1	2009	0.24	0.81				-61.4771	2.51054	-0.01633
	Model 3	2009	0.26	0.57	0.10	0.84		-56.24845	7.73919	0.09155
	Model 4	2009	0.31	0.64	0.14	0.86	0.98	-49.58318	14.4045	0.0007899
Gould Brook	Model 1	1999, 2007, 2012	0.71	0.20				-59.97822	0	0.003266
	Model 2	1999, 2007, 2012			0.24	0.74		-59.41378	0.56444	-0.03252
	Model 3	1999, 2007, 2012	0.61	0.22	0.32	0.52		-52.05889	7.91933	-0.05409
	Model 4	1999, 2007, 2012	0.96	0.82	0.12	0.28	0.12	-49.49707	10.4812	0.1029

Table 3.7 continued.

Stream Name	Model	Years Interpolated	Temp	Temp Lag 1 Year	Precip	Precip Lag 1 Year	Temp:Precip	AICc	Change	Adjusted R2
Narraguagus River	Model 2	2012			0.61	0.14		-69.0998	0	0.02922
	Model 1	2012	0.82	0.63				-66.64556	2.45424	-0.1317
	Model 3	2012	0.99	0.88	0.63	0.21		-59.4578	9.642	-0.1434
	Model 4	2012	0.84	0.85	0.82	0.30	0.58	-53.31506	15.7847	-0.2172
Northern Stream	Model 2	None			0.12	0.13		-60.29096	0	0.135
	Model 1	None	0.42	0.73				-57.59574	2.69522	-0.02368
	Model 3	None	0.61	0.52	0.21	0.12		-52.76354	7.52742	0.1074
	Model 4	None	0.84	0.35	0.38	0.19	0.44	-47.11912	13.1718	0.07888
Old Stream	Model 1	None	0.442	0.564				-39.65337	0	0.01095
	Model 2	None			0.47	0.953		-37.87166	1.78171	-0.1055
	Model 3	None	0.435	0.476	0.308	0.924		-31.67722	7.97615	-0.04968
	Model 4	None	0.397	0.734	0.447	0.838	0.667	-25.32166	14.3317	-0.1324
Seavey Stream	Model 2	None			0.207	0.564		-52.86893	0	0.04077
	Model 1	None	0.884	0.328				-51.94741	0.92152	-0.0161
	Model 3	None	0.895	0.513	0.306	0.709		-44.34186	8.52707	-0.0537
	Model 4	None	0.983	0.457	0.44	0.65	0.684	-37.95395	14.915	-0.1391

Table 3.8 Results of dynamic regression Models 1 – 4 at the drainage level as well as all stream combined, examining the relationship between seasonally averaged summer temperature (°C), precipitation (cm), and Atlantic salmon condition (Log_e+1) between 1999 and 2015. Values listed represent p-values unless otherwise stated.

Stream Name	**Model**	**Temp**	**Temp Lag 1 Year**	**Precip**	**Precip Lag 1 Year**	**Temp:Precip**	**AICc**	**Change**	**Adjusted R^2**
DE Drainage *(Dennys River, Cathance Stream)*	Model 1	0.08	0.94				-44.25329	0	0.1625
	Model 2			0.40	0.94		-40.06856	4.18473	-0.08786
	Model 3	0.12	0.87	0.56	0.99		-35.09497	9.15832	0.04299
	Model 4	0.11	0.67	0.48	0.90	0.60	-28.88682	15.3665	-0.02297
EM Drainage *(Beaverdam Stream, East Machias River, Northern Stream, Seavey Stream)*	Model 2			0.04	0.69		-45.81655	0	0.1833
	Model 1	0.46	0.64				-42.3162	3.50035	-0.01646
	Model 3	0.56	0.75	0.07	0.66		-37.52051	8.29604	0.1157
	Model 4	0.64	0.73	0.12	0.73	0.86	-30.90369	14.9129	0.03028
MC Drainge									
NG Drainage *(Narraguagus River, Gould Brook)*	Model 1	0.65	0.21				-52.75437	0	-0.007976
	Model 2			0.58	0.56		-51.68036	1.07401	-0.07796
	Model 3	0.69	0.32	0.69	0.77		-43.52404	9.23033	-0.157
	Model 4	0.90	0.96	0.34	0.91	0.15	-40.38007	12.3743	-0.0212
All Streams Combined	Model 2			0.03	0.64		-36.94906	0	0.2097
	Model 1	0.81	0.67				-31.54352	5.40554	-0.1079
	Model 3	0.96	0.78	0.05	0.63		-27.46	9.48906	0.07811
	Model 4	0.85	0.99	0.06	0.58	0.67	-21.10583	15.8432	0.005535

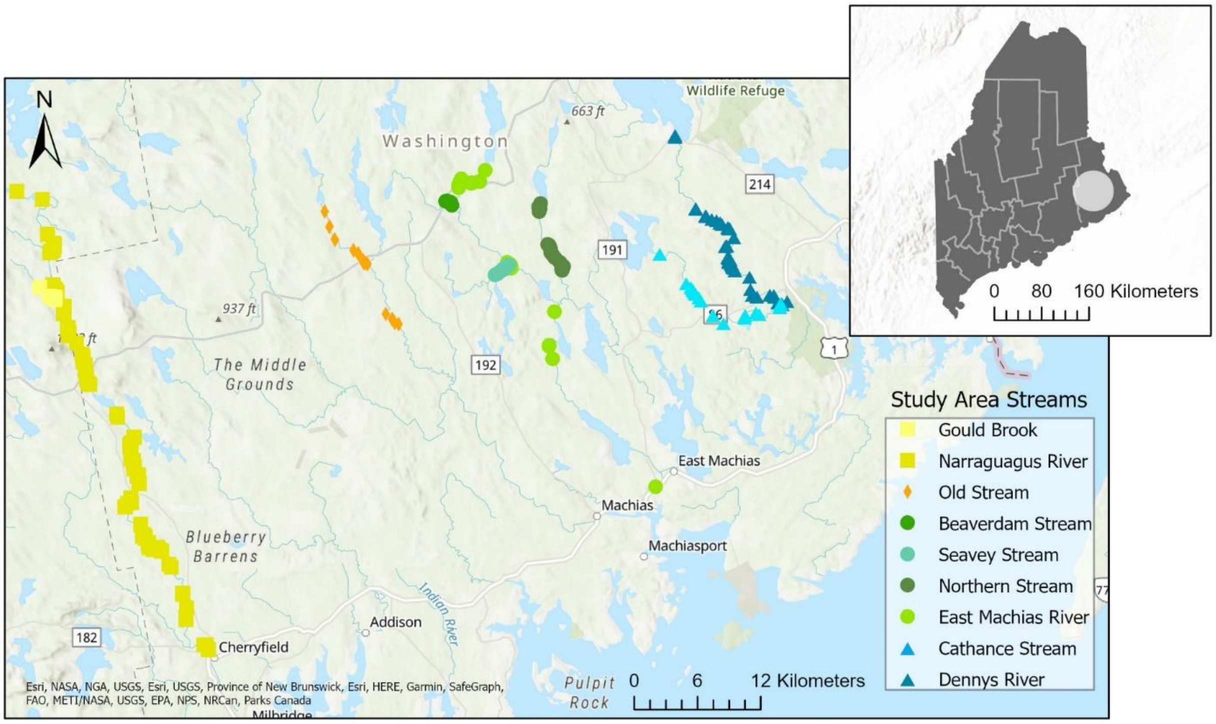


Figure 3.1 Geographic location of all streams included in our dynamic regression models. Symbol type represents drainage, many of which contain multiple streams. Symbol color identifies specific streams. Symbology: Squares represent Narraguagus Drainage, Diamonds represent Machias Drainage, Circles represent East Machias Drainage, and Triangles represent Dennys Drainage. Multiple points mapped along each stream represent locations where the Department of Marine Resources has conducted surveys between 1975 – 2015. Inset map: All streams are located in Downeast Maine, as indicated by the grey locator circle on the State of Maine map. Nearly all sites fall within the Washington County Boundary. Map was created using ArcGIS Pro, version 2.6 and Maine Office of GIS Maine Boundaries County Lines (CNTY24L) shapefile.

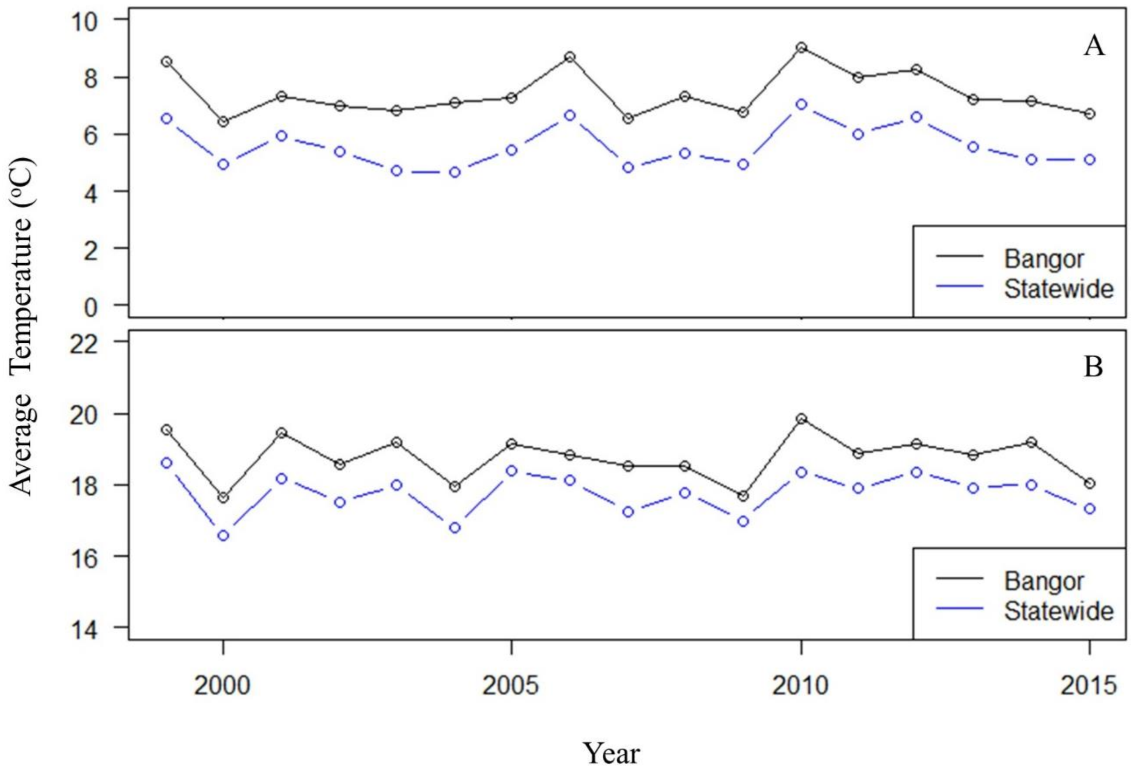


Figure 3.2 Average annual temperature (Panel A) and seasonally averaged summertime (June, July, and August) temperatures (Panel B) for Bangor and the State of Maine between 1999 and 2015.

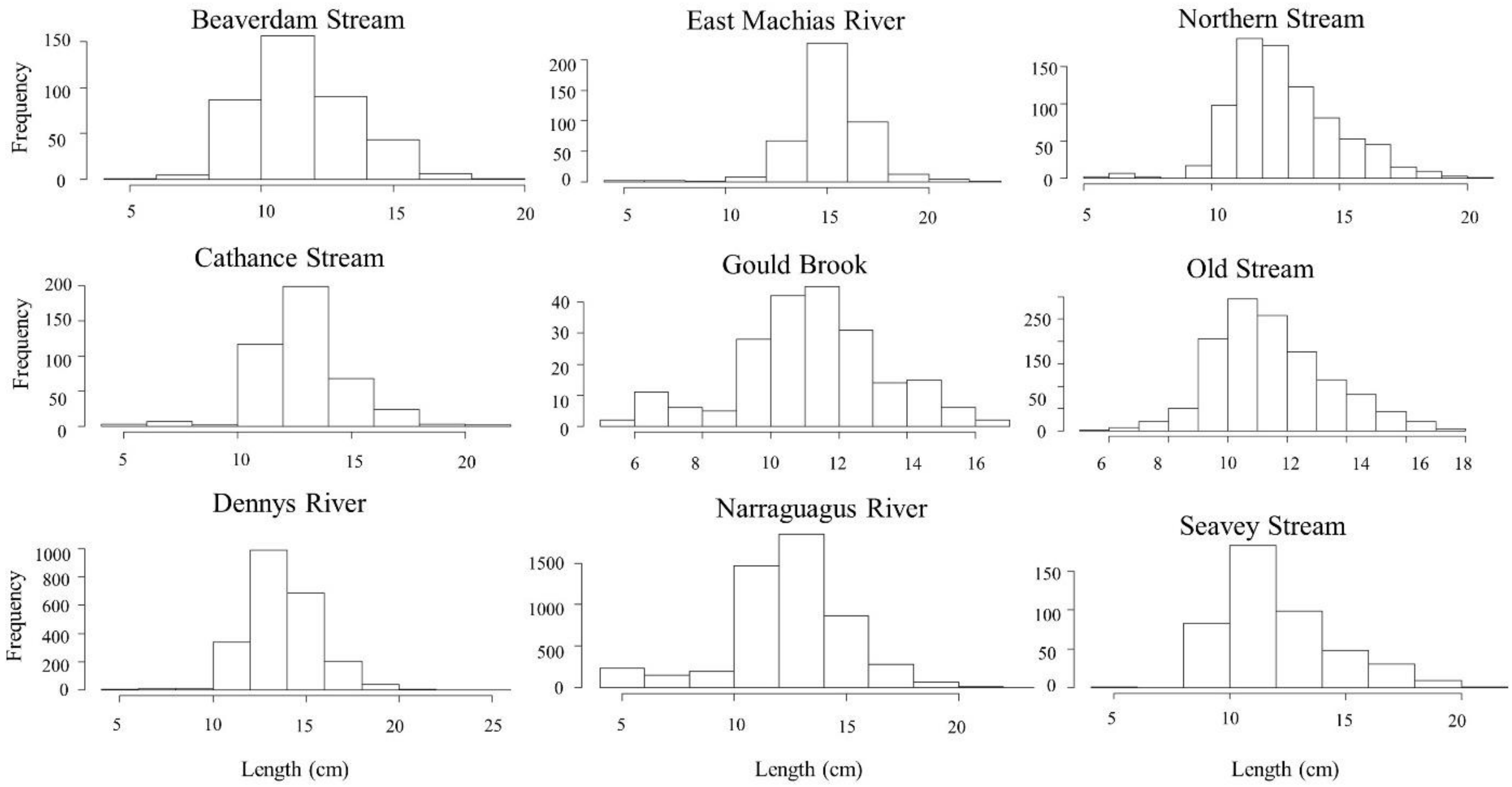


Figure 3.3 Histograms of juvenile Atlantic salmon length by stream for individuals included in the analyses.

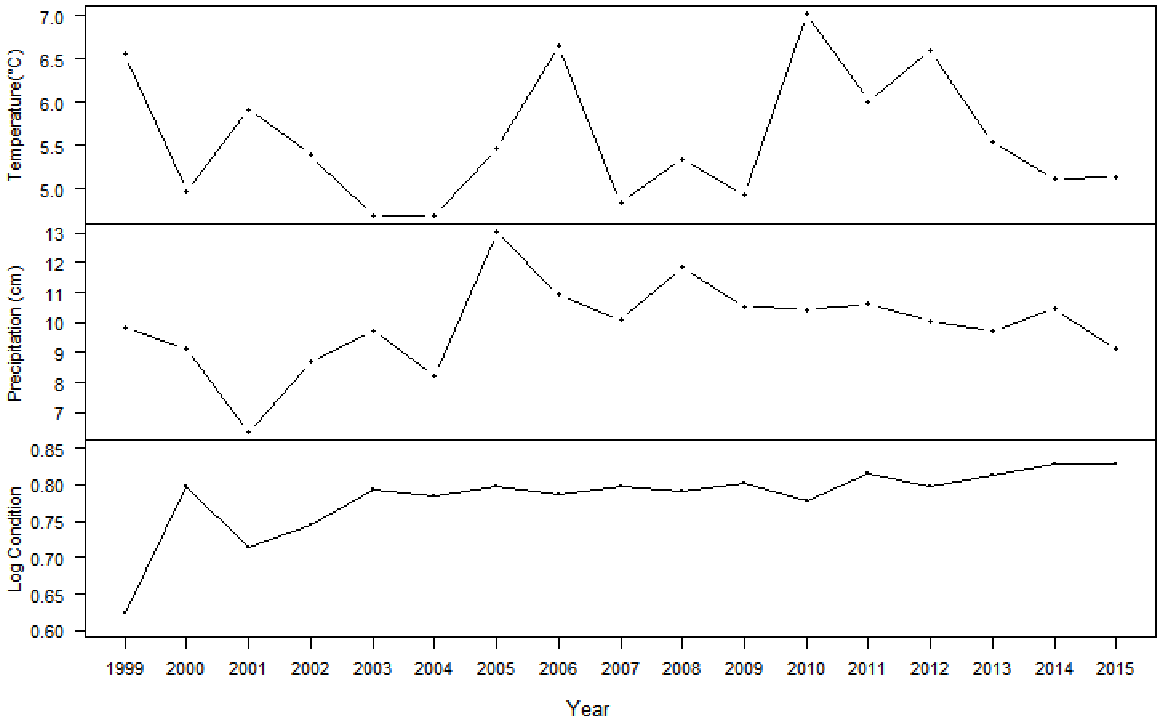


Figure 3.4 Average annual temperature (°C), precipitation (cm), and Atlantic salmon condition (Log_e +1) factor for Dennys River between 1999 and 2015.

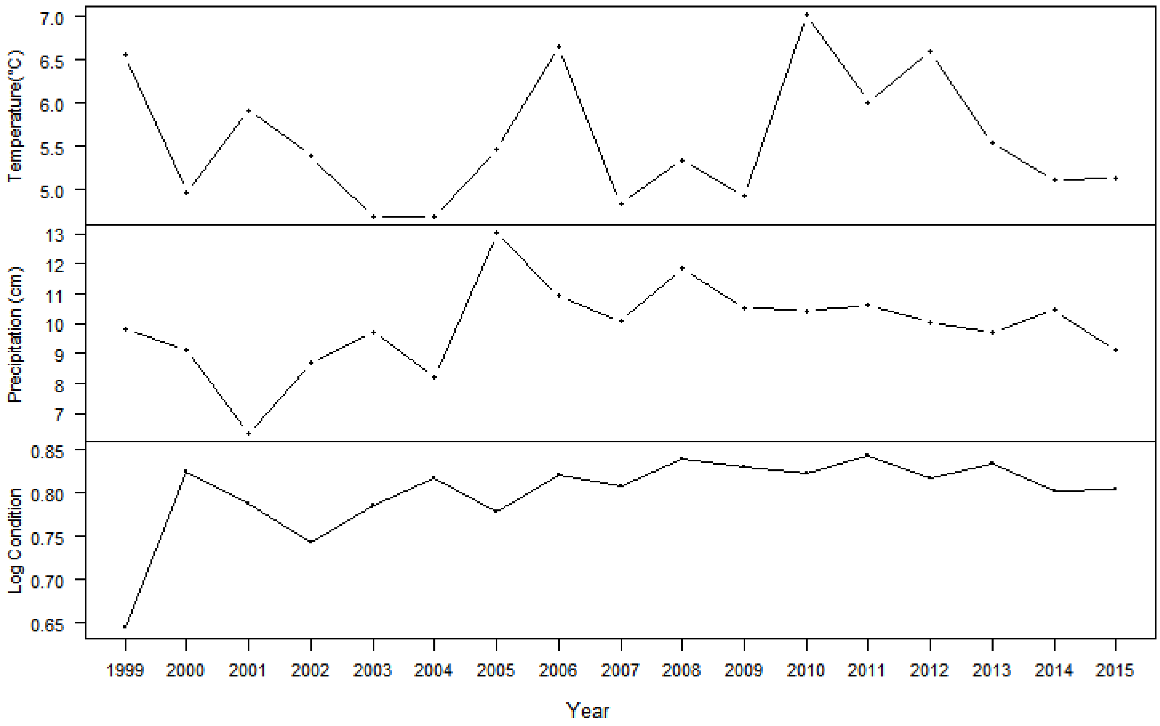


Figure 3.5 Average annual temperature (°C), precipitation (cm), and Atlantic salmon condition (Log_e +1) factor for East Machias River between 1999 and 2015.

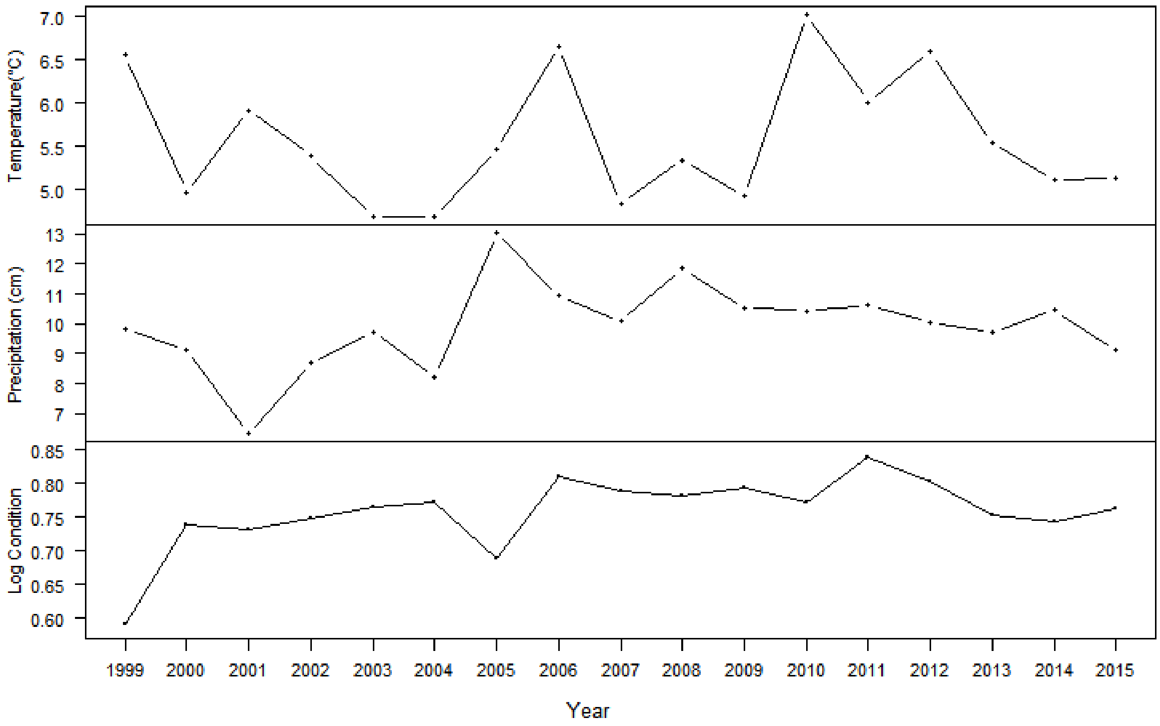


Figure 3.6 Average annual temperature (°C), precipitation (cm), and Atlantic salmon condition (Log_e +1) factor for Seavey Stream between 1999 and 2015.

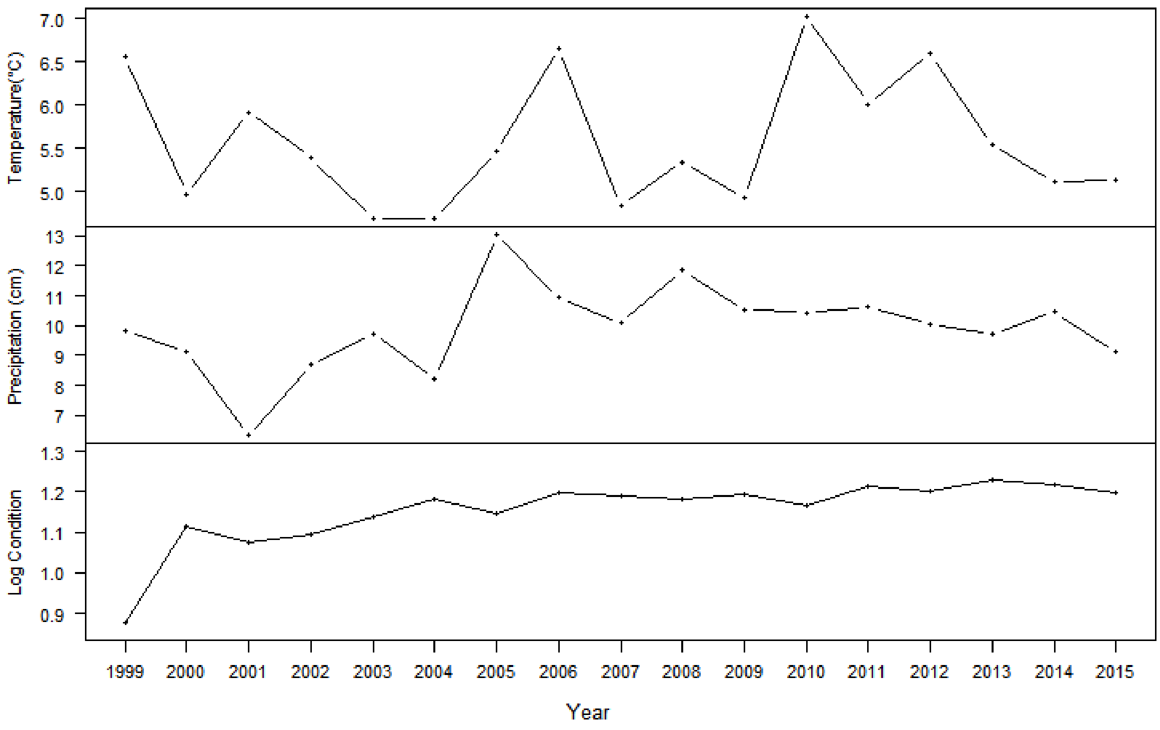


Figure 3.7 Average annual temperature (°C), precipitation (cm), and Atlantic salmon condition (Log_e +1) factor for all streams combined between 1999 and 2015.

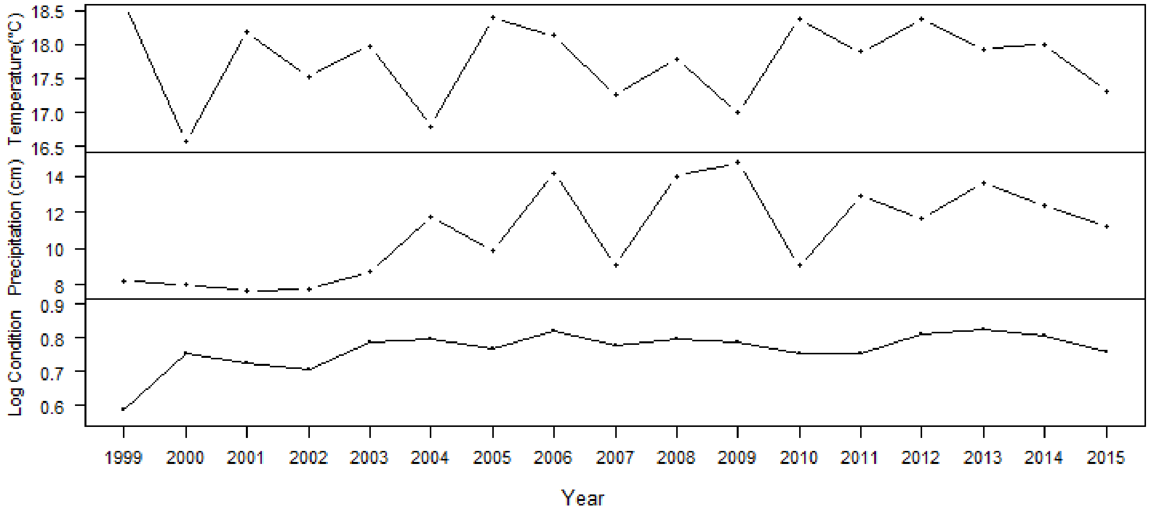


Figure 3.8 Seasonally averaged summer temperature (°C) and precipitation (cm), along with average Atlantic salmon condition (Log_e +1) factor for Beaverdam Stream between 1999 and 2015.

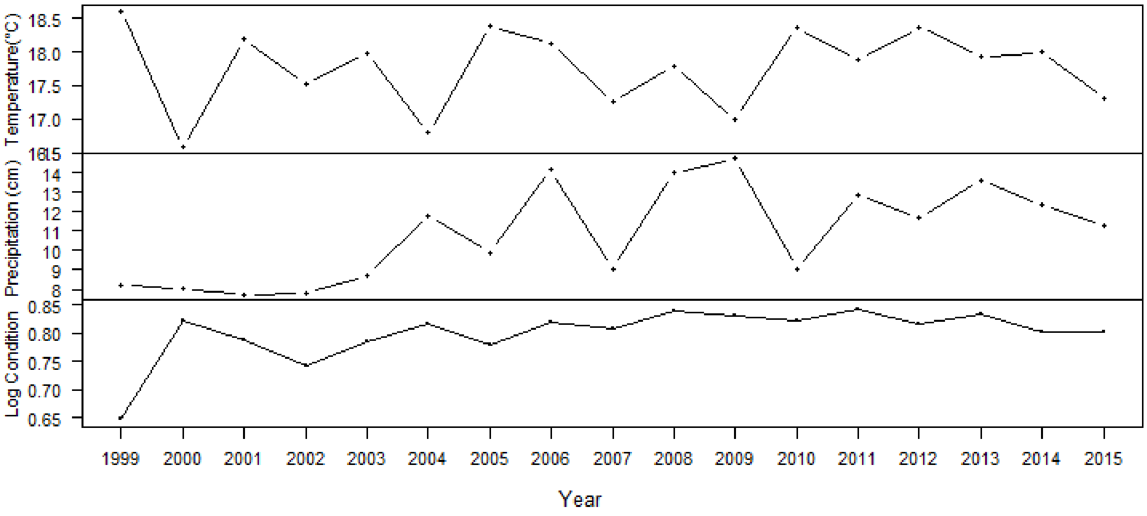


Figure 3.9 Seasonally averaged summer temperature (°C) and precipitation (cm), along with average Atlantic salmon condition (Log$_e$ +1) factor for the East Machias River between 1999 and 2015.

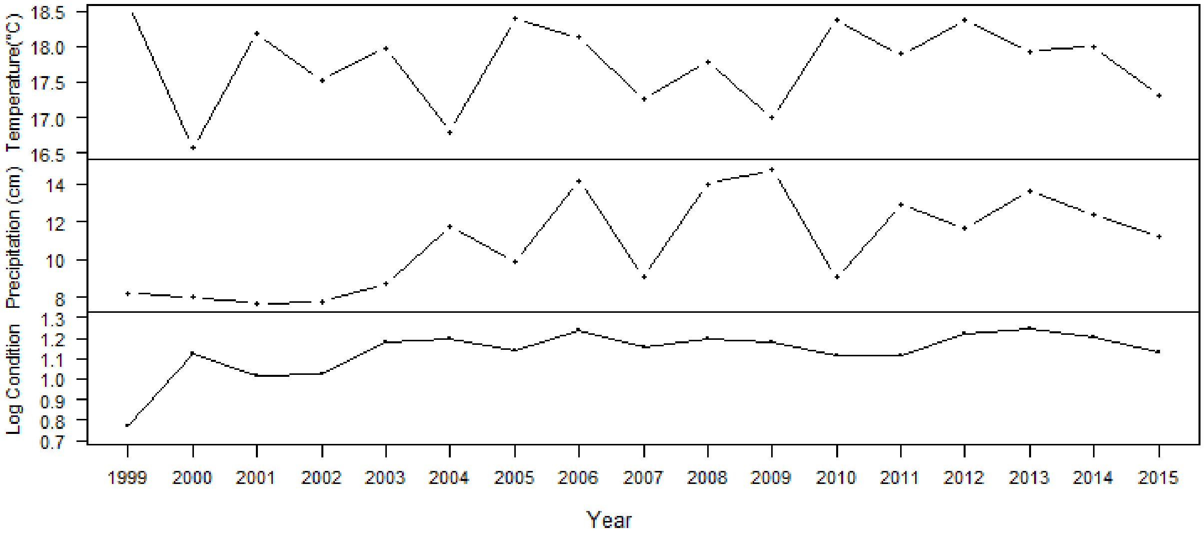


Figure 3.10 Seasonally averaged summer temperature (°C) and precipitation (cm), along with average Atlantic salmon condition (Log$_e$ +1) factor for all streams combined between 1999 and 2015.

CHAPTER 4

BOTTOM-UP EFFECTS OF NORTHERN CRAYFISH, *FAXONIUS VIRILIS*, INCREASE ATLANTIC SALMON, *SALMO SALAR*, PREY IN MAINE RIVERS

Introduction

Predation in freshwater environments can lead to shifts in the distribution, abundance, and diversity of prey (Stenroth and Nyström 2003, Nilsson et al. 2012), resulting in indirect effects that cascade from one trophic level to the next and ultimately impact food web dynamics (Carpenter et al. 1987, Mcqueen et al. 1989, Rosemond et al. 2001). Therefore, consumer presence and interactions between consumers can influence community structure (De Bernardi 1981, Polis and Holt 1992) as well as carbon and nutrient cycling (Vanni et al. 2002, McIntyre et al. 2008). Furthermore, intraguild interactions can shape community assemblages (Wallace and Webster 1996, Covich et al. 1999) and affect basal resources that sustain stream food webs (Cummins 1974, Stevenson et al. 1996, Mancinelli et al. 2007). For instance, predation by benthic versus drift feeding fish often has contrasting influences over prey resources, with benthic feeders having a stronger impact on invertebrate assemblage and abundance compared to drift feeders (Dahl and Greenberg 1996, Dahl 1998, Miyasaka and Nakano 1999). Moreover the impact of stream dwelling fish on invertebrate communities are altered by competition among fish species (Hanson and Leggett 1986, Mittelbach 1988, Diehl 1992, Flecker 1992, Leduc et al. 2015) and with large-bodied invertebrates such as crayfish and shrimp (Soluk and Collins 1988, Pringle and Hamazaki 1998, Huhta et al. 1999, Turner et al. 1999). However, many taxa are both predators as well as consumers of detritus or algae (Momot 1995, Pringle and Hamazaki 1998) and less is known about how interactions between these omnivores and predatory fish alter top-down control of freshwater ecosystems.

Here I investigate the food-web implications of interactions between omnivorous crayfish and predatory Atlantic Salmon, *Salmo salar* (Holm 1989, Griffiths et al. 2004, Findlay et al. 2014). Atlantic salmon, Gulf of Maine, Distinct Population Segment, are a Federally Endangered Species and Maine currently harbors the last wild populations of Atlantic salmon in the United States (Buchsbaum et al. 2005, Saunders et al. 2006, Schmitt 2015). Juvenile salmon spend approximately 1-3 years in Maine streams, where they are predators of macroinvertebrates and occasionally smaller fish (Fay et al. 2006). In comparison, crayfish are omnivores that can act as shredders, scavengers, grazers, and predators (Momot 1995). Crayfish impact multiple trophic levels simultaneously (Nyström et al. 1996, Whitledge and Rabeni 1997, Geiger et al. 2005) and may function as a keystone species (Creed, Robert P. 1994, Nyström et al. 1996, Whitledge and Rabeni 1997, Joaquín Gutiérrez-Yurrita et al. 1998, Woodward et al. 2008, Phillips et al. 2009).

Fish and crayfish share a complex dynamic that extends through multiple life stages of each species (Reynolds 2011). Crayfish first prey upon fish eggs and even small fish (Miller and Savino 1992, Findlay et al. 2014). When juvenile fish become larger, both organisms often occupy similar niches where they compete for shelter and prey (Stenroth and Nyström 2003, Hirsch and Fischer 2008, Peay et al. 2009) and when fish become large enough, they often prey upon crayfish (Hepworth and Duffield 1987, Rabeni 1992). This suggests that Atlantic salmon are likely interacting with crayfish in Maine streams in multiple ways. Yet limited knowledge exists regarding salmon and crayfish interactions or the impacts of these two important macroconsumers on stream macroinvertebrate assemblages, algal production, and the breakdown of terrestrial detritus.

We conducted an in-situ stream channel experiment to examine the roles and interactive effects of Atlantic salmon and northern crayfish, *Faxonius virilis* (formerly *Orconectes*), a species common to Maine streams since the 1970's (Crocker 1979, Martin 1997). Stream channels naturally colonized with invertebrates were populated with salmon, crayfish, or both salmon and crayfish individuals. The design enabled us to investigate 1) macroinvertebrate community responses in both cobble and leaf substrate, and 2) indirect effects of these consumers on algal growth and leaf breakdown rates. Within these broad objectives we tested several hypotheses. First, given that both salmon and crayfish function as predators but vary in feeding modes (Momot 1995, Fay et al. 2006), we hypothesized that the impact of these consumers on macroinvertebrate community structure would differ between species. Salmon are primarily drift feeders (Wańkowski 1981) and as such they are likely to have stronger impacts on mobile prey in cobble substrates compared to invertebrates found in leaf packs. Crayfish are also benthic predators and shredders (Bobeldyk et al. 2010, Dunoyer et al. 2014), which suggests they would have a stronger impact on leaf pack invertebrates than those on cobble substrate.

Our second hypothesis was that these differences in the effects of salmon and crayfish on invertebrate communities would have cascading effects on basal resources. Given crayfish both consume detritus and potentially alter leaf pack invertebrate communities, we expected them to have a stronger impact on leaf breakdown rates than salmon. In contrast, cobble-dwelling invertebrates are especially vulnerable to salmonids who both consume invertebrates and alter their grazing behavior, so we predicted increased algal biomass in the presence of Atlantic salmon. Despite the fact that crayfish function as detritivores (Momot 1995), they are often described as impacting algal pathways by consuming grazers (Lodge et al. 1994). Therefore, we expected to see increased algal biomass when crayfish were present. Finally, interactions between salmon and crayfish could lead to novel effects on both invertebrate and basal resources, either through agonistic encounters that depress feeding (Stein and Magnuson 1976) or by facilitation of drift feeding fish by benthic activity of crayfish (Holm 1989). Therefore, we included salmon and crayfish interactions as a factor in our analyses.

Methods

We examined the roles of Atlantic salmon and northern crayfish in Maine streams within stream channels (n=24) placed in a third order forested stream (Sunkhaze Stream, Milford, Maine). Stream channels were subject to the same environmental conditions (i.e. flow, water depth, and temperature) as the rest of the surrounding stream. Stream temperature from trial start to end date ranged from 15.3 - 27.6°C, with a mean temperature of 21.4°C. The channels (measuring 183 x 46 x 23 cm) were constructed out of a wood U-shaped frame and a corrugated plastic bottom (Figure 4.1). Mesh (6 mm openings) attached at both ends allowed for stream water to flow through the channel and a 2 mm mesh lid allowed access into the channels (Haghkerdar et al. 2019). Channel substrate was provided by adding a bed of small cobbles (6 – 12cm diameter), two leaf packs suspended from the channel frame, four white porcelain tiles (5.08 x 5.08cm) placed equidistant throughout the stream channel, and four large cobbles (approximately 15-17cm diameter) to provide shelter. Channels were installed 19-20 June 2018, 3 weeks prior to the experiment to enable the colonization by macroinvertebrates through open mesh ends. We supplemented natural colonization by adding the contents of one 0.16m^2 Surber sample to each channel that had been collected downstream of the experimental reach. Surber contents were added to the upstream end of each stream channel and a D-net held at the end of the channel for 30 seconds following the addition allowed us to return any invertebrates that initially drifted out of the channel.

Juvenile Atlantic salmon (n=36, range of length 5.5-7.0cm, median length 6.3cm, mean length 6.34cm± 0.37 S.D.) were provided by Green Lake Hatchery in Ellsworth, Maine, while northern crayfish (n=36, range of length 3.2 – 7.5cm, median length 4.2cm, mean length 4.69cm±1.38 S.D.) were captured in minnow traps baited with beef liver that were placed at the field site overnight. On 9 July 2018, salmon were acclimated to stream conditions and were held in live wells. In order to obtain individual-specific data during the trial, fish were marked using VIE tagging protocols (McFarlane et al. 1990, Frederick 1997, Olsen and Vøllestad 2001) and crayfish carapaces were marked with nailpolish. At the time of tagging on 14 July 2018, length and weight measurements were recorded. Salmon and crayfish were then placed into one of the following treatments: Atlantic salmon only (n=4 individuals), northern crayfish only (n=4 individuals), or a combination of Atlantic salmon and northern crayfish (n=2 salmon, 2 crayfish); we also had a control containing neither species. We acknowledge that, because overall density of consumers did not vary, this experimental design does not allow us to distinguish between interspecific effects of crayfish from overall density-dependent effects. All treatments were replicated 6 times and were randomized across 6 blocks, each containing one stream channel per treatment. Stream channels were then left undisturbed for approximately 3 weeks aside from routine channel inspections to clear the mesh ends every 1-3 days.

On 2 August 2018, stream channels were systematically broken down and removed from the stream. Starting with the block furthest downstream, fish and crayfish were first removed from the channels using a net. Fish were euthanized with a lethal dose of buffered MS-222 before being placed on ice. Crayfish were removed from stream channels and immediately placed on ice. Both weight (g) and length (cm) measurements for fish (fork length) and crayfish (total length) were recorded again, allowing us to assess growth as change in mass over time. We collected invertebrate samples from both the cobble lining the stream channel as well as the leaf packs fixed in each channel. Cobbles lining the bottom of the channel were rinsed over a 500-µm mesh sieve to collect colonized insects that were preserved in 70 percent ethanol for later identification. Leaf packs (including invertebrates) and algae tiles were placed on ice and frozen for further analysis. Leaf packs were then thawed and invertebrate samples were picked from the leaves and preserved in 70 percent ethanol. Invertebrate samples from both the cobble and leaf pack samples were identified to family using standard taxonomic keys (Peckarsky et al. 1990, Merritt et al. 2008) as small instars of many taxa prevented reliable identification to genus.

Leaf Litter Decay Rate

After all invertebrates had been picked from the leaf pack samples, the leaves were placed in a 1mm sieve and washed to remove any remaining fine particulate organic matter (FPOM). The remaining leaves or coarse particulate organic matter (CPOM), were dried to constant mass (48h at 60 ^{o}C) to obtain dry weight, combusted at 550 ^{o}C for 4h, and then reweighed to enable the calculation of ash-free dry mass (AFDM). We then calculated rate of decay of the leaf litter (Benfield 2007) for the duration of the experiment whereby decay, *k* =

$$1 * \left(ln \left(\frac{Final\ AFDM\ (g)\ /\ Initial\ AFDM\ (g)}{Duration\ of\ Experiment\ (days)} \right) \right)$$

In order to address whether crayfish density may be impacting leaf litter decay rate we also calculated per capita decay rate. Mean *k* from the control treatment served as a baseline value (i.e., breakdown in the absence of salmon or crayfish) and was substracted from from the mean *k* for the crayfish and SxC treatments at the block level. This difference was then divided by the number of crayfish individuals in both the SxC (2 individuals) and crayfish only treatment (4 individuals), yielding a per capita *k* value.

Algal Biomass

Tiles were frozen for approximately one year and were thawed before being processed. The four tiles per channel were pooled into two sets of two, with each pair of tiles added to a whirlpack with 20mL of 90% buffered ethanol for 18h to extract Chlorophyll-*a* pigments. Concentrations were determined through standard acidification spectrophotometric method for Chl*a* analysis (Eaton et al. 2005). Algal biomass, was expressed as µg Chl*a* / cm^2.

Salmon and Crayfish Stomach Contents

We quantified salmon and crayfish diet to document the functional feeding roles that individuals assumed in the experimental venue and whether diet composition was altered by the presence of competitors. Salmon and crayfish individuals were thawed and the contents of their stomachs were removed and preserved in 70% ethanol. All invertebrates sampled from the salmon stomach contents were identified to the level of family. Crayfish stomach contents were preserved in 70% ethanol in individual 3 dram vials and stained using Congo Red. Congo Red is an effective method for staining animal material that may otherwise be indistinguishable from other stomach contents (Wissinger et al. 2018). Stained stomach contents were examined under a microscope at 100x resolution using a Sedgewick-Rafter Counting Chamber slide (Wildco®). One row was randomly selected using a random number table and 7 consecutive grids in that row were examined. For each grid, the amount of coarse plant debris (> 1 µm), amorphous material, algal cells, and invertebrate material (stained red) was quantified. To provide a sample representative of the entire vile, 3 samples were processed for each vial and averaged per individual for statistical analysis.

Statistical Analysis

All analyses were conducted using R, version 3.4.4. Generalized linear models (GLM) were conducted to determine the main and interactive effects of salmon and crayfish presence on algal biomass, leaf litter decay rates, as well as invertebrate richness and evenness in the cobble and leaf pack samples. Block was initially included in all models and was retained in the final models if block was significant ($P < 0.05$) and it improved model fit (adjusted R^2). Richness was calculated using the 'Rarefy' package in R to account for differences in total invertebrate abundance among channels, while Pielou's equitability (Shannon index divided by the log of the number of species) was calculated to represent evenness using the R package, 'Vegan.' Since there were two leaf packs per channel, all samples were averaged per stream channel for all leaf pack analyses. Furthermore, mean per-capita leaf litter decay rates were compared between crayfish only and SxC treatments using a two-sample t-test. MANOVA with Pillai's trace as a test of significance was used to test the effect of salmon presence on crayfish diet to account for non-independence among diet categories (coarse plant debris, amorphous material, algal cells, and invertebrate material). Data for crayfish diet were proportional and a logit transformation was performed which improved the normality of the data. We used GLM to test for a difference in salmon growth between salmon only and salmon x crayfish treatments, treatment block was included as a main effect. Meanwhile, GLM was used to compare crayfish growth in the presence and absence of salmon, treatment block was also included as a factor in the model.

We examined the impact of crayfish and salmon presence and their interactive effects on the invertebrate community in both the cobble and leaf pack samples with a Redundancy Analysis (RDA) on a Hellinger-transformed family abundance matrix using the R-package 'Vegan.' The RDA model included crayfish presence, salmon presence, and the salmon x crayfish interaction term as factors. The significance of these terms in the model was tested with a permANOVA with 999 permutations and channel as the unit of replication. Given that there was a significant effect of treatment block for the cobble samples, we ran a Partial Redundancy Analysis (pRDA) with block as a conditioning factor in the cobble analysis. Lastly, RDA on a Hellinger-transformed species abundance matrix was used to examine the impacts of crayfish presence on salmon diet. This analysis reflected the higher level of taxonomic resolution in salmon diet contents compared to broad diet categories for crayfish. Given that there was a significant effect of treatment block, we ran a Partial Redundancy Analysis with crayfish presence and block as a conditioning factor with 999 permutations.

Results

Cobble Invertebrate Samples

Overall, 6,292 invertebrates were sampled from the cobble. Heptageniidae, Ameletidae, and Ephemeridae mayflies (Ephemeroptera), and Chironomids (Diptera) comprised the majority of the invertebrates found in the cobble. The next most abundant taxon was Megaloptera, followed by Plecoptera and Trichoptera. Odonata, Zygoptera, Gastropoda, Decapoda, and Coleoptera were present in low abundance (*Appendix A1*). The partial redundancy analysis revealed that crayfish presence effected the community composition of invertebrates in the cobble samples (Table 4.1), with a higher abundance of Heptageniidae, Ameletidae mayflies and Perlidae stoneflies in stream channels with crayfish (Figure 4.2A). In contrast, no effect was found for Atlantic salmon on invertebrate communities and no interaction between these two factors was detected (Table 4.1, Figure 4.2A). Invertebrate species richness in cobble substrate was lower when crayfish were present (Table 4.1, Figure 4.3) and post hoc Tukey tests revealed this difference was likely driven by differences between salmon only and crayfish only treatments (p=0.0906). Both salmon presence and salmon x crayfish interaction had no influence on species richness (Table 4.1). Family evenness was not influenced by any of the treatments (Table 4.1).

Leaf Pack Invertebrate Samples

Overall, 5,043 invertebrates were sampled from the leaf packs Chironomids (Diptera) Leptophlebiidae and Heptageniidae (Ephemeroptera) comprised the majority of the invertebrates found in the leaf pack samples. The next most abundant taxon was Zygoptera, followed by Megaloptera, Trichoptera, Plecoptera, and Coleoptera. The remaining taxa collected all equaled approximately 1 percent of the total inverts collected: Decapoda, Gastropoda, Hemiptera, Hydrachnidia, Odonata, and Oligochaeta (*Appendix A2*). The redundancy analysis revealed that crayfish had a significant effect on invertebrate community composition in the leaf pack samples, with a higher abundance of Calopterygidae damselflies and Ameletidae mayflies (Table 4.2, Figure 4.2B), while no effect was found for Atlantic salmon, block, or interactive effects between salmon and crayfish presence (Table 4.2). We found that invertebrate species richness was not impacted by crayfish or salmon presence and no interaction between crayfish and salmon presence was found (Table 4.2). Similarly for evenness, we found no effect of crayfish or salmon presence and no interaction between crayfish and salmon presence (Table 4.2).

Salmon and Crayfish Stomach Content Samples

Overall, 131 organisms were counted in the salmon stomachs. We found that salmon diet was largely categorized by Ephemeroptera, Diptera, and Trichoptera. In the treatments where crayfish were present, Ephemeroptera comprised 76 percent of the stomach content items sampled and only 45 percent for salmon in salmon only treatments. Interestingly, in salmon only treatments, 30 percent of salmon diet was Diptera and when crayfish were present 10 percent of the diet was Diptera. However, RDA indicated that crayfish presence did not significantly impact the composition of salmon diet ($F_{(1,9)}$ = 2.31, p=0.071, Figure 4.4). Furthermore, crayfish presence did not affect the richness ($F_{(1,9)}$ 1.92, p=0.224) or evenness ($F_{(1,9)}$ = 2.84, p=0.169) of invertebrates found in salmon stomachs. Similarly, crayfish diet was not impacted by the presence of salmon (Table 4.3). Overall, the majority of the crayfish stomach contents were amorphous material and coarse plant detritus (Figure 4.5).

We found an effect of crayfish presence on salmon growth (F=6.81, df= 1,31, p=0.013), whereby salmon lost mass in salmon only treatments and gained mass in SxC treatments; no effect of treatment block was found (F=1.14, df=1,31, p=0.293; Figure 4.6). Crayfish growth was not impacted by the presence of salmon (F=0.492, df=1,9, p=0.500) or block (F=0.076, df=1,9, p=0.789).

Algal Biomass and Leaf Litter Decay Rate

Crayfish presence was associated with a significant increase in algal abundance (F=4.91, df=1,20, P=0.04, Figure 4.7A), but there was no effect of salmon (F=1.30, df=1,20, p=0.27) or of the interaction between crayfish and salmon (F=0.0535, df=1,20, p=0.81941). Leaf decay rate significantly increased when crayfish were present (F=25.60, df=1,20, $p \leq 0.001$), and decreased when salmon were present (F=6.41, df=1,20, p=0.016), and we found an interactive effect between salmon and crayfish presence on decay rate (F=6.97, df=1,20, p=0.016) whereby the positive effects of crayfish on breakdown rate was stronger when salmon were absent (Figure 4.7b). Nevertheless, mean per-capita decay rate was twice as high in the SxC treatment compared to the crayfish only treamtent ($t_{(7.35)}$= -2.199, p = 0.06).

Discussion

Our results suggest that the crayfish, a large invertebrate consumer filling multiple functional roles, has greater influence in Maine stream food webs than predatory juvenile

Atlantic salmon. As we predicted, composition of the benthic invertebrate community in both the cobble and leaf pack samples were impacted by the presence of crayfish. We also found that crayfish presence resulted in lower familial richness of invertebrates on cobble samples but not leaf packs. Finally, the effect of crayfish was largely independent of salmon presence, with the only significant salmon x crayfish interaction detected in leaf litter breakdown rates.

Responses in Cobble Substrate

Faxonius crayfish are known for having extensive impacts to the biotic and abiotic elements of the systems they inhabit (Phillips et al. 2009, Roessink et al. 2017). While the impact of crayfish on stream food webs could be driven by differences in metabolic rates between crayfish and other stream organisms, aquatic invertebrates and aquatic ecothermic vertebrates (i.e., fish) have similar mass specific metabolic rates 0.56 (W kg^{-1}) and 0.38 (W kg^{-1}), respectively (Makarieva et al. 2008). Matching our predictions, more algal biomass was found in treatments when crayfish were present compared to when salmon were present. Initially we surmised that predation of scrapers by crayfish may have caused a simple trophic cascade resulting in increased algal biomass; as this has previously been shown before for *Faxonius* species including the northern crayfish (Lodge et al. 1994, Luttenton et al. 1998). Crayfish presence could have also impacted algal biomass through trait mediated-indirect effects by altering prey behavior through scaring (Lima 1998, Peckarsky et al. 2008, Matassa and Trussell 2011) which led to decreased feeding and increased algae. However, crayfish are known predators of benthic invertebrates and invertebrate material is a known component of the crayfish diet (Momot 1995, Whitledge and Rabeni 1997, Joaquín Gutiérrez-Yurrita et al. 1998). While we too found that invertebrate material was present in crayfish stomachs (Figure 4.5), scrapers (Heptagenaiidae and Ameletidae mayflies) were more abundant in our cobble samples when crayfish were present compared to when they were absent. These compositional changes could be in response to an increase in algal resources which may have in turn facilitated higher abundances of predatory Perlidae stoneflies that regularly feed on smaller mayfly taxa (Peckarsky 1979).

Increased algal biomass when crayfish are present could be due to bioturbation, a process where crayfish activity removes silt and dead cells from patches of algal growth, leading to increased algal productivity (Whitmore 1997). Dorn and Wojdak (2004) found increased Chl*a* in ponds containing northern crayfish and rusty crayfish for the first year of a two-year experiment; they attributed this to bioturbation from crayfish. Stenroth and Nyström (2003), also found increased algal biomass when signal crayfish were present, which they attributed to crayfish activity. If bioturbation is the main driver of increased algal biomass in crayfish treatments, we would expect that invertebrate taxa tracking algal resources, such as scraping mayflies, may decrease the presence of rarer, less competitive invertebrates and result in the lower richness observed in the cobble samples (Figure 4.3). Several other studies have also associated reduced richness and changes in invertebrate abundance with crayfish presence (Nyström et al. 1996, Stenroth and Nyström 2003, Nilsson et al. 2012).

Interestingly, we did not find any evidence that salmon influenced algal biomass via trophic cascades. This was surprising given that numerous studies have shown the direct and indirect impacts of salmonids on scrapers often results in increased algal biomass (McIntosh and Townsend 1996, Rosenfeld 2000, Simon and Townsend 2003, Buria et al. 2010). However, top-down pressure from predators is not the only factor regulating algal biomass in streams. A combination of nutrient and light availability, along with grazing pressure, could moderate algal biomass (Rosemond 1993, Rosemond et al. 1993) and the strength of cascades (Pace et al. 1999).

For example, Biggs et al. (2000) found that algal production was sensitive to nutrient enrichment despite strong influence of Galaxidae predators on invertebrates in New Zealand streams. Similarly, Winkelmann et al. (2014) found that despite the strong top-down impacts of benthivorous fish on algal production, cascades were regulated by light availability, with top-down effects dominating during fall months when light availability was lowest. Thus, algal biomass in our stream channels may have been limited by light or nutrient availability and not by grazing, dampening top-down control often associated with salmonid presence. The increase in algal biomass in channels with crayfish lends further weight to this hypothesis, as the removal of light limitation is the primary mechanism by which bioturbation by crayfish promotes algal growth.

Salmon diet was dominated by Ephemeroptera, and Diptera, mainly chironomids. While not all mayflies sampled from salmon stomachs could be identified to the level of family, Ameletidae comprised the majority of the identifiable samples. Perhaps the lower abundance of Ameletidae mayflies in the absence of crayfish, could partially be explained by their large representation in salmon diet. Other Ephemeroptera included Ephemeridae, Heptageniidae, and Leptophlebiidae. These results are similar to that of Keeley and Grant (1997), who found that chironomids and mayflies made up a large portion of juvenile salmon diet in New Brunswick, Canada. However, unlike their findings, the majority of organisms consumed in our study were mayflies rather than chironomids. Salmon predominately feed on drifting invertebrates and drift feeding predators often have less of an impact on benthic prey compared to benthic feeding predators (Dahl and Greenberg 1996, Dahl 1998). Thus, it was not entirely unexpected that salmon presence did not yield significant effects on invertebrate community composition, richness, or evenness in either the cobble or the leaf pack samples.

Despite the fact that crayfish have been shown to compete with fish species for prey items (Momot 1995, Phillips et al. 2009), salmon diet was not altered by the presence of crayfish. In fact, no significant differences in invertebrate composition, richness, or evenness at the level of order were detected for the samples collected from salmon's stomachs. We suspect that a drastic shift in community composition or in the abundance of key prey items would have to occur, in order for crayfish presence to significantly impact salmon diet. However, there is the potential that salmon could actually benefit from crayfish presence. In examining the interactions between juvenile Atlantic salmon and noble crayfish, *Astacus Astacus*, Holm (1989) found that crayfish activity in the sediment actually forced prey items to become resuspended in the drift and this led to an increase in salmon growth. We also found increased salmon growth in enclosures where crayfish were present (Figure 4.6). Increased salmon growth could be due to a release of intraspecific competition in crayfish SxC treatment, a non-linear response to salmon density, crayfish activity making prey items readily available for salmon consumption via physical disturbance or facilitation of algal production, or a combination of these factors. However, since we did not conduct a density-controlled experiment we are unable to distinguish between these underlying mechanisms. Nevertheless, the absence of a salmon effect on macroinvertebrate abundance and community composition provides evidence that salmon did not depress the availability of prey resources when at high abundance (i.e., 4 salmon per channel), which suggests release from density-dependent intraspecific competition in salmon was less likely responsible for higher salmon growth with crayfish.

Responses in Leaf Packs

Significantly higher rates of detrital breakdown occurred in channels with crayfish (Figure 4.7B) which is consistent with several other studies (Bobeldyk et al. 2010, Moore et al.

2012, Dunoyer et al. 2014). However, two mechanisms can generate this effect: crayfish directly consuming detritus, or an indirect effect mediated by changes in shredder abundance or behavior in response to crayfish that cascaded through the food web. Only 3 taxa described as shredders were found in the leaf packs, Diptera *Tipulidae*, Plecoptera *Capniidae,* and Plecoptera *Leuctridae,* and they were found in low abundance in comparison to other functional feeding groups such as collector-gatherers, predators, and scrapers. Rather, the significant effect of crayfish on leaf pack invertebrate communities was primarily through an increase in Leptophlebidae, which feed on FPOM and biofilms, Ameletidae scrapers, and predatory Perlidae stoneflies and Calopterygidae damselflies. Thus there is no strong evidence that crayfish altered shredder assemblages in leaf packs. Furthermore, analysis of the crayfish stomach contents revealed mostly amorphous material or unidentifiable organic matter not belonging to insects, followed by course plant detritus, algal cells, and invertebrate material (Figure 4.5). These findings are consistent with other studies which report large quantities of amorphous material and suggest that detritus plays an important role in *Faxonius* diet (Momot et al. 1978, Whitledge and Rabeni 1997, Evans-White et al. 2001). Low abundance of shredders in the leaf packs coupled with the large quantity of detritus found in the crayfish stomachs, suggest that crayfish were the leading cause of increased leaf litter breakdown observed when crayfish were present; lending support to the notion that crayfish often function as shredders in stream environments (Anderson and Sedell 1979, Usio and Townsend 2001).

Crayfish had the largest effect on leaf litter breakdown in treatments when salmon were absent compared to treatments where both species were present. This suggests that allochthonous detritus is a more important source of energy for crayfish than for salmon. Our results were not surprising considering that isotope analysis has suggested that crayfish cluster closer to detrital and algal food sources than fish (Evans-White et al. 2001). We did find an interaction between salmon and crayfish presence, where we observed increased detrital breakdown in crayfish treatments when salmon were absent. We observed an intermediate amount of detrital breakdown when both species were present. We suspected the significantly moderate effects of leaf litter breakdown when both species were present could have been an artifact of the reduced crayfish and salmon density in the SxC treatment. Indeed, we found that per capita breakdown in the SxC treatment was twice as high as the crayfish only treatment. This suggests that crayfish feeding rates were density-dependent and food may have become limiting when 4 individuals were present in the crayfish only treatment compared to when only 2 individuals were present in the SxC treatment.

Conclusion

Given that Maine harbors the last wild populations of Atlantic salmon in the United States, insight into the role that juveniles assume during their time in freshwater is integral to informing adaptive management policies surrounding their recovery. Our results suggest that while salmon function as predators of macroinvertebrates in streams, crayfish impact multiple trophic levels simultaneously and therefore, have a larger impact to stream food webs and basal resources than juvenile Atlantic salmon. While crayfish are often regarded as a keystone species and even ecosystem engineers (Creed and Reed 2004), our results indicate that crayfish at the very least, demonstrated the potential to be an important macroconsumer in Maine's freshwater systems. We found that crayfish altered macroinvertebrate community composition. As shredders, crayfish increased the rate of leaf litter breakdown, influencing detrital pathways and potentially increasing allochthonous carbon flow through food webs. Lastly, crayfish activity also increased algal biomass despite evidence that some grazing by crayfish occurred. These activities appeared to have increased salmon growth, leading us to posit that stronger bottom-up processes may occur when crayfish are present. Thus, the impact that crayfish have on algal biomass and detrital breakdown could extend beyond carbon and nutrient cycling by promoting increased availability of macroinvertebrates important to salmon diet. These results demonstrate the role that consumer interactions have in shaping stream food webs and highlight the importance of maintaining diverse assemblages in Maine Streams.

Table 4.1 Results of the partialRDA analysis examining community composition (conditioned on experimental block) and GLM analyses examining richness and evenness for invertebrates sampled in the cobble substrates.

Source of Variation	df	F	P
pRDA- Community Composition			
Crayfish Presence	1,19	6.26	<0.01
Salmon Presence	1,19	0.99	0.39
Crayfish x Salmon Presence	1,19	0.28	0.99
GLM - Richness			
Crayfish Presence	1,20	6.62	0.02
Salmon Presence	1,20	1.08	0.31
Crayfish x Salmon Presence	1,20	0.06	0.81
GLM - Evenness			
Crayfish Presence	1,20	1.35	0.26
Salmon Presence	1,20	0.14	0.71
Crayfish x Salmon Presence	1,20	0.22	0.64

Table 4.2 Results of the RDA analysis examining community composition and GLM analyses examining richness and evenness for invertebrates sampled in the leaf packs.

Source of Variation	df	F	P
RDA - Community Composition			
Crayfish Presence	1,19	3.87	<0.01
Salmon Presence	1,19	0.52	0.88
Crayfish x Salmon Presence	1,19	0.51	0.87
GLM - Richness			
Crayfish Presence	1,20	1.13	0.30
Salmon Presence	1,20	<0.01	0.99
Crayfish x Salmon Presence	1,20	1.90	0.18
GLM - Evenness			
Crayfish Presence	1,20	2.18	0.16
Salmon Presence	1,20	0.21	0.65
Crayfish x Salmon Presence	1,20	2.23	0.16

Table 4.3 MANOVA results testing the effect of salmon presence on the percentage of algal cells, amorphous detritus, coarse plant detritus, and invertebrate material found in crayfish stomach samples.

Response Variable	df	Pillai	F	P
Multivariate				
All categories	1,10	0.50	0.26	0.24
Univariate				
Algal Cells	1,10	NA	0.10	0.75
Amorphous Detritus	1,10	NA	0.16	0.69
Coarse Plant Detritus	1,10	NA	0.14	0.72
Invertebrate Material	1,10	NA	3.06	0.11

Figure 4.1 Image of stream channels placed in Sunkhaze Stream, Maine, during the Summer 2018 field season. Stream channels were placed directly in streams to mimic natural stream conditions. Mesh attached at both ends allowed for stream water to flow through the channel, supporting natural invertebrate colonization and a mesh lid allowed access to the channels.

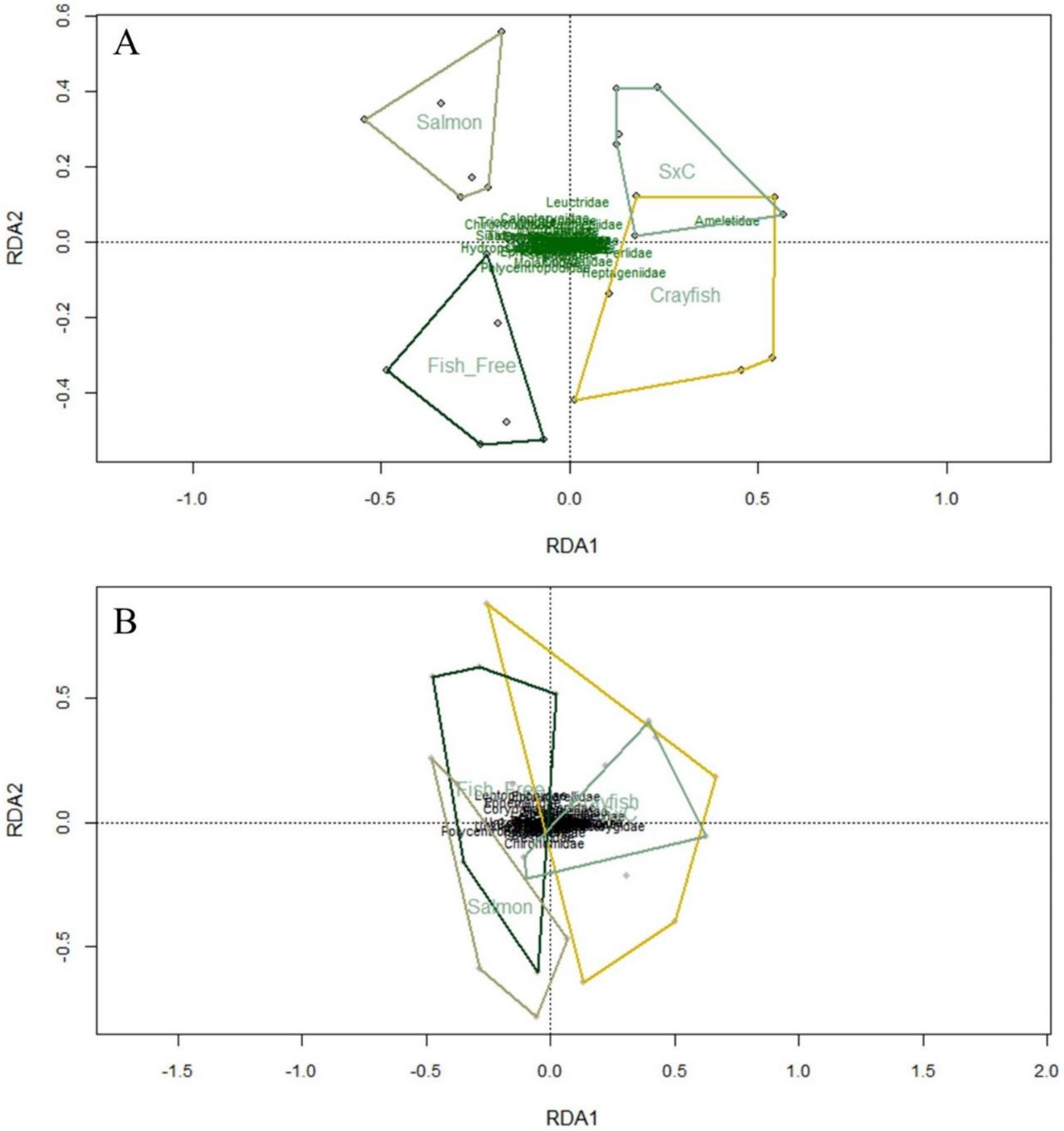


Figure 4.2 Results of the partialRDA analysis examining the effects of salmon and crayfish presence on familial invertebrate community composition in the cobble samples (Panel A) and in the leaf packs (Panel B). Polygons enclose all 6 replicates for each treatment combination.

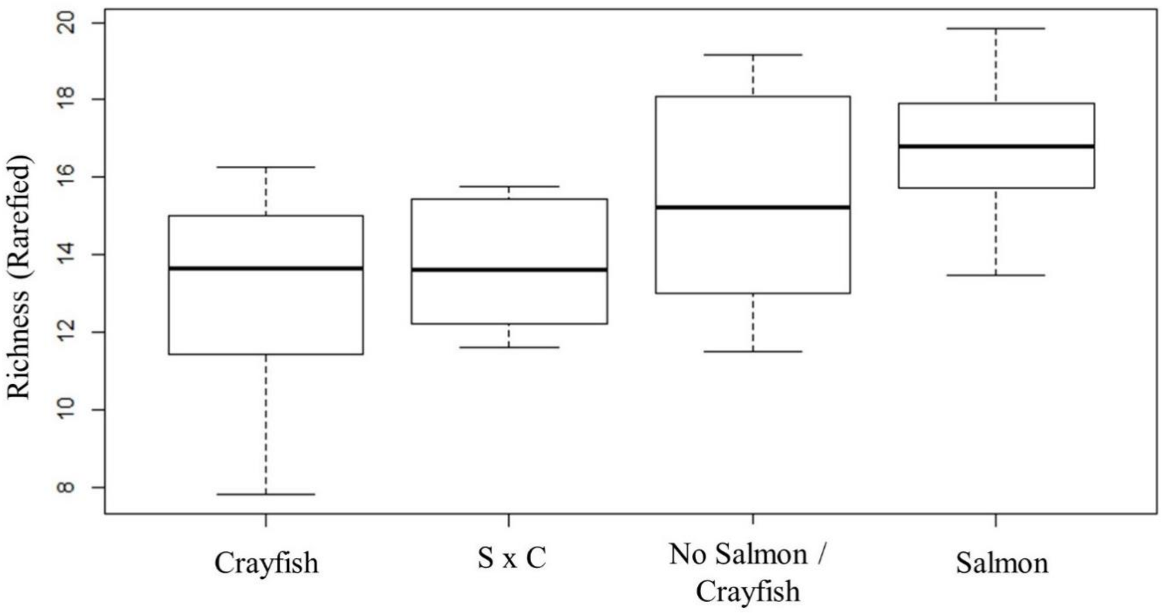


Figure 4.3 Effect of salmon and crayfish presence on invertebrate familial richness (rarefied) found in the cobble substrate.

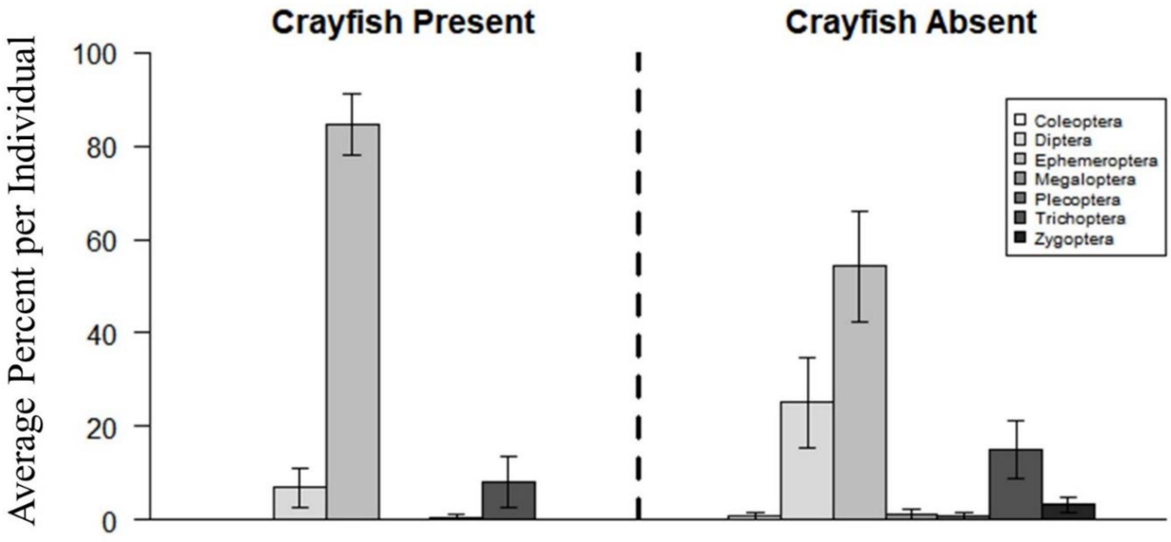


Figure 4.4 Average percentage of invertebrate orders (± 1 SE) identified in salmon stomachs in stream channels with and without crayfish.

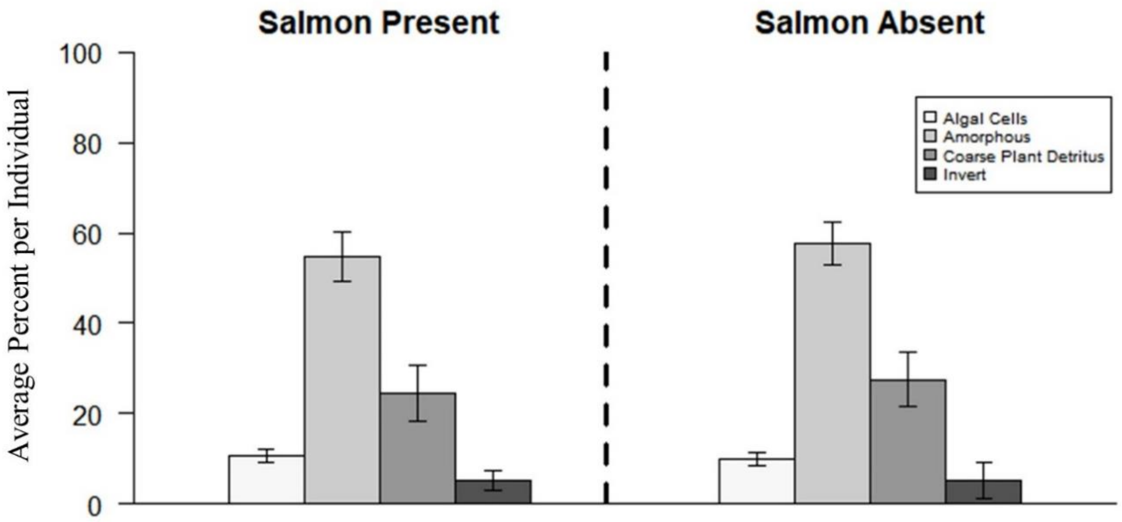


Figure 4.5 Average percentage of algal cells, amorphous detritus, coarse plant detritus (cell walls visible), and invertebrate material found in the stomachs of northern crayfish individuals in the presence and absence of salmon.

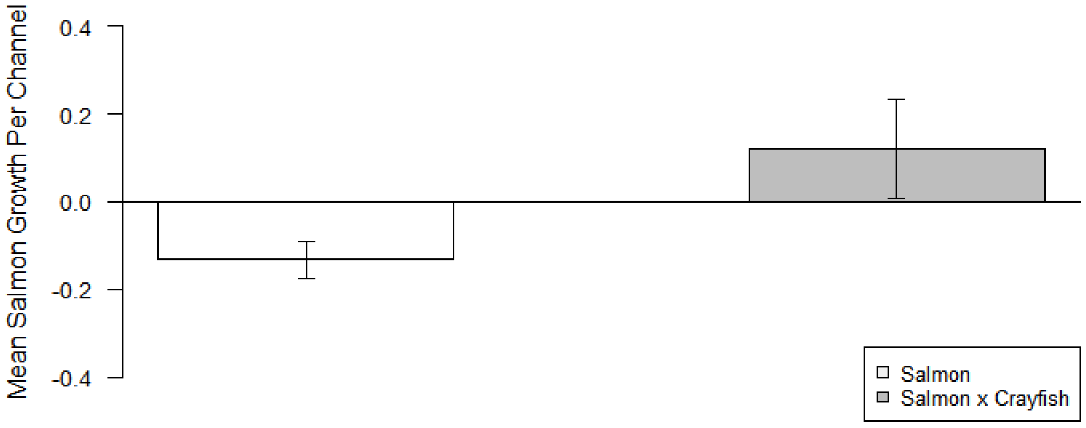


Figure 4.6 Mean growth (change in mass over time) when crayfish were present in the Salmon x Crayfish treatment compared to when crayfish were absent in the salmon only treatment.

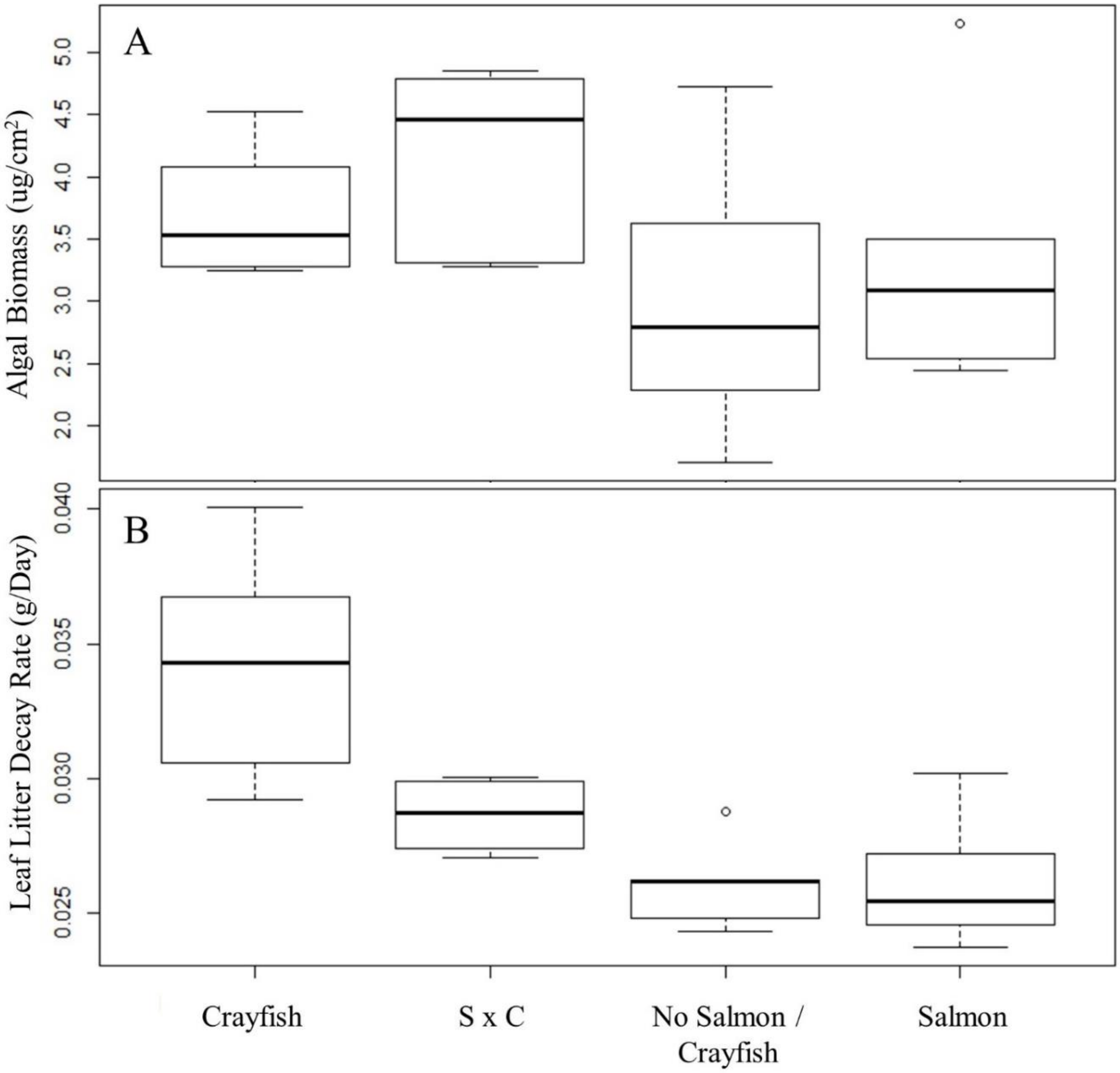


Figure 4.7 Algal biomass (ug/cm^2), Chl*a*, accumulation on tiles over the duration of the experiment by crayfish and salmon presence. (Panel A) Decay rate, *k*, of leaf litter in stream channels in the presence and absence of salmon and crayfish (Panel B).

CHAPTER 5

GENERAL CONCLUSION AND IMPLICATIONS

The case of Atlantic salmon declines over the last century, and the looming threat of Atlantic salmon extinction, serves as a stark reminder that society has strong influence over the well-being of natural systems. This situation also serves as a reminder that humans can greatly affect the recovery of species in peril. This is exemplified through the efforts of multiple agencies and organizations working to restore salmon waters and increase chances of survival for juvenile Atlantic salmon in Maine streams (NMFS 2016, U.S. Fish and Wildlife Service and NMFS 2018). However, changes in climate continue to pose serious risk to freshwater fisheries (Ficke et al. 2007, Woodward et al. 2016), including Atlantic salmon populations (Hare et al. 2016). The results presented here reinforce that both temperature and precipitation impact juvenile Atlantic Salmon in Maine streams. Warming waters could force Atlantic salmon to perform in sub-optimal conditions that impede their ability to effectively compete for resources. Furthermore, outcomes from experiments in Chapter 2 suggest that non-native smallmouth bass have the potential to outcompete Atlantic salmon as waters continue to warm. This is concerning given that the range of smallmouth bass is expected to expand as temperatures rise, which could increase the likelihood of salmon and bass interactions in streams.

However, it is important to recognize that not all salmonid populations will be uniformly impacted by changes in climate. This was demonstrated by the results of Chapter 3, which investigated whether juvenile Atlantic salmon condition was correlated with annual changes in temperature and precipitation at multiple scales over a 16-year period. For example, I found that annual temperature was a better predictor of salmon condition in the Dennys River, while annual precipitation with a 1-year lag was a better predictor of salmon condition in East Machias River and Seavey Stream. Therefore, the results presented here reinforce the importance of scale when studying salmon populations (Poff and Huryn 1998) and reinforce suggestions that studies need to capture trends across multiple spatial and temporal scales to gain a more complete picture of the population and community dynamics of freshwater organisms (Fausch et al. 2002, Snelder and Biggs 2002).

Lastly, species interactions at the stream level often drive patterns in community composition that influence the structure and functioning of stream food webs (Carpenter et al. 1985, Rosemond et al. 1998). Changes in climate that threaten to alter the performance of individuals could lead to alterations in the functioning of stream food webs (Winder and Schindler 2004, Woodward et al. 2010, 2016). The final portion of my work in Chapter 4 aimed to better understand the relative influence of predatory juvenile Atlantic salmon and omnivorous northern crayfish on invertebrate community structure and basal resources in Maine streams. I found that omnivorous crayfish assuming multiple trophic roles have a larger impact to stream food webs and basal resources than predatory Atlantic salmon. These results further suggest that strong bottom-up processes occur when crayfish are present, whereby increased algal growth could promote the availability of macroinvertebrates important to salmon diet, highlighting the importance of maintaining species diversity in stream food webs.

Earth’s freshwater environments are fascinatingly complex systems with a wealth of diversity that easily captures the imagination. However, as climate across the globe continues to change, it is important to recognize the inherent intricacies of ecological systems and acknowledge that humans do not exist in isolation from the natural world. Just as the availability of freshwater along with the resources it contains impacts humanity, the decisions that we make can have lasting and profound impacts on the systems we rely so heavily upon for our own survival. Unfortunately, for Atlantic salmon in the United States, this story is known all too well. While perfect solutions are unlikely to exist for multifaceted issues stemming from climate change, including that of Atlantic salmon recovery, informed decisions based on sound science underlie practical and attainable management goals. It is my hope that the research presented herein informs future adaptive management and policy efforts striving to enhance the resiliency of endangered Atlantic salmon populations in Maine streams. While the path to Atlantic salmon recovery may be arduous, it is not one that salmon must travel alone.

REFERENCES

Abrams, P. A. 2000. The evolution of predator-prey interactions: Theory and evidence. Annual Review of Ecology and Systematics 31:79–105.

Allan, J., and A. Benke. 2005. Rivers of North America. Elsevier Academic Press, Burlington, MA.

Allen, J. D., and M. M. Castillo. 2007. Stream Ecology Structure and function of running waters. Second Edi. Springer, Dorderecht, Netherlands.

Anderson, M. T., J. M. Kiesecker, D. P. Chivers, and A. R. Blaustein. 2001. The direct and indirect effects of temperature on a predator–prey relationship. Canadian Journal of Zoology 79:1834–1841.

Angilletta, M. J., R. B. Huey, and M. R. Frazier. 2010. Thermodynamic Effects on Organismal Performance: Is Hotter Better? Physiological and Biochemical Zoology 83:197–206.

Angilletta, M. J., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. Journal of Thermal Biology 27:249–268.

Arnold, G. P., P. W. Webb, and B. H. Holford. 1991. The role of the pectoral fins in station-holding of Atlantic salmon parr (Salmo salar L.). Journal of Experimental Biology 156:625–629.

Bacon, P. J., S. C. F. Palmer, J. C. MacLean, G. W. Smith, B. D. M. Whyte, W. S. C. Gurney, and A. F. Youngson. 2009. Empirical analyses of the length, weight, and condition of adult Atlantic salmon on return to the Scottish coast between 1963 and 2006. ICES Journal of Marine Science 66:844–859.

Bar-Yam, Y. 1997. Dynamics of Copmlex Systems. Westview Press, New York, New York.

Benfield, E. F. 2007. Decomposition of leaf material. Page (R.F. Hauer and G. A. Lamberti, Eds.) Methods in Steam Ecology. Academic Press, Burlington, MA.

De Bernardi, R. 1981. Biotic interactions in freshwater and effects on community structure. Italian Journal of Zoology 48:353–371.

Biggs, B. J. F., S. N. Francoeur, A. D. Huryn, R. Young, C. J. Arbuckle, and C. R. Townsend. 2000. Trophic cascades in streams: effects of nutrient enrichment on autotrophic and consumer benthic communities under two different fish predation regimes. Canadian Journal of Fisheries and Aquatic Sciences 57:1380–1394.

Bobeldyk, A. M., G. A. Lamberti, and A. M. Bobeldyk. 2010. Stream Food Web Responses To a Large Omnivorous Invader, Orconectes Rusticus (Decapoda, Cambaridae). Crustaceana 83:641–657.

Boisclair, D. 2004. The status of Atlantic salmon (Salmo salar): Populations and habitats. Canadian Journal of Fisheries and Aquatic Sciences 61:2267–2270.

Brett, J. R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (Oncorhynchus nerkd). Integrative and Comparative Biology.

Brett, J. R., and T. D. D. Groves. 1979. Physiological energetics. Fish physiology 8:280–352.

Brooker, M. P., D. L. Morris, and R. J. Hemsworth. 1977. Mass Mortalities of Adult Salmon , Salmo salar , in the R . Wye , 1976. Journal of Applied Ecology 14:409–417.

Buchsbaum, R., J. Pederson, and W. E. Robinson. 2005. The decline of fisheries in New England: evaluating the impact of overfishing, contamination, and habitat degradation. Page MIT Sea Grant College Program Publication.

Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30:492–507.

Buria, L., R. Albariño, V. D. Villanueva, B. Modenutti, and E. Balseiro. 2010. Does predation by the introduced rainbow trout cascade down to detritus and algae in a forested small stream in Patagonia? Hydrobiologia 651:161–172.

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23–35.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading Trophic Interactions and Lake Productivity. BioScience 35:634–639.

Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cochran, and J. J. Elser. 1987. Regulation of lake primary productivity by food web structure. Ecology 68:1863–1876.

Clarke, A., and K. P. P. Fraser. 2004. Why does metabolism scale with temperature? Functional Ecology 18:243–251.

Climate Reanalyzer. (n.d.). . (https://ClimateReanalyzer.org), Climate Change Institute, University of Maine, USA.

Comte, L., L. Buisson, M. Daufresne, and G. Grenouillet. 2013. Climate-induced changes in the distribution of freshwater fish: Observed and predicted trends. Freshwater Biology 58:625–639.

Comte, L., and G. Grenouillet. 2013. Do stream fish track climate change? Assessing distribution shifts in recent decades. Ecography 36:1236–1246.

Copeland, T., and K. A. Meyer. 2011. Interspecies synchrony in salmonid densities associated with large-scale bioclimatic conditions in central Idaho. Transactions of the American Fisheries Society 140:928–942.

Covich, A. P., M. A. Palmer, and T. A. Crowl. 1999. The role of benthic invertebrate species in freshwater ecosystems: Zoobenthic species influence energy flows and nutrient cycling. BioScience 49:119–127.

Creed, Robert P., J. 1994. Direct and Indirect Effects of Crayfish Grazing in a Stream Community. Ecology 75:2091–2103.

Creed, R. P., and J. M. Reed. 2004. Ecosystem engineering by crayfish in a headwater stream community. Journal of the North American Benthological Society 23:224–236.

Crocker, D. W. 1979. The Crayfish of New England. Proceedings of the Biological Society of Washington 92:225–252.

Cummins, K. W. 1974. Structure and Function of Stream Ecosystems. BioScience 24:631–641.

Cutts, C. J., N. B. Metcalfe, and A. C. Taylor. 1998. Aggression and growth depression in juvenile Atlantic salmon: The consequences of individual variation in standard metabolic rate. Journal of Fish Biology 52:1026–1037.

Dahl, J. 1998. Effects of a benthivorous and a drift-feeding fish on a benthic stream assemblage. Oecologia 116:426–432.

Dahl, J., and L. Greenberg. 1996. Nordic Society Oikos Impact on Stream Benthic Prey by Benthic vs Drift Feeding Predators : A Meta-Analysis. Oikos 77:177–181.

Dell, A. I., S. Pawar, and V. M. Savage. 2014. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. Journal of Animal Ecology 83:70–84.

Desmarais, B. A., and J. J. Harden. 2013. Testing for zero inflation in count models: Bias correction for the Vuong test. Stata Journal 13:810–835.

Diehl, S. 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology 73:1646–1661.

Dorn, N. J., and J. M. Wojdak. 2004. The role of omnivorous crayfish in littoral communities. Oecologia 140:150–159.

Dudley, R. W., and G. A. Hodgkins. 2002. Trends in streamflow, river ice, and snowpack for coastal river basins in Maine during the 20th century.

Dugdale, S. J., J. Franssen, E. Corey, N. E. Bergeron, M. Lapointe, and R. A. Cunjak. 2016. Main stem movement of Atlantic salmon parr in response to high river temperature. Ecology of Freshwater Fish 25:429–445.

Dunoyer, L., L. Dijoux, L. Bollache, and C. Lagrue. 2014. Effects of crayfish on leaf litter breakdown and shredder prey: Are native and introduced species functionally redundant? Biological Invasions 16:1545–1555.

Eaton, A. D., L. S. Clesceri, and A. E. Greenberg. 2005. Standard methods for the examination of water and wastewater. 21st edition. APHA, Washington, D.C.

Einum, S., and I. A. Fleming. 1997. Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. Journal of Fish Biology 50:634–651.

Einum, S., and I. A. Fleming. 2000. Selection against late emergence and small offspring in Atlantic salmon (Salmo salar). Evolution 54:628–639.

Elliott, J. M. 1976. The Energetics of Feeding, Metabolism and Growth of Brown Trout (Salmo trutta L.) in Relation to Body Weight, Water Temperature and Ration Size. The Journal of Animal Ecology:273–289.

Elliott, J. M. 1991. Tolerance and resistance to thermal stress in juvenile Atlantic salmon, Salmo salar. Freshwater Biology 25:61–70.

Elliott, J. M., and J. A. Elliott. 2010. Temperature requirements of Atlantic salmon Salmo salar, brown trout Salmo trutta and Arctic charr Salvelinus alpinus: Predicting the effects of climate change. Journal of Fish Biology 77:1793–1817.

Evans-White, M., W. K. Dodds, L. J. Gray, and K. M. Fritz. 2001. A comparison of the trophic ecology of the crayfishes (Orconectes nais (Faxon) and Orconectes neglectus (Faxon)) and the central stoneroller minnow (Campostoma anomalum (Rafinesque)): Omnivory in a tallgrass prairie stream. Hydrobiologia 462:131–144.

Falke, J. A., and K. D. Fausch. 2010. From Metapopulations to Metacommunities: Linking Theory with Empirical Observations of the Spatial Population Dynamics of Stream Fishes. American Fisheries Society Symposium 73:207–233.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 63:441–451.

Fausch, K. D. 1998. Interspecific competition and juvenile Atlantic salmon (Salmo salar): on testing effects and evaluating the evidence across scales. Canadian Journal of Fisheries and Aquatic Sciences 55:218–231.

Fausch, K. D., Y. Taniguchi, S. Nakano, G. D. Grossman, and C. R. Townsend. 2001. Flood Disturbance Regimes Influence Rainbow Trout Invasion Success among Five Holarctic Regions. Ecological Applications 11:1438–1455.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to Riverscapes: Bridging the Gap between Research and Conservation of Stream Fishes. BioScience 52:483–498.

Fay, C., M. Bartron, S. Craig, A. Hecht, J. Pruden, R. Saunders, T. Sheehan, and J. Trial. 2006. Status Review for Anadromous Atlantic Salmon (Salmo salar) in the United States. Report to the National Marine Fisheries Service and U.S. Fish and Wildlife Service.:294.

Fenderson, O. C., and M. R. Carpenter. 1971. Effects of crowding on the behaviour of juvenile hatchery and wild landlocked Atlantic salmon (Salmo salar L.). Animal Behaviour 19:439–447.

Fernandez, I. J., C. Schmitt, E. Stancioff, S. D. Birkel, A. Pershing, I. J. ; Fernandez, C. ; Schmitt, S. D. ; Birkel, A. ; Pershing, J. ; Runge, G. L. Jacobson, and P. A. Mayewski. 2015. Maine' s Climate Future: 2015 Update Repository Citation.

Fernandez, I., C. Schmitt, S. Birkel, E. Stancioff, A. Pershing, J. Kelley, J. Runge, G. Jacobson, and P. Mayewski. 2020. Maine's Climate Future 2020 Update.

Ficke, A. D., C. A. Myrick, and L. J. Hansen. 2007. Potential impacts of global climate change on freshwater fisheries. Reviews in Fish Biology and Fisheries 17:581–613.

Findlay, J. D., W. D. Riley, and M. Lucas. 2014. Signal crayfish (Pacifastacus leniusculus) predation upon Atlantic salmon (Salmo salar) eggs. Aquatic conservation: marine and freshwater ecosystems 25:250–258.

Finstad, A. G., and B. Jonsson. 2012. Effect of incubation temperature on growth performance in Atlantic salmon. Marine Ecology Progress Series 454:75–82.

Flecker, A. S. 1992. Fish predation and the evolution of invertebrate drift periodicity: Evidence from neotrohpical streams. Ecology1 73:438–448.

Forseth, T., M. A. Hurley, A. J. Jensen, and J. M. Elliott. 2001. Functional models for growth and food consumption of Atlantic salmon parr, Salmo salar, from a Norwegian river. Freshwater Biology 46:173–186.

Frederick, J. L. 1997. Evaluation of flourescent elastomer injection as a method for marking small fish 61:399–408.

Geiger, W., P. Alcorlo, A. Baltanás, and C. Montes. 2005. Impact of an introduced Crustacean on the trophic webs of Mediterranean wetlands. Biological Invasions 7:49–73.

Giannico, G. R., and S. G. Hinch. 2003. The effect of wood and temperature on juvenile coho salmon winter movement, growth, density and survival in side-channels. River Research and Applications 19:219–231.

Gibson, R. J. 1993, March. The Atlantic salmon in fresh water: spawning, rearing and production. Kluwer Academic Publishers.

Gibson, R. J. 2015. Some behavioural and ecological factors affecting distribution, biomass and production of juvenile Atlantic salmon. Ecology of Freshwater Fish 24:397–411.

Gilbert, B., T. D. Tunney, K. S. Mccann, J. P. Delong, D. A. Vasseur, V. Savage, J. B. Shurin, A. I. Dell, B. T. Barton, C. D. G. Harley, H. M. Kharouba, P. Kratina, J. L. Blanchard, C. Clements, M. Winder, H. S. Greig, and M. I. O'Connor. 2014. A bioenergetic framework for the temperature dependence of trophic interactions. Ecology Letters 17:902–914.

Gregory, R., J. Arvai, and L. R. Gerber. 2013. Structuring Decisions for Managing Threatened and Endangered Species in a Changing Climate. Conservation Biology 27:1212–1221.

Griffiths, S. W., P. Collen, and J. D. Armstrong. 2004. Competition for shelter among over-wintering signal crayfish and juvenile Atlantic salmon. Journal of Fish Biology 65:436–447.

Grossman, G. D. 2014. Not all drift feeders are trout: A short review of fitness-based habitat selection models for fishes. Environmental Biology of Fishes 97:465–473.

Grossman, G. D., and T. N. Simon. 2020. Density-dependent effects on salmonid populations: A review. Ecology of Freshwater Fish 29:400–418.

Haghkerdar, J. M., J. R. McLachlan, A. Ireland, and H. S. Greig. 2019. Repeat disturbances have cumulative impacts on stream communities. Ecology and Evolution 9:2898–2906.

Handeland, S. O., A. K. Imsland, and S. O. Stefansson. 2008. The effect of temperature and fish size on growth, feed intake, food conversion efficiency and stomach evacuation rate of Atlantic salmon post-smolts. Aquaculture 283:36–42.

Hanson, J. M., and W. C. Leggett. 1986. Effect of competition between two freshwater fishes on prey consumption and abundance. Canadian Journal of Fisheries and Aquatic Sciences 43:1363–1372.

Hare, J. A., W. E. Morrison, M. W. Nelson, M. M. Stachura, E. J. Teeters, R. B. Griffis, M. A. Alexander, J. D. Scott, L. Alade, R. J. Bell, A. S. Chute, K. L. Curti, T. H. Curtis, D. Kircheis, J. F. Kocik, S. M. Lucey, C. T. McCandless, L. M. Milke, D. E. Richardson, E. Robillard, H. J. Walsh, M. C. McManus, K. E. Marancik, and C. A. Griswold. 2016. A vulnerability assessment of fish and invertebrates to climate change on the northeast u.s. continental shelf. PLoS ONE 11:1–30.

Hayes, J. W., J. D. Stark, and K. A. Shearer. 2000. Transactions of the American Fisheries Society Development and Test of a Whole-Lifetime Foraging and Bioenergetics Growth Model for. Transactions of the American Fisheries Society 129:315–332.

Heggenes, J., and R. Borgstrøm. 1991. Effect of habitat types on survival, spatial distribution, and production of an allopatric cohort of Atlantic salmon, Salmo salar L., under conditions of low competition. Journal of Fish Biology 38:267–280.

Heino, J., R. Virkkala, and H. Toivonen. 2009. Climate change and freshwater biodiversity: Detected patterns, future trends and adaptations in northern regions.

Hendry, A. P., M. T. Kinnison, M. Heino, T. Day, T. B. Smith, G. Fitt, C. T. Bergstrom, J. Oakeshott, P. S. Jørgensen, M. P. Zalucki, G. Gilchrist, S. Southerton, A. Sih, S. Strauss, R. F. Denison, and S. P. Carroll. 2011. Evolutionary principles and their practical application. Evolutionary Applications 4:159–183.

Hepworth, D. K., and D. J. Duffield. 1987. Interactions between an Exotic Crayfish and Stocked Rainbow Trout in Newcastle Reservoir, Utah. North American Journal of Fisheries Management 7:554–561.

Hirsch, P. E., and P. Fischer. 2008. Interactions between native juvenile burbot (Lota lota) and the invasive spinycheek crayfish (Orconectes limosus) in a large European lake. Canadian Journal of Fisheries and Aquatic Sciences 65:2636–2643.

Hodgkins, G. A., R. W. Dudley, and T. G. Huntington. 2005. Summer Low Flows in New England During the 20Th Century. Journal of the American Water Resources Association 41:403–411.

Hodgkins, G. A., I. C. James II, and T. G. Huntington. 2002. Historical changes in lake ice-out dates as indicators of climate change in New England, 1850-2000. International Journal of Climatology 22:1819–1827.

Holm, J. C. 1989. Atlantic salmon parr (Salmo salar) and noble crayfish (Astacus astacus) in duoculture. Aquacultural Engineering 8:79–94.

Horning II, W. B., and R. E. Pearson. 1973. Growth Temperature Requirements and Lower Lethal Temperatures for Juvenile Smallmouth Bass (Micropterus dolomieui). Journal of the Fisheries Research Board of Canada 30:1226–1230.

Huey, R. B., and J. G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. Trends In Ecology & Evolution 4:131–135.

Huey, R. B., and R. D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. Integrative and Comparative Biology 19:357–366.

Hughes, N. F., and L. M. Dill. 1990. Position choice by drift-feeding salmonids: Model and test for Arctic Grayine (Thymallus arcticus) in subarctic mountain streams, interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences:2039–2048.

Huhta, A., T. Muotka, A. Juntunen, and M. Yrjönen. 1999. Behavioural interactions in stream food webs: The case of drift-feeding fish, predatory invertebrates and grazing mayflies. Journal of Animal Ecology 68:917–927.

Huntingford, F. A., D. Aird, P. Joiner, K. E. Thorpe, V. A. Braithwaite, and J. D. Armstrong. 1999. How juvenile Atlantic salmon, Salmo salar L., respond to falling water levels: Experiments in an artificial stream. Fisheries Management and Ecology 6:357–364.

IPCC. 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovern- mental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xi. Cambridge University Press, Cambridge, United Kingdom and New York, NY.

IPCC. 2018. Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of cli. Page In Press.

Isaak, D. J., S. Wollrab, D. Horan, and G. Chandler. 2012. Climate change effects on stream and river temperatures across the northwest U.S. from 1980-2009 and implications for salmonid fishes. Climatic Change 113:499–524.

Jackson, D. A. 2002. Ecological Effects of Micropterus Introductions : the Dark Side of Black Bass. Black Bass: Ecology, Conservation, and Management:221–232.

Joaquín Gutiérrez-Yurrita, P., G. Sancho, M. Á. Bravo, Á. Baltanás, and C. Montes. 1998. Diet of the Red Swamp Crayfish Procambarus clarkii in Natural Ecosystems of the Doñana National Park Temporary Fresh-Water Marsh (Spain). Journal of Crustacean Biology 18:120–127.

Jonsson, B., and N. Jonsson. 2006. Cultured Atlantic salmon in nature : a review of their ecology and interaction with wild fish 1181:1162–1181.

Jonsson, B., and N. Jonsson. 2009. A review of the likely effects of climate change on anadromous Atlantic salmon Salmo salar and brown trout Salmo trutta, with particular reference to water temperature and flow. Journal of Fish Biology 75:2381–2447.

Karmalkar, A. V., and R. S. Bradley. 2017. Consequences of global warming of 1.5 °c and 2 °c for regional temperature and precipitation changes in the contiguous United States. PLoS ONE 12:1–17.

Keeley, E. R., and J. W. A. Grant. 1997. Allometry of diet selectivity in juvenile Atlantic salmon (Salmo salar) 1.

Keenleyside, M. H. A., and F. T. Yamamoto. 1962. Territorial Behaviour of Juvenile Atlantic Salmon (Salmo salar L. Page Source: Behaviour.

Kingsolver, J. G., and R. B. Huey. 2008. Size, temperature, and fitness: Three rules. Evolutionary Ecology Research 10:251–268.

Lake, P. S. 2000. Disturbance , patchiness , and diversity in streams. Journal of the North American Benthological Society 19:573–592.

Lake, P. S. 2003. Ecological effects of perturbation by drought in flowing waters. Freshwater Biology 48:1161–1172.

Lambert, D. 1992. Zero-inflated poisson regression, with an application to defects in manufacturing. Technometrics 34:1–14.

Lawrimore, J. H., M. J. Menne, B. E. Gleason, C. N. Williams, D. B. Wuertz, R. S. Vose, and J. Rennie. 2011. Global Historical Climatology Network - Monthly (GHCN-M), Version 3. [Temperature and Precipitation]. NOAA National Centers for Environmental Information.

Ledger, M. E., and A. M. Milner. 2015. Extreme events in running waters. Freshwater Biology 60:2455–2460.

Leduc, A. O. H. C., E. M. Da Silva, and J. S. Rosenfeld. 2015. Effects of species vs. functional diversity: Understanding the roles of complementarity and competition on ecosystem function in a tropical stream fish assemblage. Ecological Indicators 48:627–635.

Lima, S. L. 1998. Nonlethal Effects in the Ecology of Predator-Prey Interactions. BioScience 48:25–34.

Lindenmayer, D., R. J. Hobbs, R. Montague-Drake, J. Alexandra, A. Bennett, M. Burgman, P. Cale, A. Calhoun, V. Cramer, P. Cullen, D. Driscoll, L. Fahrig, J. Fischer, J. Franklin, Y. Haila, M. Hunter, P. Gibbons, S. Lake, G. Luck, C. MacGregor, S. McIntyre, R. Mac Nally, A. Manning, J. Miller, H. Mooney, R. Noss, H. Possingham, D. Saunders, F. Schmiegelow, M. Scott, D. Simberloff, T. Sisk, G. Tabor, B. Walker, J. Wiens, J. Woinarski, and E. Zavaleta. 2008. A checklist for ecological management of landscapes for conservation. Ecology Letters 11:78–91.

Liu, J., T. Dietz, S. R. Carpenter, C. Folke, M. Alberti, C. L. Redman, S. H. Schneider, E. Ostrom, A. N. Pell, J. Lubchenco, W. W. Taylor, Z. Ouyang, P. Deadman, T. Kratz, and W. Provencher. 2007. Coupled human and natural systems. Ambio 36:639–49.

Lodge, D. M., M. W. Kershner, J. E. Aloi, and A. P. Covich. 1994. Effects of an omnivorous crayfish (Orconectes rusticus) on a freshwater littoral food web. Ecology 75:1265–1281.

Luttenton, M. R., M. J. Horgan, and D. M. Lodge. 1998. Effects of Three Orconectes Crayfishes on Epilithic Microalgae : A Laboratory Experiment. Crustaceana 71:845–855.

MacCrimmon, H. R., and W. H. Robbins. 1981. Influence of temperature, water current, illumination, and time on activity and substrate selection in juvenile smallmouth bass (Micropterus dolomieui). Canadian Journal of Zoology 59:2322–2330.

MacRae, P. S., and D. A. Jackson. 2001. The influence of smallmouth bass (Micropterus dolomieu) predation and habitat complexity on the structure of littoral zone fish assemblages. Canadian Journal of Fisheries and Aquatic Sciences 58:342–351.

Makarieva, A. M., V. G. Gorshkov, B. A. Li, S. L. Chown, P. B. Reich, and V. M. Gavrilov. 2008. Mean mass-specific metabolic rates are strikingly similar across life's major domains: Evidence for life's metabolic optimum. Proceedings of the National Academy of Sciences of the United States of America 105:16994–16999.

Mancinelli, G., M. L. Costantini, and L. Rossi. 2007. Top-down control of reed detritus processing in a lake littoral zone: Experimental evidence of a seasonal compensation between fish and invertebrate predation. International Review of Hydrobiology 92:117–134.

Mangel, M. 1994. Climate change and salmonid life history variation. Deep-Sea Research Part II 41:75–106.

Martin, S. M. 1997. Crayfish of Maine. Northeastern Naturalist 4:165–188.

Matassa, C. M., and G. C. Trussell. 2011. Landscape of fear influences the relative importance of consumptive and nonconsumptive predator effects. Ecology 92:2258–2266.

McCormick, S. D., L. P. Hansen, T. P. Quinn, and R. L. Saunders. 1998. Movement, migration, and smolting of Atlantic salmon (Salmo salar). Canadian Journal of Fisheries and Aquatic Sciences 55:77–92.

McFarlane, G. A., R. S. Wydoski, and E. D. Prince. 1990. External Tags and Marks. American Fisheries Society Symposium 7:9–29.

McIntosh, A. R., and C. R. Townsend. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: A trophic cascade mediated by fish-induced changes to grazer behaviour? Oecologia 108:174–181.

McIntyre, P. B., A. S. Flecker, M. J. Vanni, J. M. Hood, B. W. Taylor, and S. A. Thomas. 2008. Fish distributions and nutrient cycling in streams: Can fish create biogeochemical hotspots? Ecology 89:2335–2346.

Mcqueen, D. J., M. R. S. Johannes, J. R. Post, T. J. Stewart, and R. S. Lean. 1989. Bottom-Up and Top-Down Impacts on Freshwater Pelagic Community Structure. Ecological Monographs 59:289–309.

Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. An Introduction to the Aquatic Insects of North America. Fourth Edi. Kendall Hunt Publishing.

Metcalfe, N. B., F. A. Huntingford, and J. E. Thorpe. 1988. Feeding Intensity , Growth Rates , and the Establishment of Life-History Patterns in Juvenile Atlantic Salmon Salmo salar. Journal of Animal Ecology 57:463–474.

Miller, J. E., and J. F. Savino. 1992. Competition for food between crayfish (Orconectes virilis) and the slimy sculpin (Cottus cognatus). Journal of Freshwater Ecology 7:127–136.

Mills, K. E., A. J. Pershing, T. F. Sheehan, and D. Mountain. 2013. Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. Global Change Biology 19:3046–3061.

Mittelbach, G. G. 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. Ecology 69:614–623.

Miyasaka, H., and S. Nakano. 1999. Effects of drift- and benthic-foraging fish on the drift dispersal of three species of mayfly nymphs in a Japanese stream. Oecologia 118:99–106.

Mohseni, O., H. G. Stefan, and J. G. Eaton. 2003. Global Warming and Potential Changes in Fish Habitat. Environmental Protection 59:389–409.

Momot T, W., and P. L. Hauta. 1995. Effects of growth and mortality phenology on the cohort P/B of the crayfish, Orconectes virilis. Freshwater Crayfish 8:265–275.

Momot, W. T. 1995. Redefining the Role of Crayfish in Aquatic Ecosystems. Reviews in Fisheries Science.

Momot, W. T., H. Gowing, and P. Jones. 1978. The Dynamics of Crayfish and Their Role in Ecosystems 99:10–35.

Moore, J. W., S. M. Carlson, L. A. Twardochleb, J. L. Hwan, J. M. Fox, and S. A. Hayes. 2012. Trophic Tangles through Time? Opposing Direct and Indirect Effects of an Invasive Omnivore on Stream Ecosystem Processes. PLoS ONE 7.

Moore, R. D., D. L. Spittlehouse, and A. Story. 2005. Riparian Microclimate. Journal of the American Water Resources Association 41:813–834.

Moyle, P. B., and T. Light. 1996. Biological Invasions of Freshwater: Empirical rules and assembly theory. Biological Conservation 78:149–161.

Murphy, M. H. 2004. Ecology of young-of-the-year Atlantic salmon: evaluation of strain differences and over-winter survival. College of Environmental Science and Forestry, Syracuse, NY.

Murphy, M. H., M. J. Connerton, and D. J. Stewart. 2006. Evaluation of Winter Severity on Growth of Young-of-the-Year Atlantic Salmon. Transactions of the American Fisheries Society 135:420–430.

Nash, R. D. M., A. H. Valencia, and A. J. Geffen. 2006. The origin of Fulton’s condition factor - Setting the record straight. Fisheries 31:236–238.

Nekola, J. C., and J. H. Brown. 2007. The wealth of species: Ecological communities, complex systems and the legacy of Frank Preston. Ecology Letters 10:188–196.

Nicieza, A. G., and N. B. Metcalfe. 1999. Costs of rapid growth: The risk of aggression is higher for fast-growing salmon. Functional Ecology 13:793–800.

Nilsson, E., C. T. Solomon, K. A. Wilson, T. V. Willis, B. Larget, and M. J. Vander Zanden. 2012. Effects of an invasive crayfish on trophic relationships in north-temperate lake food webs. Freshwater Biology 57:10–23.

Nislow, K. H., A. J. Sepulveda, and C. L. Folt. 2004. Mechanistic Linkage of Hydrologic Regime to Summer Growth of Age-0 Atlantic Salmon. Transactions of the American Fisheries Society 133:79–88.

NMFS. 2016. Species in the Spotlight. Priority Actions: 2016-2020. Atlantic Salmon Salmo salar. Species in the Spotlight.

Noble, C., S. Kadri, D. F. Mitchell, and F. A. Huntingford. 2007. Influence of feeding regime on intraspecific competition, fin damage and growth in 1+ Atlantic salmon parr (Salmo salar L.) held in freshwater production cages. Aquaculture Research 38:1137–1143.

Nyström, P., C. Brönmark, and W. Granéli. 1996. Patterns in benthic food webs: A role for omnivorous crayfish? Freshwater Biology 36:631–646.

Odum, E. P. 1959. Fundamentals of ecology. 2d ed. W.B. Saunders Company, Philadelphia and London.

Olsen, E. M., and L. A. Vøllestad. 2001. Estimates of survival of stream-dwelling brown trout using mark-recaptures. Journal of Fish Biology 59:1622–1637.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution 14:483–488.

Paukert, C. P., A. J. Lynch, and J. E. Whitney. 2016. Effects of Climate Change on North American Inland Fishes: Introduction to the Special Issue. Fisheries 41:329–330.

Peay, S., N. Guthrie, J. Spees, E. Nilsson, and P. Bradley. 2009. The impact of signal crayfish (Pacifastacus leniusculus) on the recruitment of salmonid fish in a headwater stream in Yorkshire, England . Knowledge and Management of Aquatic Ecosystems:12.

Peckarsky, B. L. 1979. A Review of the Distribution , Ecology , and Evolution of the North American Species of Acroneuria and Six Related Genera (Plecoptera : Perlidae). Journal of Kansas Entomological Society 52:787–809.

Peckarsky, B. L., P. A. Abrams, D. I. Bolnick, L. M. Dill, H. Grabowski, B. Luttbeg, J. L. Orrock, S. D. Peacor, E. L. Preisser, J. Oswald, G. C. Trussell, L. Peckarsky, I. Bolnick, P. A. Abrams, M. Dill, H. Grabowski, J. L. Orrock, L. Preisser, S. D. Peacor, and C. Trussell. 2008. Revisiting the Classics : Considering Nonconsumptive Effects in Textbook Examples of Predator — Prey Interactions. Ecology 89:2416–2425.

Peckarsky, B. L., P. R. Fraissinet, M. Penton, and D. Conklin Jr. 1990. Freshwater Macroinvertebrates of Northeeastern North America. Cornell University Press.

Perkins, D. M., B. G. McKie, B. Malmqvist, S. G. Gilmour, J. Reiss, and G. Woodward. 2010. Environmental warming and biodiversity-ecosystem functioning in freshwater microcosms. Partitioning the effects of species identity, richness and metabolism. Advances in Ecological Research 43:177–209.

Phillips, I. D., R. D. Vinebrooke, and M. A. Turner. 2009. Ecosystem consequences of potential range expansions of Orconectes virilis and Orconectes rusticus crayfish in Canada - A review. Environmental Reviews 17:235–248.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, P. K.L., B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: A paradigm for river conservation and restoration. BioScience 47:769–784.

Poff, N. L., J. D. Allan, M. A. Palmer, D. D. Hart, B. D. Richter, A. H. Arthington, K. H. Rogers, J. L. Meyer, and J. A. Stanford. 2003. River flows and water wars: emerging science for environmental decision making. Frontiers in Ecology and the Environment 1:298–306.

Poff, N. L. R., and A. D. Huryn. 1998. Multi-scale determinants of secondary production in Atlantic salmon (Salmo salar) streams. Canadian Journal of Fisheries and Aquatic Sciences 55:201–217.

Poff, N. L., and J. K. H. Zimmerman. 2010. Ecological responses to altered flow regimes: A literature review to inform the science and management of environmental flows. Freshwater Biology 55:194–205.

Polis, G., and R. Holt. 1992. Intraguild predation: The dynamics of complex trophic interactions. Trends in Ecology & Evolution 7:151–154.

Poole, G. C., and C. H. Berman. 2001. An ecological perspective on in-stream temperature: Natural heat dynamics and mechanisms of human-caused thermal degradation. Environmental Management 27:787–802.

Pörtner, H. O. 2002. Physiological basis of temperature-dependent biogeography: trade-offs in muscle design and performance in polar ectotherms. The Journal of experimental biology 205:2217–2230.

Pörtner, H. O., P. L. M. Van Dijk, I. Hardewig, and A. Sommer. 2000. Levels of Metabolic Cold Adaptation: Tradeoffs in Eurythermal and Stenothermal Ectotherms. Pages 201–122 *in* W. Davison, C. Howard-Williams, and P. Broady, editors. Antarctic Systems: models for wider ecological understanding. Caxton Press, Christchurch, New Zealand.

Pörtner, H. O., and M. A. Peck. 2010. Climate change effects on fishes and fisheries: Towards a cause-and-effect understanding. Journal of Fish Biology 77:1745–1779.

Pringle, C. M., and T. Hamazaki. 1998. The Role of Omnivory in a Neotropical Stream: Separating Diurnal and Nocturnal Effects. Ecology 79:269–280.

Rabeni, C. F. 1992. Trophic Linkage between Stream Centrarchids and Their Crayfish Prey. Canadian Journal of Fisheries and Aquatic Sciences.

Rahel, F. J., and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. Conservation Biology 22:521–533.

Rao, P., and T. Bullock. 1954. Q10 as a Function of Size and Habitat Temperature in Poikilotherms . Pampapathi Rao and Theodore H . Bullock Source : The American Naturalist , Vol . 88 , No . 838 (Jan . - Feb ., 1954), pp . 33-44 Published by : The University of Chicag. The American Naturalist 88:33–44.

Regier, H. A., and J. D. Meisner. 2004. Anticipated Effects of Climate Change on Freshwater Fishes and Their Habitat. Fisheries 15:10–15.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The Role of Disturbance in Stream Ecology. Journal of the North American Benthological Society 7:433–455.

Reynolds, J. D. 2011. A review of ecological interactions between crayfish and fish, indigenous and introduced. Knowledge and Management of Aquatic Ecosystems 401:1–21.

Richards, S. A. 2005. Testing ecological theory using the information-theoretic approach: Examples and cautionary results. Ecology 86:2805–2814.

Roessink, I., R. Gylstra, P. G. M. Heuts, B. Specken, and F. Ottburg. 2017. Impact of invasive crayfish on water quality and aquatic macrophytes in the Netherlands. Aquatic Invasions 12:397–404.

Rosemond, A. D. 1993. Interactions among irradiance , nutrients , and herbivores. Oecologia 94:585–594.

Rosemond, A. D., P. J. Mulholland, and J. W. Elwood. 1993. Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. Ecology 74:1264–1280.

Rosemond, A. D., C. M. Pringle, and A. Ramirez. 1998. Macroconsumer effects on insect detritivores and detritu processing in a tropical stream. Freshwater Biology 39:515–523.

Rosemond, A. D., C. M. Pringle, A. Ramírez, and M. J. Paul. 2001. A test of top-down and bottom-up control in a detritus-based food web. Ecology 82:2279–2293.

Rosenfeld, J. 2000. Effects of fish predation in erosional and depositional habitats in a temperate stream. Canadian Journal of Fisheries and Aquatic Sciences 57:1369–1379.

Roussel, J. M. 2007. Carry-over effects in brown trout (Salmo trutta): Hypoxia on embryos impairs predator avoidance by alevins in experimental channels. Canadian Journal of Fisheries and Aquatic Sciences 64:786–792.

Ruzzante, D. E. 1994. Domestication effects on aggressive and schooling behavior in fish. Aquaculture 120:1–24.

Sabo, M. J., E. J. Pert, and K. O. Winemiller. 1996. Agonistic Behavior of Juvenile Largemouth Bass and Smallmouth Bass. Journal of Freshwater Ecology 11:115–118.

Saltveit, S. J., J. H. Halleraker, J. V. Arnekleiv, and A. Harby. 2001. Field experiments on stranding in juvenile atlantic salmon (Salmo salar) and brown trout (Salmo trutta) during rapid flow decreases caused by hydropeaking. Regulated Rivers: Research & Management 17:609–622.

Saunders, R., M. A. Hachey, and C. W. Fay. 2006. Maine ' s Diadromous Fish Community Maine ' s Diadromous Past , Present , and Implications. Fisheries 31:537–541.

Scheraga, J. D., and A. E. Grambsch. 1998. Risks, opportunities, and adaptation to climate change. Climate Research 10:85–95.

Schmitt, C. 2015. The President's Salmon: Restoring the King of Fish and Its Home Waters. Down East Books.

Shumway, R. H., and D. S. Stoffer. 2017. Time Series Analysis and Its Applications with R Examples. Page (G. Casella, S. Fienberg, and I. Olkin, Eds.) Revista do Hospital das Clínicas. Third Edit. Springer, New York, Dordrecht, Heidelberg, London.

Simon, K. S., and C. R. Townsend. 2003. Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences. Freshwater Biology 48:982–994.

Slaney, P. A., and T. G. Northcote. 1974. Effects of Prey Abundance on Density and Territorial Behavior of Young Rainbow Trout (Salmo gairdneri) in Laboratory Stream Channels. Journal of the Fisheries Research Board of Canada 31:1201–1209.

Smith, J. J., and H. W. Li. 1983. Energetic factors influencing foraging tactics of juvenile steelhead trout, Salmo gairdneri. Pages 173–180 Predators and Prey Fishes. Springer.

Snelder, T. H., and B. J. F. Biggs. 2002. Multiscale river environment classification for water resources management. Journal of the American Water Resources Association 38:1225–1239.

Soluk, D. A., and N. C. Collins. 1988. Synergistic Interactions between Fish and Stoneflies: Facilitation and Interference among Stream Predators. Oikos 52:94–100.

Spotila, J., and E. Standora. 1985. Energy budgets of ectothermic vertebrates. American Zoologist 25:973–986.

Stein, R. A., and J. J. Magnuson. 1976. Behavioral Response of Crayfish to a Fish Predator. Ecology 57:751–761.

Stenroth, P., and P. Nyström. 2003. Exotic crayfish in a brown water stream: Effects on juvenile trout, invertebrates and algae. Freshwater Biology 48:466–475.

Stevenson, J., M. Bothwell, and R. Lowe. 1996. Algal Ecology: Freshwater Benthic Ecosystems. Academic Press.

Swansburg, E., G. Chaput, D. Moore, D. Caissie, and N. El-Jabi. 2002. Size variability of juvenile Atlantic salmon: Links to environmental conditions. Journal of Fish Biology 61:661–683.

Sykes, G. E., C. J. Johnson, and J. M. Shrimpton. 2009. Temperature and Flow Effects on Migration Timing of Chinook Salmon Smolts. Transactions of the American Fisheries Society 138:1252–1265.

Symons, P. E. K. 1968. Increase in Aggression and in Strength of the Social Hierarchy among Juvenile Atlantic Salmon Deprived of Food. Journal of the Fisheries Research Board of Canada 25:2387–2401.

Townsend, C. R., and M. R. Scarsbrook. 1997. The intermediate disturbance hypothesis , and biodiversity in streams. American Society of Limnology and Oceanography, Inc. 42:938–949.

Turnbull, J., C. E. Adams, R. H. Richards, and D. A. Robertson. 1998. Attack site and resultant damage during aggressive encounters in Atlantic salmon (Salmo salar L .) parr. Aquaculture 159:345–353.

Turner, A. M., S. A. Fetterolf, and R. J. Bernot. 1999. Predator identity and consumer behavior: Differential effects of fish and crayfish on the habitat use of a freshwater snail. Oecologia 118:242–247.

U.S. Fish and Wildlife Service and NMFS. 2018. Recovery Plan for the Gulf of Maine Distinct Population Segment of Atlantic Salmon (Salmo salar):74pp.

Valois, A., R. . Curry, and S. . Coghlan. 2009. Smallmouth Bass (Micropterus dolomieu) Invasion of Gulf Region Rivers: Evaluating the Impacts on Atlantic Salmon (Salmo salar) Populations 3848:28 pp.

Vanni, M. J., A. S. Flecker, J. M. Hood, and J. L. Headworth. 2002. Stoichiometry of nutrient recycling by vertebrates in a tropical stream: Linking species identity and ecosystem processes. Ecology Letters 5:285–293.

Vucic-Pestic, O., R. B. Ehnes, B. C. Rall, and U. Brose. 2011. Warming up the system: Higher predator feeding rates but lower energetic efficiencies. Global Change Biology 17:1301–1310.

Wallace, J. B., and J. R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. Annual review of entomology 41:115–139.

Walther, G. R. 2010. Community and ecosystem responses to recent climate change. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2019–2024.

Wańkowski, J. W. J. 1981. Behavioural aspects of predation by juvenile Atlantic salmon (Salmo salar L.) on particulate, drifting prey. Animal Behaviour 29:557–571.

Wańkowski, J. W. J., and J. E. Thorpe. 1979. The role of food particle size in the growth of juvenile Atlantic salmon (Salmo salar L.). Journal of Fish Biology 14:351–370.

Ward, D. M., K. H. Nislow, and C. L. Folt. 2009. Increased Population Density and Suppressed Prey Biomass: Relative Impacts on Juvenile Atlantic Salmon Growth. Transactions of the American Fisheries Society 138:135–143.

Ward, J. V, and J. A. Stanford. 1982. Evolutionary Ecology of Aquatic Insects. Annuael Review of Entomology:97–117.

Warner, K. 2005. Smallmouth Bass Introductions in Maine. Fisheries 30:20–26.

Warren, C. E., and G. E. Davis. 1967. Laboratory studies on the feeding, bioenergetics, and growth of fish. The Biological Basis of Freshwater Fish Production:175–214.

Wathen, G., J. Zydlewski, S. M. Coghlan, and J. G. Trial. 2012. Effects of smallmouth bass on Atlantic salmon habitat use and diel movements in an artificial stream. Transactions of the American Fisheries Society 141:174–184.

Webb, J. H., and H. A. McLay. 1996. Variation in the time of spawning of Atlantic salmon (Salmo salar) and its relationship to temperature in the Aberdeenshire Dee, Scotland. Canadian Journal of Fisheries and Aquatic Sciences 53:2739–2744.

White, R. S. A., P. A. McHugh, and A. R. McIntosh. 2016. Drought survival is a threshold function of habitat size and population density in a fish metapopulation. Global Change Biology 22:3341–3348.

White, S. M., G. Giannico, and H. Li. 2014. A ‘behaviorscape’ perspective on stream fish ecology and conservation: linking fish behavior to riverscapes. Wiley Interdisciplinary Reviews: Water 1:385–400.

Whitledge, G., and C. Rabeni. 1997. Energy sources and ecological role of crayfishes in an Ozark stream: insights from stable isotopes and gut analysis. Canadian Journal of Fisheries and Aquatic Sciences 54:2555–2563.

Whitledge, G. W., R. S. Hayward, and C. F. Rabeni. 2002. Effects of temperature on specific daily metabolic demand and growth scope of sub-adult and adult smallmouth bass. Journal of Freshwater Ecology 17:353–361.

Whitledge, G. W., R. S. Hayward, R. D. Zweifel, and C. F. Rabeni. 2003. Development and Laboratory Evaluation of a Bioenergetics Model for Subadult and Adult Smallmouth Bass. Transactions of the American Fisheries Society 132:316–325.

Whitmore, N. 1997. Population Ecology of the Freshwater Crayfish Paranephrops Zealandicus and Its Effect on the Community Structure of a Lowland Bush Stream. University of Otago, Dunedin, New Zealand.

Winder, M., and D. E. Schindler. 2004. Climate Change Uncouples Trophic Interactions in an. Ecology 85:2100–2106.

Winkelmann, C., J. Schneider, D. Mewes, S. I. Schmidt, S. Worischka, C. Hellmann, and J. Benndorf. 2014. Top-down and bottom-up control of periphyton by benthivorous fish and light supply in two streams. Freshwater Biology 59:803–818.

Wissinger, S. A., M. E. Perchik, and A. J. Klemmer. 2018. Role of animal detritivores in the breakdown of emergent plant detritus in temporary ponds.

Woodward, G., N. Bonada, L. E. Brown, R. G. Death, I. Durance, C. Gray, S. Hladyz, M. E. Ledger, A. M. Milner, S. J. Ormerod, R. M. Thompson, and S. Pawar. 2016. The effects of climatic fluctuations and extreme events on running water ecosystems. Philosophical Transactions of the Royal Society B: Biological Sciences 371.

Woodward, G., G. Papantoniou, and R. B. Lauridsen. 2008. Trophic trickles and cascades in a complex food web: impacts of a keyston predator on stream community structure and ecosystem processes. Oikos 117:683–692.

Woodward, G., D. M. Perkins, and L. E. Brown. 2010. Climate change and freshwater ecosystems: Impacts across multiple levels of organization. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2093–2106.

Wuellner, M. R., B. D. S. Graeb, D. W. Willis, B. J. Galster, T. M. Selch, and S. R. Chipps. 2011. Competitive interactions between walleye (Sander vitreus) and smallmouth bass (Micropterus dolomieu) under various controlled conditions. Journal of Freshwater Ecology 26:299–314.

Xenopoulos, M. a, D. M. Lodge, J. Alcamo, M. Marker, K. Schulze, and D. P. Van Vuuren. 2005. Scenarios of freshwater fish extinctions from climate change and water withdrawal. Global Change Biology 11:1557–1564.

Zanden, M. J. Vander, J. M. Casselman, and J. B. Rasmussen. 1999. 1999- Vander Zanden et al-Stable isotope evidence for the food web consequences of species invasions in lake.pdf 401:1997–2000.

Vander Zanden, M. J., J. D. Olden, J. H. Thorne, and N. E. Mandrak. 2004. Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. Ecological Applications 14:132–148.

APPENDIX A

MEAN ABUNDANCE OF INVERTEBRATES FOUND IN SUNKHAZE SAMPLES

Table A1 – Mean abundance (number of individuals per family) of invertebrates found in the cobble samples by treatment.

Order	Family	Crayfish	Salmon	SxC	Salmon/Crayfish Free
Coleoptera	Elmidae	1.42	0.67	1.17	1.00
Coleoptera	Psephenidae	0.00	0.00	0.04	0.00
Decapoda	Cambaridae	0.00	0.00	0.00	0.08
Diptera	Athericidae	1.00	0.58	0.67	0.83
Diptera	Chironomidae	54.58	69.08	49.67	56.00
Diptera	Dixidae	0.00	0.08	0.00	0.00
Diptera	Empididae	0.08	0.00	0.00	0.00
Diptera	Tabanidae	0.00	0.08	0.00	0.00
Diptera	Tipulidae	0.08	0.06	0.00	0.03
Ephemeroptera	Ameletidae	2.00	0.42	1.25	0.67
Ephemeroptera	Ephemerellidae	1.17	0.58	1.17	1.08
Ephemeroptera	Ephemeridae	0.25	0.67	0.17	1.33
Ephemeroptera	Heptageniidae	2.06	1.29	1.75	1.65
Ephemeroptera	Leptophlebiidae	8.25	11.71	5.75	10.67
Ephemeroptera	Tricorythidae	2.83	3.42	2.83	2.42
Gastropoda	Planorbidae	0.00	0.00	0.08	0.00
Hempitera	Notonectidae	0.00	0.08	0.00	0.00
Hempitera	Veliidae	0.00	0.08	0.00	0.00
Hydrachnidia	Unknown	0.00	0.00	0.08	0.00
Megaloptera	Corydalidae	2.25	5.75	3.83	5.00
Megaloptera	Sialidae	0.08	0.08	0.08	0.17
Odonata	Aeshnidae	0.08	0.50	0.25	0.17
Odonata	Petaluridae	0.00	0.25	0.00	0.17
Oligochaeta	Unknown	0.08	0.58	0.42	0.25
Plecoptera	Capniidae	0.75	0.00	0.33	0.08
Plecoptera	Leuctridae	0.67	0.92	0.67	1.08
Plecoptera	Perlidae	0.46	0.08	0.67	0.38
Plecoptera	Perlodidae	0.33	0.00	0.08	0.00
Trichoptera	Hydropsychidae	0.83	0.25	1.08	0.21
Trichoptera	Leptoceridae	0.08	0.17	0.00	0.00
Trichoptera	Polycentropodidae	1.00	3.92	0.83	2.33
Zygoptera	Calopterygidae	6.25	3.83	5.92	2.92
Zygoptera	Coenagrionidae	0.00	0.08	0.00	0.17

Table A2 – Mean abundance (number of individuals per family) of invertebrates found in the leaf pack samples by treatment.

Order	Family	Crayfish	Salmon	SxC	Salmon/Crayfish Free
Coleoptera	Elmidae	1.42	0.67	1.17	1.00
Coleoptera	Psephenidae	0.00	0.00	0.04	0.00
Decapoda	Cambaridae	0.00	0.00	0.00	0.08
Diptera	Athericidae	1.00	0.58	0.67	0.83
Diptera	Chironomidae	54.58	69.08	49.67	56.00
Diptera	Dixidae	0.00	0.08	0.00	0.00
Diptera	Empididae	0.08	0.00	0.00	0.00
Diptera	Tabanidae	0.00	0.08	0.00	0.00
Diptera	Tipulidae	0.08	0.06	0.00	0.03
Ephemeroptera	Ameletidae	2.00	0.42	1.25	0.67
Ephemeroptera	Ephemerellidae	1.17	0.58	1.17	1.08
Ephemeroptera	Ephemeridae	0.25	0.67	0.17	1.33
Ephemeroptera	Heptageniidae	2.06	1.29	1.75	1.65
Ephemeroptera	Leptophlebiidae	8.25	11.71	5.75	10.67
Ephemeroptera	Tricorythidae	2.83	3.42	2.83	2.42
Gastropoda	Planorbidae	0.00	0.00	0.08	0.00
Hempitera	Notonectidae	0.00	0.08	0.00	0.00
Hempitera	Veliidae	0.00	0.08	0.00	0.00
Hydrachnidia	Unknown	0.00	0.00	0.08	0.00
Megaloptera	Corydalidae	2.25	5.75	3.83	5.00
Megaloptera	Sialidae	0.08	0.08	0.08	0.17
Odonata	Aeshnidae	0.08	0.50	0.25	0.17
Odonata	Petaluridae	0.00	0.25	0.00	0.17
Oligochaeta	Unknown	0.08	0.58	0.42	0.25
Plecoptera	Capniidae	0.75	0.00	0.33	0.08
Plecoptera	Leuctridae	0.67	0.92	0.67	1.08
Plecoptera	Perlidae	0.46	0.08	0.67	0.38
Plecoptera	Perlodidae	0.33	0.00	0.08	0.00
Trichoptera	Hydropsychidae	0.83	0.25	1.08	0.21
Trichoptera	Leptoceridae	0.08	0.17	0.00	0.00
Trichoptera	Polycentropodidae	1.00	3.92	0.83	2.33
Zygoptera	Calopterygidae	6.25	3.83	5.92	2.92
Zygoptera	Coenagrionidae	0.00	0.08	0.00	0.17

BIOGRAPHY OF THE AUTHOR

Nicole Ramberg-Pihl was born in Ridgewood, New Jersey on May 15, 1988. She was raised in the Hudson Valley, New York and moved to New Hampshire following High School with her family. She attended Plymouth State University and graduated in 2009 with a degree in Environmental Biology. She continued her academic career at Plymouth State University, receiving a Master of Science degree in Biology in 2012. Nicole started teaching as an adjunct faculty member during graduate school and continued teaching until she moved to Maine to pursue her PhD in Ecology and Environmental Sciences in 2015. Nicole entered the University of Maine as an NSF IGERT Fellow interested in addressing multifaceted issues stemming from abrupt climate change through interdisciplinary research. While completing her dissertation work, she also completed two terms with the NASA DEVELOP National Program, a capacity building program that strives to bridge the gap between NASA Earth observations and local environmental issues. Nicole is a candidate for the Doctor of Philosophy degree in Ecology and Environmental Science from the University of Maine in August 2020.