

**THE INTERACTIVE ECOLOGY OF JUVENILE ATLANTIC SALMON AND
SMALLMOUTH BASS: COMPETITION FOR HABITAT**

By

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THESIS
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Thesis Co-Advisors: Dr. Stephen Coghlan and Dr. Joseph Zydlewski

An abstract of the Thesis Presented
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Anadromous Atlantic salmon populations in New England have declined precipitously and now persist in only a handful of Maine rivers. Smallmouth bass have been established in most of the last remaining watersheds containing endangered anadromous Atlantic salmon, yet little is known about the ecological interactions between the species. The goal of this research is fill key gaps in knowledge regarding the effects of competition for habitat from smallmouth bass on Atlantic salmon.

We used snorkel observation to identify the degree and timing of overlap in habitat use and to describe habitat shifts by Atlantic salmon in the presence of smallmouth bass in natural conditions. We also used a simulated stream, to monitor age 0 Atlantic salmon and age 0 smallmouth bass diel habitat use and movements in sympatry and allopatry.

In late July, 2008, we observed substantial overlap in depths and mean water column velocities used by both species in sympatry, and an apparent shift by age 0 Atlantic salmon to shallower water coinciding with the period of high overlap. We

detected no overlap or habitat shifts by age 0 Atlantic salmon in the presence age 1 smallmouth bass, and low overlap and no habitat shifts of Atlantic salmon and age 0 smallmouth bass in fall 2008. Summer floods in 2009 resulted in a near complete reproductive failure of smallmouth bass in our study streams, thus compromising our ability to replicate our 2008 experiments. In laboratory experiments Atlantic salmon did not change their habitat use in the presence of conspecific or heterospecific invaders. However, Atlantic salmon did forced smallmouth bass out of riffle habitats during daytime. Atlantic salmon and smallmouth bass displayed different diel activity patterns, which were affected by heterospecific introductions.

From our field experiments, we suggest that environmental conditions of temperature and discharge mediate interactions of these species, and may determine the potential outcomes of competition. In our laboratory experiments the level of interspecific competition for habitat was low. Under certain conditions, Age 0 Atlantic salmon and smallmouth bass may be able to avoid intense interspecific competition through spatial and temporal habitat partitioning.

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CHAPTER 1:
THE EFFECTS OF COMPETITION FROM AN EXOTIC SPECIES: DO
INVASIVE SMALLMOUTH BASS IMPACT ENDANGERED ATLANTIC
SALMON?

Introduction

Historically, the Atlantic salmon, often referred to as “the king of fishes”, thrived in most major rivers in New England from the Housatonic (CT) north to the St. Croix (ME; Behnke, 2002). Today, wild Atlantic salmon populations have declined precipitously and persist in only a handful of Maine rivers. Part of the remaining population (Distinct Population Segments) is now federally protected under the Endangered Species Act (NOAA 2009), but the species still faces extirpation. Declines in range and numbers are due primarily to anthropogenic disturbances, including pollution, loss of habitat, disruption of river hydrology, and over-fishing. Although Atlantic salmon have received much conservation attention, little research has addressed the ecological effects of invasive species, and no data exist on interactions with smallmouth bass. The goal of this research is fill key gaps in knowledge regarding the effects of sympatric smallmouth bass on Atlantic salmon.

In 2005 the Maine Atlantic Salmon Commission (now the Department of Marine Resources Bureau of Sea-Run Fisheries and Habitat) released a 10 year strategic plan to facilitate the conservation, recovery, and restoration of Atlantic salmon populations in Maine waters (ASC 2005). In their report, the Commission outlined the most pressing threats to the persistence of wild Atlantic salmon in the Gulf of Maine rivers, one of

which was competition and predation from smallmouth bass. Exotic smallmouth bass pose a significant predation threat to native salmonines elsewhere; for example, in the Lake Washington Basin (WA), up to 38% of the diet of smallmouth bass consisted of juvenile Pacific salmon migratory smolts (Fayram and Sibley, 2000). Here in Maine, an earlier field study found no evidence of smallmouth bass predation on Atlantic salmon smolts in the Penobscot River, but a complementary laboratory experiment showed that smallmouth bass will consume Atlantic salmon smolts (Van den Ende 1993). Though no prior research exists on habitat selection of sympatric Atlantic salmon and smallmouth bass, similar habitat preferences at early life stages of both species in allopatry indicate that juveniles in rivers could overlap in habitat, which could result in competition. Furthermore, young-of-year smallmouth bass might have a competitive advantage over similar-sized salmon due to the smallmouth bass's larger gape size, aggressive behavior, and increased tolerance for harsh environmental conditions during summer months (i.e. high water temperatures and lower flow). Thus, smallmouth bass may pose a severe competitive and predatory threat to Atlantic salmon, which could facilitate the extirpation of wild, endangered Atlantic salmon from United States waters.

Atlantic salmon in Maine

Life cycle

Atlantic salmon emerge from eggs buried within well oxygenated substrate in which they were laid the preceding fall. The young "alevins" remain in the redd (nest) for about 6 weeks after they hatch, gaining nutrients from the yolk sac attached to their abdomen. Once the yolk sac is depleted the alevins emerge from the gravel, start feeding

actively in the stream, as “fry”. Embryo to fry survival in Maine is estimated to be from 15 to 35% (Mackenzie and Moring 1988). Fry develop quickly into parr as noted by the development of camouflaging vertical parr marks along their flanks. The parr typically reside in their natal stream for 2-3 years where they feed on drifting invertebrates. After spending their nursery period in streams most parr begin a downstream migration towards the Atlantic Ocean. During the migration the young salmon undergo dramatic physiological transformations to prepare for life at sea. The parr marks disappear as they take on a silvery appearance and enter the smolt stage. Survival from embryo to smolt is estimated to be in the range of 0.2 – 3.2% (Hutchings and Jones 1998). Some salmon do not undergo smoltification; instead, they become sexually mature while they are still in freshwater environments. These fish are known as “precocious parr” and are thought to increase genetic diversity in offspring of returning spawning cohorts (Fay et al. 2006).

Once the smolts reach the sea water they typically spend 1-3 years migrating through the North Atlantic Ocean, feeding mainly on amphipods, euphasiids, and fish (Hislop and Shelton 1993). Some salmon return to spawn after one winter at sea (i.e., grilse), while others may stay at sea for more than 5 years. Survival from the smolt to grilse stage is estimated to be between 1.3 – 17.5% (Hutchings and Jones 1998). When returning to freshwater most Atlantic home to natal river (Stabell 1984). This homing tendency is key to the maintenance of “stocks”, which allow fish to spawn with others who have similar life histories or characteristics that allow them to exploit resources distinct to their natal rivers (Ghaerrett and Smoker 1993; Dittman and Quinn 1996). Every spring, returning Atlantic salmon make their way back to their natal streams. As with out-migration, the spawning run back to freshwater requires a series of physiological

adjustments in response to changing salinity. Unlike adult Pacific salmon, which spawn only once, Atlantic salmon are iteroparous – they have the ability to spawn multiple times.

Atlantic salmon evolved a complex lifecycle in which individuals take advantage of both freshwater and marine environments. Juvenile salmon spend the most vulnerable stage of their lives in environments where naturally occurring competition and predators are minimized. Once salmon grow large enough, they move to marine environments rich with food where they can grow into mature adults. This unique life cycle has led to the proliferation of Atlantic salmon over the whole of the North Atlantic Ocean, and the major rivers that drain into it. However, in the past 200 years, anthropogenic effects have affected Atlantic salmon negatively in both marine and freshwater habitats.

State of the salmon

Historically, most major rivers in New England contained Atlantic salmon runs, including possibly as many as 34 rivers in Maine (Beland 1984). Annual runs of Atlantic salmon in the United States are speculated to have been as high as 500,000 fish (Beland 1984; Saunders et al. 2006). However, these runs began to decrease in the early 1800's. Over fishing, barriers to migration like hydro-electric dams, and water quality degradation were the major causes of Atlantic salmon decline. Due to increased anthropogenic disturbances, the Atlantic salmon was extirpated in its southern range by 1865 (Fay et al. 2006). Large-scale artificial propagation efforts were put into place, but yielded limited early success at increasing adult salmon populations. Over the years, numbers of returning adult spawners continued to decline. By the middle of the 20th

century, a once thriving population of wild Atlantic salmon had been reduced to less than 2,000 spawning individuals in the United States, and limited to only a handful of rivers in eastern Maine (Fay et al. 2006).

Today Maine is the only state in the US that supports a population of naturally reproducing Atlantic salmon. The core of the Gulf of Maine Distinct Population Segment (DPS) of Atlantic salmon is found in eleven rivers in Maine: the Sheepscot, Ducktrap, Narraguagas, Pleasant, Machias, East Machias, Dennys, Penobscot, Kennebec, Androscoggin and Cove Brook. DPS salmon are protected under the endangered species act, and great strides have been made to preserve the last vestiges of a wild population. Federal and state agencies have banned commercial fishing for Atlantic salmon, retrofitted dams with fish passage facilities, and enacted strict regulations to improve water quality. Despite conservation efforts and extensive fry and smolt stocking, the returning adult population does not show signs of returning to historic numbers. Unquestionably myriad factors affect salmon survivorship, many of which affect the freshwater stages creating a possible population bottleneck (Armstrong 2005). Therefore, further research into factors affecting Atlantic salmon survival in their freshwater life stage is needed.

Smallmouth bass in Maine

Life history

Smallmouth bass, native to the upper Mississippi River basin are a freshwater fish that persist in fluvial and lacustrine habitats. In fluvial systems, mature fish spawn in the early summer, choosing nest sites in shallow, slow moving water (Ridgway et al. 1989).

Nests typically contain ~6200 embryos (Raffetto et al. 1990), of which 15-34% are viable and, of those, 26-33% survive to the post larval stage (Clady 1975). After emergence the adult male will guard the nest aggressively for up to a month, seldom foraging (Ridgway 1988) but often striking at intruders or angler's lures. Age 0 smallmouth bass can use a wide range of habitats during their first summer (Sabo and Orth 1994), but maximize net energy gain in faster, shallower micro-habitats than do older conspecifics (Sabo et al. 1996). During warmer months, age 1 and older fish typically occupy pool habitats with rocky substrate, proximal to overhead cover (Probst et al. 1984; Todd and Rabeni 1989). As water temperatures decrease below 15° C with the onset of winter, smallmouth bass seek habitats with minimal current and decrease their activity until the water starts to warm in spring (Munther 1970). Juvenile fish forage predominantly on aquatic insects, but as they mature, they shift to a diet dominated by higher caloric items (i.e. other fish and crayfish) once gape size allows (Olson and Young 2003). Smallmouth bass growth rates are highly dependent on temperature; maximal growth occurs between 22 - 24° C (Sabo et al. 1996; Whitley et al. 2002). Thus, the northward expansion of the smallmouth bass' range in Ontario is thought to be limited by water temperature (Jackson and Mandrak 2002).

Introduction and proliferation

State agencies introduced smallmouth bass to seven Maine ponds in 1868 to fill a perceived void left by over-harvested brook trout (Warner, 2005). Initially, managers took great precaution to avoid introduction in any waters containing native salmonines. However, in 1881 the Maine Commissioners for Fisheries could no longer fund

smallmouth bass introduction efforts, and ceded management responsibility to the public. By that time, smallmouth bass had been introduced to 51 suitable ponds, but undoubtedly little precaution was taken once non-regulated public introductions began. Introductions of smallmouth bass to new watersheds continued due to the fish's rising popularity among anglers. The invasive smallmouth bass has now established itself across the state, permeating even the most highly regarded strongholds for native brook trout and Atlantic salmon. As of 2000, the smallmouth bass was known to exist in 471 lakes and ponds, uncounted streams and rivers in Maine (Warner 2005), and virtually every warm and cool-water watershed in the United States once historically occupied by anadromous Atlantic salmon.

Effects of smallmouth bass invasions

Smallmouth bass are endemic to the upper Mississippi River basin and parts of the Great Lakes basin, but are now among the most widely distributed fish in the world due to their popularity among anglers. Because of the reputation smallmouth bass have as prized sport fish, little attention has been given to the ecological impact they cause (Jackson 2002). Smallmouth bass are known as “one of world's most disastrous invasive species” (Kei'ichiro et al. 2004) because of their adaptability and ability to exploit resources in novel environments at the expense of native species. Smallmouth bass introductions have caused niche shifts in (Vander Zanden et al. 1999), and extirpations of, native species, due to direct predation (Jackson 2002). In Ontario (Canada) lakes, Jackson (2002) observed that cyprinids chose more complex habitats in the presence of invasive smallmouth bass, to avoid predation. These habitat restrictions could limit the

foraging area, which, in turn, may affect growth rate and fecundity. Predatory effects of smallmouth bass on prey fish abundance and behavior can spur trophic cascades, as a shift in prey fish foraging behavior may trigger changes in plankton assemblages (Jackson 2002). The introduction of smallmouth bass to aquatic environments can have detrimental effects on native piscivores due to resource competition (Vander Zanden et al. 1999; Vander Zanden et al. 2004a; Weidel et al. 2007). In a study conducted in Ontario lakes, Vander Zanden (1999) found that introduced smallmouth bass out-competed native lake trout for littoral prey fish, forcing lake trout to rely on invertebrates for sustenance, which in turn resulted in a decline in growth rate and fecundity of the native salmonine.

Competition

Birch (1957) put forth one of the more accepted definitions of competition:

“Competition occurs when a number of animals (of the same or different species) use common resources the supply of which is short; or if the resources are not in short supply, competition occurs when the animals seeking that resource nevertheless harm one another in the process”.

Resource competition can be a driving force in shaping ecological communities, as well as a major factor influencing evolution, in part because it can occur interspecifically (among species) and intraspecifically (within a species). There are two types of competition: resource and interference, both of which can be seen in salmonine fishes. One species' exploitation of a resource, thereby limiting the access to another species “scramble competition”, is most common in roaming pool foragers such as coho salmon (Nielsen 1992). Interference competition is common in Atlantic salmon, and is marked by territorial defense whereby the species uses intimidation to maintain a discrete

territory (Symons and Heland 1978). Agonistic displays, previous residency, and sheer body size are salmonines' territorial defense mechanisms. Both exploitive and interference competition can change the availability of a resource and interrupt the energy balance of the competitors (Hall et al. 1992).

Competition as a result of an exotic species introduction can alter the structure of native biotic communities. Research to elucidate the effects of competition from invasive salmonines on native salmonines has documented that the exotics: displace native salmonines from preferred habitats (Fausch and White 1986; Hasegawa and Maekawa 2006), alter within-stream dominance hierarchies (Hasegawa et al. 2004), decrease native salmonine foraging rates (Nakano et al. 1998), and disrupt niche partitioning mechanisms evolved by co-existing species (Hasegawa and Maekawa 2006). Exclusion or depletion of resources by exotic species can reduce growth rates, which would presumably affect survival rates (Rose 1986). Exotic competitors can also alter native salmonine diel activity patterns that could increase susceptibility to predation (Blanchet et al. 2008). If native and exotic fish overlap in resource use, negative effects could be incurred by the native species due to the absence of resource partitioning mechanisms (Gunckel et al. 2002). However, if differences in spatial and temporal resource use exist, competition can be minimized and species that are not naturally sympatric can co-exist (Kocik and Taylor 1996).

What fish compete for in streams

Atlantic salmon nursery streams in Maine are typically a mixture of pool, riffle, and run habitat. For stream dwelling fish, faster moving water may increase the energetic

demand of maintaining position, but simultaneously increases the opportunity to feed on drift (Smith and Li 1983). Slower, deeper habitats offer refugia from fast currents, allowing fish to expend less energy to maintain position, but they are also areas of decreased drift. In streams, food and habitat are usually the limiting resource for salmonines (Chapman 1966). Because invertebrate drift constitutes a majority of diet for most stream salmonines, optimal habitat consists of low water velocities with immediate access to swifter currents in order to increase drift feeding opportunities (Fausch 1984). Fish increase their net energy gain by occupying habitats where the difference between the benefits of high foraging opportunities and energy expended to maintain position are minimized (Hill and Grossman 1993). Competitive exclusion from energetically profitable habitats can reduce growth rate and survival (Nakano et al. 1998).

Naturally co-existing brook trout and Atlantic salmon parr partition themselves in streams. Parr prefer faster, shallower water, whereas brook trout prefer slower deeper pools (Gibson 1978). Partitioning of microhabitats allows Atlantic salmon and brook trout to co-exist while minimizing competition for resources. Atlantic salmon and brook trout have had millennia to co-evolve the behavioral and morphological traits that allow resource partitioning. Because of the relatively short period of sympatry between Atlantic salmon and smallmouth bass, we expect that behavioral mechanisms to partition habitat have not had enough time to evolve. As impetus for this study, we expected that juvenile smallmouth bass and Atlantic salmon rely on similar resources, setting the stage for interspecific competition.

Resource overlap between juvenile Atlantic salmon and smallmouth bass

It is imperative for age 0 Atlantic salmon to occupy optimal foraging habitat, as access to favorable feeding areas increases Atlantic salmon survival during their critical first summer (Nislow et al. 1999). Salmonines select focal points based on access to food supply, water velocity characteristics, and in stream dominance hierarchy (Fausch 1984). During summer months, age 0 Atlantic salmon show a strong preference for microhabitat predicted to maximize consumption rates (Nislow et al. 1999). Survival of juvenile Atlantic salmon is higher in streams where the salmon occupy swifter current speeds, which are predicted to maximize food item consumption. Nislow et al. (1999) found that current speeds of 12.8 cm/s, with a range of 8 cm/s provided optimal prey encounter rate vs. capture success for age 0 Atlantic salmon. As salmon grow and are able to withstand increased current velocities, they shift to faster deeper water, presumably to increase foraging opportunities (Rimmer et al. 1985; Morantz et al. 1987; Nislow et al. 2000). Habitat suitability indices indicate depths of 20 to 50 cm are most amenable to Age 1 and older parr (Stanley and Trial 1995). Mature smallmouth bass tend to occupy pools > 60 cm in depth (Todd and Rabeni 1989), indicating that older Atlantic salmon and smallmouth bass may not overlap in habitat.

In streams, age 0 smallmouth bass use different mesohabitats during development. Age 0 fish may move from the pools in which they were spawned into faster riffle mesohabitats to increase their rate of energy gain (Sabo and Orth 1994; Sabo et al. 1996). This shift into shallow and fast habitats occurs 6-8 weeks after fry leave the nest (Sabo et al. 1996). In Virginia streams, juvenile smallmouth bass occupied mean depths of 56.5

cm and mean velocities of 7.8 cm/s (Sabo et al. 1996). These shallow areas with high water velocities tend to be the most energetically profitable habitats in the stream system (Sabo and Orth 1994). Furthermore age 0 smallmouth bass may occupy shallow habitats to avoid predation from large smallmouth bass in adjacent pool habitats (Schlosser 1987).

If species do not naturally co-exist but are present in the same environment, there is a greater probability that interspecific competition occur (Hearn 1987). Both juvenile Atlantic salmon and juvenile smallmouth bass tend to occupy shallow stream habitats, and maximize net energy gain at similar velocities (7.2 cm/s for smallmouth bass and 12.8 cm/s for Atlantic salmon), thus, we presumed interspecific competition to be likely between the two species. Maine's rivers have the potential to support five to ten large parr per hundred square meters (Baum 1997), therefore the freshwater stage is a density-dependent part of the life cycle that creates a bottleneck for survival (Jonsson and Jonsson 2004; Scott et al. 2005). If juvenile Atlantic salmon cannot access optimal foraging stations due to competition from smallmouth bass, growth rate may decrease which could decrease overall survival

Another point of concern is the effect of Maine's late summer water temperatures on the competitive ability of Atlantic salmon. As streams warm during the summer, temperatures may reach the range of 22-24°C, the peak growth potential for juvenile smallmouth bass (Sabo et al. 1996; Whitley et al. 2002), and surpass the 15 - 19°C optimal temperature range of juvenile Atlantic salmon (Elliot 1991; Murphy 2003). Competitive dominance between fish with different thermal optima can be governed by water temperatures (Taniguchi et al. 1998; Coghlan and Ringler 2005). High summer

water temperatures, optimal for smallmouth bass and stressful for Atlantic salmon, could result in a competitive advantage for smallmouth bass.

In a population regulated by density-dependant processes, position in a dominance hierarchy can have a direct effect on a fish's preparedness for the harsh conditions of winter. In a study conducted on competition and energetic costs in rainbow trout, dominant individuals tended to grow faster and have higher fat content than subordinate fish (Li and Brocksen 1977). Overwinter survival rate increases with an increase of body size in brook and brown trout (Cunjak and Power 1987). However, Connolly and Petersen (2003) found that larger juvenile steelhead were at a survival disadvantage in warmer winters. Nicieza and Metcalfe (1999) observed that dominant fish had increased energetic and physiological costs which may compromise overwinter survival in Atlantic salmon. Atlantic salmon overwinter survival success is positively correlated with individual energy content, not fish size (Finstad et al. 2004). If the presence of smallmouth bass negatively impacts energy acquisition or increases agonistic behavior in Atlantic salmon, then Atlantic salmon may experience decreased overwinter survival rates.

Assessing Competition for habitat between Atlantic salmon and smallmouth bass

The goal of our research was to determine if competition for habitat exists between Atlantic salmon and smallmouth bass by; 1) determining if the two species overlap in habitat use, and if so, at what life stages and during what time of the year; and 2) determining if the presence of smallmouth bass cause a shift in Atlantic salmon habitat use and activity patterns. To meet our objectives we conducted experiments in natural

and laboratory conditions, as recommended by Fausch (1998a). We observed of fish habitat use in streams where Atlantic salmon occurred in allopatry and in sympatry with smallmouth bass at multiple periods during the summer (Chapter 2). Using a combined additive and substitutive design (Fausch 1998a), we quantified Atlantic salmon habitat use before and after the introduction of potential competitors (either smallmouth bass or additional Atlantic salmon) in enclosed sections of streams (Chapter 2). As a complement, we conducted a similar experiment in an artificial stream channel to test effects of inter and intraspecific competition on Atlantic salmon and smallmouth bass habitat use, daily movement, diel activity patterns (Chapter 3). Understanding the important ecological factors that affect habitat use in nursery streams which may compromise growth and survival is critical to the conservation of the endangered Atlantic salmon.

CHAPTER 2:
COMPETITION FOR HABITAT BETWEEN NATIVE ATLANTIC SALMON
(*SALMO SALAR*) AND INVASIVE SMALLMOUTH BASS (*MICROPTERUS*
***DOLOMIEU*)**

Abstract

Exotic smallmouth bass have invaded much of the historic freshwater habitat of Atlantic salmon in North America, yet little is known about ecological interactions between the two species. We investigated the possibility of competition for habitat between Atlantic salmon and smallmouth bass using two *in situ* experiments. We used snorkel observation to identify the degree and timing of overlap in habitat use and to describe habitat shifts by Atlantic salmon in the presence of smallmouth bass. In late July, 2008, we observed substantial overlap in depths and mean water column velocities used by both species in sympatry, and an apparent shift by age 0 Atlantic salmon to shallower water coinciding with the period of high overlap. We detected no overlap or habitat shifts by age 0 Atlantic salmon in the presence age 1 smallmouth bass, and low overlap and no habitat shifts of Atlantic salmon and age 0 smallmouth bass in fall 2008. Summer floods of 2009, with sustained high flows and low temperatures, resulted in a near complete reproductive failure of smallmouth bass in our study streams, thus compromising our ability to replicate our 2008 experiments. We suggest that environmental conditions of temperature and discharge mediate interactions of these species, and thus determine the outcomes of potential competition.

Introduction

Once abundant in New England rivers, anadromous Atlantic salmon (*Salmo salar*) have been reduced to a fraction of their historic numbers and range. Atlantic salmon have declined due to both natural causes (e.g., declines in ocean productivity) and anthropogenic perturbations (e.g., barriers to migration, loss of habitat, pollution and overharvest). By the 1950's, the entire population in the US consisted of only a few hundred fish persisting in five rivers in Maine (Behnke 2002; Fay et al. 2006). Since that time, continued efforts to restore the Atlantic salmon's population and habitat have been met with limited success. In 2000 and in 2009, several river-specific stocks within the Gulf of Maine Distinct Population Segment were listed under the Endangered Species Act (NOAA 2009). In 2005 the Maine Atlantic Salmon Commission released a 10-year strategic plan to facilitate the conservation, recovery, and restoration of Atlantic salmon populations in the Gulf of Maine and tributaries (Atlantic Salmon Commission 2005). In their report, the Commission outlined the most pressing threats to the persistence of Atlantic salmon in Maine rivers, one of which was competition and predation from invasive species such as smallmouth bass (*Micropterus dolomieu*).

Smallmouth bass, native to the upper Mississippi River drainage, have been introduced throughout New England since the 1860's, and the northeastern limit of their range now extends into New Brunswick, Canada (Jackson 2002; Warner 2005). Smallmouth bass have invaded virtually every major watershed in the state of Maine (Warner 2005). These fish were recently detected in Miramichi Lake, NB (Valois et al. 2009), which drains into the Mirimichi River, home of the largest naturally reproducing

population of Atlantic salmon in North America. The smallmouth bass' large gape size, aggressive behavior, wide thermal tolerance, and ability to colonize and persist in riverine and lacustrine habitats have made them a favorite sport-fish, and a formidable competitor and predator of native fishes (Vander Zanden et al. 2004b; Weidel et al. 2007). Due to their ecological impacts) smallmouth bass are considered one of the world's "most disastrous invasive species" (Kei'ichiro et al. 2004). Competition from, and predation by invasive smallmouth bass have evinced niche shifts, changes in trophic structure, and extirpations of native fishes (Vander Zanden et al. 1999; Findlay et al. 2000; Jackson 2002). Numerous studies have documented smallmouth bass predation on outmigrating Pacific salmon smolts (Rieman et al. 1991; Fayram and Sibley 2000). In large Maine rivers, adult smallmouth bass may consume 10 Atlantic salmon smolts per day (Van den Ende 1993). Previous research has demonstrated that predation by adult smallmouth bass may limit juvenile Atlantic salmon survival (Van den Ende 1993); however competitive interactions between juveniles are not yet characterized. Many studies have investigated competition for habitat between Atlantic salmon and other native and non-native salmonines (Fausch 1988; Fausch 1998), but few have focused on competition between salmonines and centrarchids (Ebert and Filipek 1991).

In order for interspecific competition to exist, potential competitors must overlap in use of a scarce resource, and one species' use of the resource must evince a change in resource use of the other species, usually to the detriment of one or both species' survival, growth, or fecundity (Birch 1957). Independent habitat selection studies on early life-stages of Atlantic salmon and smallmouth indicate the possibility for considerable overlap (Valois et al. 2009). Juvenile Atlantic salmon in allopatry use a

wide range of habitats (DeGraaf and Bain 1986) but select primarily for fast shallow riffles (Heggenes and Saltveit 1990; Heggenes et al. 1999). Adult smallmouth bass occupy deep pool habitats (Walters and Wilson 1996) typically avoided by juvenile Atlantic salmon, suggesting a minimal amount of habitat overlap between these life stages. However, juvenile smallmouth bass are habitat generalists (Sabo and Orth 1994), and age 0 fish maximize their net energy gain by feeding in fast, shallow riffles (Sabo et al. 1996) similar to those selected by Atlantic salmon fry and parr (Nislow et al. 1998). Simultaneous occupancy of these habitats by juveniles of both species may result in significant overlap and subsequent competition for habitat, which in stream-dwelling salmonines, translates into competition for food (Chapman 1966).

Timing of habitat overlap can amplify the competitive effects of one species on another (Werner and Hall 1979). Even if competition for habitat between two species occurs only briefly, negative effects on growth rate can occur if competition exists during a vulnerable life stage for one or both species (Rose 1986). For stream fishes, maintaining position in optimal foraging habitats allows individuals to maximize their net energy gain by increasing access to invertebrate drift while minimizing the energetic demand of maintaining positions against the current (Fausch 1984; Facey and Grossman 1992; Hill and Grossman 1993). Optimal habitat is a function of fish size, temperature, current velocity, and food abundance and thus changes over the growing season (Smith and Li 1983; Rosenfeld 2003). Exclusion from energetically profitable habitats as a result of interspecific competition between stream-dwelling salmonines can cause a decrease in growth rate and survival (Nakano et al. 1998; Gunckel et al. 2002) in one or both species. Access to energetically-profitable foraging habitat increases age 0 Atlantic

salmon survival during their critical first summer (Nislow et al. 1999). If Atlantic salmon are displaced from energetically profitable habitats by smallmouth bass during their first summer, we would expect survival and/or growth to decrease.

The goal of our research was to determine if competition for habitat exists between Atlantic salmon and smallmouth bass by; 1) determining if the two species overlap in habitat use, and if so, at what life stages and during what time of the year; and 2) determining if the presence of smallmouth bass cause a shift in Atlantic salmon habitat use. We hypothesized that juvenile smallmouth bass overlap in habitat use with Atlantic salmon during the summer months, and that the presence of the smallmouth bass causes Atlantic salmon to shift into faster and shallower habitats as a result of interspecific competition. To test these hypotheses we carried out two field studies using snorkel observation of fish habitat use. Our “open observations” of fish habitat use were conducted in streams where Atlantic salmon occurred in allopatry and in sympatry with smallmouth bass at multiple periods during the summer. The “controlled invasion” experiment involved quantifying Atlantic salmon habitat use before and after the introduction of potential competitors (either smallmouth bass or additional Atlantic salmon) in isolated sections of streams.

Methods

Study fish

Atlantic salmon in all but one of our study sites were offspring of sea-run adults returning to the Penobscot River and captured at the Veazie Fish Trap. Adults were spawned in November, and embryos were incubated over the winter at US Fish and

Wildlife Service, Craig Brook National Fish Hatchery (East Orland, ME). In late May, personnel from the Maine Department of Marine Resources Bureau of Sea-Run Fisheries and Habitat (DMR) stocked Atlantic salmon fry into our study riffles at a density of 1 fish per m². The remaining study site, the Crooked River (a tributary to the Machias River), contained fry of natural origin and thus was not stocked with hatchery-raised fry.

For the open observation experiment, all juvenile smallmouth bass observed were the result of natural reproduction within study streams. For the controlled invasion experiment, we obtained juvenile smallmouth bass by boat electro-fishing from the Piscataquis River near Howland, Maine (July 2008), and by backpack electrofishing from Kenduskeag Stream near Corinth, Maine (September 2009). In 2008, we used age 1 smallmouth bass (TL = 90.7mm ± 7.0 SD), because we were concerned that age 0 smallmouth bass available at the time of collection were too small (TL = ~30 mm) to interact strongly with the Atlantic salmon (TL = 48.6 ± 4.3 mm) used in the study. For reasons described below we use age 0 smallmouth bass (TL = 50.7 ± 5.0 mm) and Atlantic salmon (TL = 60.0 ± 5.3 mm) in 2009.

Open observations

We chose study riffles in streams containing two different combinations of our study species: Atlantic salmon in allopatry (2008: Chandler Brook (46°24'56 N, 68°46'46 W), Mooseluk Stream (46°25'09 N, 68°47'23 W) – Aroostook County; 2009: Narraguagus River (44°50'37 N, 68°04'12 W), Crooked River (44°55'40 N, 67°52'08 W) – Washington County), and Atlantic salmon and smallmouth bass in sympatry (2008 and 2009: Union River (44°54'04 N, 68°04'12 W) – Hancock County, Great Works Stream

(44°55'00 N, 68°19'49 W) – Penobscot County) (Figure 2.1). Temperature data loggers were installed in or near each study riffle.

We quantified habitat use of juvenile Atlantic salmon and smallmouth bass in pre-selected 50 m riffles reaches from streams where the two species occurred in sympatry and Atlantic salmon occurred in allopatry. On three separate occasions in 2008 and 2009 we assessed habitat use of age 0 Atlantic salmon and smallmouth bass by snorkel observation (see below for detailed methodology). Directly after each event we obtained a sample of Atlantic salmon ($n = 10-15$) by backpack electrofishing for total length and mass measurements. For each sampling period we calculated spatial overlap indices for depth and mean water column velocities (hereto after referred as “velocity”) used by Atlantic salmon and smallmouth bass. We compartmentalized velocity measurements into increments of 0.05 m/s and total depth into increments of 0.05 m (Moyle and Vondracek 1985). We chose Morisita’s index of similarity (“ C ”) (Morisita 1959) to measure niche overlap due to its minimal bias compared to other overlap measures (Krebs 1989). Calculated C values are on a scale from 0-1. We assumed that C values > 0.67 indicated high resource overlap, values between 0.66 and 0.33 indicated moderate resource overlap, and values < 0.33 were and indication of low overlap (Zaret and Rand 1971; Brown and Moyle 1991; Scoppettone 1993). We used analysis of variance (ANOVA) to compare depths and velocities used by Atlantic salmon at different sampling events. We used a post-hoc Tukey’s HSD test to test for differences in depths and velocity used between sampling events. All statistical tests were two-tailed, and an α level of 0.05 was the significance criterion. Data on Atlantic salmon

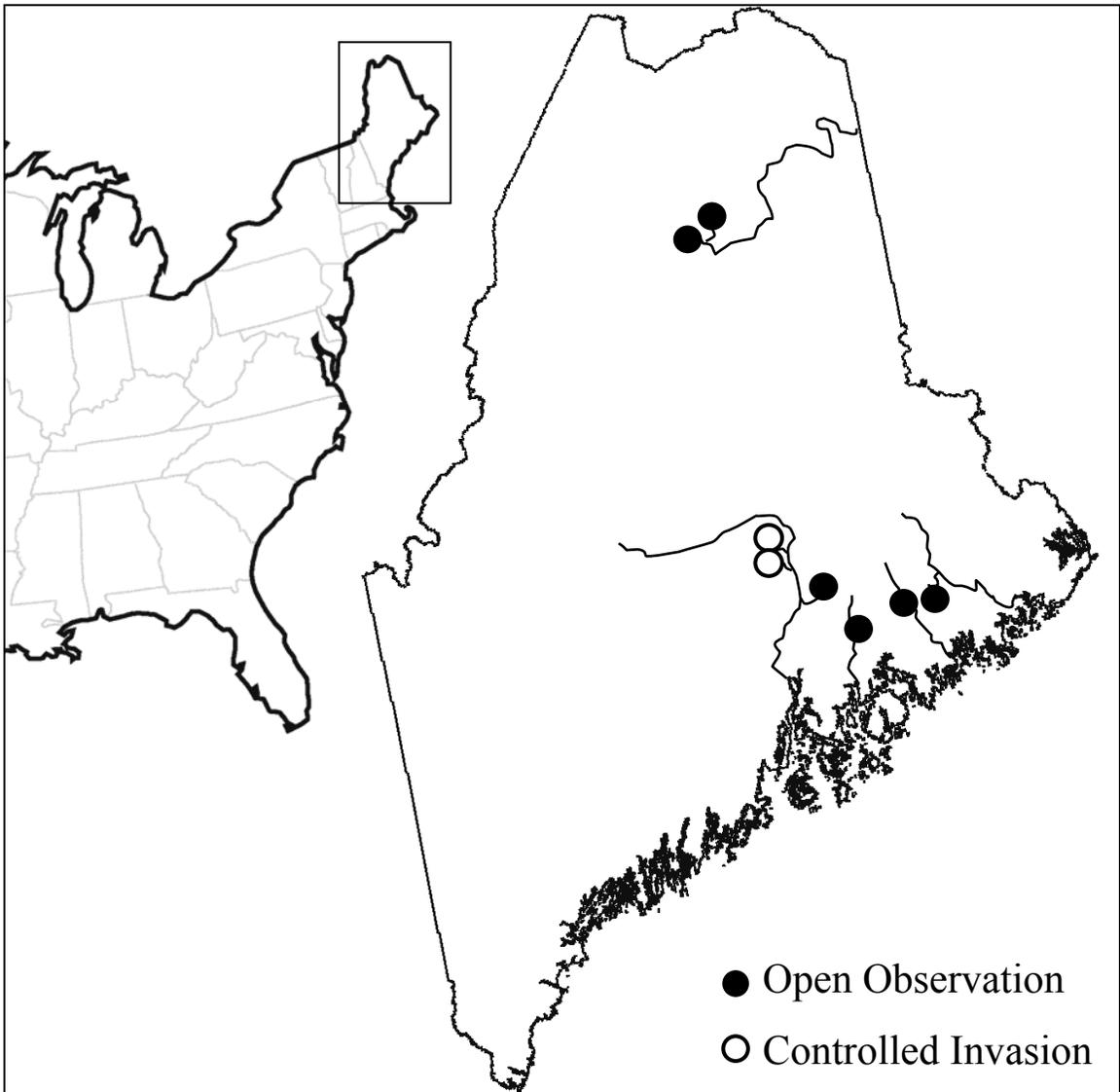


Figure 2.1 – Approximate locations of streams in Maine, USA with black and white circles indicating if sites were included in controlled invasion studies or where habitat use observations were made.

habitat use from the first sampling event in 2008 were not included in analysis due to low sample size ($N = 7$) as a result of near flood conditions and turbid waters.

Controlled invasions

In 2008 we selected study riffles on Hemlock ($45^{\circ}05'04$ N, $68^{\circ}40'12$ W) and Pollard ($45^{\circ}10'28$ N, $68^{\circ}38'06$ W) Brooks (Figure 2.1) both 3rd order adventitious tributaries of the Penobscot River (Penobscot County, Maine). In 2009 we utilized two riffles on Pollard Brook and omitted Hemlock Brook. Streams were selected because they were of similar size and discharge, close to each other, were historic Atlantic salmon nursery habitat, and are stocked annually with Atlantic salmon fry by DMR.

From July 8th – 15th of 2008 and September 9th – 21st of 2009 we conducted experiments testing for shifts in Atlantic salmon habitat use after the introduction of heterospecifics (smallmouth bass) and conspecifics (more Atlantic salmon) in a stream section. At each site, we installed blocking nets (4-mm mesh) at 0m, 25m, and 50m to create two 25 m reaches. We then removed > 95% of resident fishes, including stocked Atlantic salmon, by 3-pass electrofishing reductions (Zippin 1956). All age 0 Atlantic salmon parr collected from the study reaches were kept in an in-stream holding tank until removals were complete, and then some of those parr (2008 $N = 40$, 2009 $N = 30$) were reintroduced to each 25 m isolated reach. Reintroduced fish were allowed a minimum of 48 hours to re-acclimate before snorkel observations commenced. We conducted snorkel observations (see below for detailed methodology) between 09:00 and 12:00 EST. After entering the stream, observers remained motionless for 5 min before the observation period commenced.

Directly after the first snorkel sampling we spread additional fish (either smallmouth bass or Atlantic salmon) throughout study reaches. We introduced smallmouth bass to the downstream 25m reach in each stream section and a matching number of Atlantic salmon to the upstream reach (2008 $N = 19$, 2009 $N = 20$). Following the second set of introductions, we allowed for a 48 hour acclimation period before repeating snorkel observations and habitat use measurements. A three-pass reduction estimate (Zippin 1956) was conducted after all snorkel observations. This was used to assess detectability of fishes (numbers of fish observed previously / numbers of fish collected subsequently) and to make sure there was no migration between 25 m sections.

In 2009, after snorkel observation sampling, we repeated the experiment in one reach using PIT tag technology to identify fish locations. During snorkel observations, detectability in one of the study reaches was very low (mean percentage of fish detected in four sampling events = 14%). The low detectability was a result of difficult snorkeling conditions (shallow depths) and observed hiding behavior by both species (presumably due to low temperatures; Cunjak 1988). In this experiment all fish were anesthetized with buffered MS-222 (80 mg/L, 0.2 mM NaCO₃, pH = 7.0) and implanted with PIT tags (Biomark, Boise, ID. 12mm: TX1411SSL) (Gries and Letcher 2002). The first group of re-introduced Atlantic salmon ($N = 30$) was allowed 48 hours for re-acclimation before sampling. We used a PIT-pack (Hill et al. 2006; Kurth et al. 2007) to locate fish by slowly moving upstream while interrogating the entire wetted area of each reach. Once a fish was identified by PIT-packing, its position was marked so that depth, velocity and estimated dominant substrate could be measured. A second group of 20 Atlantic salmon

and 20 smallmouth bass were introduced into the lower and upper reaches respectively, and allowed a 48 hour acclimation period before the second PIT-pack sampling.

For data collected using snorkel observations we used paired t-tests to compare depths and velocities used by Atlantic salmon habitat before and after the second introduction of fish. For data collected using a PIT-pack we used a Friedman's non-parametric ANOVA to detect differences in Atlantic salmon habitat use between treatments. To compare data collected by snorkel observation to data collected using a PIT-pack we used paired t-tests to compare depths and velocities of pre-invasion Atlantic salmon from the reach in which both interrogation techniques were used. For categorical substrate data we used a Fischer's exact test to test for differences in substrate use between treatments. We used the Cochran-Mantel-Haenszel test to quantify differences in detectability of Atlantic salmon before and after competitor introduction.

Snorkel observations

At the beginning of each sampling event, two snorkelers would enter the stream downstream of the study reach and work their way slowly into the reach, recording only fish within the delineated area. We visually divided each reach longitudinally into two sections, and each snorkeler was responsible for observing fish in only his/her section. Snorkelers moved in parallel, slowly upstream and across each section in a zigzag pattern (Cunjak and Power 1986). Upon sighting a fish, we observed its behavior and physical features to ensure that it had not moved to that particular position as a result of the our presence, and that it had not been counted previously. Once we were confident that the fish was undisturbed we recorded species, presumed age class (length-frequency

distributions of age 0 and > age 1 classes do not overlap in Maine streams; J. Trial personal observation), and estimated focal point height. We then placed a marker directly below each fish's focal point. Upon the completion of observations within the reach, we returned to each marker, and measured total depth, mean water column (60% of depth) velocity, snout water velocity (based on estimated focal point height), and estimated the dominant substrate type (modified Wentworth Scale) in a 0.25 m radius around the marker. Focal point velocities were often heavily influenced by surrounding substrate and difficult to accurately obtain; therefore, we used mean water column velocities in all of our analyses. Because foraging habitat selection in stream salmonines is a function of the juxtaposition of slow focal point current and nearby faster advective current, as quantified by mean water column velocities (e.g., Fausch 1993), we were confident that mean water column velocity provided a reliable descriptor of foraging habitat used. Due to the homogeneous nature of substrate in our study riffles, and evidence from other studies findings that substrate size is relatively unimportant for age 0 Atlantic salmon habitat selection and riffles (DeGraaf and Bain 1986), we did not include substrate measurements in our open observation analysis.

To quantify habitat availability in each of our study riffles we set up a series of ten equally spaced transects perpendicular to flow along the study reach. At seven points on each transect we measured total depth, mean water column velocity, water velocity at bottom, and estimated dominant substrate in a 0.25 m radius around each sample point.

Results

Open observations

Over two years we quantified the habitat use of 908 Atlantic salmon and 86 smallmouth bass (Table 2.1). In our first set of 2008 snorkel observations, we observed no smallmouth bass of any year class in our designated study reaches. By late July, once stream discharge had subsided and temperature increased, age 0 smallmouth were abundant in sympatric study riffles ($N = 34$ in Great Works Stream, $N = 41$ in Union River). During this sampling period, Atlantic salmon and smallmouth bass in sympatry showed a high degree of overlap in velocity in both study streams, high depth overlap in the Union River, and moderate depth overlap in Great Works Stream (Table 2.2). This period of high overlap corresponded with a shift in depths used by Atlantic salmon ($P < 0.001$) over time. Atlantic salmon in sympatry used significantly shallower depths in late July than in mid-June ($P = 0.001$). In both sympatric and allopatric streams, there were no significant differences in velocities used by Atlantic salmon among sampling events.

Snorkel observations conducted in late summer/fall revealed that smallmouth bass had either moved to slower, deeper habitats or had left study riffles altogether (Figure 2.2). In sympatric streams, Atlantic salmon had shifted back to deeper water by the third sampling event ($P < 0.001$), such that depths used in September were similar to those used in June ($P = 0.655$; Figure 2.3). Overlap indices from this time indicate a low overlap in velocity, and a moderate overlap in depths in the Union River. No overlap indices were calculated from third sampling on Great Works stream because only one smallmouth bass was detected within the study reach. In allopatric streams, Atlantic salmon were detected in shallower ($P = 0.003$) habitats in September than in July.

Table 2.1 – Number of Atlantic salmon and smallmouth bass observed and measured at open observation sampling events. Mean (\pm SD) total length and mass of a sample of fish obtained from study reaches after snorkel observations. Data from both allopatric and sympatric streams are pooled.

Year	Snorkel event; date (mo./day)	Number of fish observed (measured)	Total length (mean \pm SD)	Mass (mean \pm SD)
Atlantic salmon in allopatry				
2008	1; June 25, 26	7 (-)	-	-
	2; August 23, 24	48 (18)	63.7 \pm 3.7	2.4 \pm 0.4
	3; September 25, 26	40 (11)	68.7 \pm 5.2	2.8 \pm 0.6
2009	1; June 10, 15	68 (15)	40.1 \pm 5.0	0.5 \pm 0.1
	2; July 02, 13	110 (21)	51.0 \pm 5.5	1.2 \pm 0.3
	3; August 02, 03	55 (21)	56.5 \pm 5.0	1.8 \pm 0.5
Atlantic salmon in sympatry				
2008	1; June 13, 14	168 (21)	36.0 \pm 3.9	0.5 \pm 0.2
	2; July 30, 31	81 (22)	55.1 \pm 5.4	1.7 \pm 0.5
	3; September 23, 24	63 (22)	72.8 \pm 5.5	3.5 \pm 0.8
2009	1; June 16, 17	178 (32)	41.2 \pm 5.2	0.6 \pm 0.1
	2; July 14, 17	55 (31)	50.0 \pm 6.0	1.1 \pm 0.5
	3; August 05, 06	35 (26)	56.2 \pm 5.5	2.1 \pm 0.7
Smallmouth bass in sympatry				
2008	1; June 13, 14	0 (-)	-	-
	2; July 30, 31	75 (11)	49.3 \pm 5.9	1.6 \pm 0.5
	3; September 23, 24	11 (1)	70.0 \pm	4.1 \pm
2009	1; June 16, 17	0 (-)	-	-
	2; July 14, 17	0 (-)	-	-
	3; August 05, 06	0 (-)	-	-

Table 2.2 – Relative overlap (Morisita's Overlap Index C), in depths and mean water column velocities of habitat used by Atlantic salmon and smallmouth bass in two streams where they occurred in sympatry for three sampling periods. One asterisk denotes moderate overlap, two asterisks denote high overlap.

Stream	Sample Period	Depth	Velocity
Great Works	1	0	0
	2	0.57 *	0.97 **
	3	0	0
Union River	1	0	0
	2	0.98 **	0.83 **
	3	0.52 *	0.11

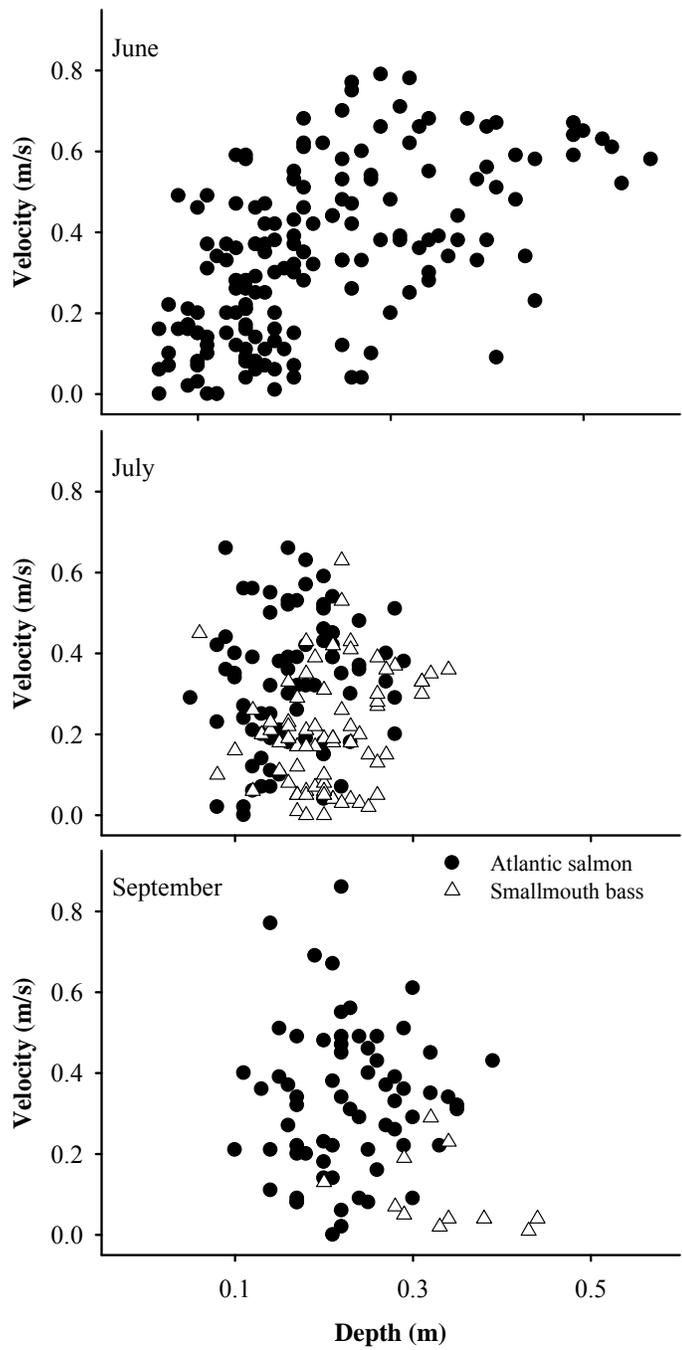


Figure 2.2 – Depths and mean water column velocities used by Atlantic salmon and smallmouth bass during open observations in sympatric streams (Great Works Stream and Union River) at three sampling events in the 2008.

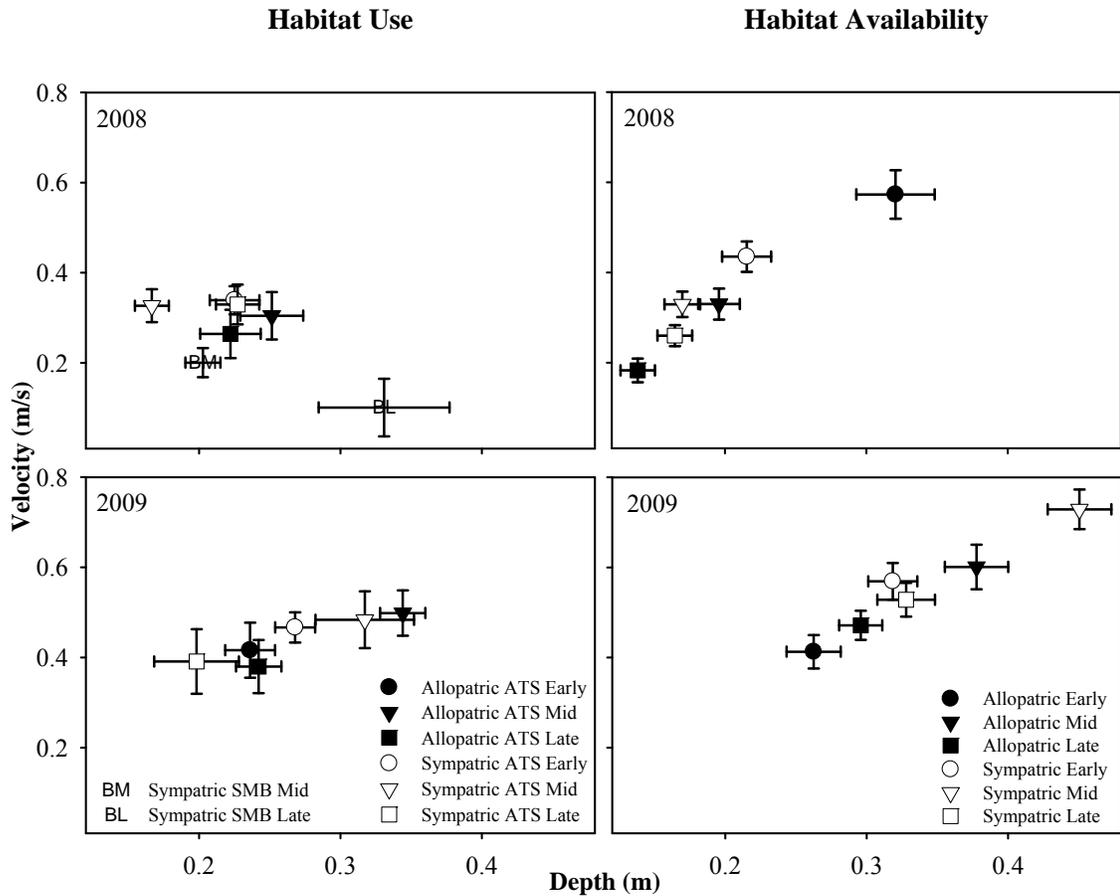


Figure 2.3 – Mean depths (x-axis) and water column velocities (y-axis) used and available to Atlantic salmon and smallmouth bass in allopatric and sympatric streams. Each graph depicts either fish habitat use or habitat availability at three different times during two summers (early, middle, and late). Error bars are 95% confidence intervals around the mean. Data on allopatric Atlantic salmon habitat use from the early sampling of 2008 were excluded from the graph due to in-stream flood conditions which affect habitat use, and low number of detections (n=7). Observations of smallmouth bass were made only in mid and late sampling periods 2008 (BM, BL respectively).

In 2009 we did not find any age 0 smallmouth bass in either of our sympatric study systems. Adult smallmouth bass were observed in pools upstream and downstream of study reaches but no data were collected on their habitat use, thus we did not compute overlap indices. There were significant differences in depths ($P < 0.001$) and velocities ($P = 0.009$) used by Atlantic salmon between observational periods in allopatric streams. Mirroring the increases in available depths and velocities, Atlantic salmon shifted to deeper faster habitats in the July sampling. Likewise there were significant differences in velocities ($P < 0.001$), but not depths ($P = 0.057$) used by Atlantic salmon in sympatric streams, even though there were no age 0 smallmouth bass present in study reaches (Figure 2.3). In sympatric streams Atlantic salmon used the fastest water velocities during the July sampling event.

Differences in precipitation levels and water temperatures between our two study seasons may explain the lack of smallmouth bass detected in our 2009 open observations. At the National Oceanic and Atmospheric Administration weather station in Old Town, ME total precipitation for both months was 337 mm in 2009 and 191 mm in 2008; mean temperature was 16.7° C in 2009 and 18.7° C in 2008 (NOAA 2008-2009). Increased early summer stream discharge and lower than expected water temperatures were observed across the state, as typified by the Narraguagus River (USGS 2008-2009). Lower early summer water temperatures were mirrored in our sympatric study reaches (e.g., Union River; Figure 2.4).

Water Temperature and Discharge

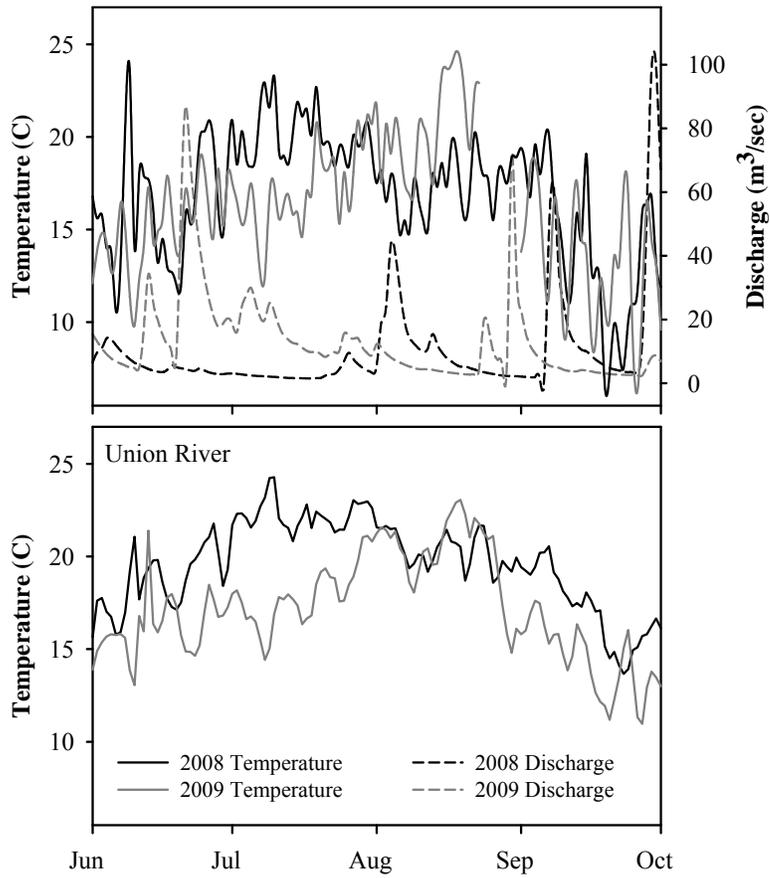


Figure 2.4 – Water temperature and stream discharge profiles from the Narraguagus River (Data courtesy of USGS National Water Information System monitoring station on the Narraguagus River at Deblois, Maine) and water temperature from the Union River over four months during the summers of 2008 and 2009.

Controlled invasions

In 2008 we observed no significant change in depths or velocities used by Atlantic salmon after introducing age 1 smallmouth bass (Figure 2.5). We saw a shift in substrate used in Pollard Brook ($P = 0.036$) but not in Hemlock Brook. In reaches containing Atlantic salmon only, we did not detect a difference in depths used by fish at low and high densities (i.e., before and after introduction of additional Atlantic salmon). However, we did detect a small but significant shift to higher water velocities ($P = 0.041$) and finer substrates ($P = 0.030$) after an increase in Atlantic salmon density in one reach, but not in the other ($P = 0.549$ for velocity, $P = 0.421$ for substrate).

In both sympatric reaches, Atlantic salmon detectability decreased ($P = 0.015$, 0.0001) after the introduction of age 1 smallmouth bass, averaging 56% before and 26% after introduction. In both allopatric reaches, detectability of Atlantic salmon was similar at low densities and high densities (i.e., before and after introductions; 42% and 50%, respectively)

In 2009 we did not detect a shift in habitat use by Atlantic salmon after the introduction of age 0 smallmouth bass, using snorkel observations (Figure 2.5). Likewise, there was no shift in depths and velocities used by Atlantic salmon in allopatric reaches before and after conspecific introductions. Similarly, using a PIT-pack to locate fish, we detected no difference in depths and velocities in the allopatric reach (Figure 2.5) and no difference in the sympatric reach. We detected no difference in depths and velocities of fish interrogated by PIT-pack versus snorkel observation.

Snorkeling detectability of Atlantic salmon did not change after invasion in either allopatric (27% vs. 24%) or sympatric (34% vs. 22%) sections. PIT-packing was more

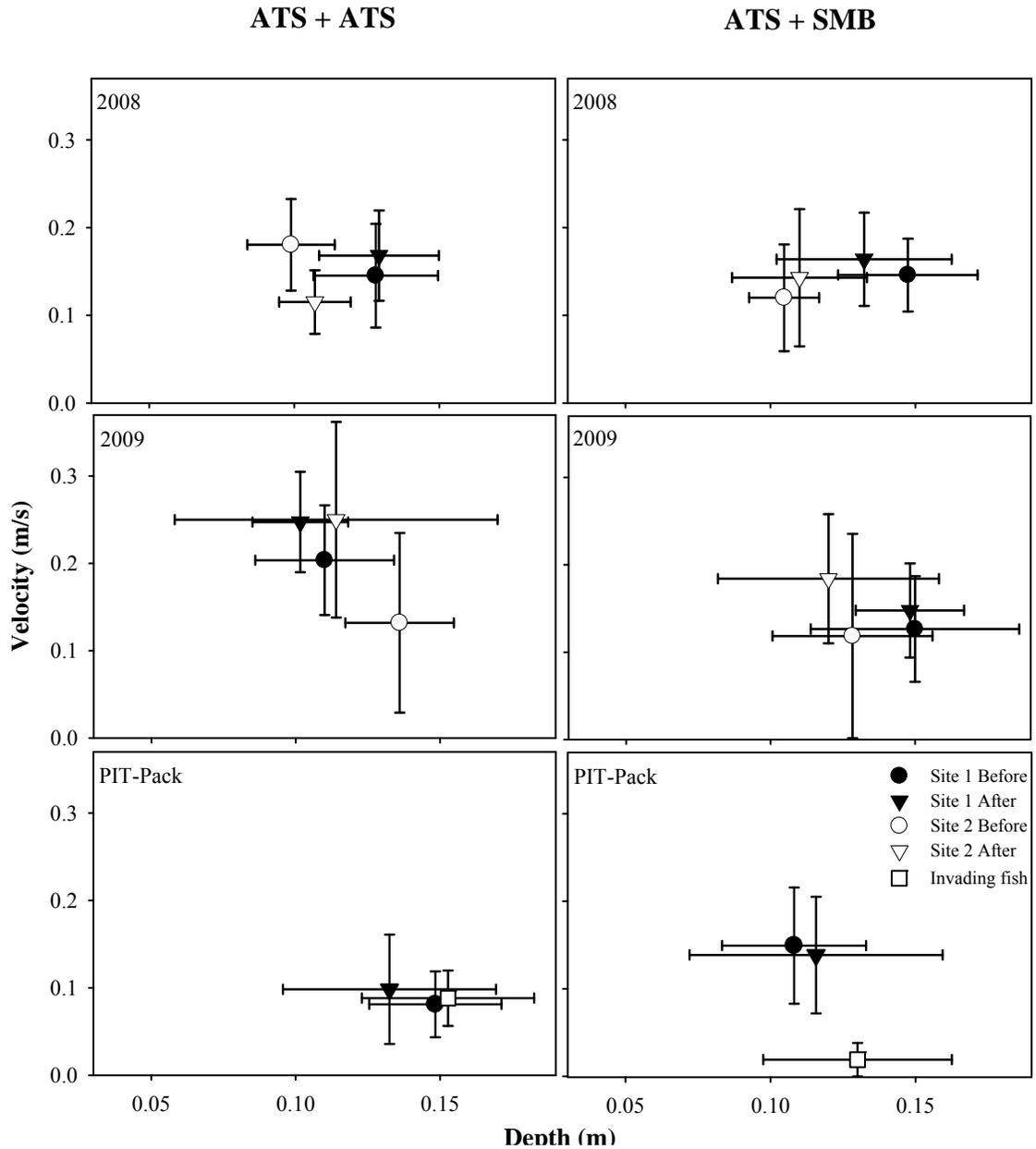


Figure 2.5 – Mean depths (x-axis) and water column velocities (y-axis) used by Atlantic salmon before and after the introduction of either more Atlantic salmon (ATS + ATS) or smallmouth bass (ATS + SMB) in controlled invasion experiments from 2008, 2009, and PIT-Pack 2009. Habitat variables used by “invading fish” from the experiment utilizing PIT-Pack interrogation are included in bottom graphs. Error bars are 95% confidence intervals around the mean.

effective at locating fish in our study reaches. In the allopatric reach we accounted for 60% of the fish before introduction, and 68% after introduction. In the sympatric reach we detected 53% before the introduction and 62% after the introduction.

Discussion

We found that under certain conditions, age 0 Atlantic salmon and age 0 smallmouth bass overlap substantially in their habitat use during mid-summer. Furthermore, salmon in sympatry shifted to shallow habitats during the period of high overlap while salmon in allopatry were found in deeper habitats, suggesting that the presence of age 0 smallmouth bass in nursery riffles altered Atlantic salmon behavior. We were unable to document explicit shifts in Atlantic salmon habitat as a result of controlled smallmouth bass introductions, although we showed that salmon in the presence of age-1 bass are much less detectable than salmon in the presence of other salmon.

Open observations

In 2008, we saw a considerable overlap in velocities and depths used by age 0 Atlantic salmon and age 0 smallmouth bass during mid-summer months. The influx of age 0 smallmouth bass into study riffles is consistent with those fish selecting foraging habitats that maximize their net energy gain (Sabo et al. 1996) while avoiding predation from large smallmouth bass in adjacent pool habitats (Schlosser 1987). The period of high overlap occurred during late July, when streams in Maine typically experience low discharge and high water temperatures. Mean and maximum daily stream temperature

during the second set of snorkel observations were 23.0° C and 25.1° C, respectively, in the Union River, which exceeds the 16° C to 19° C optimal temperature range for growth of Atlantic salmon (Murphy 2003) but within or near the 22° C to 24° C optimal range for smallmouth bass (Sabo et al. 1996; Whitley et al. 2002).

Previous research has demonstrated that competition between native Atlantic salmon and exotic rainbow trout (*Oncorhynchus mykiss*) is temperature-dependent, with the more cold-water adapted rainbow trout competitively-dominant at temperatures near its thermal optimum (Coghlan and Ringler 2005). Similarly, Taniguchi et al. (1998) demonstrated that a warm water adapted cyprinid was competitively superior to two salmonine species at higher water temperatures. Mid-to-late summer is also typically a time when drifting invertebrate abundance in the water column is low (Brittain and Eikeland 1988; Romaniszyn et al. 2007). At higher water temperatures, it is plausible that Atlantic salmon are competitively inferior to the warm-water adapted smallmouth bass for habitats that provide sufficient quantities of scarce prey.

Our data from 2008 show a shift by Atlantic salmon to shallower waters in the presence of age 0 smallmouth bass during our mid-summer sampling. This observed shift to shallower mid-summer habitats was not mirrored in our allopatric study reaches and contradicts the well-documented ontogenetic shifts of Atlantic salmon to faster, deeper water through their first summer (Rimmer et al. 1985; Morantz et al. 1987; Nislow et al. 2000). This shift may have been a result of interference competition from age 0 smallmouth bass, as smallmouth bass occupied depths similar to what sympatric Atlantic salmon used during the June and September observations. Decreases in available water depths were much more pronounced in allopatric streams than in sympatric streams.

Therefore, it is more likely that the shift to shallower habitats by allopatric Atlantic salmon in late September was simply a result of decreases in water levels that limited the availability of deeper habitats.

Salmonines excluded from preferred habitats, via competition, can experience reductions in net energy gain (Fausch 1984; Vander Zanden et al. 2004b). A shift away from favorable foraging areas as a result of smallmouth bass presence could decrease net energy gain and survival of Atlantic salmon similar to what Nislow et al. (1999) observed for juvenile Atlantic salmon in streams containing less preferred habitat. Energetic demands govern Atlantic salmon diurnal activity patterns (Orpwood et al. 2006). Atlantic salmon are primarily nocturnal foragers during winter months (Cunjak 1988), and at higher summer water temperatures (Orpwood et al. 2006). Because smallmouth bass are primarily active during the daytime (Demers et al. 1996), diel segregation of foraging activities between Atlantic salmon and smallmouth bass is a possible mechanism for competition avoidance. However, altered diel patterns of juvenile Atlantic salmon in the presence of a competitor could increase daytime activity levels, thereby increasing vulnerability to diurnal predators (Blanchet et al. 2008).

In June and July of 2009 the state of Maine experienced atypically high rainfall and low air temperatures. We believe that the combination of increased stream discharge and lower water temperature during the smallmouth bass' emergence period caused near year class failures in many Maine streams, including our study systems. Increased water velocities and decreased temperatures can cause nest abandonment by adult males (Cleary 1956; Simonson and Swenson 1990) which decreases emergence success and fry survival (Bain and Helfrich 1983; Ridgway 1988; Ridgway and Shuter 1997). Increases

in discharge can also displace juvenile smallmouth bass (Harvey 1987), and reduce first year growth and survival (Swenson et al. 2002).

High water events in 2009 may also explain the shifts in depths and velocities used by Atlantic salmon, particularly in July in both types of streams. These shifts track closely with increases in mean depths and velocities of available habitat during that period, indicating patterns in habitat use were primarily determined by in-stream conditions.

Controlled invasion

In the 2008 controlled invasion study we observed no effects of age 1 smallmouth bass on Atlantic salmon habitat use. We conducted these experiments two weeks before we observed age 0 smallmouth bass co-habiting with Atlantic salmon in our open observation riffles. At the time, we believed that age 1 smallmouth bass would pose a greater competitive threat to juvenile Atlantic salmon due to their size advantage. However, during this experiment smallmouth bass were found in the slowest deepest habitats available in the enclosed reaches. It seemed that age 1 smallmouth bass avoided habitats used characteristically by juvenile Atlantic salmon. Given the lack of age 1 or older smallmouth bass present in our open observation study riffles and the evidence from the controlled invasion experiments, we believe competition for habitat between age 0 Atlantic salmon and age 1 smallmouth bass is minimal. However, detectability of age 0 Atlantic salmon decreased significantly with the introduction of age 1 smallmouth bass. Other salmonines have been shown to increase their use of shelter refugia in the presence of predators (Alvarez and Nicieza 2003). Decreased daily activity levels have been

observed for juvenile Atlantic salmon in the presence of predators (Vehanen 2003). The decrease in detectability of age 0 Atlantic salmon, plus a change in substrates used in one study reach, is probably indicative of increased hiding behavior caused by the threat of predation by age 1 smallmouth bass, and suggests that the Atlantic salmon that change their habitat use the most may not have been observed.

In 2009, we repeated the controlled invasion experiments with age 0 Atlantic salmon and age 0 smallmouth bass. Our intentions were to conduct this experiment in early to mid-August, a time at which we expected a high level of habitat use overlap between the two species. By mid-August, after searching in many central Maine streams, we were able to locate only one fluvial age 0 smallmouth bass cohort (Kenduskeag Stream), which showed dramatically delayed development. Mean weight of age 0 smallmouth bass in Kenduskeag Stream was 1.9g in September 2009, compared to 6.1g in September 2007 (S. Coghlan, unpublished data). We waited until mid-September to conduct the 2009 controlled invasion experiment in an effort to minimize the size discrepancy between the species. By the time our experiments began, smallmouth bass were on average 10 mm (TL) smaller than Atlantic salmon. Greater fish size is often the major determining factor for competitive ability (Fausch and White 1986; Glova 1986; Young 2004), although prior residence is important in some cases (Volpe et al. 2001). Atlantic salmon used in the 2009 controlled invasion experiment had a clear size advantage, which may partially explain our results.

We observed no significant change in age 0 Atlantic salmon habitat use before and after the introduction of either age 0 smallmouth bass or additional Atlantic salmon and thus did not detect inter- or intra-specific competition for habitat. The lack of

response to hetero- and con-specific introductions could have been the result of one or many of the following factors: 1) insufficient densities of fish to cause habitat saturation, thus obviating competition for habitat and habitat use shifts (Bult et al. 1999), 2) habitat partitioning by 0 Atlantic salmon and smallmouth bass, similar to natural habitat partitioning by Atlantic salmon and brook trout (Gibson 1973), 3) inferior competitive abilities of fish at a distinct size disadvantage (Glova 1986), and 4) timing of the experiment and associated water temperatures (mean water temperature during snorkel observations = 14.5°C) that were below the optimal foraging range smallmouth bass and Atlantic salmon (Sabo et al. 1996; Murphy 2003). Many Atlantic salmon and smallmouth bass were observed hiding in interstitial spaces. Both Atlantic salmon (Gibson 1978) and smallmouth bass (Munther 1970) are known to decrease activity levels as temperatures decrease, and the observed hiding behavior may be an indicator that conditions that promote habitat overlap between the two species were not present.

The similarity between depths and velocities used by fish detected by PIT-packing compared to snorkel observation may indicate that PIT-packing can be advantageous as a method for identifying fish locations due to higher detection success and shorter sampling time. In our narrow reaches, PIT-pack interrogations took less than one half hour and required minimal wading. On the other hand, snorkel observations took two hours per reach to complete and required sampling in shallow habitats where the method is less effective (Heggenes et al. 1990). In the two reaches where we compared data between sampling techniques, means of used velocities were 0.05 m/s slower in PIT-pack interrogated reaches. This was not a significant difference but a low sample size ($N = 26, 28$) resulted in low statistical power ($1-\beta = 0.20, 0.39$ respectively), increasing the

probability of type two error. Unquestionably, PIT-packing locates hiding fish more effectively. The overhead stimulus of the PIT-Pack antenna may have triggered Atlantic salmon hiding behavior, but Hill et al. (2005) found that 86% of their study fish did not change position when detected by PIT-pack. Other investigators have used electrofishing to locate stream salmonines and quantify habitat use with success (e.g., Johnson and Douglass 2009). Once fish are tagged, PIT-packing is much less intrusive and stress-inducing than electrofishing.

Despite the fact that we were not able to conduct controlled invasion experiments under ideal conditions, our results did provide verification of insights gained during open observation studies. Controlled invasion experiments from 2008 revealed that interference competition for habitat between juvenile Atlantic salmon and age 1 smallmouth bass is highly unlikely, but that a predation risk from bass may alter behavior of Atlantic salmon. Our 2009 experiments revealed that competition for habitat from developmentally-delayed age 0 smallmouth bass in early fall does not cause a shift in juvenile Atlantic salmon's habitat use.

Implications

Overall, we saw that under typical summer conditions in Maine streams, age 0 Atlantic salmon and smallmouth bass overlap in their habitat use during mid-summer months, and habitat shifts by Atlantic salmon coincide with the timing of highest overlap. Early and mid-summer flows and water temperature likely set the stage for competitive interactions. The variation in weather between the two years of our study made replicating experiments impossible, but the differential responses of Atlantic salmon

among years was evidence that habitat use and competitive interactions depend at least in part on stream temperature and discharge.

Mean July air temperature limits the northward expansion of smallmouth bass range in Ontario, Canada (Jackson and Mandrak 2002). Global climate change scenarios predict increases in both air and water temperatures throughout New England (Jacobson et al. 2009), which will result in more thermally-suitable habitat for the smallmouth bass at the expense of Atlantic salmon. Even though we suggest that the period for competition between Atlantic salmon and smallmouth bass is relatively short, it occurs at an energetically-challenging time for age 0 Atlantic salmon, when discharge is low, water temperatures are high, and aquatic drift is diminished. Our results suggest that as streams continue to warm, the period of competition and its resultant negative effects will increase in duration and severity. In light, Atlantic salmon recovery efforts should be focused in watersheds that smallmouth bass have yet to invade, or are colder than optimal for smallmouth bass. Furthermore, removal efforts of smallmouth bass from Atlantic salmon habitats should target streams where smallmouth bass still occur at low densities, or take advantage of natural recruitment bottlenecks by targeting cohorts already impacted by cold, wet summers (like the one Maine experienced in 2009).

CHAPTER 3:
EFFECTS OF SMALLMOUTH BASS (*MICROPTERUS DOLOMIEU*) ON
ATLANTIC SALMON (*SALMO SALAR*) HABITAT USE AND DIEL
MOVEMENTS IN AN ARTIFICIAL STREAM

Abstract

For over 150 years, smallmouth bass have been established in some of the last remaining watersheds containing wild anadromous Atlantic salmon, yet little is known about the ecological interactions between the species. We used a simulated stream, equipped with a PIT tag antenna array, to monitor habitat use and movements of age 0 Atlantic salmon and age 0 smallmouth in sympatry and allopatry. We used a combined additive and substitutive design to test for changes in habitat use, diel movements, and diel activity patterns of prior resident fish as a result of inter- and intra-specific competition from invaders. Atlantic salmon did not change their habitat use in the presence of conspecific or heterospecific invaders. However, Atlantic salmon did cause smallmouth bass to use riffle habitats less during daytime. Atlantic salmon and smallmouth bass displayed different diel activity patterns, which were affected by heterospecific introductions. Because both species tended to favor different habitat types and displayed different activity patterns, we suggest under the conditions tested, the level of interspecific competition for habitat was low. Age 0 Atlantic salmon and smallmouth bass may be able to avoid intense interspecific competition through spatial and temporal habitat partitioning.

Introduction

The introduction and establishment of exotic species has caused the extirpation of native salmonine populations, and has limited the success of re-introducing endemic species to their historic habitats (Harig et al. 2000; Levin et al. 2002; Scott et al. 2005). Competition for resources from invasive species can have negative effects on individuals and populations of native species (Callaway and Aschehoug 2000), by depleting or limiting access to resources. In turn, this competition from an invasive species can reduce native fish survival, growth, and thus fitness (Nakano et al. 1998; Gunckel et al. 2002). The potential for competition from exotic salmonines to limit the recovery of native Atlantic salmon in the Great Lakes has been evaluated (Fausch 1998b; Coghlan and Ringler 2005; Scott et al. 2005), yet little is known about the threat of interspecific competition to re-establishing wild Atlantic salmon populations in the Gulf of Maine watershed.

Atlantic salmon (*Salmo salar*) are endangered or have been extirpated from much of their historic range within the United States. Multiple anthropogenic effects have contributed to the decline of Atlantic salmon populations including habitat loss, barriers to migration, overharvest, and pollution. State and federal management efforts and extensive resources have been devoted to remediate the effects of previous practices in hopes of restoring Atlantic salmon populations, yet most populations in the United States are listed under the Endangered Species Act (NOAA 2009).

Over two million Atlantic salmon fry and parr are stocked annually in rivers draining into the Gulf of Maine, yet adult returns are drastically lower than historic numbers. Oceanic conditions impact Atlantic salmon mortality (Scarnecchia 1984), but

the major population bottleneck may be the freshwater foraging stage of the Atlantic salmon life-cycle (Armstrong 2005; Scott et al. 2005). For Atlantic salmon to complete their freshwater life stage, they must avoid predation, endure harsh winters, and successfully transition through the physiological changes of smoltification. Access to energetically-profitable foraging habitat increases age 0 Atlantic salmon survival during their first summer (Nislow et al. 1999), the period in which they are most susceptible to mortality (Scott et al. 2005). Exclusion from profitable habitats by a competitor can reduce net energy gain (Fausch 1984), and can also alter activity patterns, possibly making Atlantic salmon more susceptible to predation (Blanchet et al. 2008).

Through out most of their North American range Atlantic salmon co-occur with brook trout (*Salvelinus fontinalis*); these two species have co-evolved habitat partitioning mechanisms that minimize resource use overlap, thereby avoiding intense competition (Gibson 1973; Gibson 1978). Smallmouth bass (*Micropterus dolomeiu*), were introduced to New England in the middle of the 19th century, and since have invaded almost every historic Atlantic salmon watershed in the United States and many in Canada (Warner 2005; Valois et al. 2009). In watersheds where they occur in sympatry, smallmouth bass may compete with Atlantic salmon for physical habitat and food either spatially, temporally, or both.

In streams, habitat selection reflects balancing food quality and supply with energy expended on prey capture (Smith and Li 1983). Juvenile smallmouth bass maximize net energy gain in fast (> 10 cm/s) shallow (< 60 cm) habitats (Sabo et al. 1996). Nislow et al. (1999) estimated the optimal current velocity for age 0 Atlantic salmon foraging to be 12.8 cm/s and Stanley and Trial (1995) estimated depths of 10-40

cm most suitable for Atlantic salmon fry. The similarity of energetically-profitable habitats for juvenile Atlantic salmon and smallmouth bass may result in habitat overlap and competition for habitat between juveniles of both species. Atlantic salmon and smallmouth bass have not co-evolved niche-partitioning mechanisms. Without niche-partitioning mechanisms, competitive interactions can be intensified in fish (Fausch 1998b).

Diel activity patterns in freshwater fishes should be determined primarily by maximizing foraging opportunities while minimizing predation risks. Atlantic salmon forage primarily at night during winter (Cunjak and Power 1987; Metcalfe et al. 1998), at higher summer water temperatures (Gries et al. 1997; Orpwood et al. 2006), and presumably forage diurnally only when required to sustain growth (Orpwood et al. 2006). Blanchet et al. (2008) observed increased diurnal activity of juvenile Atlantic salmon in the presence of exotic rainbow trout, which may increase daytime predation rates of the latter on the former. Juvenile smallmouth bass are primarily diurnal foragers (Sabo et al. 1996), but little is known of the impacts of smallmouth bass presence on Atlantic salmon diel activity patterns. Competition can restrict competitively-inferior fish to sub-optimal foraging times, but temporal partitioning is also thought to minimize competition and allow for co-habitation (Alanara and Brannas 1997; Brannas and Alanara 1997; David et al. 2007).

The goal of this study was to assess effects of heterospecific and conspecific introductions on Atlantic salmon and smallmouth bass habitat use and activity patterns. We used a combined additive and substitutive design (Fausch 1998b) to test for effects of inter- and intraspecific competition on habitat use and movements in an artificial stream

channel for both species of fish. We analyzed data so as to detect shifts in habitat use, differences in the amount of daily movement, and altered diel activity patterns due to the presence of a putative competitor.

Artificial streams have been used widely to explore the competitive interactions between species. They allow researchers to focus on hypothesized driving variables, manipulate assemblages and densities, all while minimizing the environmental stochasticity and logistical issues of conducting research in natural systems. Furthermore, ideal studies combine research conducted in natural settings with laboratory research to form a more comprehensive understanding of mechanisms of competition (Fausch 1998b). Our study was designed to be a complement to research conducted in natural conditions during spring through fall, 2008 – 2009 (Chapter 2). In situ studies provided information on Atlantic salmon and smallmouth bass habitat use, and timing of habitat overlap. By complementing field research with these laboratory studies, we sought to obtain additional information on time spent in different habitats, movements, and diel activity patterns.

Methods

Study fish

Sea-run Atlantic salmon adults returning to the Penobscot River were captured at the Veazie Fish Trap (Penobscot County, Maine), and spawned in November as part of normal rearing. Embryos were incubated over the winter at US Fish and Wildlife Service, Craig Brook National Fish Hatchery (East Orland, Maine). In late May, personnel from the Maine Department of Marine Resources Bureau of Sea-Run Fisheries

and Habitat (DMR) stocked Atlantic salmon fry into Pollard Brook (45°10'28 N, 68°38'06 W; Penobscot County, Maine), a tributary of the Penobscot River, at a density of 1 fish per m². Smallmouth bass used in experiments were naturally produced within Kenduskeag Stream (44°58'22 N, 69°01'18 W; Penobscot County, Maine), another tributary to the Penobscot River.

We collected all fish using a backpack electrofisher (Smith-Root LR-24). We obtained age 0 smallmouth bass (50.7 ± 1.8 mm TL, 1.8 ± 0.2 g wet weight) on 9/11/2009, and age 0 Atlantic salmon (60.0 ± 2.0 mm TL, 2.1 ± 0.2 g wet weight) on 9/21/2009. We intended to collect fish of similar sizes, but the summer of 2009 was anomalously wet and cold (NOAA 2008-2009) which may have caused year class failures and slow growth of smallmouth bass in central Maine. Smallmouth bass have reduced growth rates in cooler water at higher discharges (Swenson et al. 2002), which explains why bass were smaller than we expected. Fish were brought to the Aquaculture Research Center (University of Maine campus, Orono, Maine), where a subset of fish was anesthetized with buffered MS-222 (80 mg/L, 0.2 mM NaCO₃, pH = 7.0) and implanted with PIT tags (Biomark, Boise, ID. 12mm: TX1411SSL) through a small incision between the pelvic fins and anus (Gries and Letcher 2002). All fish were then held in allopatry in holding tanks for at least a nine day acclimation period before being used in an experiment. During the acclimation period all fish were fed previously frozen chironomid larvae (0.1 g / fish / day; San Francisco Bay Brand).

The tank

We conducted competition experiments in an annular artificial stream channel constructed on the University of Maine campus, Orono, Maine (Figure 3.1). The dimensions of the fiberglass channel are: diameter of 5.2 m, 1.4 m channel width, and 1.2 m height (total bottom area = 17.6 m²). The substrate was comprised of river rocks (20-260 mm diameter) oriented to create two distinct pool and riffle habitats (mean depth pool = 43.3 cm, riffle = 22.9 cm). Experimental tank temperature was kept at 18° C to match the thermal conditions in Kenduskeag Stream on the day we collected smallmouth bass. Two pumps propelled well water through 24 adjustable outlets spaced equally

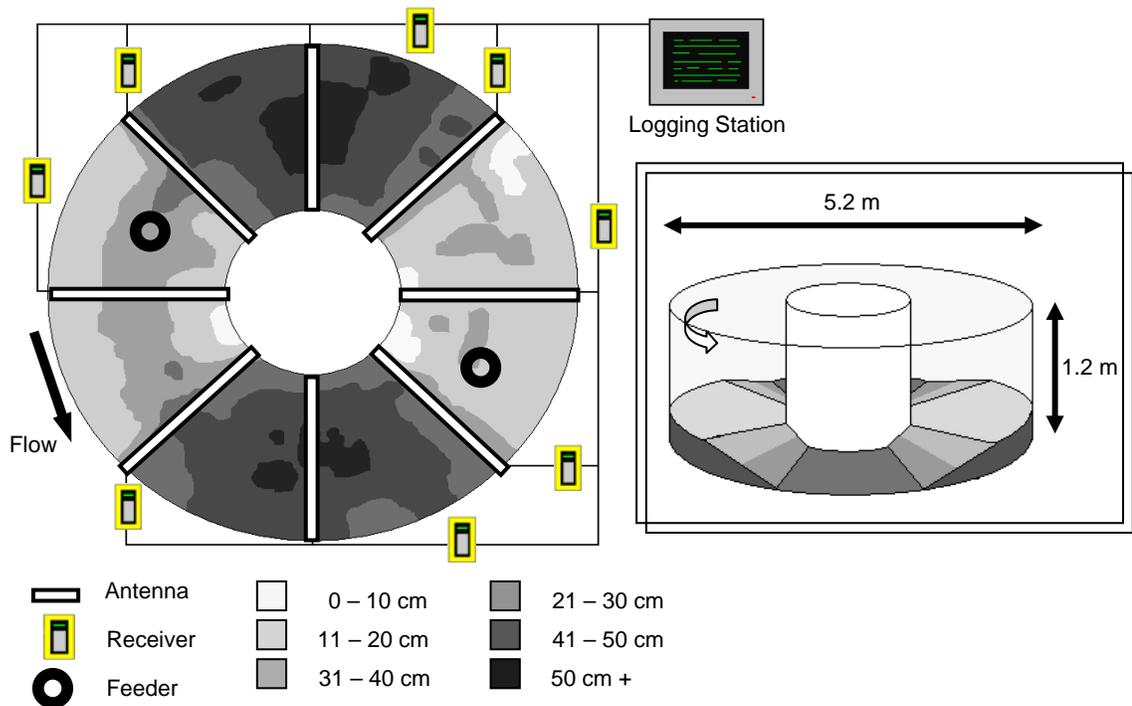


Figure 3.1 – Schematic of an overhead (left) and 3-D view (right) of the annular simulated stream tank used in competition experiments. Grayscale in overhead view diagram corresponds to water depths. An array of eight equally spaced PIT tag antennae was used to detect fish habitat use and movements. Flow ran in a counter clockwise direction.

along the inside and outside walls of the channel. These outlets created a counter-clockwise flow characterized by higher velocities in the riffles (mean water column velocities = 0.15 m/s +/- 0.08 SD) and lower velocities in pools (60% depth velocities = 0.07 m/s +/- 0.06 SD). We maintained a photoperiod of L:D 13.5 : 10.5 with sunrise at 0630 EST. Light was provided by eight full spectrum light bulbs positioned symmetrically above the tank.

We used eight equally-spaced, vertically-oriented PIT tag antennae to monitor fish habitat use and movement during the course of experiments (Figure 1). Six rectangular antennae (1.35 cm x 39 cm) were positioned at the transition between pool and riffle habitats (four) and in riffle habitats (two). Two larger antennae (1.35 cm x 65 cm) were positioned in the middle of both pool habitats. The larger antennae were built in a figure eight pattern to increase efficacy. We used individual PIT-tag readers (Destron Fearing FS 200IF-ISO) unique to each antenna to transmit detection data (tag ID, time and date, and antenna number) to a central logging station. We used MiniMon software (PSMFC) to record and store detection data.

Competition experiments

We conducted four trials to evaluate inter- and intra-specific competition for habitat in the simulated stream: (1) Atlantic salmon prior residents, Atlantic salmon invaders (ATS + ATS; 10/13/2009 – 10/20/2009); (2) Atlantic salmon prior residents, smallmouth bass invaders (ATS + SMB; 9/30/2009 – 10/5/2009); (3) smallmouth bass prior residents, smallmouth bass invaders (SMB + SMB; 9/21/2009 – 9/26/2009); and (4) smallmouth bass prior residents, Atlantic salmon invaders (SMB + ATS; 10/07/2009 –

10/12/2009). In pilot studies evaluating the effect of fish density on movement patterns, we found that at densities of 3 fish per m², Atlantic salmon moved less frequently and occupied specific territories for longer periods. Thus, invader and prior resident fish density for each trial was 1.5 fish /m² or half of presumed habitat saturation. In each experiment we introduced twenty five PIT-tagged fish as “prior residents”. The first group of fish was allowed 72 hours to establish territories before the second group of twenty five fish was introduced to the tank (Note: in the SMB + SMB experiment we introduced only 24 “invaders” because there was a “prior resident” mortality).

We were concerned with the possibility of swamping PIT-tag antennas with too many tags during experiments (i.e., “tag collisions”); therefore, we inserted PIT-tags into no more than 15 “invading” fish (SMB + SMB experiment no invaders tagged; ATS + SMB 10 invaders tagged; SMB + ATS 12 invaders tagged; ATS + ATS 15 invaders tagged). Competition trials were conducted for 72 hours.

During all trials, we introduced 5.6 g of previously frozen chironomid larvae (San Francisco Bay Brand) twice daily (0800 and 1700 EST.) over approximately 20 minutes using automatic feeders at the upstream end of each riffle habitat. The chironomid larvae landed in the center of the stream channel but were dispersed rapidly by the turbulent flows typical in the riffle habitats.

Data collection and analysis for habitat use

We applied four rules to the data collected in the trials to determine which habitats fish used, and for how long: 1) If a fish was detected two or more times consecutively by the same antenna (with a minimum of one second between detections),

then we termed this a continuous detection, assessed a duration time between the first and last detection time, and assumed that the fish was either at or around that antenna for the entire duration. 2) If a fish was detected by one antenna and the next detection occurred at an adjacent antenna immediately upstream or downstream of the first, then we inferred that the duration of time between the detections was the duration of time the fish spent in the habitat between the two antennae. 3) If a fish was detected by the antenna at the edge of a pool or riffle, and the next detection occurred at the other edge of that same pool or riffle then the duration of time between detections was the duration of time that fish spent in the pool or riffle (these types of detections would occur only if the antenna in the middle of the habitat failed to detect the fishes movement). Likewise, if a fish was detected in the middle of one habitat type and in the middle of the adjacent habitat, but was missed by the antenna at the habitat transition zone, we called this habitat use “edge”. These type of detections accounted for 11.2% of all detections. 4) Finally, if two or more consecutive antennae failed to detect a fish during movements, no habitat designation was assigned (9.7% of all detections), and these non-detections were omitted from the analyses.

Habitat detection rules created forty possible habitat use scenarios, which we combined into four mesohabitat use groups: pool, riffle, edge upstream of pool (US edge), and edge downstream of pool (DS edge). We analyzed habitat use as time spent in each mesohabitat category during the designated timeframe. Not all fish had identical total times of detection; therefore, we standardized times by multiplying the hours of the diel period by the proportion of total time detected that fish were in each mesohabitat type.

Pilot experiments indicated that after two days fish movements stabilized, suggesting a 48 hour acclimation period. Therefore, we only analyzed habitat use after prior residents had been in the tank for two days, then again when invaders had been in the tank for two days. We analyzed day and night habitat use separately. We first tested for habitat selection in all trials, and then tested for changes in prior resident habitat use after invader introductions.

Selection - We used Friedman's non-parametric analysis of variance to determine whether, in each trial, individual fish were selecting habitats or using habitats randomly (i.e., proportional to availability). For these analyses we used fish as blocks, habitat types as groups, and the ranks of time spent in each habitat type for each fish as the dependant variable.

Invader effects - We also used Friedman's tests to test for differences in the habitat use in each habitat type for individual prior-resident fish before and after the introduction of invaders. For each experiment, and for day and night, we ranked the differences in hours spent in each habitat type, from before and after invasions, for all fish. Again, we used fish as blocks and habitat types as groups. By using a Friedman's test, we minimized variability between fish; however, not all individuals responded to invasions equally. To better understand the magnitude of how fish changed habitat use after invasion we assigned a maximum percent habitat use change value for each fish, in each trial, for both day and night diel periods. Maximum changes were the absolute value of the greatest percent change in any of the habitat categories from before and after invasions. For example: if an Atlantic salmon used US Edge 15% less, DS edge 8% more, pool 30% more, and riffle 23% less then its maximum change was 30%.

Data collection and analysis for movements

We quantified movements during competition trials by determining the number of movements between antennas for each fish during each hour of the experiment. We treated a movement from one antenna to an adjacent antenna as one “distance unit”. We also recorded the direction of each movement (either upstream or downstream). To test for differences between number movements before and after the introductions of invading fish, day and night periods, and the interaction term, we used a randomized block ANOVA, treating individual fish as blocks. We used transformed ($\ln(x + 1)$) data in the analysis due to the non-normal distribution of the raw data. Again, we only analyzed movements from two 24 hour periods (sunrise to sunrise), starting at day two (before the introduction) and day five (after introduction). We also used a two factor ANOVA to quantify differences between prior resident and invader diel activity patterns.

Results

Habitat use

Selection – During day and night, and before and after invader introductions individual prior resident fish selected for habitats ($P < 0.05$), in all but one trial (Table 3.1); Atlantic salmon during the day in the ATS + SMB trial ($P = 0.252$ before introduction, $P = 0.254$ after introduction). Atlantic salmon used riffles most frequently, whereas smallmouth bass used pools most frequently (Figure 3.2).

Table 3.1 – Habitat selection results for prior resident (first treatment heading) age 0 Atlantic salmon (ATS) and smallmouth bass (SMB) using a Freidman’s non-parametric analysis of variance. Selection evaluated separately for each treatment, before and after invaders, and during day and night.

Treatment	Introduction	Diel	Rank sums for each habitat				P-value
			DS Edge	Pool	Riffle	US Edge	
ATS + ATS	Before	Day	43	69	84	54	<0.001
		Night	56	66	79	49	0.006
	After	Day	44	71	74	61	0.004
		Night	43.5	59.5	78	69	0.001
ATS + SMB	Before	Day	56	65	72	57	0.252
		Night	47.5	66	73.5	63	0.033
	After	Day	55.5	71.5	65.5	57.5	0.254
		Night	51	70.5	74	54.5	0.018
SMB + SMB	Before	Day	39	90	65	46	<0.001
		Night	41	77	58	64	0.001
	After	Day	45	87	66	42	<0.001
		Night	42	81	62	55	<0.001
SMB + ATS	Before	Day	41	97	73	39	<0.001
		Night	34	84	71	61	<0.001
	After	Day	42.5	96	61	50.5	<0.001
		Night	39	90	59	62	<0.001

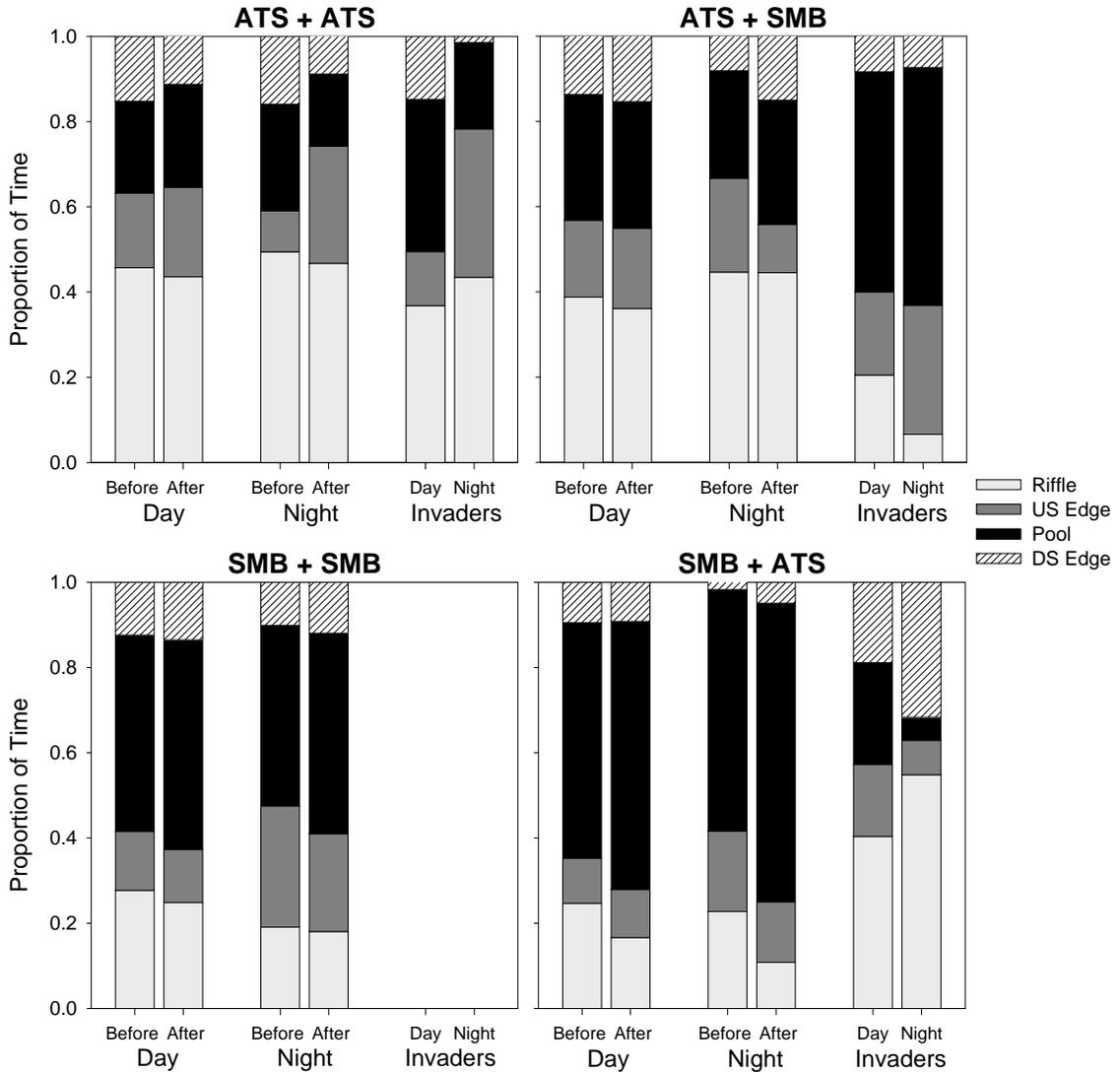


Figure 3.2 – Proportions of habitat type used by age 0 prior resident Atlantic salmon (ATS) or smallmouth bass (SMB) fish (first species) before and after the introduction of invaders (second species) in an annular stream tank, for day and night diel periods. Available data on invader day and night habitat use is on the right side of each graph.

Invader effect – The largest difference in individual habitat use after invasion was observed in the daytime of the SMB + ATS trial (P = 0.051). In this trial the smallest ranked sum was associated with riffle habitats, indicating prior resident smallmouth bass moved out of riffle habitats (Table 3.2). In all other trials, calculated P-values were > 0.271, indicating no statistical difference between the amount of time individual fish spent in habitat types before and after invasions.

Table 3.2 – Results from a Freidman’s non-parametric analysis of variance of habitat use (amount of time spent in each meso habitat category) of prior resident (first treatment heading) age 0 Atlantic salmon (ATS) and smallmouth bass (SMB) before and after the introduction of invaders (second heading) for day and night periods separately.

Trial	Diel	Rank sums for each habitat				P-value
		DS Edge	Pool	Riffle	US Edge	
ATS +	Day	59	64	58	69	0.605
ATS	Night	62	54	62	72	0.271
ATS +	Day	64	63	63	60	0.975
SMB	Night	64.5	64	65.5	56	0.709
SMB +	Day	57	56	64	63	0.741
SMB	Night	62	65	59	54	0.648
SMB +	Day	62	70	48	70	0.051
ATS	Night	63	71	54	62	0.323

In the daytime of the SMB + ATS trial fifteen out of twenty five fish showed a maximal change value < 20% (Figure 3.3), indicating that the observed change in habitat use was the result of many fish changing habitat use patterns slightly. In each trial the largest maximal change values occurred at night. In trials where Atlantic salmon were prior residents, fifteen fish exhibited maximum change values > 60% during the day as opposed to eight individuals at night. In trials where smallmouth bass were prior

residents, no fish showed a maximum change value > 60% during the day, but twenty two had values > 60% at night.

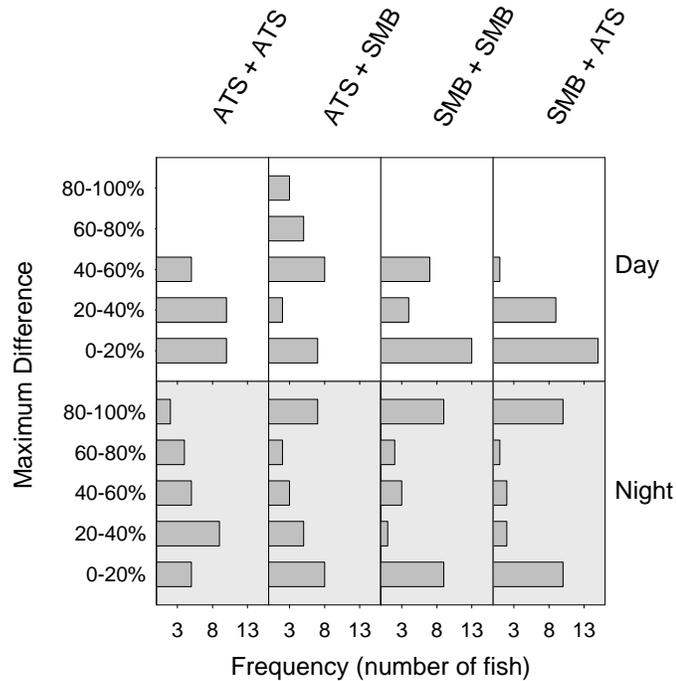


Figure 3.3 – Frequencies of maximum difference in habitat use in prior resident (first heading) age 0 Atlantic salmon (ATS) and smallmouth bass (SMB) before and after the introduction of invaders (second heading) during day and night diel periods. Maximum difference values are defined as the greatest proportional change in use of any habitat type (DS edge, pool, riffle, US edge) for each prior resident fish before and after invasion.

Movements

In general, diel movement patterns of Atlantic salmon and smallmouth bass were nearly opposite. In day one of experiments the highest daily movements of prior resident Atlantic salmon occurred at night (Figure 3.4). As the Atlantic salmon acclimatized, individual fish moved an average of 791 distance units by day and 1029 distance units at night. In addition to the decrease in activity as they acclimatized, Atlantic salmon made very few directional movements except during the first night of the ATS + ATS trial

(Figure 3.5). Conversely, smallmouth bass movements increased in daylight (mean daytime moves = 2451), and decreased at night (mean nighttime moves= 461).

Furthermore, daytime movements were almost always in the upstream direction.

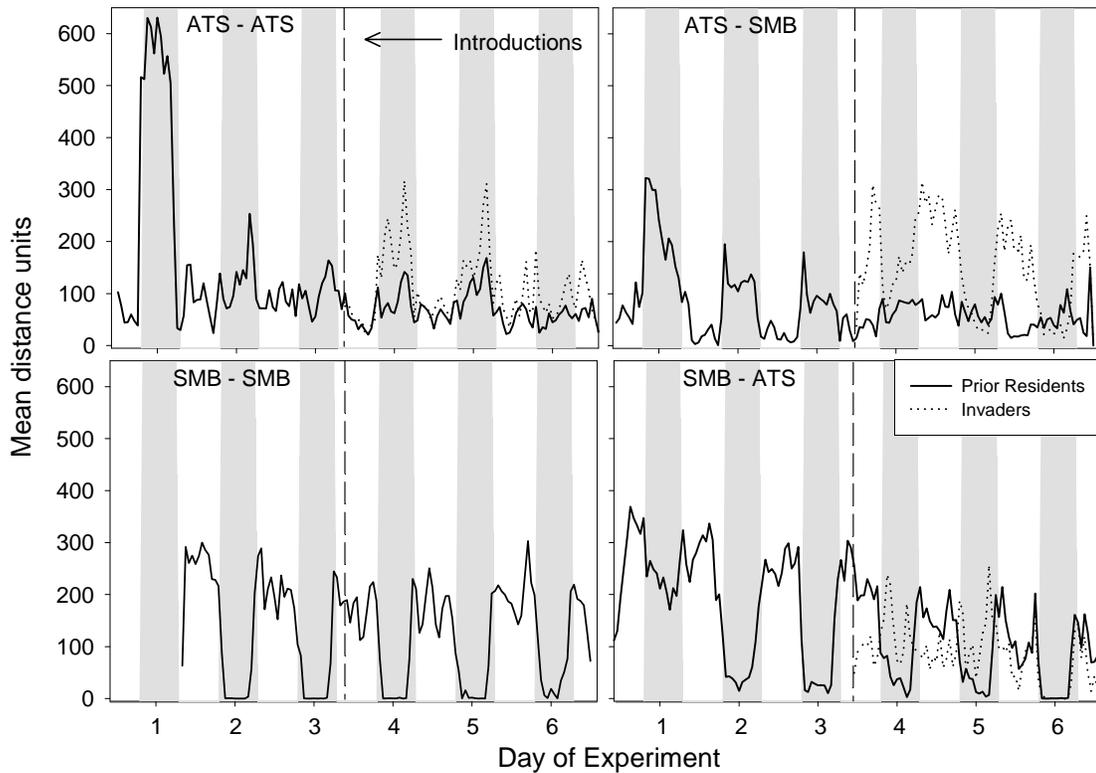


Figure 3.4 – Mean number of distance units moved in an annular experimental tank by a cohort of prior resident (first in heading) and invading (second in heading) young of the year smallmouth bass (SMB) and Atlantic salmon (ATS) in six day experiments. White vertical bars denote hours of daylight, gray vertical bars denote hours of darkness. Vertical dashed line indicates introduction time of invading fish.

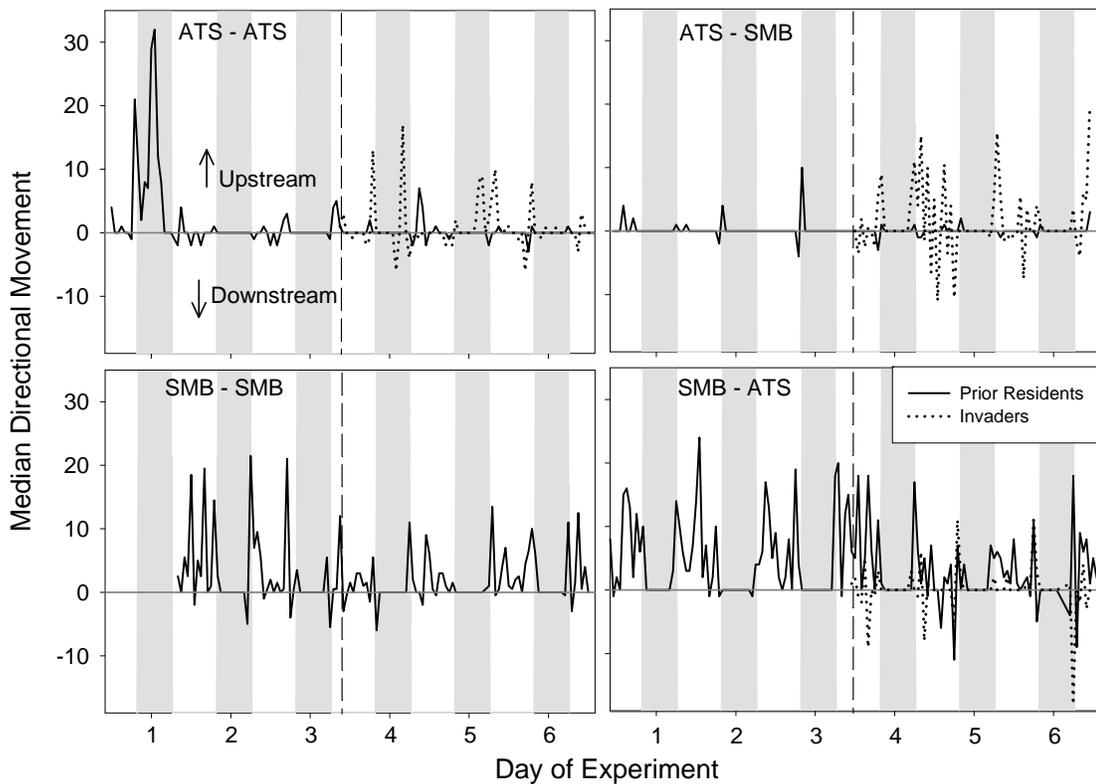


Figure 3.5 – Median directional movements of a cohort of prior resident (first heading) and invading (second heading) age 0 Atlantic salmon (ATS) and smallmouth bass (SMB) in six day experiments. White vertical bars denote hours of daylight, gray vertical bars denote hours of darkness. Dashed vertical line indicates introduction time of invading fish. Positive values indicate upstream movement, negative values indicate downstream movement.

In the ATS + ATS trial there was no significant difference in prior resident Atlantic salmon movements (mean distance units) between day and night, before and after the introduction of invader Atlantic salmon, or the diel pattern (interaction term). The prior resident Atlantic salmon moved less than the invaders ($P = 0.005$), but showed a similar diel pattern. In the ATS + SMB trial, there was a significant difference in diel movement patterns of Atlantic salmon before and after the introduction of smallmouth bass (interaction term: $P = 0.041$). The invading smallmouth bass moved more than the Atlantic salmon ($P < 0.001$), but diel patterns of the two species were not different. In

the SMB + SMB trial smallmouth bass moved more in the day time than they did in the night ($P < 0.001$), irrespective of the presence of the invading smallmouth bass.

Similarly smallmouth bass moved less in the night than in the day ($P < 0.001$) in the SMB + ATS trial, but also moved less in the presence of invading Atlantic salmon ($P = 0.014$), and displayed a different diel pattern with the addition of Atlantic salmon ($P = 0.016$). There was no difference between the number of movements or the diel pattern between the prior resident smallmouth bass and the invading Atlantic salmon.

Discussion

By conducting this research in a controlled setting we have eliminated a set of important ecological factors that may affect habitat use, movement, and diel activity patterns of juvenile Atlantic salmon and smallmouth bass. Predation, interaction with other species, migration, multiple food sources, temperature, and heterogeneous habitat are a few of the natural factors absent from our experiments that may play important roles in facilitating or alleviating competition for habitat between the species. However, the level of detail in our observations of amount of habitat use and movements over diurnal and nocturnal periods would have been prohibitively difficult in a natural setting.

Habitat use

As juveniles, both Atlantic salmon and smallmouth bass may use a wide range of fluvial habitats (DeGraaf and Bain 1986; Sabo and Orth 1994). In our experiments we observed both species using every available mesohabitat, but not in equal proportions. In 88% of trials we observed habitat selection in prior resident fish. We did not detect

daytime habitat selection by Atlantic salmon in the ATS + SMB trial before or after invasion, probably because of high variability in habitat use among fish. Habitat use for Atlantic salmon was highest in riffles in five of six analyses. This observation aligns with many other studies that documented Atlantic salmon selection for riffle habitats (Gibson 1978; Heggenes and Saltveit 1990; Heggenes et al. 1999). Conversely, smallmouth bass habitat use was highest in pools in all experiments, and at night they used pools almost exclusively. One study of lacustrine smallmouth bass in Maine found that adult smallmouth bass moved to deeper habitats at night (Cole and Moring 1997). Although previous research has documented maximal net energy gain by juvenile smallmouth bass in velocities > 10 cm/s and depths < 60 cm (Sabo et al. 1996); smallmouth bass in our experiments used slower deeper pool habitats more frequently. Depth and velocity conditions in our experimental stream's riffles were within the optimal range (mean velocity = 0.15 m/s, mean depth = 22.9 cm) for age 0 smallmouth bass. However, our work was conducted later in the season and at lower water temperatures than those by Sabo et al. (1996), both of which factors may have influenced habitat selection. A previous study of smallmouth bass habitat selection in simulated streams found that sub-adult smallmouth bass (TL: 140-160 mm) select for slower currents (Sechnick et al. 1986), similar to the age 0 smallmouth bass in our experiments.

We observed a daytime shift away from riffle habitats by smallmouth bass in the presence of invading Atlantic salmon. Though small in magnitude, this shift was made by enough smallmouth bass to be evident. In all trials, the experimental stream tank was kept at 18° C, within the 16° C to 19° C optimal temperature range for growth of Atlantic salmon (Murphy 2003) but below the 22° C to 24° C optimal range for smallmouth bass

(Sabo et al. 1996; Whitley et al. 2002). Furthermore, Atlantic salmon used in experiments had, on average, a 9.7 mm total length size advantage over smallmouth bass. Sub-optimal temperatures and a size disadvantage may explain why introduced smallmouth bass had no effect on prior resident Atlantic salmon habitat use, while Atlantic salmon seemed to displace smallmouth bass from riffles.

In other trials, we did not observe a significant shift in habitats used by prior resident fish after the introduction of invaders, indicating that the level of competition for habitat within the tank was not strong enough to elicit a shift in habitat use. Some plausible explanations are that 1) there were insufficient densities of fish to cause habitat saturation, thus obviating competition for habitat and habitat use shifts (Bult et al. 1999), 2) there was habitat partitioning by Atlantic salmon and smallmouth bass, similar to natural habitat partitioning by Atlantic salmon and brook trout (Gibson 1973) and 3) that prior residency could be a determining factor for habitat occupation (Volpe et al. 2001).

In all trials the largest differences in individual habitat use were observed at night, indicating that density may be an important driver of nocturnal Atlantic salmon and smallmouth bass habitat use. Previous research has documented changes in diel habitat use and activity patterns of subordinate stream fish with the increases in levels of intraspecific competition (Alanara et al. 2001; David et al. 2007). Therefore, the larger changes in habitat use we observed at night from a few individuals were probably the result of subordinate fish being displaced at higher densities.

Movements

In natural conditions, juvenile Atlantic salmon move a considerable amount after emergence, but as they grow their movements decrease (Heggenes 1991), and they become territorial (Keenleyside and Yamamoto 1962). Our observations of juvenile Atlantic salmon movements are consistent with what we would expect from age 0 parr at the beginning of fall placed into our experimental stream, which is that daily movement decreased over time, presumably as foraging territories were established.

In streams, adult smallmouth bass have been described as roving foragers (Rankin 1986) that move primarily in an upstream direction (Rankin 1986; Todd and Rabeni 1989). Previous research has shown increased activity at dawn and dusk (Reynolds and Casterlin 1976; Todd and Rabeni 1989), and increased daytime movements (Demers et al. 1996) of adult smallmouth bass. Our simulated stream studies documented that age 0 smallmouth bass had similar activity patterns to adult smallmouth bass. Smallmouth bass in our experiments were most active during daylight hours, did not seem to hold territories like Atlantic salmon, and typically moved upstream.

Despite different diel movement patterns, there was an effect of interspecific introductions on both Atlantic salmon and smallmouth bass movements. In the ATS + ATS trial there was no difference in movement before and after conspecific introductions; however, introducing smallmouth bass in with prior resident Atlantic salmon evinced a change in diel movement patterns of Atlantic salmon. Similarly, prior resident smallmouth bass changed their diel movement patterns in the presence of invading Atlantic salmon, but no such change was observed with the conspecific invader. In both interspecific experiments there were changes in diel movement patterns,

indicating that the presence of heterospecifics caused a disruption of prior resident diel patterns. Competitor-induced shifts in salmonine diel movement patterns could affect energy acquisition, as less competitive fish can be prevented from foraging during optimal feeding times by socially dominant fish (Alanara and Brannas 1997). For many animals the probability of predation is dynamic over a diel cycle (Lima and Dill 1990), and often predation risk influences diel activity (Kronfeld-Schor and Dayan 2003). Presence of smallmouth bass may change the activity patterns of Atlantic salmon, this in turn may lead to increased susceptibility to predation (Blanchet et al. 2008) and disrupt optimal foraging behaviors (David et al. 2007). However, Atlantic salmon can also alter foraging behavior in the event of a competitor mediated change in diel activity, thereby maintaining a similar growth trajectory (Blanchet et al. 2008).

In our experiments, differences in most frequently used habitat, and diel movement patterns, suggest that under the tested conditions, age 0 Atlantic salmon and smallmouth bass may avoid competing for habitat by spatially and temporally partitioning habitat. Spatial partitioning has been observed in sympatric Atlantic salmon and brook trout (Gibson 1973). Likewise, temporal partitioning of activity patterns can reduce direct competition for resources (Kronfeld-Schor and Dayan 2003). In the case of giant kokopu (*Galaxias argenteus*), differences in diel activity patterns allow dominant and subordinate fish to overlap in pool habitats while minimizing interference competition for space (David et al. 2007). Though the period of cohabitation is short on an evolutionary scale, the independently evolved ecologies of juvenile Atlantic salmon and smallmouth bass may be different enough so that high levels of competition for habitat are avoided.

That being said, our results are probably specific to season, temperature, and fish size. Thus, under alternative scenarios results may differ. In a complementary field study we observed a period of high habitat overlap between age 0 Atlantic salmon and age 0 smallmouth bass during the summer of 2008 (Chapter 2). This overlap occurred in mid to late summer when water levels were low, water temperatures were high (~22° C), and fish were similar in size. Our intention was to replicate these conditions in our simulated stream, but an unusually cool and wet summer (2009) resulted in the retarded development of age 0 smallmouth bass and a delayed start time of our experiments at lower water temperature. Temperature influences behavior and habitat use of stream fishes strongly (Magnuson et al. 1979). At temperatures closer to their thermal optima, the competitive ability and resource selection of age 0 smallmouth bass may differ from our tank observations. However, Atlantic salmon can shift to nocturnal foraging at higher temperatures (Orpwood et al. 2006), a diel period where our data suggest that age 0 smallmouth bass are minimally active. It is plausible that even at higher temperatures, where smallmouth bass might be a more formidable competitor, partitioning of diel foraging activity may minimize interspecific resource competition between the two species.

With our documented spatial and temporal partitioning, we are not suggesting that the presence of smallmouth bass has no impact on Atlantic salmon, rather that efforts to re-establish Atlantic salmon in waters containing smallmouth bass may not be in vain. Competition from, and predation by invasive smallmouth bass have evinced niche shifts, changes in trophic structure, and extirpations of native fishes across North America (Vander Zanden et al. 1999; Findlay et al. 2000; Jackson 2002). Little research exists on

smallmouth bass predation on Atlantic salmon (Van den Ende 1993), but our study is the second (Chapter 2) to explore competition between the two species. Competition trials under different scenarios are warranted, but our research suggests that competition for habitat from smallmouth bass, under these particular conditions, may not be a substantial threat to Atlantic salmon persistence.

The size of the fish, timing of the experiment, and the temperature of the simulated stream used in these experiments represent conditions typical of an anomalously cold wet summer. Future experiments on competition for habitat between Atlantic salmon and smallmouth bass should mimic conditions expected from a warmer dryer summer. Repeating experiments under various temperature regimes and with differing size advantages between species will provide a better understanding of the competitive threat smallmouth bass pose to Atlantic salmon in different watersheds, and under multiple climate change scenarios.

REFERENCES

- Alanara, A., and E. Brannas. 1997. Diurnal and nocturnal feeding activity in Arctic char (*Salvelinus alpinus*) and rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* **54**:2894-2900.
- Alanara, A., M. D. Burns, and N. B. Metcalfe. 2001. Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. *Journal of Animal Ecology* **70**:980-986.
- Alvarez, D., and A. G. Nieceza. 2003. Predator avoidance behaviour in wild and hatchery-reared brown trout: the role of experience and domestication. *Journal of Fish Biology* **63**:1565-1577.
- Armstrong, J. D. 2005. Spatial variation in population dynamics of juvenile Atlantic salmon: implications for conservation and management. *Journal of Fish Biology* **67**:35-52.
- ASC. 2005. ATS 2015: Maine Atlantic Salmon Commission's 10-year strategic plan. State of Maine, Atlantic Salmon Commission, Augusta, ME.
- Atlantic Salmon Commission, A. 2005. ATS 2015: Maine Atlantic Salmon Commission's 10-year strategic plan. State of Maine, Atlantic Salmon Commission, Augusta, ME.
- Bain, M. B., and L. A. Helfrich. 1983. Role of male parental care in survival of larval bluegills. *Transactions of the American Fisheries Society* **112**:47-52.
- Baum, E. 1997. *Maine Atlantic Salmon: A National Treasure*. Atlantic Salmon Unlimited, Hermon, Maine.
- Behnke, R. J. 2002. *Trout and Salmon of North America*. The Free Press, New York.
- Beland, K. F. 1984. Strategic plan for management of Atlantic salmon in the state of Maine., Atlantic Sea Run Salmon Commission, Bangor, ME.
- Birch, L. C. 1957. The meanings of competition. *American Naturalist* **91**:5-18.
- Blanchet, S., G. Loot, L. Bernatchez, and J. J. Dodson. 2008. The effects of abiotic factors and intraspecific versus interspecific competition on the diel activity patterns of Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Sciences* **65**:1545-1553.
- Brannas, E., and A. Alanara. 1997. Is diel dualism in feeding activity influenced by competition between individuals? *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **75**:661-669.

- Brittain, J. E., and T. J. Eikeland. 1988. Invertebrate drift - a review. *Hydrobiologia* **166**:77-93.
- Brown, L. R., and P. B. Moyle. 1991. Changes in habitat and microhabitat partitioning within an assemblage of stream fishes in response to predation by Sacramento squawfish (*Ptychocheilus grandis*). *Canadian Journal of Fisheries and Aquatic Sciences* **48**:849-856.
- Bult, T. P., S. C. Riley, R. L. Haedrich, R. J. Gibson, and J. Heggenes. 1999. Density-dependent habitat selection by juvenile Atlantic salmon (*Salmo salar*) in experimental riverine habitats. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:1298-1306.
- Callaway, R. M., and E. T. Aschehoug. 2000. Invasive plants versus their new and old neighbors: A mechanism for exotic invasion. *Science* **290**:521-523.
- Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. *The American Naturalist* **100**:345-357.
- Clady, M. D. 1975. Early survival and recruitment of smallmouth bass in northern Michigan. *The Journal of Wildlife Management* **39**:194-200.
- Cleary, R. E. 1956. Observations on Factors Affecting Smallmouth Bass Production in Iowa. *The Journal of Wildlife Management* **20**:353-359.
- Coghlan, S. M., and N. H. Ringler. 2005. Temperature-dependent effects of rainbow trout on growth of Atlantic salmon parr. *Journal of Great Lakes Research* **31**:386-396.
- Cole, M. B., and J. R. Moring. 1997. Relation of adult size to movements and distribution of smallmouth bass in a central Maine lake. *Transactions of the American Fisheries Society* **126**:815-821.
- Connolly, P. J., and J. H. Petersen. 2003. Bigger is not always better for overwintering young-of-year steelhead. *Transactions of the American Fisheries Society* **132**:262-274.
- Cunjak, R. A. 1988. Behaviour and microhabitat of young Atlantic salmon (*Salmo salar*) during winter. *Canadian Journal of Fisheries and Aquatic Sciences* **45**:2156-2160.
- Cunjak, R. A., and G. Power. 1987. The feeding and energetics of stream-resident trout in winter. *Journal of Fish Biology* **31**:493-511.
- David, B. O., G. P. Closs, S. K. Crow, and E. A. Hansen. 2007. Is diel activity determined by social rank in a drift-feeding stream fish dominance hierarchy? *Animal Behaviour* **74**:259-263.

- DeGraaf, D. A., and L. H. Bain. 1986. Habitat use by and preferences of juvenile Atlantic salmon in to Newfoundland rivers. Transactions of the American Fisheries Society **115**:671-681.
- Demers, E., R. S. McKinley, A. H. Weatherley, and D. J. McQueen. 1996. Activity patterns of largemouth and smallmouth bass determined with electromyogram biotelemetry. Transactions of the American Fisheries Society **125**:434-439.
- Dittman, A. H., and T. P. Quinn. 1996. Homing in Pacific salmon: Mechanisms and ecological basis. Journal of Experimental Biology **199**:83-91.
- Ebert, D. J., and S. P. Filipek. 1991. Evaluation of feeding and habitat competition between native smallmouth bass (*Micropterus dolomieu*) and rainbow trout (*Oncorhynchus mykiss*) in a coolwater stream. First International Smallmouth Bass Symposium:49-54.
- Elliot, J. M. 1991. Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. Freshwater Biology **25**:61-70.
- Facey, D. E., and G. D. Grossman. 1992. The relationship between water velocity, energetic costs, and microhabitat use in four North American stream fishes. Hydrobiologia **239**:1-6.
- Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology **62**:441-451.
- Fausch, K. D. 1988. Tests of competition between native and introduced salmonids in streams: what have we learned? Canadian Journal of Fisheries and Aquatic Sciences **45**:2238-2246.
- Fausch, K. D. 1993. Experimental-analysis of microhabitat selection by juvenile steelhead (*Oncorhynchus-mykiss*) an coho salmon (*Oncorhynchus-kisutch*) in a British-Colombia stream. Canadian Journal of Fisheries and Aquatic Sciences **50**:1198-1207.
- 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., and R. J. White. 1986. Competition among juveniles of coho salmon, brook trout, and brown trout in a laboratory stream, and implications for Great Lakes tributaries. Transactions of the American Fisheries Society **115**:363-381.
- Fay, C., M. Barton, 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.

- Fayram, A. H., and T. H. Sibley. 2000. Impact of predation by smallmouth bass on sockeye salmon in Lake Washington, Washington. *North American Journal of Fisheries Management* **20**:81-89.
- Findlay, C. S., D. G. Bert, and L. Zheng. 2000. Effects of introduced piscivores on native minnow communities in Adirondack lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **57**:570-580.
- Finstad, A. G., O. Ugedal, T. Forseth, and T. F. Næsje. 2004. Energy-related juvenile winter mortality in a northern population of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **61**:2358-2368.
- Ghaerrett, A. J., and W. W. Smoker. 1993. A perspective on the adaptive importance of genetic infrastructure in salmon populations to ocean ranching in Alaska. *Fisheries Research* **18**:45-58.
- Gibson, R. J. 1973. Interactions of juvenile Atlantic salmon (*Salmo salar* L.) and brook trout (*Salvelinus fontinalis* Mitchell). Special Publication Series, International Atlantic Salmon Foundation **4**:181-202.
- Gibson, R. J. 1978. The behavior of juvenile Atlantic salmon (*Salmon salar*) and brook trout (*Salvelinus fontinalis*) with regard to temperature and water velocity. *Transactions of the American Fisheries Society* **107**:703-712.
- Glova, G. J. 1986. Interaction for food and space between experimental populations of juvenile coho salmon (*Oncorhynchus-kisutch*) and costal cutthroat trout (*Salmo-clarki*) in a laboratory stream. *Hydrobiologia* **131**:155-168.
- Gries, G., and B. H. Letcher. 2002. Tag retention and survival of age-0 Atlantic salmon following surgical implantation with passive integrated transponder tags. *North American Journal of Fisheries Management* **22**:219-222.
- Gries, G., K. G. Whalen, F. Juanes, and D. L. Parrish. 1997. Nocturnal activity of juvenile Atlantic salmon (*Salmo salar*) in late summer: evidence of diel activity partitioning. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:1408-1413.
- Gunckel, S. L., A. R. Hemmingsen, and J. L. Li. 2002. Effect of bull trout and brook trout interactions on foraging habitat, feeding behavior, and growth. *Transactions of the American Fisheries Society* **131**:1119-1130.
- Hall, C. A. S., J. A. Stanford, and R. Hauer. 1992. The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients. *Oikos* **65**:377-390.
- Harig, A. L., K. D. Fausch, and M. K. Young. 2000. Factors influencing success of greenback cutthroat trout translocations. *North American Journal of Fisheries Management* **20**:994-1004.

- Harvey, B. C. 1987. Susceptibility of young-of-year fishes to downstream displacement by flooding. *Transactions of the American Fisheries Society* **116**:851-855.
- Hasegawa, K., and K. Maekawa. 2006. The effects of introduced salmonids on two native stream-dwelling salmonids through interspecific competition. *Journal of Fish Biology* **68**:1123-1132.
- Hasegawa, K., T. Yamamoto, M. Murakami, and K. Maekawa. 2004. Comparison of competitive ability between native and introduced salmonids: evidence from pairwise contests. *Ichthyological Research* **51**:191-194.
- Hearn, W. E. 1987. Interspecific competition and habitat segregation among stream-dwelling trout and salmon: a review. *Fisheries* **12**:24-31.
- Heggenes, J. 1991. Comparisons of habitat availability and habitat use by an allopatric cohort of juvenile Atlantic salmon *Salmo salar* under conditions of low competition in a Norwegian stream. *Holarctic Ecology* **14**:51-62.
- Heggenes, J., J. L. Bagliniere, and R. A. Cunjak. 1999. Spatial niche variability for young Atlantic salmon (*Salmo salar*) and brown trout (*S-trutta*) in heterogeneous streams. *Ecology of Freshwater Fish* **8**:1-21.
- Heggenes, J., A. Brabrand, and S. J. Saltveit. 1990. Comparison of three methods for studies of stream habitat use by young brown trout and Atlantic salmon. *Transactions of the American Fisheries Society* **119**:101-111.
- Heggenes, J., and S. J. Saltveit. 1990. Seasonal and spatial microhabitat selection and segregation and young Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) and a Norwegian River *Journal of Fish Biology* **36**:707-720.
- Hill, J., and G. D. Grossman. 1993. An energetic model of microhabitat use for rainbow-trout and roside dace. *Ecology* **74**:685-698.
- Hill, M. S., G. B. Zydlewski, J. D. Zydlewski, and J. M. Gasvoda. 2006. Development and evaluation of portable PIT tag detection units: PITpacks. *Fisheries Research* **77**:102-109.
- Hislop, J. R. G., and R. G. J. Shelton. 1993. Marine predators and prey of Atlantic salmon (*Salmo Salar*).in D. Mills, editor. *Salmon in the Sea and New Enhancement Strategies*. Fishing News Books, Oxford.
- Hutchings, J. A., and M. E. B. Jones. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences* **55**:22-47.
- Jackson, D. A. 2002. Ecological Effects of *Micropterus* Introductions: The Dark Side of Black Bass. Pages 221-232 in D. P. Philipp and M. S. Ridgway, editors. Black

- Bass: Ecology, Conservation, and Management. American Fisheries Society, Symposium 31, Bethesda, Maryland.
- Jackson, D. A., and N. E. Mandrak. 2002. Changing fish biodiversity: predicting the loss of cyprinid biodiversity due to global climate change. Pages 89-98 in N. A. McGinn, editor. Fisheries in a Changing Climate. American Fisheries Society, Symposium 32, Bethesda, Maryland.
- Jacobson, G. L., I. J. Fernandez, P. A. Mayewski, and C. V. Schmitt. 2009. Maine's climate future: an initial assessment. University of Maine, Orono, ME.
- Johnson, J. H., and K. A. Douglass. 2009. Diurnal stream habitat use of juvenile Atlantic salmon, brown trout and rainbow trout in winter. Fisheries Management and Ecology **16**:352-359.
- Jonsson, B., and N. Jonsson. 2004. Factors affecting marine production of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **61**:2369-2383.
- Keenleyside, M. H. A., and F. T. Yamamoto. 1962. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). Behaviour **19**:139-169.
- Kei'ichiro, I., Y. Taiga, and M. Naoto. 2004. Spawning and brood defense of smallmouth bass under the process of invasion into a novel habitat. Environmental Biology of Fishes **70**:219-225.
- Kocik, J. F., and W. W. Taylor. 1996. Effect of juvenile steelhead on juvenile brown trout habitat use in a low-gradient great lakes tributary. Transactions of the American Fisheries Society **125**:244-252.
- Krebs, C. J. 1989. Niche overlap and diet analysis. Ecological Methodology. Harper and Row Publishers, New York.
- Kronfeld-Schor, N., and T. Dayan. 2003. Partitioning of time as an ecological resource. Annual Review of Ecology Evolution and Systematics **34**:153-181.
- Kurth, J., C. Loftin, J. Zydlewski, and J. Rhymer. 2007. PIT tags increase effectiveness of freshwater mussel recaptures. Journal of the North American Benthological Society **26**:253-260.
- Levin, P. S., S. Achord, B. E. Feist, and R. W. Zabel. 2002. Non-indigenous brook trout and the demise of Pacific salmon: a forgotten threat? Proceedings of the Royal Society B-Biological Sciences **269**:1663-1670.
- Li, H. W., and R. W. Brocksen. 1977. Approaches to the analysis of energetic costs of intraspecific competition for space by rainbow trout (*Salmo Gairdneri*). Journal of Fish Biology **11**:329-341.

- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**:619-640.
- Mackenzie, C., and J. R. Moring. 1988. Estimating survival of Atlantic salmon during the intragravel period. *North American Journal of Fisheries Management* **8**:45-49.
- Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an ecological resource. *Integrative and Comparative Biology* **19**:331.
- Metcalf, N. B., N. H. C. Fraser, and M. D. Burns. 1998. State-dependent shifts between nocturnal and diurnal activity in salmon. *Proceedings of the Royal Society B: Biological Sciences* **265**:1503.
- Morantz, D. L., R. K. Sweeney, C. S. Shirvell, and D. A. Longard. 1987. Selection of microhabitat in summer by juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **44**:120-129.
- Morisita, M. 1959. Measuring of interspecific association and similarity between communities. *Memoirs of the Faculty of Science, Kyushu University, Series E (Biology)* **3**:65-80.
- Munther, G. L. 1970. Movement and distribution of smallmouth bass in the Middle Snake River. *Transactions of the American Fisheries Society* **99**:44-&.
- Murphy, M. H. M. 2003. Ecology of young-of-the-year Atlantic salmon (*Salmo salar*): evaluation of strain differences and overwinter survival. State University of New York College of Environmental Science and Forestry, Syracuse, NY.
- Nakano, S., S. Kitano, K. Nakai, and K. D. Fausch. 1998. Competitive interactions for foraging microhabitat among introduced brook charr, *Salvelinus fontinalis*, and native bull charr, *S. confluentus*, and westslope cutthroat trout, *Oncorhynchus clarki lewisi*, in a Montana stream. *Environmental Biology of Fishes* **52**:345-355.
- 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.
- Nielsen, J. L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. *Transactions of the American Fisheries Society* **121**:617-634.
- Nislow, K. H., C. Folt, and M. Seandel. 1998. Food and foraging behavior in relation to microhabitat use and survival of age-0 Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **55**:116-127.
- Nislow, K. H., C. L. Folt, and D. L. Parish. 1999. Favorable foraging locations for young Atlantic salmon: application to habitat and population restoration. *Ecological Applications* **9**:1085-1099.

- Nislow, K. H., C. L. Folt, and D. L. Parrish. 2000. Spatially explicit bioenergetic analysis of habitat quality for age-0 Atlantic salmon. *Transactions of the American Fisheries Society* **129**:1067-1081.
- NOAA. 2008-2009. US Climate Reference Network, Monthly Summary: ME Old Town 2 W. National Climatic Data Center. Available: <http://www.ncdc.noaa.gov/crn/station.htm?stationId=1034>. (January 2010)
- NOAA. 2009. Endangered and Threatened Species; Designation of Critical Habitat for Atlantic Salmon (*Salmo salar*) Gulf of Maine Distinct Population Segment; Final Rule. *Federal Register* **74**:39903-39907.
- Olson, M. H., and B. P. Young. 2003. Patterns of Diet and Growth in Co-occurring Populations of Largemouth Bass and Smallmouth Bass. *Transactions of the American Fisheries Society* **132**:1207-1213.
- Orpwood, J. E., S. W. Griffiths, and J. D. Armstrong. 2006. Effects of food availability on temporal activity patterns and growth of Atlantic salmon. *Journal of Animal Ecology* **75**:677-685.
- Probst, W. E., C. F. Rabeni, W. G. Covington, and R. E. Marteney. 1984. Resource Use by Stream-Dwelling Rock Bass and Smallmouth Bass. *Transactions of the American Fisheries Society* **113**:283-294.
- Raffetto, N. S., J. R. Baylis, and S. L. Serns. 1990. Complete estimates of reproductive success in a closed population of smallmouth bass (*Micropterus Dolomieu*). *Ecology* **71**:1523-1535.
- Rankin, E. T. 1986. Habitat selection by smallmouth bass in response to physical characteristics in a natural stream. *Transactions of the American Fisheries Society* **115**:322-334.
- Reynolds, W. W., and M. E. Casterlin. 1976. Activity rhythms and light intensity preferences of *Micropterus salmoides* and *M. dolomieu*. *Transactions of the American Fisheries Society* **105**:400-403.
- Ridgway, M. S. 1988. Developmental stage of offspring and brood defense in smallmouth bass (*Micropterus-dolomieu*). *Canadian Journal of Zoology* **66**:1722-1728.
- Ridgway, M. S., G. P. Goff, and M. H. A. Keenleyside. 1989. Courtship and spawning behavior in smallmouth bass (*Micropterus dolomieu*). *American Midland Naturalist* **122**:209-213.
- Ridgway, M. S., and B. J. Shuter. 1997. Predicting the effects of angling for nesting male smallmouth bass on production of age-0 fish with an individual-based model. *North American Journal of Fisheries Management* **17**:568-580.

- Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Colombia River Transactions of the American Fisheries Society **120**:448-458.
- Rimmer, D. M., R. L. Saunders, and U. Paim. 1985. Effects of temperature and season on the position holding performance of juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Zoology **63**:92-96.
- Romaniszyn, E. D., J. J. Hutchens, and J. B. Wallace. 2007. Aquatic and terrestrial invertebrate drift in southern Appalachian Mountain streams: implications for trout food resources. Freshwater Biology **52**:1-11.
- Rose, G. A. 1986. Growth decline in subyearling brook trout (*Salvelinus-fontinalis*) after emergence of rainbow-trout (*Salmo-gairdneri*). Canadian Journal of Fisheries and Aquatic Sciences **43**:187-193.
- Rosenfeld, J. 2003. Assessing the habitat requirements of stream fishes: An overview and evaluation of different approaches. Transactions of the American Fisheries Society **132**:953-968.
- Sabo, M. J., and D. J. Orth. 1994. Temporal variation in microhabitat use by age-0 smallmouth bass in the North Anna River, Virginia. Transactions of the American Fisheries Society **123**:733-746.
- Sabo, M. J., D. J. Orth, and E. J. Pert. 1996. Effect of stream microhabitat characteristics on rate of net energy gain by juvenile smallmouth bass, *Micropterus dolomieu*. Environmental Biology of Fishes **46**:393-403.
- Saunders, R., M. A. Hachey, and C. W. Fay. 2006. Maine's Diadromous Fish Community. Fisheries **31**:537-547.
- Scarnecchia, D. L. 1984. Climatic and oceanic variations affecting yield of icelandic stocks of Atlantic salmon (*Salmo-salar*) Canadian Journal of Fisheries and Aquatic Sciences **41**:917-935.
- Schlosser, I. J. 1987. The role of predation in age-related and size-related habitat use by stream fishes. Ecology **68**:651-659.
- Scoppettone, G. G. 1993. Interactions between native and nonnative fishes of the upper Muddy River, Nevada. Transactions of the American Fisheries Society **122**:599-608.
- Scott, R. J., M. S. Poos, D. L. G. Noakes, and F. W. H. Beamish. 2005. Effects of exotic salmonids on juvenile Atlantic salmon behavior. Ecology of Freshwater Fish **14**:283-288.

- Sechnick, C. W., R. F. Carline, R. A. Stein, and E. T. Rankin. 1986. Habitat selection by smallmouth bass in response to physical characteristics of a simulated stream. *Transactions of the American Fisheries Society* **115**:314-321.
- Simonson, T. D., and W. A. Swenson. 1990. Critical stream velocities for young-of-year smallmouth bass in relation to habitat use. *Transactions of the American Fisheries Society* **119**:902-909.
- Smith, J. J., and H. W. Li. 1983. Energetic factors influencing foraging tactics of juvenile steelhead trout, *Salmo gairdneri*. Pages 173-180 in D. G. Lindquist, G. S. Helfman, and J. A. Ward, editors. *Predators and prey fishes*. Dr W. Junk Publishers, The Hague, Netherlands.
- Stabell, O. B. 1984. Homing and olfaction in salmonids: A critical review with special reference to the Atlantic salmon. *Biological Review of the Cambridge Philosophical Society* **59**:333-388.
- Stanley, J. G., and J. G. Trial. 1995. Habitat suitability index models: nonmigratory freshwater life stages of Atlantic salmon. *Biological Science Report* **3**:1-17.
- Swenson, W. A., B. J. Shuter, D. J. Orr, and G. D. Heberling. 2002. The effects of stream temperature and velocity on first-year growth and year-class abundance of smallmouth bass in the Upper Mississippi River. Pages 101-113 in D. P. Philipp and M. S. Ridgway, editors. *Black Bass: Ecology, Conservation, and Management*. American Fisheries Society, Symposium 31, Bethesda, Maryland.
- Symons, P. K. E., and M. Heland. 1978. Stream habitats and behavioral interactions of underyearling and yearling Atlantic salmon (*Salmon salar*). *Journal of the Fisheries Research Board of Canada* **35**:175-183.
- Taniguchi, Y., F. J. Rahel, D. C. Novinger, and K. G. Geron. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. *Canadian Journal of Fisheries and Aquatic Sciences* **55**:1894-1901.
- Todd, B. L., and C. F. Rabeni. 1989. Movement and habitat use by stream-dwelling smallmouth bass. *Transactions of the American Fisheries Society* **118**:229-242.
- USGS. 2008-2009. USGS Real-Time Water Data for Maine. National Water Information System: Web Interface. Available: <http://waterdata.usgs.gov/me/nwis/current/?type=flow>. (January 2010).
- Valois, A., R. A. Curry, and S. M. Coghlan. 2009. Smallmouth bass (*Micropterus dolomeiu*) invasion of Gulf Region rivers: evaluating the impact n Atlantic salmon (*Salmo salar*) populations.

- Van den Ende, O. 1993. Predation on Atlantic salmon smolts (*Salmo salar*) by smallmouth bass (*micropterus dolomeiu*) and chain pickerel (*Esox niger*) in the Penobscot River, Maine. University of Maine, Orono.
- Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* **401**:464-467.
- Vander Zanden, M. J., J. D. Olden, J. H. Thorne, and N. E. Mandrak. 2004a. Predicting Occurrences and Impacts of Smallmouth Bass Introductions in North Temperate Lakes. *Ecological Applications* **14**:132-148.
- Vander Zanden, M. J., J. D. Olden, J. H. Thorne, and N. E. Mandrak. 2004b. Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. *Ecological Applications* **14**:132-148.
- Vehanen, T. 2003. Adaptive flexibility in the behaviour of juvenile Atlantic salmon: short-term responses to food availability and threat from predation. *Journal of Fish Biology* **63**:1034-1045.
- Volpe, J. P., B. R. Anholt, and B. W. Glickman. 2001. Competition among juvenile Atlantic salmon (*Salmo salar*) and steelhead (*Oncorhynchus mykiss*): relevance to invasion potential in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:197-207.
- Walters, J. P., and J. R. Wilson. 1996. Intraspecific habitat segregation by smallmouth bass in the Buffalo River, Arkansas. *Transactions of the American Fisheries Society* **125**:284-290.
- Warner, K. 2005. Smallmouth bass introductions in Maine: history and management implications. *Fisheries* **30**:20-26.
- Weidel, B. C., D. C. Josephson, and C. E. Kraft. 2007. Littoral fish community response to smallmouth bass removal from an Adirondack lake. *Transactions of the American Fisheries Society* **136**:778-789.
- Werner, E. E., and D. J. Hall. 1979. Foraging efficiency and habitat switching in competing sunfishes. *Ecology* **60**:256-264.
- 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.
- Young, K. A. 2004. Asymmetric competition, habitat selection, and niche overlap in juvenile salmonids. *Ecology* **85**:134-149.
- Zaret, T. M., and A. S. Rand. 1971. Competition in tropical stream fishes - support for competitive exclusion principle. *Ecology* **52**:336-&.

Zippin, C. 1956. An evaluation of the removal method of estimating animal populations.
Biometrics **12**:163-189.

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