Habitat Selection and Overlap of Atlantic Salmon and Smallmouth Bass Juveniles in Nursery Streams

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Available online: 20 Sep 2011

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Abstract

Introduced smallmouth bass *Micropterus dolomieu* have invaded much of the historic freshwater habitat of Atlantic salmon *Salmo salar* in North America, yet little is known about the ecological interactions between the two species. We investigated the possibility of competition for habitat between age-0 Atlantic salmon and age-0 and age-1 smallmouth bass by means of in situ observations and a mesocosm experiment. We used snorkel observation to identify the degree and timing of overlap in habitat use in our in situ observations and to describe habitat shifts by Atlantic salmon in the presence of smallmouth bass in our mesocosm experiments. In late July 2008, we observed substantial overlap in the depths and mean water column velocities used by both species in sympatric in situ conditions and an apparent shift by age-0 Atlantic salmon to shallower water that coincided with the period of high overlap. In the mesocosm experiments, 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 2009. In 2009, summer floods with sustained high flows and low temperatures resulted in the nearly complete reproductive failure of the smallmouth bass in our study streams, and we did not observe a midsummer habitat shift by Atlantic salmon similar to that seen in 2008. Although this prevented us from replicating our 2008 experiments under similar conditions, the virtual year-class failure of smallmouth bass itself is enlightening. We suggest that future studies incorporate the effects of varying temperature and discharge to determine how abiotic factors affect the interactions between these species and thus mediate the outcomes of potential competition.

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 owing to both natural causes (e.g., declines in marine survival) and anthropogenic perturbations (e.g., barriers to migration, loss of habitat, pollution, and overharvest; Fay et al. 2006). By the 1950s, the entire Atlantic salmon population in the United States 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 2009, several river-specific stocks within the Gulf of Maine Distinct Population Segment were listed under the U.S. 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 and the Laurentian Great Lakes, have been introduced throughout New England since the 1860s, and the northeastern limit of their range now extends into New Brunswick (Jackson 2002; Warner 2005). Smallmouth bass have invaded virtually every major watershed in the state of Maine (Warner 2005). These fish were detected recently in Miramichi Lake, New Brunswick (Valois et al. 2009), which drains into the Miramichi River, home of one of the largest naturally reproducing population of Atlantic salmon in North America (Chaput 1995). The large gape size of the smallmouth bass, its 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. 2004; Weidel et al. 2007). Competition from and predation by invasive smallmouth bass have caused 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 out-migrating Pacific salmon smolts (Rieman et al. 1991; Fayram and Sibley 2000). In large Maine rivers, one adult smallmouth bass may consume 10 Atlantic salmon smolts per day (Van den Ende 1993). 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 nonnative salmonines (Fausch 1988, 1998), but few have focused on competition between salmonines and centrarchids (Ebert and Filipek 1991).

For interspecific competition to exist, potential competitors must overlap in their use of a limiting resource and the use of the resource by one species must cause a change in that of the other species, usually to the detriment of the survival, growth, or fecundity of one or both species (Birch 1957). Independent habitat selection studies on early life stages of Atlantic salmon and smallmouth bass indicate the possibility for considerable overlap (Valois et al. 2009). In allopatry, juvenile Atlantic salmon 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 sig-

nificant overlap and subsequent competition for habitat, which in stream-dwelling salmonines, translates into competition for food (Chapman 1966).

In stream salmonines, many co-evolved species exhibit niche-partitioning mechanisms that appear to obviate the negative effects of competition in sympatry (e.g., Atlantic salmon and brook trout *Salvelinus fontinalis*; Johnson 2008). In other co-evolved species pairs, competition is probably not important because of innate interspecific differences in habitat use and foraging behavior (e.g., coho salmon *Oncorhynchus kisutch* and steelhead *O. mykiss* (anadromous rainbow trout); Johnson and Ringler 1980). However, in pairs of potentially competing salmonines that do not share co-evolutionary history, results are mixed. Some introduced species pairs interact little if at all (e.g., brown trout *Salmo trutta* and steelhead; Kocik and Taylor 1991), some native species undergo niche shifts when confronted with an exotic species to the detriment of the native species (e.g., brown trout and brook trout; Fausch and White 1986), and some native species forego a niche shift but bear the brunt of interference competition (e.g., bull trout *Salvelinus confluentus* and brook trout; Gunckel et al. 2002).

The goal of our research was to determine whether competition for habitat exists between Atlantic salmon and smallmouth bass by determining (1) whether the two species overlap in habitat use, and if so, at what life stages and during what time of the year; and (2) whether the presence of smallmouth bass causes 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.—In all but one of our study sites, Atlantic salmon were the 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 U.S. 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 unfed Atlantic salmon fry into our study riffles at a density of 1 fish/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. We observed no discernable difference in behavior of fry of natural and hatchery origin.

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 electrofishing 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 (total length [TL] = 90.7 ± 7.0 mm [mean ± 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 used 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. The first consisted of Atlantic salmon in allopatry in 2008 in Chandler Brook (46°24′56″N, 68°46′46″W; average bankfull width [ABW], 9.3 m) and Mooseluk Stream (46°25′09″N, 68°47′23″W; ABW, 15.1 m) in Aroostook County, and in 2009 in Narraguagus River (44°50′37″N, 68°04′12″W; ABW, 20.5 m) and Crooked River (44°55′40″N, 67°52′08″W; ABW, 8.5 m) in Washington County. The second consisted of Atlantic salmon and smallmouth bass in sympatry in both 2008 and 2009 in Union River (44°54′04″N, 68°04′12″W; ABW, 24.9 m) in Hancock County, and in Great Works Stream (44°55′00″N, 68°19′49″W; ABW, 8.4 m) in Penobscot County (Figure 1).
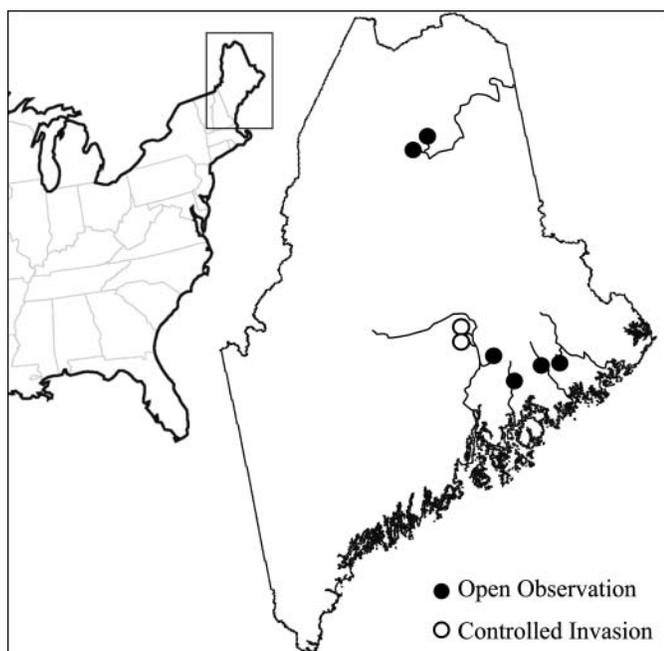

FIGURE 1. Approximate locations of streams in which controlled-invasion studies were done or habitat use observations were made.

Temperature data loggers were installed in or near each study riffle.

We quantified the habitat use of juvenile Atlantic salmon and smallmouth bass in preselected 50-m reaches comprising riffles from streams where the two species occurred in sympatry and Atlantic salmon occurred in allopatry. Because juvenile Atlantic salmon select for riffle habitats (Heggenes and Saltveit 1990; Heggenes et al. 1999) we limited our study sites to homogeneous riffles. We selected specific study sites based on abundance of suitable depths and velocities for juvenile Atlantic salmon (Stanley and Trial 1995), their compatibility with snorkel observation, and their status as annual Atlantic salmon fry stocking sites by DMR.

On three separate occasions in 2008 and 2009 (Table 1), we assessed the habitat use of age-0 Atlantic salmon and smallmouth bass by snorkel observation (see the section on snorkel observations for detailed methodology). Directly after each event we obtained a sample of Atlantic salmon (N = 10–15) by backpack electrofishing for TL and mass measurements (Table 1). 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 with other overlap measures (Krebs 1989). Calculated C values are on a scale from 0 to 1. We assumed that C values greater than 0.67 indicated high spatial overlap, values between 0.66 and 0.33 indicated moderate resource overlap, and values less than 0.33 were an 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 posthoc Tukey's honestly significantly different (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 habitat use from the first sampling event in 2008 were not included in analysis owing 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°05′04″N, 68°40′12″W; ABW, 6.7 m) and Pollard (45°10′28″N, 68°38′06″W; ABW, 5.5 m) brooks (Figure 1), both of which are third-order adventitious tributaries of the Penobscot River (Penobscot County, Maine). In 2009 we used two riffles on Pollard Brook and omitted Hemlock Brook. Streams were selected because they were of similar size and discharge, were close to each other, and were historic Atlantic salmon nursery habitat. We selected specific study sites based on abundance of suitable depths and velocities for juvenile Atlantic salmon (Stanley and Trial 1995) and their status as annual Atlantic salmon fry stocking sites by DMR.

TABLE 1. Number of age-0 Atlantic salmon and age-0 smallmouth bass observed and measured at open-observation sampling events, along with the mean $\pm$ SD total length (TL) and mass of a sample of fish obtained from study reaches after snorkel observations. Data from allopatric and sympatric streams are pooled.

Year	Snorkeling event; date	Number of fish observed (measured)	TL (mm)	Mass (g)
Atlantic salmon in allopatry				
2008	1; Jun 25, 26	7 (0)		
	2; Aug 23, 24	48 (18)	63.7 ± 3.7	2.4 ± 0.4
	3; Sep 25, 26	40 (11)	68.7 ± 5.2	2.8 ± 0.6
2009	1; Jun 10, 15	68 (15)	40.1 ± 5.0	0.5 ± 0.1
	2; Jul 2, 13	110 (21)	51.0 ± 5.5	1.2 ± 0.3
	3; Aug 2, 3	55 (21)	56.5 ± 5.0	1.8 ± 0.5
Atlantic salmon in sympatry				
2008	1; Jun 13, 14	168 (21)	36.0 ± 3.9	0.5 ± 0.2
	2; Jul 30, 31	81 (22)	55.1 ± 5.4	1.7 ± 0.5
	3; Sep 23, 24	63 (22)	72.8 ± 5.5	3.5 ± 0.8
2009	1; Jun 16, 17	178 (32)	41.2 ± 5.2	0.6 ± 0.1
	2; Jul 14, 17	55 (31)	50.0 ± 6.0	1.1 ± 0.5
	3; Aug 5, 6	35 (26)	56.2 ± 5.5	2.1 ± 0.7
Smallmouth bass in sympatry				
2008	1; Jun 13, 14	0 (0)		
	2; Jul 30, 31	75 (11)	49.3 ± 5.9	1.6 ± 0.5
	3; Sep 23, 24	11 (1)	70.0	4.1
2009	1; Jun 16, 17	0 (0)		
	2; Jul 14, 17	0 (0)		
	3; Aug 5, 6	0 (0)		

From July 8 to 15, 2008, and from September 9 to 21, 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 0, 25, and 50 m to create two 25-m reaches. We then removed more than 95% of the resident fishes, including stocked Atlantic salmon, by three-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 all fish were removed, and then some of those parr (2008, $N = 40$; 2009, $N = 30$) were reintroduced to each 25-m isolated reach. The numbers of fish used in experiments were selected to mirror approximated densities found in the wild. Reintroduced fish were allowed a minimum of 48 h to reacclimate before snorkel observations commenced. We conducted snorkel observations (see section on snorkel observations for detailed methodology) between 0900 hours and 1200 hours. After entering the stream, observers remained motionless for 5 min before the observation period commenced.

Directly after the first snorkel sampling we distributed additional fish (either smallmouth bass or Atlantic salmon) throughout the study reaches. We introduced smallmouth bass to the downstream 25-m reach in each stream section and a matching number of Atlantic salmon to the upstream reach (2008: $N = 19$; 2009: $N = 20$). After the second set of introductions, we allowed

for a 48-h 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 $\div$ 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 with passive integrated transponder (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 tricaine methanesulfonate (MS-222; 80 mg/L, 0.2 mM NaCO3, pH = 7.0) and implanted with PIT tags (12 mm; TX1411SSL, Biomark, Boise, Idaho; Gries and Letcher 2002). The first group of reintroduced Atlantic salmon ($N = 30$) was allowed 48 h for reacclimation 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-h acclimation period before the second PIT-pack sampling.

For data collected by means of snorkel observations we used paired *t*-tests to compare depths and velocities in the habitat used by Atlantic salmon before and after the second introduction of fish. For data collected with a PIT-pack we used a Friedman's nonparametric ANOVA to detect differences in Atlantic salmon habitat use between treatments. To compare data collected by snorkel observation with data collected with a PIT-pack we used paired *t*-tests to compare depths and velocities of preinvasion 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 entered the stream downstream of the study reach and worked their way slowly into the reach, recording only fish within the delineated area. We visually divided each reach longitudinally into two sections, and snorkelers were responsible for observing fish in only their own section. Snorkelers moved in parallel, slowly upstream, and across each section in a zigzag pattern (Cunjak and Power 1986). Upon sighting a fish, snorkelers observed its behavior and physical features to ensure that it had not moved to that particular position as a result of snorkeler 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 older than age-1 fish do not overlap in Maine streams; J. G. Trial, personal observation), and estimated focal point height. We then placed a marker directly below each fish's focal point. When observations were completed 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 salmonine fishes 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. Owing 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 in 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 10 equally spaced transects perpendicular to the flow along the study reach. At seven points on each transect we measured total depth, mean water column velocity, water velocity at the bottom, and estimated dominant substrate in a 0.25-m radius around each sample point.

RESULTS

Open Observations

Over 2 years we quantified the habitat use of 908 Atlantic salmon and 86 smallmouth bass (Table 1). In our first set of snorkel observations from 2008, 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 bass 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 use in both study streams, high depth overlap in the Union River, and moderate depth overlap in Great Works Stream (Table 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 the study riffles altogether (Figure 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 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 the 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. Relative overlap (Morisita's overlap index [*C*]) in depths and mean water column velocities of habitat used by age-0 Atlantic salmon and age-0 smallmouth bass in two watercourses where they occurred in sympatry for three sampling periods. One asterisk denotes moderate overlap, two asterisks high overlap.

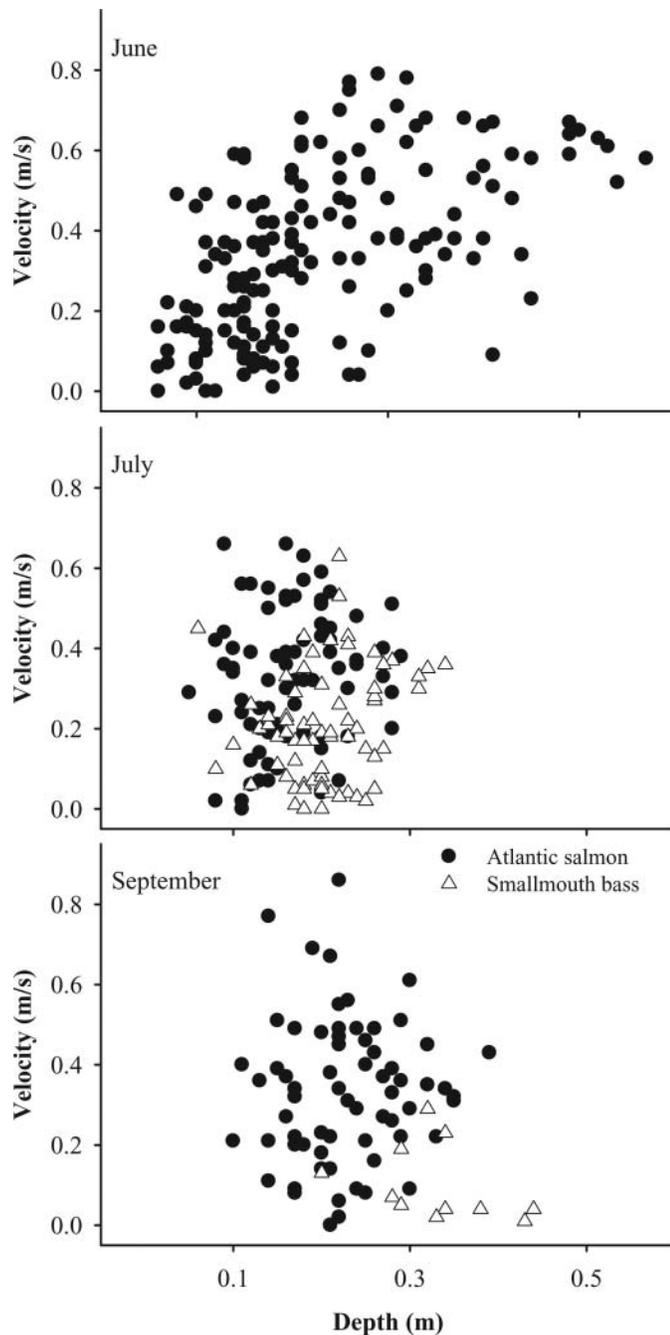| Stream	Sample period	Depth	Velocity
Great Works Stream	1	0	0
	2	0.57*	0.97**
	3	0	0
Union River	1	0	0
	2	0.98**	0.83**
	3	0.52*	0.11

FIGURE 2. Depths and mean water column velocities used by age-0 Atlantic salmon and age-0 smallmouth bass during open observations in sympatric streams (Great Works Stream and the Union River) at three sampling events in 2008.

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 from 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 3). In sympatric streams Atlantic salmon used the fastest water velocities during the July sampling event.

Differences in precipitation level and water temperature between our two study seasons may explain the failure to detect smallmouth bass in our 2009 open observations. At the National Oceanic and Atmospheric Administration weather station in Old Town, Maine, 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 4).

Controlled Invasions

In 2008 we observed no significant change in the depths or velocities used by Atlantic salmon after introducing age-1 smallmouth bass (Figure 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, the detectability of Atlantic salmon decreased ($P = 0.015$ and 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 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 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% versus 24%) or sympatric (34% versus 22%) sections. PIT-packing was more effective at

Habitat Use   **Habitat Availability**
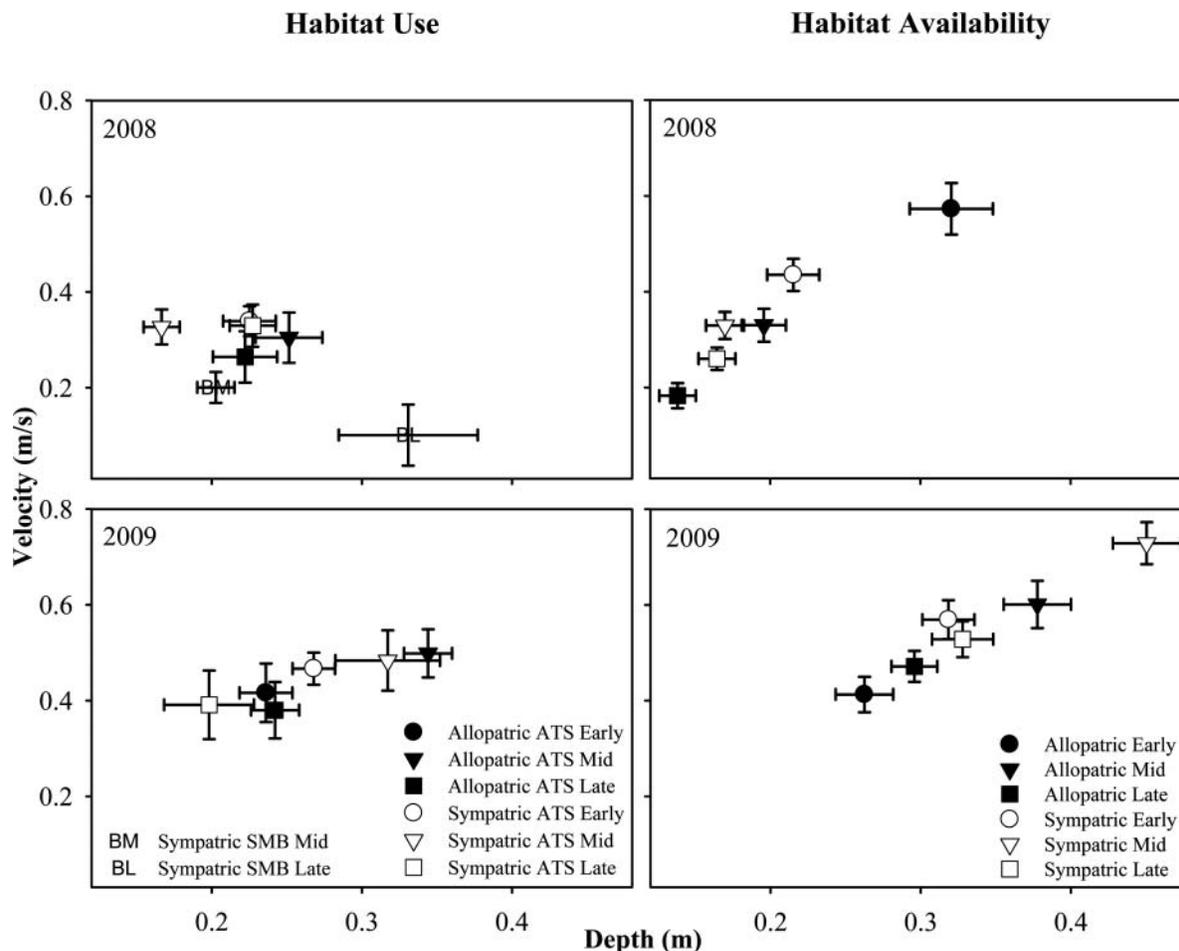

FIGURE 3.   Mean depths and water column velocities used by and available to age-0 Atlantic salmon and age-0 smallmouth bass in allopatric and sympatric streams. Each graph depicts either fish habitat use or habitat availability at three different times (early, middle, and late) during two summers. The error bars are 95% confidence intervals around the means. Data on allopatric Atlantic salmon habitat use from the early 2008 sampling were excluded owing to in-stream flood conditions, which affect habitat use, and the low number of detections ($N = 7$). Observations of smallmouth bass were made only in the mid and late sampling periods in 2008 (BM and BL, respectively).

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

Under certain conditions, age-0 Atlantic salmon and age-0 smallmouth bass overlap substantially in their habitat use during midsummer. 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 salmon in the presence

of age-1 bass were much less detectable than salmon in the presence of other salmon.

Open Observations

In 2008, we saw a considerable overlap in the velocities and depths used by age-0 Atlantic salmon and age-0 smallmouth bass during midsummer 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 16–19°C optimal temperature range for growth of Atlantic salmon (Murphy 2003) but is
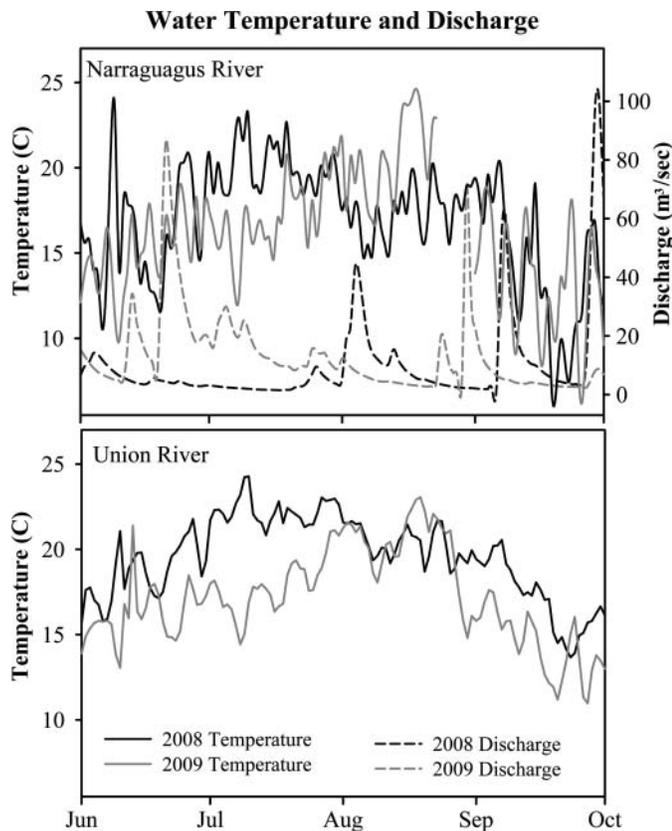
Water Temperature and Discharge

FIGURE 4.   Water temperature and stream discharge profiles from the Nar-
raguagus River (data courtesy of the U.S. Geological Survey's National Water
Information System monitoring station at Deblois, Maine) and water temper-
ature from the Union River over 4 months during the summers of 2008 and
2009.

within or near the 22–24°C optimal range for smallmouth bass
(Sabo et al. 1996; Whitledge et al. 2002).

Competition between native Atlantic salmon and intro-
duced rainbow trout is temperature dependent, with the more
coldwater-adapted rainbow trout competitively dominant at
temperatures near its thermal optimum (Coghlan and Ringler
2005). Similarly, Taniguchi et al. (1998) demonstrated that
a warmwater-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 warmwater-adapted smallmouth bass for habitats that
provide sufficient quantities of scarce prey.

Our data from 2008 show a shift by Atlantic salmon to shal-
lower waters in the presence of age-0 smallmouth bass dur-
ing our midsummer sampling. This observed shift to shallower
midsummer 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 competi-
tion from age-0 smallmouth bass, as smallmouth bass occupied
depths similar to those 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.

The timing of habitat overlap can amplify the competitive ef-
fects 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 forag-
ing 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 causes a de-
crease in growth rate and survival (Nakano et al. 1998; Gunckel
et al. 2002) in one or both species. Access to energetically prof-
itable 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, growth, or both to decrease.

Salmonine fishes excluded from preferred habitats, via
competition, experience reductions in net energy gain (Fausch
1984; Vander Zanden et al. 2004). A shift away from favorable
foraging areas as a result of smallmouth bass presence could de-
crease 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, but see Gries et al. 1997).
Because smallmouth bass are primarily active during the day-
time (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 com-
petitor 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 emergence period for small-
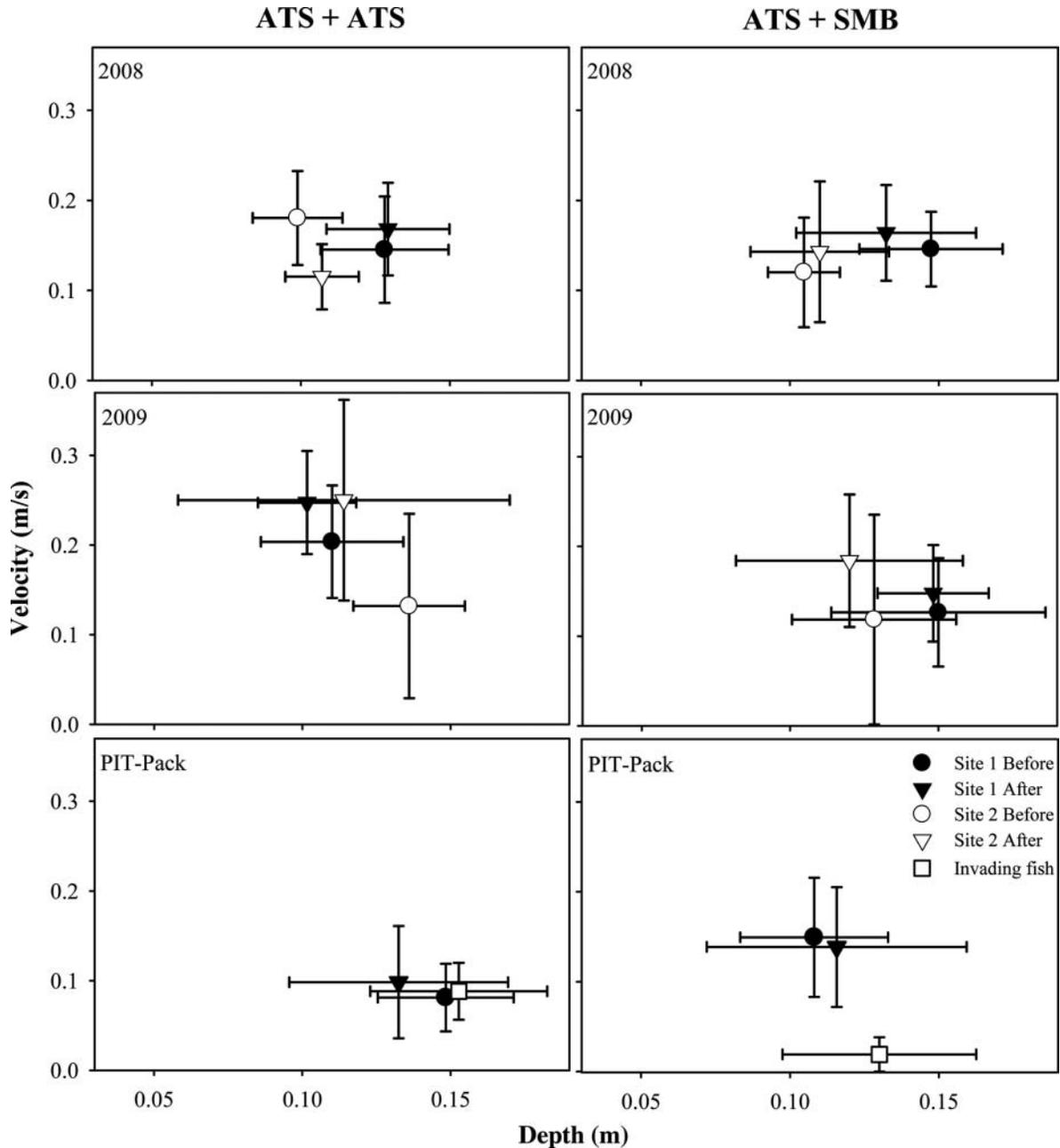mouth bass caused near year-class failures in many Maine

FIGURE 5. Mean depths and mid–water column velocities used by age-0 Atlantic salmon (ATS) before and after the introduction of either more age-0 Atlantic salmon or smallmouth bass (SMB) in controlled-invasion experiments from 2008 (age-1 SMB), 2009 (age-0 SMB), and PIT-pack 2009 (age-0 SMB). Habitat variables used by "invading fish" from the experiment using PIT-Pack interrogation are included in the bottom graphs. The error bars are 95% confidence intervals around the means.

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 is known to decrease emergence success and fry survival (Bain and Helfrich 1983; Ridgway 1988; Ridgway and Shuter 1997). Increases in discharge 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 depth and velocitie 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 2 weeks before we observed age-0 smallmouth bass cohabitating 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 owing 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 can 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 are probably indicative of increased hiding behavior caused by the threat of predation by age-1 smallmouth bass and suggest 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 when 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 1.9 g in September 2009, compared with 6.1 g in September 2007 (S. M. 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. Body size is often the major determining factor for competitive ability in stream fishes (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 intraspecific competition for habitat. The lack of response to hetero- and conspecific introductions could have been the result of one or more of the following factors: (1) densities of fish that were insufficient to cause habitat saturation, thus obviating competition for habitat and habitat use shifts (Bult et al. 1999); (2) habitat partitioning by age-0 Atlantic salmon and smallmouth bass similar to the natural habitat partitioning by Atlantic salmon and brook trout (Gibson 1973); (3) the inferior competitive abilities of fish at a distinct size disadvantage (Glova 1986); and (4) water temperatures (mean water temperature during snorkel observations was $14.5°C$) that were below the optimal foraging temperature range for smallmouth bass and Atlantic salmon as a result of the timing of the experiment (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 the depths and velocities used by fish detected by PIT-packing rather than snorkel observation may indicate that PIT-packing is advantageous as a method for identifying fish locations owing 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 2 h 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 ($N = 26$ and 28) resulted in low statistical power ($1 - \beta = 0.20$ and 0.39 respectively), increasing the probability of a type II 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. (2006) 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 the insights gained during the 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 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 midsummer months and habitat shifts by Atlantic salmon coincide with the timing of the highest overlap. Early and midsummer flows and water temperature probably set the stage for competitive interactions. The variation in weather between the 2 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 the smallmouth bass's range in Ontario (Jackson and Mandrak 2002). Global climate change scenarios predict increases in both air and water temperatures throughout New England (Jacobson et al. 2009), and historic data suggest there are continuing trends toward earlier spring runoff, increased spring discharge, earlier summer low-flow periods, and decreased summer discharge (Hodgkins and Dudley 2005), all of which should result in more thermally suitable habitat for the smallmouth bass at the expense of Atlantic salmon. Effects of this earlier onset of hydrological spring on in-stream physical habitat (e.g., depth and velocity distributions of microhabitats) during midsummer is harder to predict for Atlantic salmon given the complex interactions among body size at, timing of, and environmental conditions during emergence or stocking (e.g., Nislow et al. 1999; Letcher et al. 2004; Kennedy et al. 2008), but most likely these effects would be favorable for smallmouth bass. Even though we suggest that the period for possible 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 (Brittain and Eikeland 1988; Romaniszyn et al. 2007). If streams continue to warm owing to global climate change, we suspect that the period of spatial overlap and possible 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 in which temperatures are colder than optimal for smallmouth bass.

ACKNOWLEDGMENTS

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