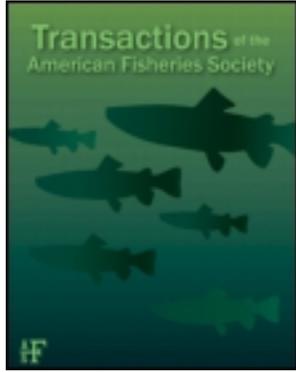


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ARTICLE

Effects of Smallmouth Bass on Atlantic Salmon Habitat Use and Diel Movements in an Artificial Stream

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Abstract

Invasive smallmouth bass *Micropterus dolomieu* have been introduced to some of the last remaining watersheds that contain wild anadromous Atlantic salmon *Salmo salar*, yet little is known about the interactions between these species. We used an artificial stream equipped with passive integrated transponder tag antenna arrays to monitor habitat use and movements of age-0 Atlantic salmon and age-0 smallmouth bass in sympatry and allopatry. We used additive and substitutive designs to test for changes in habitat use, diel movements, and diel activity patterns of prior-resident Atlantic salmon or smallmouth bass resulting from the addition of conspecifics or heterospecifics. Atlantic salmon prior residents did not change their habitat use in the presence of conspecific or heterospecific invaders. However, Atlantic salmon invaders did lessen riffle habitat use by smallmouth bass prior residents during daytime. Atlantic salmon and smallmouth bass displayed different diel activity patterns of movement (Atlantic salmon were more nocturnal; smallmouth bass were more diurnal), which were affected by heterospecific introductions. Because the two species tended to favor different habitat types and displayed different diel activity patterns, we suggest that 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. These data do not, however, predict the potential for competition under different seasonal or ontogenetic circumstances.

The introduction and establishment of nonnative species have caused the extirpation of native salmonine populations and have limited the success of reintroductions of native species to their historical habitats (Harig et al. 2000; Levin et al. 2002; Scott et al. 2005). Competition for resources from invasive species can deplete or limit native species access to resources (Callaway and Aschehoug 2000). In turn, this competition can directly reduce fitness of native fish by decreasing survival and growth (Nakano et al. 1998; Gunckel et al. 2002). Competition from exotic salmonines has limited the recovery of native Atlantic salmon *Salmo salar* in the Great Lakes (Fausch 1998; Coghlan and Ringler 2005; Scott et al. 2005), but little is known about the threats of interspecific competition to wild

anadromous Atlantic salmon populations in the Gulf of Maine watershed.

Throughout most of their North American range, Atlantic salmon co-occur with brook trout *Salvelinus fontinalis*; these two species have coevolved habitat partitioning mechanisms (i.e., differences in body morphology and metabolic rate) that minimize resource use overlap, thereby avoiding intense competition (Gibson 1973, 1978; Tucker and Rasmussen 1999). Smallmouth bass *Micropterus dolomieu* were introduced to New England in the middle of the 19th century and since have invaded almost every historical Atlantic salmon watershed in the USA and many in Canada (Warner 2005; Valois et al. 2009). Competition from and predation by invasive smallmouth bass

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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). In watersheds where they occur in sympatry, smallmouth bass and Atlantic salmon may compete for physical habitat and food both spatially and temporally.

In streams, habitat selection reflects balancing food quality and supply with energy expended on prey capture (Smith and Li 1983). Age-0 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 that depths of 10–40 cm were 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. Wathen et al. (2011) found a high degree of habitat overlap between sympatric age-0 smallmouth bass and age-0 Atlantic salmon in warm, low-water conditions. Because Atlantic salmon and smallmouth bass have not coevolved niche partitioning mechanisms, competitive interactions may intensify (Fausch 1998).

Analogous to physical habitat selection, diel activity patterns in freshwater fishes represent a balance of costs and benefits that maximize foraging opportunities while minimizing predation risks. Atlantic salmon forage primarily at night during winter (Cunjak and Power 1987; Metcalfe et al. 1998) and at higher summer water temperatures (Gries et al. 1997; Orpwood et al. 2006); they presumably forage diurnally only when required to sustain growth (Orpwood et al. 2006). Competition can restrict competitively inferior fish to suboptimal foraging times, but temporal partitioning is also thought to minimize competition and allow for cohabitation among coevolved fishes (Alanara and Brannas 1997; Brannas and Alanara 1997; David et al. 2007). Interactions with exotic or nonnative species may shift these tendencies. Blanchet et al. (2008) observed increased diurnal activity of juvenile Atlantic salmon in the presence of nonnative rainbow trout *Oncorhynchus mykiss*; greater diurnal activity may increase susceptibility to predation. Juvenile smallmouth bass are primarily diurnal foragers (Sabo et al. 1996). Smallmouth bass may affect Atlantic salmon diel activity patterns during periods of high growth.

Our goal in this study was to assess the effects of heterospecific and conspecific introductions on the habitat use and diel activity patterns of Atlantic salmon and smallmouth bass in an artificial stream channel. We used a combination of additive and substitutive designs to test for effects of interspecific and intraspecific competition on habitat use and movement patterns while controlling for increases in density (Underwood 1986; Fausch 1988, 1998). We analyzed data to look for shifts in proportions of habitat types used, differences in the frequency of daily movement, and altered frequency in diel activity patterns due to the presence of a putative competitor. We hypothesized that (1) Atlantic salmon would select for riffle habitats and small-

mouth bass would select for pool habitats, (2) habitat overlap during heterospecific interactions would cause both species to increase selected habitat use, and (3) heterospecific interactions would cause changes in diel activity patterns of both species.

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 2008. Embryos were incubated over the winter at the Craig Brook National Fish Hatchery (U.S. Fish and Wildlife Service, East Orland, Maine). In late May, personnel from the Bureau of Sea-Run Fisheries and Habitat (Maine Department of Marine Resources) stocked the fry at a density of 1 fish/m² into Pollard Brook (45°10'28"N, 68°38'06"W; Penobscot County), a tributary of the Penobscot River. Smallmouth bass used in experiments were naturally produced within Kenduskeag Stream (44°58'22"N, 69°01'18"W; Penobscot County), another tributary to the Penobscot River.

We subsequently collected experimental fish from these streams by use of a backpack electrofisher (Smith-Root Model LR-24). Age-0 smallmouth bass (mean total length = 51 mm, SD = 2; mean wet weight = 1.8 g, SD = 0.2) were collected on September 11, 2009, and age-0 Atlantic salmon (mean total length = 60 mm, SD = 2; mean wet weight = 2.1 g, SD = 0.2) were collected on September 21, 2009. While we intended to collect fish of similar sizes, the 2009 smallmouth bass year-class suffered poor recruitment and slow growth due to an anomalously wet and cold early summer (Swenson et al. 2002; NOAA 2008–2009). Fish were brought to the Aquaculture Research Center (University of Maine, Orono), where a subset of fish were anesthetized with tricaine methanesulfonate (MS-222 at 80 mg/L of water; buffered with 0.2-mM NaCO₃, pH = 7.0) and received 12-mm passive integrated transponder (PIT) tags (Model TX1411SSL; Biomark, Boise, Idaho) that were implanted through a small incision between the pelvic fins and anus (Gries and Letcher 2002). All fish were then held in species-segregated holding tanks to acclimatize for at least 9 d before being used in an experiment. Individual fish were only used in one experiment. During the acclimation period, all fish were fed previously frozen chironomid larvae (0.1 g/fish daily; San Francisco Bay Brand).

Experimental Stream Tank

We conducted competition experiments in an annular artificial stream channel constructed on the University of Maine campus (Figure 1). The substrate was composed of river rocks (2–26 cm), creating two distinct pool (mean depth = 43.3 cm) and riffle habitats (mean depth = 22.9 cm). Water temperature was maintained at 18°C, matching the thermal conditions in Kenduskeag Stream on the date of the smallmouth bass collection. Two pumps propelled well water through 24 adjustable outlets spaced equally along the inside (8 outlets) and outside

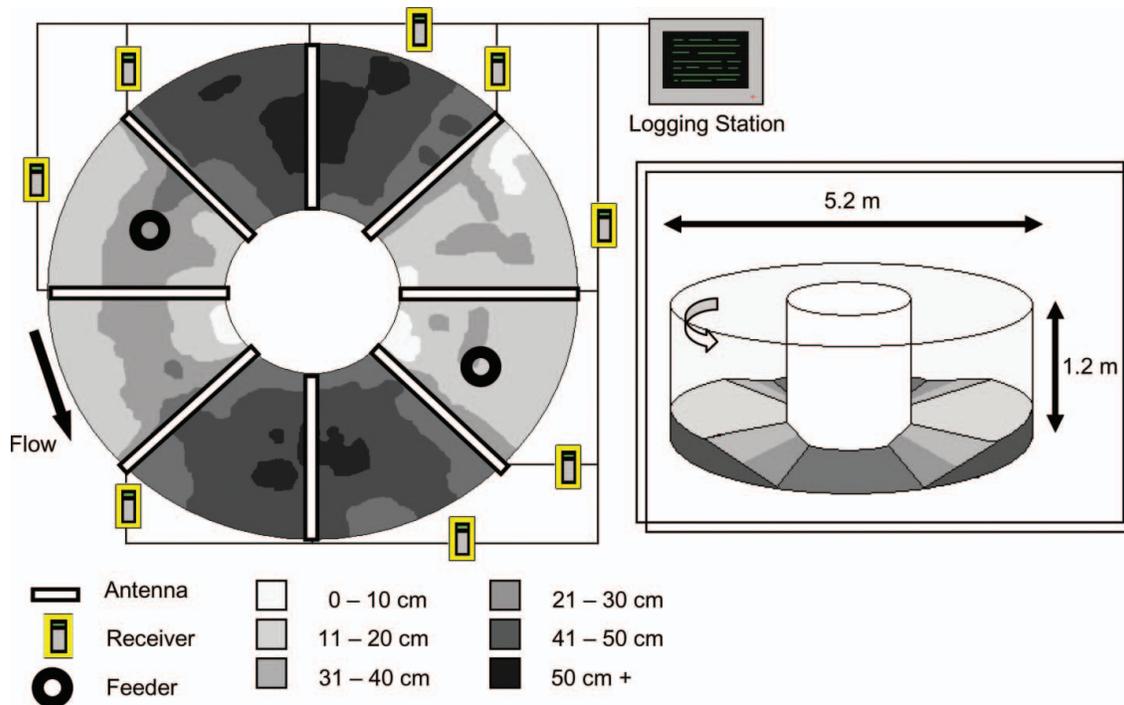


FIGURE 1. Schematics of an overhead view (left) and three-dimensional view (right) of the annular simulated stream tank used in experiments examining competition between Atlantic salmon and smallmouth bass. The channel width was 1.4 m; the total bottom area was 17.6 m². Grayscale in the overhead view corresponds to water depth (cm). An array of eight equally spaced passive integrated transponder tag antennae was used to detect habitat use and movements by fish. [Figure available online in color.]

(16 outlets) walls of the channel. These outlets created a counterclockwise flow characterized by higher velocities in the riffles (mean water column velocity = 15 cm/s; SD = 8) and lower velocities in pools (60% depth velocity = 7 m/s; SD = 6). Our intent in designing the habitat mosaic of the artificial stream channel was to provide water depths and velocities close to the optimal foraging conditions for both Atlantic salmon (Stanley and Trial 1995; Nislow et al. 1999) and smallmouth bass (Sabo et al. 1996). We maintained a photoperiod of 13.5 h light : 10.5 h dark (sunrise was set at 0630 hours Eastern Standard Time). Light was provided by eight full-spectrum light bulbs (40 W) positioned symmetrically above the tank (about 2 m above the water surface). No light was provided during the nighttime.

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 × 39 cm) were positioned at the transition between pool and riffle habitats (4 antennae) and in riffle habitats (2 antennae). Two larger antennae (1.35 × 65 cm) were positioned in the middle of both pool habitats. The larger antennae were built in a figure-eight pattern to increase read efficacy. We used individual PIT tag readers (Destron Fearing Model FS 200IF-ISO) that were unique to each antenna to transmit detection data (tag code, time and date, and antenna number) to a central logging station. We used MiniMon software (Infineon Technologies; www.infineon.com) to record and store detection data.

Competition Experiments

We conducted four trials in 2009 to evaluate interspecific and intraspecific competition for habitat in the simulated stream: (1) Atlantic salmon prior residents and Atlantic salmon invaders (ATS + ATS; October 13–20); (2) Atlantic salmon prior residents and smallmouth bass invaders (ATS + SMB; September 30–October 5); (3) smallmouth bass prior residents and smallmouth bass invaders (SMB + SMB; September 21–26); and (4) smallmouth bass prior residents and Atlantic salmon invaders (SMB + ATS; October 7–12). Due to the complexity of the artificial stream channel, we were unable to conduct trials simultaneously and with replication. In pilot studies evaluating the effect of fish density on movement patterns, we found that at a density of 3 fish/m², Atlantic salmon moved less frequently and occupied specific territories for longer periods. Thus, prior-resident fish density for each trial was set at 1.5 fish/m² (or half of presumed habitat saturation level), to which invaders were added at a density of 1.5 fish/m², thus bringing the total trial density to the saturation level (3.0 fish/m²). In each experiment, we introduced 25 PIT-tagged fish as prior residents; they were allowed 72 h to establish territories before the second group of 25 fish (invaders) was introduced to the tank (i.e., at the beginning of day 3). In the SMB + SMB experiment, we introduced only 24 invaders because one of the prior residents died.

We were concerned with the possibility of swamping the PIT tag antennae with too many tags during experiments (i.e., “tag

collisions"); therefore, we inserted PIT tags into no more than 15 invading fish. The number of tagged invaders was zero in the SMB + SMB trial, 10 in the ATS + SMB trial, 12 in the SMB + ATS trial, and 15 in the ATS + ATS trial. Competition trials were conducted for 72 h.

During all trials, we introduced 5.6 g of previously frozen chironomid larvae (San Francisco Bay Brand) twice daily (0800 and 1700 hours) over approximately 20 min by 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 were used and the duration of use. First, if a fish was detected two or more times consecutively by the same antenna (with a minimum of 1 s between detections), then we termed this a continuous detection, assessed the elapsed time between the first and last detections, and assumed that the fish was either at or around that antenna for the entire duration. Second, 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 elapsed time between the detections was time the fish spent in the habitat between the two antennae. Third, 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 elapsed time between detections was the 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 fish's 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, then this habitat use was referred to as "edge" habitat use; these types of detections accounted for 11.2% of all detections and did not differ between trials. Fourth, 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 nondetections were omitted from the analyses.

Habitat detection rules created 40 possible habitat use scenarios, which we combined into four mesohabitat use groups: (1) pool, (2) riffle, (3) edge upstream of pool (upstream [US] edge), and (4) edge downstream of pool (downstream [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 detection time for which fish were in each mesohabitat type.

Pilot experiments during which fish were held for 10 d indicated that after 2 d, fish movements stabilized, suggesting a 48-h acclimation period. Therefore, we statistically analyzed data on habitat use by prior residents after they had been in the tank for 2 d (i.e., the 24-h period of day 3). Likewise, we next analyzed

habitat use 2 d after invaders were added to the tank on day 4 (i.e., the 24-h period of day 6). We analyzed subjective daytime and nighttime habitat use separately. We first tested for habitat selection in all trials and then tested for changes in habitat use by prior residents after invader introductions.

Selection and invader effects.—We used Friedman's non-parametric analysis of variance (ANOVA) to determine whether individual fish in each trial 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 dependent variable.

We also used Friedman's ANOVA to assess differences in habitat use by prior residents before and after the introduction of invaders. For each experiment and for daytime and nighttime, the differences in hours spent in each habitat type before and after the invasion were ranked for all fish. We again used fish as blocks and habitat types as groups. By using Friedman's ANOVA, we minimized variability among 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 within each trial for both daytime and nighttime 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 after invasion, then its maximum change was 30%.

Movement analysis.—We quantified movements during competition trials for each fish during each hour of the 6-d experiment. We treated a movement from one antenna to an adjacent antenna as 1 distance unit. We also recorded the direction of each movement (either upstream or downstream). To test for differences in the number of movements before and after the invader introductions and between daytime and nighttime periods (and to test for significance of the interaction term), we used a randomized block ANOVA, treating individual fish as blocks. We used $\log_e(x + 1)$ -transformed data in the analysis due to the nonnormal distribution of the raw data. Again, we only analyzed movement data statistically from two 24-h periods (sunrise to sunrise), starting at day 3 (before the introduction) and at day 6 (after the introduction). We also used a two-factor ANOVA to quantify differences between prior resident and invader diel activity patterns (amount of movement between antennae in daytime versus nighttime). For all tests, significance was assessed at an α value of 0.05.

RESULTS

Habitat Use

During daytime and nighttime periods and before and after invader introductions, individual prior-resident fish selected for habitats ($P < 0.05$) in all but one trial; the exception was the

TABLE 1. Results of Friedman's nonparametric analysis of variance testing for habitat selection by prior-resident age-0 Atlantic salmon (ATS) and smallmouth bass (SMB) before and after the introduction of conspecific or heterospecific invaders (e.g., ATS + SMB = the trial in which Atlantic salmon were prior residents and smallmouth bass were the invaders) to the annular experimental tank (DS edge = downstream edge; US edge = upstream edge). Selection was evaluated separately for each trial before and after the invasion and for daytime and nighttime diel periods.

Before or after invasion	Diel period	Rank sum for each mesohabitat				<i>P</i> -value
		DS edge	Pool	Riffle	US edge	
ATS + ATS Trial						
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 Trial						
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 Trial						
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 Trial						
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

ATS + SMB trial during the daytime ($P = 0.25$; Table 1). Atlantic salmon used riffles most frequently, whereas smallmouth bass used pools most frequently (Figure 2).

The largest difference in individual habitat use after invasion was observed in the SMB + ATS trial during the daytime ($P = 0.05$). In this trial, the smallest rank sum was associated with riffle habitats, indicating that prior-resident smallmouth bass moved out of riffle habitats (Table 2). In all other trials, calculated P -values (≥ 0.271) indicated no difference between the amount of time spent by individual fish in habitat types before and after the invasion.

In the SMB + ATS trial during daytime, 15 of 25 prior-resident fish showed a maximal change value less than 20% (Figure 3), indicating that the observed change in habitat use was the result of many fish changing habitat use patterns slightly. For each trial, the largest maximal change values were observed at night. In trials where Atlantic salmon were prior residents, 15 Atlantic salmon exhibited maximum change values greater than 60% during the day, whereas 8 individuals had maximum change values greater than 60% at night. In trials where smallmouth bass were prior residents, no smallmouth bass showed a maximum change value greater than 60% during the day, but 22 fish had values greater than 60% at night.

Movements

In general, diel movement patterns of Atlantic salmon and smallmouth bass were nearly opposite. On day 1 of the experimental trials (i.e., during the acclimation period), the highest frequency of daily movements for prior-resident Atlantic salmon occurred at night (Figure 4); as they acclimated to the tank, individual Atlantic salmon moved an average of 791 distance units by day and 1,029 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 5). Conversely, smallmouth bass movements increased during daytime (mean number of movements = 2,451) and decreased at night (mean number of movements = 461). Furthermore, daytime movements were almost always in the upstream direction.

In the ATS + ATS trial, movements (mean distance units) of prior-resident Atlantic salmon did not significantly differ between daytime and nighttime, between the dates before (day 3) and after (day 6) the introduction of invading Atlantic salmon, or in the diel pattern (interaction term). The prior-resident Atlantic salmon moved less frequently than the invaders ($P = 0.005$) but showed a similar diel pattern of movement distribution between daytime and nighttime. In the ATS + SMB trial,

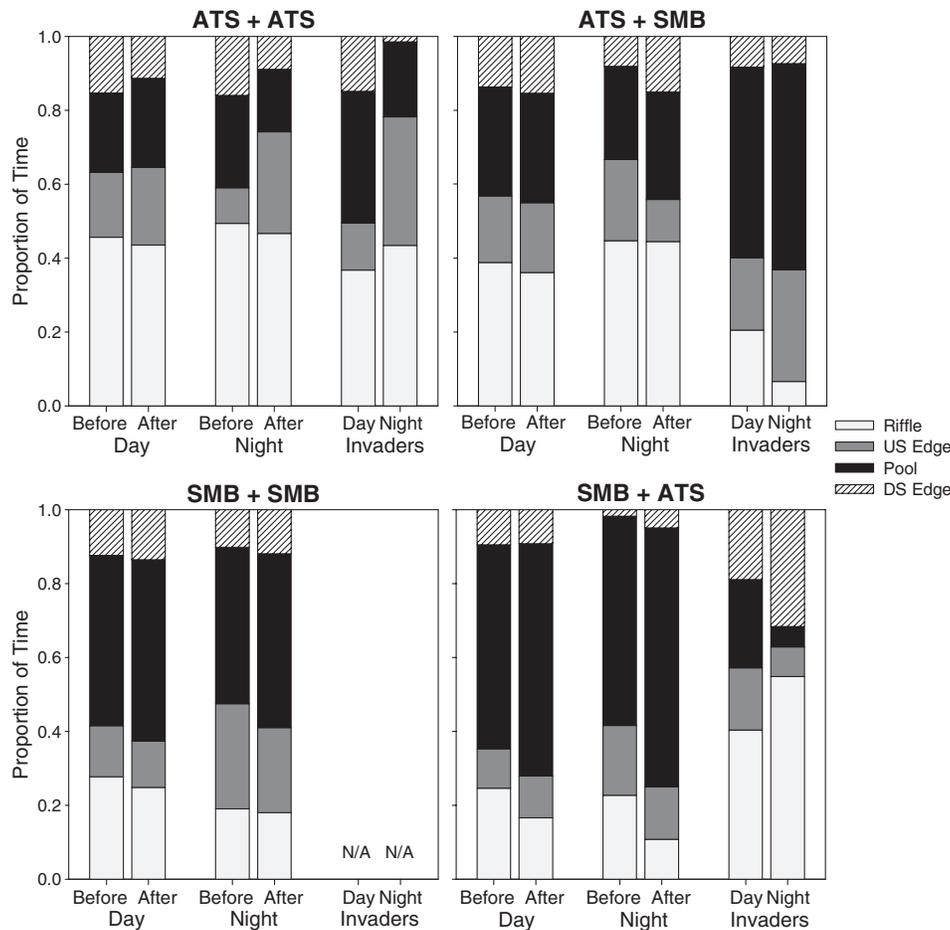


FIGURE 2. Proportions of habitat type (US edge = upstream edge; DS edge = downstream edge) used by prior-resident (acclimated for 2 d) age-0 Atlantic salmon (ATS) or smallmouth bass (SMB) within an annular stream tank before and after the introduction of conspecific or heterospecific invaders (e.g., ATS + SMB = the trial in which Atlantic salmon were prior residents and smallmouth bass were the invaders) and during daytime and nighttime diel periods. Daytime and nighttime habitat use by the invader species is also presented (rightmost two bars in each panel).

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 frequently than the Atlantic salmon ($P < 0.001$), but diel patterns of the two species did not differ. In the SMB + SMB trial, smallmouth bass moved more frequently in the daytime than at night ($P < 0.001$), irrespective of the presence of invading smallmouth bass. Similarly, smallmouth bass moved less frequently during the night than during the day ($P < 0.001$) in the SMB + ATS trial. Smallmouth bass also moved less frequently in the presence of invading Atlantic salmon ($P = 0.014$) and displayed a different diel pattern with the addition of Atlantic salmon ($P = 0.016$), moving less frequently during both daytime and nighttime after the introduction. There was no difference in the number of movements or in the diel pattern between the prior-resident smallmouth bass and the invading Atlantic salmon.

DISCUSSION

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, both species used every available mesohabitat but not in equal proportions. In 88% of trials, we observed habitat selection by 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 by Atlantic salmon was highest in riffles in five of six analyses. This observation accords with many other studies that have 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 during all experimental trials, and at night they used pools almost exclusively, which is consistent with observations

TABLE 2. Results of Friedman's nonparametric analysis of variance testing for differences in daytime and nighttime habitat use (amount of time spent in each mesohabitat category) by prior-resident age-0 Atlantic salmon (ATS) and smallmouth bass (SMB) before and after the introduction of conspecific or heterospecific invaders (e.g., ATS + SMB = the trial in which Atlantic salmon were prior residents and smallmouth bass were the invaders) to the annular experimental tank (DS edge = downstream edge; US edge = upstream edge).

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

of adult lacustrine smallmouth bass in Maine (Cole and Moring 1997).

Although previous research has documented maximal net energy gain by juvenile smallmouth bass in velocities greater

than 10 cm/s and depths less than 60 cm (Sabo et al. 1996), in our experiments the smallmouth bass used slower, deeper pool habitats more frequently. Depth and velocity conditions in riffles within our experimental stream 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 the work conducted by Sabo et al. (1996). Both of these factors may have influenced habitat selection. A previous study of smallmouth bass habitat selection in simulated streams found that subadult smallmouth bass (140–160 mm total length) 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. Although it was small in magnitude, this shift was displayed by enough smallmouth bass to be detected. In all trials, the experimental stream tank was kept at 18°C, which is within the 16–19°C optimal temperature range for growth of Atlantic salmon (Murphy 2003) but below the 22–24°C optimal range for smallmouth bass (Sabo et al. 1996; Whitledge et al. 2002). Furthermore, Atlantic salmon used in experiments had, on average, a 10-mm total length size advantage over smallmouth bass. Suboptimal temperatures and a size disadvantage may explain why introduced smallmouth bass had no effect on habitat use by prior-resident Atlantic salmon, whereas invading Atlantic salmon seemed to displace prior-resident smallmouth bass from riffles.

In other trials, we did not observe a 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 (not individually exclusive) for this result include

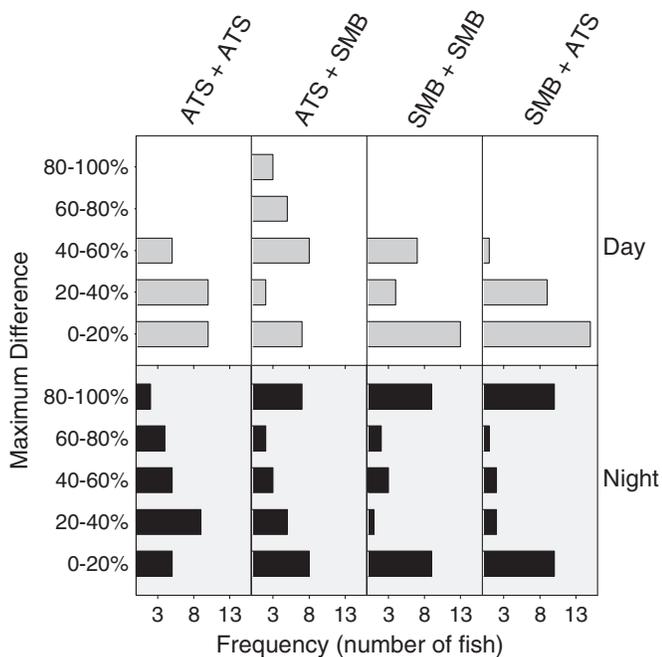


FIGURE 3. Frequencies of maximum difference in habitat use by prior-resident age-0 Atlantic salmon (ATS) or smallmouth bass (SMB) before and after the introduction of conspecific or heterospecific invaders (e.g., ATS + SMB = the trial in which Atlantic salmon were prior residents and smallmouth bass were the invaders) and during daytime and nighttime diel periods. Maximum difference values are defined as the greatest proportional change in the use of any habitat type (downstream edge, pool, riffle, or upstream edge) for each prior resident before and after the invasion.

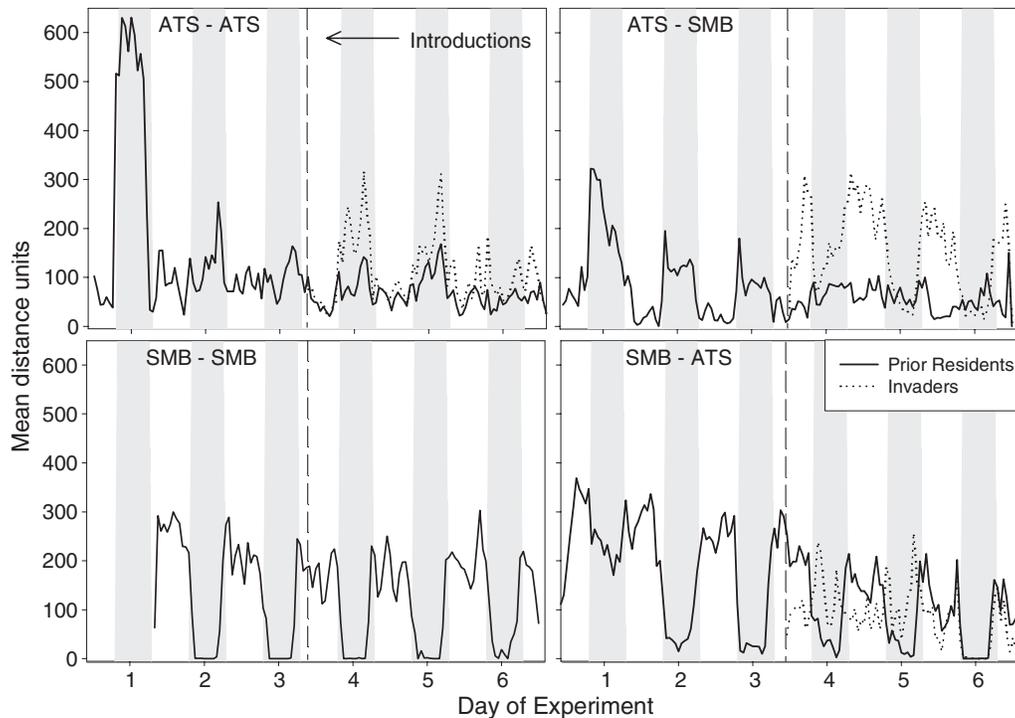


FIGURE 4. Mean number of distance units moved by prior-resident age-0 Atlantic salmon (ATS) or smallmouth bass (SMB) and by conspecific or heterospecific invaders (e.g., ATS - SMB = the trial in which Atlantic salmon were prior residents and smallmouth bass were the invaders) over a 6-d experimental period in an annular tank. White vertical bars denote hours of daylight; gray vertical bars denote hours of darkness. The vertical dashed line in each panel indicates the time of invader introduction.

the following: (1) densities of fish were insufficient 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) 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 habitat use by Atlantic salmon and smallmouth bass. Previous research has documented changes in diel habitat use and activity patterns of subordinate stream fish with increases in the level of intraspecific competition (Alanara et al. 2001; David et al. 2007). Therefore, the larger changes we observed in nighttime habitat use by 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: a decrease in daily movement over time, presumably as foraging territories are 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 of adult smallmouth bass (Demers et al. 1996). Our simulated stream studies documented that age-0 smallmouth bass had activity patterns similar to those of 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 movements of both Atlantic salmon and smallmouth bass. In the ATS + ATS trial, there was no difference in movement before and after the introduction of conspecifics. Introduction of smallmouth bass to the stream containing prior-resident Atlantic salmon evinced a change in diel movement patterns. Similarly, prior-resident smallmouth bass changed their diel movement patterns in the presence of invading Atlantic salmon, but no change was observed with the conspecific invaders. In both interspecific experiments, there were changes in diel movement patterns, indicating that the presence of heterospecifics disrupted the diel patterns of prior residents. Competitor-induced shifts in salmonine diel movement patterns

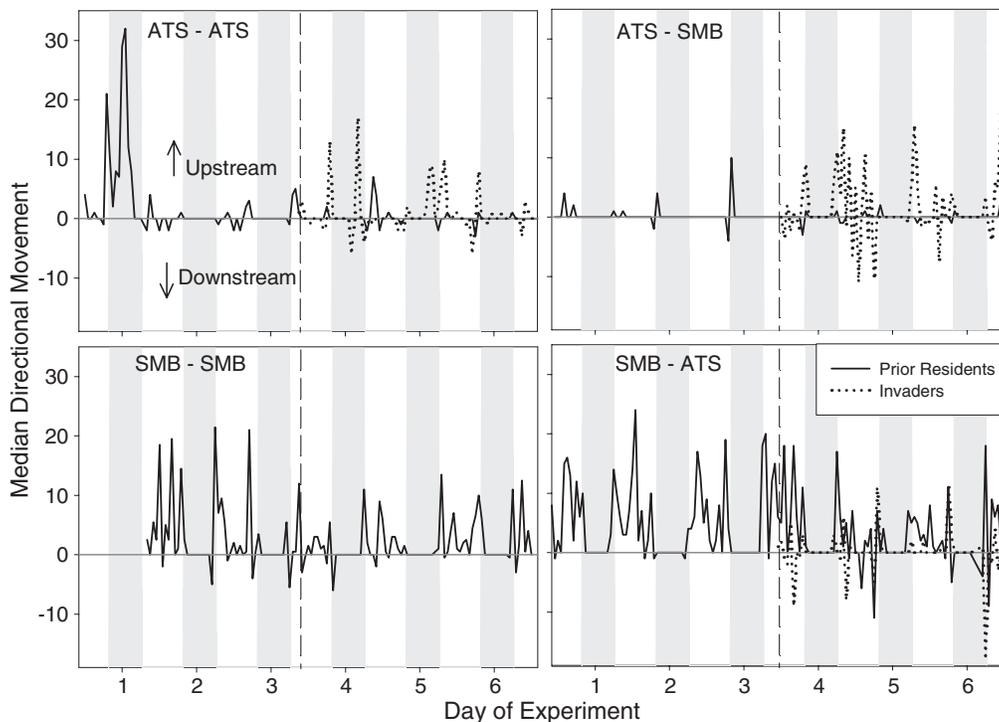


FIGURE 5. Median directional movements by prior-resident age-0 Atlantic salmon (ATS) or smallmouth bass (SMB) and by conspecific or heterospecific invaders (e.g., ATS - SMB = the trial in which Atlantic salmon were prior residents and smallmouth bass were the invaders) over a 6-d experimental period in an annular tank. White vertical bars denote hours of daylight; gray vertical bars denote hours of darkness. The dashed vertical line in each panel indicates the time of invader introduction. Positive values indicate upstream movement, and negative values indicate downstream movement.

could affect energy acquisition because socially dominant fish can prevent less-competitive fish from foraging during optimal feeding times (Alanara and Brannas 1997). For many animals, the probability of predation is dynamic over a diel cycle (Lima and Dill 1990), and predation risk often influences diel activity (Kronfeld-Schor and Dayan 2003). The 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 may disrupt optimal foraging behaviors (David et al. 2007). However, Atlantic salmon may alter diel foraging behavior in the presence of a competitor, thereby maintaining growth (Blanchet et al. 2008).

In our experiments, differences in the most frequently used habitat and differences in diel movement patterns suggested that under the tested conditions, age-0 Atlantic salmon and smallmouth bass may avoid competing for habitat by spatially and temporally partitioning the 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). Although the period of cohabitation is short on an evolutionary scale, the in-

dependently evolved ecologies of juvenile Atlantic salmon and smallmouth bass may be different enough that high levels of competition for habitat can be avoided.

That said, our results are probably specific to season, temperature, density, and fish size. The complex nature of the artificial stream added another limitation because it prevented simultaneous replicated trials. Thus, under alternative scenarios, results may differ. In a complementary field study (Wathen et al. 2011), we observed a period of high habitat overlap between age-0 Atlantic salmon and age-0 smallmouth bass during the summer of 2008. This overlap occurred in mid- to late summer, when water levels were low, water temperatures were high (about 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 (in 2009) resulted in the delayed development of age-0 smallmouth bass and therefore a delayed start time for our experiments at a lower water temperature. Temperature strongly influences behavior and habitat use of stream fishes (Magnuson et al. 1979). At temperatures closer to their thermal optima, the competitive ability of and resource selection by age-0 smallmouth bass may differ from those observed in our experimental stream. However, Atlantic salmon can shift to nocturnal foraging at higher temperatures (Orpwood et al. 2006), a diel period during which age-0 smallmouth bass are minimally active, as suggested by our data. However, it remains plausible that even at

higher temperatures in which smallmouth bass might be more formidable competitors, the partitioning of diel foraging activity may minimize interspecific resource competition between the two species.

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 that were absent from our experiments but that may play important roles in facilitating or alleviating competition for habitat between the species. However, the level of detail in our observations of habitat use and movements over diurnal and nocturnal periods would have been prohibitively difficult to achieve in a natural setting. Ideal studies combine research conducted in natural settings with laboratory research to form a more-comprehensive understanding of the mechanisms of competition (Fausch 1998). Our study was designed to be a complement to research conducted in natural conditions during the spring, summer, and fall in 2008–2009 (Wathen et al. 2011).

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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.
- 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* 75: 661–669.
- 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.
- 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.
- 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 two 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 electro-yogram biotelemetry. *Transactions of the American Fisheries Society* 125:434–439.
- 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. 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.
- 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.
- Gibson, R. J. 1973. Interactions of juvenile Atlantic salmon (*Salmo salar* L.) and brook trout (*Salvelinus fontinalis* Mitchell). *International Atlantic Salmon Foundation Special Publication Series* 4:181–202.
- Gibson, R. J. 1978. The behavior of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) with regard to temperature and water velocity. *Transactions of the American Fisheries Society* 107: 703–712.
- 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.
- 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.
- 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.

- Heggnes, J., J. L. Baglinière, 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.
- Heggnes, J., and S. J. Saltveit. 1990. Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., in a Norwegian river. *Journal of Fish Biology* 36:707–720.
- 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.
- Keenleyside, M. H. A., and F. T. Yamamoto. 1962. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). *Behaviour* 19:139–169.
- Kronfeld-Schor, N., and T. Dayan. 2003. Partitioning of time as an ecological resource. *Annual Review of Ecology Evolution and Systematics* 34:153–181.
- 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 of London B Biological Sciences* 269:1663–1670.
- 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.
- 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 of London B Biological Sciences* 265:1503.
- 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.
- 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.
- 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.
- NOAA (National Oceanic and Atmospheric Administration). 2008–2009. U.S. climate reference network, monthly summary: ME old town 2 W. National Climatic Data Center. Available: www.ncdc.noaa.gov/crn/station.htm?stationId=1034. (January 2010).
- NOAA (National Oceanic and Atmospheric Administration). 2009. Endangered and threatened species, designation of critical habitat for Atlantic salmon (*Salmo salar*) Gulf of Maine distinct population segment, final rule. *Federal Register* 74:152(10 August 2009):39903–39907.
- 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.
- 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.
- 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.
- 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.
- 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, The Hague, The Netherlands.
- 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.
- 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.
- Tucker, S., and J. B. Rasmussen. 1999. Using ¹³⁷Cs to measure and compare bioenergetic budgets of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) in the field. *Canadian Journal of Fisheries and Aquatic Sciences* 56:875–887.
- Underwood, T. 1986. The analysis of competition by field experiments. Pages 240–268 in J. Kikkawa and D. J. Anderson, editors. *Community ecology: pattern and process*. Blackwell Scientific Publications, Melbourne, Australia.
- Valois, A., R. A. Curry, and S. M. Coghlan. 2009. Smallmouth bass (*Micropterus dolomieu*) invasion of Gulf region rivers: evaluating the impact on Atlantic salmon (*Salmo salar*) populations. Department of Fisheries and Oceans, Canadian Science Advisory Secretariat Research Document 2009/075, Ottawa.
- 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.
- 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.
- Warner, K. 2005. Smallmouth bass introductions in Maine: history and management implications. *Fisheries* 30(11):20–26.
- Wathen, G., S. M. Coghlan Jr., J. Zydlewski, and J. G. Trial. 2011. Habitat selection and overlap of Atlantic salmon and smallmouth bass juveniles in nursery streams. *Transactions of the American Fisheries Society* 140:1145–1157.
- 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.