Transactions of the American Fisheries Society 132:904–912, 2003

Rheotactic Response of Two Strains of Juvenile Landlocked Atlantic Salmon: Implications for Population Restoration

MATTHEW J. NEMETH,*[1] CHARLES C. KRUEGER,[2] AND
DANIEL C. JOSEPHSON

*Department of Natural Resources, College of Agriculture and Life Sciences,
Fernow Hall, Cornell University, Ithaca, New York 14853, USA*

Abstract.—Rheotactic response—the directional response to water current—was compared between two strains of juvenile landlocked Atlantic salmon *Salmo salar* to determine the presence of inherited migratory differences. Juvenile rheotactic response was examined because it is known to be an inherited behavior in other salmonids. An inlet-spawning strain (Sebago Lake, Maine) and an outlet-spawning strain (West Grand Lake, Maine) were compared in common experimental environments. The strains were compared as newly hatched fry (age 0) and were expected to remain instream for a year. Fry movements were compared in indoor artificial stream channels in 1999 at two levels of water velocity (6 and 12 cm/s) and density (one fish/m^2 and two fish/m^2). The inlet strain fry (Sebago Lake strain) had a stronger positive rheotactic response (upstream movement) than the outlet strain fry (West Grand Lake strain). Age, density, and water velocity also affected fry movement: upstream movement was lower in older fry, downstream movement was higher at high density, and the proportion of fry that moved (either upstream or downstream) was lower at high velocity. Salmon were also compared as smolts (age 1) when they were expected to migrate lakeward. The strains were compared in outdoor artificial stream channels in 1998 and 1999. Outlet strain smolts (West Grand Lake strain) had a stronger upstream response than inlet strain smolts (Sebago Lake strain), consistent with the expectations for lakeward-migrating smolts. The fry and smolt experiments indicated that inlet and outlet strains had different rheotactic responses that changed ontogenetically. These differences may be best explained by local adaptations to native habitat conditions. Because innate movement may affect the survival of juvenile salmon stocked for population restoration or provided to sport fisheries, strain and environmental conditions must be considered when stocking landlocked salmon into new habitats.

Local adaptations are inherited traits that result from selective pressures and increase the fitness of populations in their native environments. These adaptations are well documented among salmonid fishes and include migratory behavior (Bams 1976), disease resistance (Hemmingsen et al. 1986), and reproductive traits such as size at maturity and fecundity (Healey and Heard 1984; Beacham and Murray 1987). Adaptations that affect the survival of fish transplanted into new environments have important consequences for fishery management: fish that are poorly suited to the conditions of a new environment may not survive, whereas fish with compatible adaptations may flourish (Brannon 1967; Raleigh 1967; Van Offelen et al. 1993). Consequently, local adaptations are thought to have influenced the success of salmonid conservation, restoration, and transplanting programs (Raleigh 1967), and are important considerations for population restoration (Krueger et al. 1981; Montalvo et al. 1997). Although the potential benefits of matching local adaptations with environmental conditions have long been recognized (Raleigh 1967; Krueger et al. 1981), the influence of local adaptations on the success of transplanted populations has rarely been studied (Jennings et al. 1996).

An example of locally adapted, migratory behavior is the innate response to water current that directs juvenile salmonids towards suitable rearing and feeding areas, often lakes. Salmonids that hatch in streams but rear in lakes must migrate lakewards while immature. Juvenile fish that hatch in lake outlets must eventually migrate upstream to reach the rearing lake, whereas juveniles that hatch in lake tributaries must eventually migrate downstream. Juvenile salmonids exposed to water current in laboratory experiments have often shown a rheotactic response—the directional response to water current—that would direct them lakeward in the wild. Cutthroat trout *Oncorhyn-*

---

* Corresponding author: mnemeth@lgl.com

[1] Present address: LGL Alaska Research Associates, 1101 East 76th Avenue, Suite B, Anchorage, Alaska 99518, USA.

[2] Present address: Great Lakes Fishery Commission, 2100 Commonwealth Boulevard, Suite 100, Ann Arbor, Michigan 48105-1563, USA.

Received June 18, 2002; accepted January 29, 2003

chus clarki, sockeye salmon *O. nerka*, and Arctic grayling *Thymallus arcticus* from outlet streams all had stronger positive rheotactic responses (moving upstream) than conspecifics from inlet streams when tested at the age at which they migrate lakeward in the wild (Brannon 1967; Bowler 1975; Kaya 1989). Rheotactic responses are known to be genetic because inlet and outlet strains raised and tested in common environments show different responses, the hybrid crosses of inlet and outlet strains show intermediate responses, and the offspring of adults raised in common environments retain parental differences (Raleigh 1967; Kaya 1989; Kaya and Jeanes 1995). The rheotactic response can result in local adaptations because it is heritable, can cause differential access to spawning and rearing habitats, and can thus help maintain reproductive isolation among populations.

Differences in adult migratory behavior among potential donor strains may affect the restoration of landlocked Atlantic salmon *Salmo salar* to New York. Native New York populations migrated upstream from Lake Ontario, spawning so prolifically in tributaries that Webster (1982) called them ‘‘the most striking worldwide example of freshwater colonization by the Atlantic salmon.’’ These populations became extinct in the 19th century, and subsequent efforts to replace them with strains transplanted from elsewhere in the northeastern United States have generally been unsuccessful. If salmon introduced to Lake Ontario have an inherent tendency to spawn downstream, they would migrate down the St. Lawrence River, a large river with habitat unsuitable for landlocked Atlantic salmon spawning. On the other hand, salmon with an inherent tendency to spawn upstream would access the historically productive tributaries that native populations used for spawning and juvenile rearing. Strains available for stocking in New York include a downstream-spawning strain from West Grand Lake, Maine, and an upstream-spawning strain from Sebago Lake, Maine. If the two strains express heritable migratory behaviors consistent with their native environment, the salmon from Sebago Lake may be more likely to seek spawning habitat upstream of Lake Ontario in the tributaries historically used for spawning. The juveniles that hatch in tributary headwaters may also use a greater proportion of available stream nursery habitat than juveniles that hatch lower in the tributaries (or in lake outlets) because fry may colonize habitat more easily by descending from upstream than ascending from downstream (Gibson 1993).

The conditions that influence the expression of rheotactic response, and the degree to which they do so, can vary among salmonid populations. Rheotactic response may be expressed only at specific ontogenetic stages or under limited environmental conditions, allowing it to go undetected if fish are examined at inappropriate ages or under unfavorable environmental conditions. Failure to consider such factors when testing for rheotactic response is analogous to a type II error, in which the inappropriate conditions cause a lack of response and result in the conclusion that no difference exists between the test groups. Consequently, a thorough comparison of West Grand Lake and Sebago Lake strains of landlocked Atlantic salmon should examine the fish at different ages and under a range of environmental factors known to influence movement, such as water velocity and fish density (Chapman 1966; Bjornn 1971; Crisp and Hurley 1991).

The goal of this study was to examine the innate rheotactic responses of fry and smolts of the West Grand Lake and Sebago Lake strains of landlocked salmon. The specific objectives of the study were to (1) compare the rheotactic response of fry and smolts of the West Grand Lake and Sebago Lake strains of landlocked Atlantic salmon and (2) determine whether age, stocking density, and water velocity affect the rheotactic response of fry. Newly hatched fry were expected to move little and not to show differences among strains because fry typically remain in nursery streams until the smolt life stage. In contrast, if the two strains have innate rheotactic responses that are retained after transplanting, smolts of the West Grand Lake strain should be more likely to move upstream than the Sebago Lake smolts. The expectation was that the outlet strain smolts from West Grand Lake would show a stronger positive rheotactic response (upstream movement) than the inlet strain smolts from Sebago Lake because the smolts were tested at the age when they should migrate lakeward in the wild.

Methods

The rheotactic responses of West Grand Lake and Sebago Lake salmon were compared as fry and as smolts. In each study, equal numbers of West Grand Lake and Sebago Lake strain salmon were exposed to water current in a common environment on multiple occasions, or ‘‘trials.’’ The proportion of salmon of each strain that moved upstream, downstream, and that did not move (i.e., remained in the release section) was recorded at the end of each trial. Fish that were released but

TABLE 1.—Hatchery propagation information for strains of landlocked Atlantic salmon fry and smolts tested for rheotactic response.

Life stage and year	Strain	Year-class	Egg weight (eggs/g)	Embryo survival to eye-up (%)	Embryo incubation temperature before eye-up (°C)	Parental sex ratio (M:F)	Number of families
Fry 1999	West Grand	1999	4.34	65	NA	1:1	40
Fry 1999	Sebago	1999	5.24	81	2–3	1:1	87
Smolts 1998	West Grand	1997	4.34	65	NA	1:1	40
Smolts 1998	Sebago	1997	4.34	47	2–3	1:1	38
Smolts 1999	West Grand	1998	5.24	67	NA	1:1	40
Smolts 1999	Sebago	1998	5.24	91	2–3	1:1	103

not found at the end of a trial were subtracted from the total number of potential migrants. Upstream movement was the response variable used to compare movements between the strains because it was more likely to reflect deliberate movements, whereas downstream movement may have included both deliberate movement and passive drift with the current. Fry movements were compared between 0 and 8 weeks after hatching, when fish were relatively naïve with respect to environment and acquired behaviors, and are expected to remain instream for a year in the wild. Fry were tested in artificial stream channels in an indoor laboratory at Cornell University (Ithaca, New York), allowing the control of environmental variables and the manipulation of water velocities. Smolt movements were compared between 15 and 18 months after hatching, when fish were losing parr marks and would typically migrate lakeward in the wild (Warner and Havey 1985). Smolts were tested in outdoor artificial stream channels near Old Forge, New York, at densities within the known range of wild smolt densities (approximately 1 fish/m^2; Warner and Havey 1985). None of the fish used in the tests had been exposed to directional flow, and no fish were used more than once.

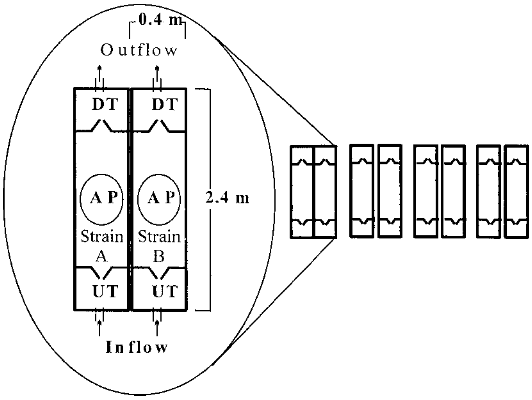

FIGURE 1.—Diagram of four pairs of artificial stream channels used to compare the rheotactic responses of the West Grand Lake and Sebago Lake strains of landlocked Atlantic salmon fry. Inset illustrates the trap locations and the flow direction of one pair. The fry were acclimated and released from central acclimation pens (AP), then recaptured in upstream (UT) and downstream (DT) traps. Each strain was randomly assigned to one side of each channel pair, and each channel pair was randomly assigned to high or low treatments of density and velocity. Strain × treatment (water velocity, density, age postswim-up) combinations were replicated from six to nine times.

Source of fish.—Gametes for all study fish were taken from 1:1 paired matings of male and female salmon by Maine Department of Inland Fish and Wildlife (MDIFW) personnel (Table 1). The fish used in each study came from a minimum of 38 paired matings. West Grand Lake gametes were taken from salmon spawning in Grand Lake Stream, the outlet of West Grand Lake. Sebago Lake gametes were taken from salmon spawning in the Jordan River, an inlet tributary to Sebago Lake. Fertilized eggs were incubated at the Little Moose Field Station operated by Cornell University near Old Forge, New York.

Fry experiments.—Fry were tested on nine occasions between 26 May 1999 and 16 July 1999. For each trial occasion, eight artificial stream channels (2.5 m long × 0.4 m wide) were grouped into four sets of pairs to achieve a 2^3 factorial split-plot design (Figure 1). Within each pair of channels, West Grand Lake fish were randomly assigned to one channel and Sebago Lake fish to the other. Two channel pairs were then randomly assigned a water velocity of 6 cm/s, and two were randomly assigned a water velocity of 12 cm/s. Within each velocity treatment, fish in one channel pair were tested at a density of 1 fish/m^2 (10 fish per channel), and fish in the other pair were tested at 2 fish/m^2 (20 fish per channel). On each test date, fish of each strain were tested at high and low water velocity, and at high and low density within each velocity treatment. Fry were also assigned a priori to two age-classes (hereafter referred to as young and old fry) to detect changes in fry rheotactic response over time. Young fry comprised fish 0–3 weeks post swim-up, and old fry comprised fish 4–8 weeks post swim-up. Dechlorinated water from Cayuga Lake, New York, was used in the stream channels.

Each strain of salmon was randomly marked with a left or right pelvic fin clip and then randomly assigned to one channel of each channel pair. High or low densities were then randomly assigned to each channel pair, and fry were placed in round holding pens (24 cm diameter) in the middle of each channel. Fry were exposed to the prescribed velocity treatment for 8 h and then allowed to disperse throughout the raceway. Fish were categorized as upstream or downstream migrants if they swam to either end of the raceway and through the 1-cm diameter trap opening (Figure 1). After 24 h, the numbers of fish in the upstream and downstream traps and in the release channel were counted.

The natural light entering the laboratory through windows was augmented with fluorescent lighting. The artificial lights were set to automatically turn on 30 min after sunrise and to turn off 30 min before sunset to achieve a natural, crepuscular transition. All tests began and ended 0.5 h before sunset, allowing fish to move throughout a complete diel cycle. Water depths ranged from 12 to 20 cm among trials. Channels were lined with gravel (mean diameter = 1.8 cm, SD = 0.75). Bricks (5.5 × 10.0 × 20.0 cm) were placed in the channel to provide cover. The water depth, velocity, and crepuscular transitions were intended to simulate environmental conditions, while the substrate and cover were added to allow fish refuge without leaving the raceway.

The ninth trial was run exclusively with extra Sebago Lake fry to increase statistical power, and only four channel pairs were used for two trial events. The methodology was identical to the eight preceding raceway trials (described above), except that no trials were conducted at the high-density treatment. Although the additional trials unbalanced the data, the analytical procedure used (described below) was able to process unbalanced data (SAS Institute 1990).

Smolt experiments.—Smolt rheotactic response was tested seven times between June 24 and August 13, 1998, and five times between August 3 and August 17, 1999. Fish were approximately 14 months after hatching and were classified as smolts because they began to lose parr marks and acquired a noticeable silver sheen. The proportion of fish with parr marks was recorded after each trial.

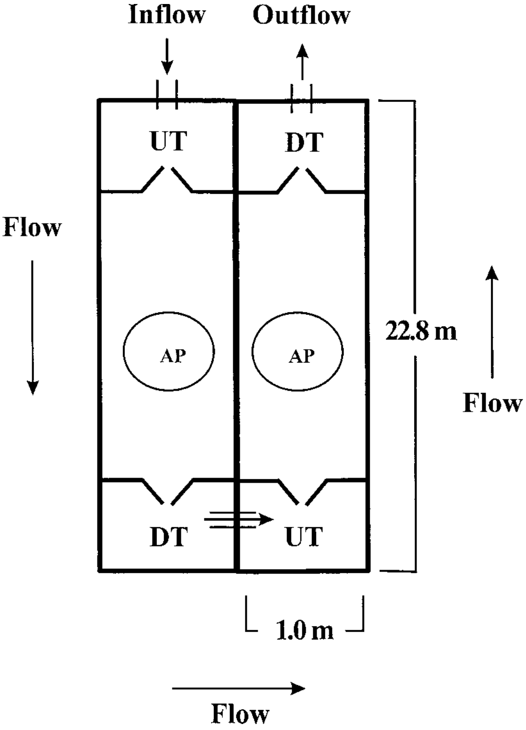

FIGURE 2.—Diagram of the artificial stream channels used to compare the rheotactic responses of West Grand Lake and Sebago Lake strains of landlocked Atlantic salmon smolts. The smolts were acclimated in central acclimation pens (AP), then released into channels and recovered in upstream (UT) and downstream (DT) traps. For each trial, 25 smolts of each strain were placed in each channel. Twelve test events were conducted in 1998, and eight events were conducted in 1999.

Stream water was diverted into the upstream ends of an in-line pair of artificial stream channels measuring 22.8 m long × 1.0 m wide (Figure 2). Strains were marked for identification with either a left or right pelvic fin clip, and 25 fish of each strain were released into holding pens in the middle of each channel. The fish were exposed to water current for approximately 12 h and then allowed to disperse throughout the raceway. Fish were categorized as upstream or downstream migrants if they swam to either end and through the 2-cm-wide trap entrance (Figure 2). The traps were closed after 24 h, and the numbers of fish in the upstream and downstream traps and in the release channel were counted.

Smolt trials began and ended 0.5 h before sunset,

TABLE 2.—Mean (SE) percent of the Sebago Lake and West Grand Lake strains of landlocked salmon fry moving upstream, downstream, and not moving. Young fry were 0 to 21 d after swim-up. Old fry were 22 to 56 d after swim-up. Significant differences between strains are indicated with asterisks ($P < 0.05$).

	Up			Down			Not moving		
Strain	All fry*	Young fry	Old fry	All fry	Young fry	Old fry	All fry	Young fry	Old fry
Sebago	42.2 (5.9)	60.9 (7.5)	28.2 (6.8)	41.1 (5.6)	29.7 (6.6)	49.7 (8.0)	16.3 (3.2)	8.6 (3.4)	22.1 (4.6)
West Grand	31.3 (5.1)	38.0 (5.6)	24.5 (8.2)	46.4 (5.6)	38.5 (7.6)	54.3 (7.8)	22.1 (3.8)	23.5 (4.8)	20.8 (6.1)

allowing fish to move throughout a complete diel cycle that included both crepuscular periods. Water velocities were recorded 1 m downstream of the upstream trap entrance on each raceway. Velocities varied from 6 to 12 cm/s among all trials because of differences in water volume available from the stream. The water depths ranged from 18 to 22 cm among all trials. The channels were lined with washed gravel. Wooden posts (10.0 × 10.0 × 244.0 cm) and concrete blocks (19.0 × 19.0 × 39.5 cm) were placed horizontally in the channels at 45° to the current to provide cover.

Data analysis.—The null hypothesis in all analyses was that no difference existed between the proportions of each strain moving upstream. For the fry trials, the proportion of fry moving upstream was compared between strains with a general linear model using the SAS MIXED procedure (SAS Institute 1990). The proportions analyzed were least squared means, the mean percentages moving in each direction after accounting for treatment effects. Proc MIXED allows for unbalanced data with random effects (SAS Institute 1990) and was thus able to analyze unbalanced strain, velocity, and density treatments. For the smolt trials, the proportion of smolts moving upstream was compared using paired *t*-tests (Snedecor and Cochran 1989). The smolt data from each year were analyzed separately (an $\alpha = 0.05$ was used to reject the null hypothesis in both fry and smolt studies).

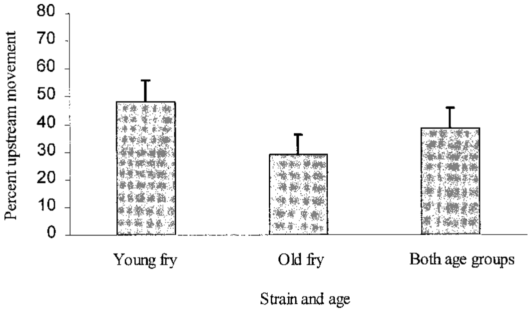

FIGURE 3.—Upstream movement of West Grand Lake and Sebago Lake fry by age-group. Columns are least-squares means, error bars are 1 SE. Young fry are 0–3 weeks posthatch, old fry are 4–8 weeks posthatch. The difference in upstream movement between young and old fry age groups is significant ($F = 9.53$, $P = 0.004$).

Results

The Sebago Lake and West Grand Lake salmon strains of landlocked Atlantic salmon had different rheotactic responses as fry and as smolts. The differences in upstream movement between the two strains reversed between the two life stages. When juvenile salmon were fry, the Sebago Lake strain was more likely to move upstream than the West Grand Lake strain; when the salmon were smolts, however, the West Grand Lake strain was more likely to move upstream than the Sebago Lake strain. An additional analysis of the effects of different variables on fry movement indicated that age (weeks after swim-up), water velocity, and fry density all affected movement.

Among fry, 42% of the Sebago Lake strain and 31% of the West Grand Lake strain moved upstream ($F = 5.12$, $P = 0.030$; Table 2). Overall upstream movement (both strains combined) dropped from 49% in young fry to 27% in old fry ($F = 9.53$, $P = 0.004$; Figure 3). The interaction between fry strain and fry age was not significant ($F = 2.09$, $P = 0.157$).

Smolt rheotactic response also differed by strain, but the upstream movement by the West Grand Lake smolts (41%) exceeded the upstream movement by the Sebago Lake smolts (30%) using 2-year averages for each strain (1998: $T = 2.66$, $P = 0.011$; 1999: $T = 1.95$, $P = 0.045$; Table 3). The upstream response by the smolts of each strain was consistent between the 1998 and 1999 trials (Table 3). The proportions of upstream-moving West Grand Lake smolts exceeded (14) or equaled (2) that of upstream-moving Sebago Lake smolts in 16 of 20 total test events. More Sebago Lake than West Grand Lake smolts moved downstream in both years, but the difference was significant only in 1998 ($T = 2.25$, $P = 0.023$; Table 3). The percentage of fish with parr marks decreased from

TABLE 3.—Mean (SE) percent of Sebago Lake and West Grant Lake strains of landlocked salmon smolts moving upstream, downstream, and not moving in 1998 and 1999 rheotactic response tests. Significant differences between strains are indicated with asterisks ($P < 0.05$).

	1998			1999		
Strain	Up*	Down*	Not moving	Up*	Down	Not moving
Sebago	32.6 (4.3)	64.0 (4.3)	3.4 (1.0)	28.4 (4.9)	60.3 (6.3)	11.3 (6.5)
West Grand	40.1 (5.9)	55.5 (5.5)	4.4 (1.3)	41.4 (5.4)	54.2 (6.1)	4.4 (2.6)

96% to 4% during the 1998 experiments, and from 30% to 10% during the 1999 experiments.

An analysis of the least-squares means of fry movements showed that density and water velocity affected fry movement but did not affect the two strains differently (Table 4). A greater proportion of fry moved downstream at high density (51%) than at low density (36%; $F = 4.78$, $P = 0.035$). Fry of both age groups were more likely to remain in the release chamber (i.e., no movement) at high water velocity (26%) than at low water velocity (10%; $F = 14.06$, $P = <0.001$). The interaction between age-class and velocity was significant ($F = 7.65$, $P = 0.009$), reflecting a greater effect of velocity on old fry (4–8 weeks) than on young fry (0–3 weeks; Table 4).

Discussion

Smolt behavior was consistent with the expectation of lakeward movement; smolts from West Grand Lake (outlet spawners) had stronger positive rheotaxis (upstream movement) than smolts from Sebago Lake (inlet spawners; Table 3). In contrast, the fry from West Grand Lake had a weaker positive rheotactic response than did the fry from Sebago Lake (Table 2). The observed differences between the two strains probably were genetically based because (1) the fish were raised under identical conditions, (2) the fish were tested under identical conditions (smolts) or the environmental conditions were controlled for in the experiments (fry; Hensleigh and Hendry 1998), and (3) similar differences in other salmonid species have been shown to be inherited (Raleigh 1967; Kaya 1989; Kaya and Jeanes 1995). The potential for nongenetic maternal effects was minimal because the test fish were from three different year-classes, the dams were of similar ages, the eggs were of similar size and condition, and the eggs were exposed to similar (until eye-up) and identical (after eye-up) temperatures (Table 1). If West Grand Lake and Sebago Lake salmon retain behavioral differences after transplanting into new environments, the two strains will be differently suited for stocking into the wild.

The greater upstream response by outlet strain smolts (West Grand Lake) in this study was consistent with the behavior of migrating juveniles of outlet populations described in other studies. Juvenile cutthroat trout, Arctic grayling, and sockeye salmon that hatch in outlets have all shown strong upstream responses to water current, either in terms of absolute numbers or relative to inlet hatching juveniles (Raleigh 1967; Raleigh and Chapman 1971; Bowler 1975; Kaya 1989). The positive rheotactic response reported in our study directs outlet smolts upstream (towards West Grand Lake) and thus should have adaptive value. The appearance and age of these fish indicated they were undergoing a physiological change associated with smolting and subsequent lakeward migration. The smolts tested in this study were losing

TABLE 4.—Mean (SE) percent of landlocked salmon fry moving upstream, downstream, and not moving in response to velocity and density treatments. Young fry were 0 to 21 d after swim-up. Old fry were 22 to 56 d after swim-up. Percent values are least-squares means. Pairs of asterisks indicate significant differences in fry movement within treatments ($P < 0.05$).

	All fry			Young fry			Old fry		
Treatment	Up	Down	Not moving	Up	Down	Not moving	Up	Down	Not moving
Density									
Low (1 fry/m^2)	42.7 (7.2)	36.4 (6.4)*	21.7 (2.5)	58.3 (8.3)	24.3 (7.8)	18.6 (3.7)	27.1 (8.1)	48.4 (7.6)	25.0 (3.5)
High (2 fry/m^2)	34.6 (7.8)	51.3 (7.2)*	13.8 (3.2)	38.2 (9.5)	50.3 (9.3)	10.6 (4.8)	31.0 (8.8)	52.2 (8.5)	17.0 (4.3)
Velocity									
Low (6 cm/s)	41.1 (7.7)	50.7 (7.0)	10.0 (2.8)*	47.6 (9.0)	41.0 (8.6)	12.4 (4.1)	34.7 (8.6)	60.4 (8.1)	7.6 (3.7)*
High (12 cm/s)	36.1 (8.2)	36.9 (7.5)	25.6 (3.0)*	48.9 (9.5)	33.7 (9.2)	16.7 (4.5)	23.4 (9.3)	40.2 (8.8)	34.4 (4.0)*

their parr marks and acquiring a silvery sheen indicative of smolting, and were moving at an age typical for wild landlocked salmon to move from streams to lakes (Warner 1965; AuClair 1982; Warner and Havey 1985).

The positive rheotactic response of inlet strain fry from Sebago Lake could be an adaptation to help newly hatched salmon remain instream and avoid premature downstream displacement. If fry remain instream for a year in the Sebago Lake drainage, as is typical for some other Maine populations (Warner and Havey 1985), the positive rheotaxis in this study may be a response that helps prevent the premature displacement of fry downstream into Sebago Lake. The strongest upstream response by Sebago Lake fry was within 3 weeks after hatching (Table 2), suggesting that an innate upstream response may be most important for newly hatched fry. In addition to preventing downstream displacement, this upstream response may also act as a dispersal mechanism to reduce density dependent effects and to maximize the use of available food and space resources.

The need to remain instream may also explain the low levels of positive rheotactic response documented in other inlet-origin salmonid populations. Inlet strain juveniles with negative rheotactic responses have typically been studied at the age that they migrate downstream in the wild (e.g., sockeye salmon, Raleigh 1967; cutthroat trout, Raleigh and Chapman 1971; Arctic grayling, Kaya 1989). Individual fry within some studies, however, have shown positive rheotactic responses (e.g., Raleigh 1967; Brannon 1972), and at least one inlet population has shown a stronger, overall positive rheotactic response than a conspecific outlet population (Kelso et al. 1981). These anomalous upstream movements by inlet-origin fish may be caused by fish with undetected, alternative life history types that require them to remain longer instream than their cohorts (Hensleigh and Hendry 1998). Some juvenile sockeye salmon may remain in inlets longer than their conspecifics, for example, and represent a ‘‘river-type’’ life history that has developed a positive rheotactic response to help maintain residence in streams (Hensleigh and Hendry 1998). The extended stream residence by the inlet-hatching Atlantic salmon used in this study is analogous to the ‘‘river-type’’ inlet sockeye salmon, and may explain the positive rheotactic response of inlet strain fry in this study.

The different rheotactic responses of the Sebago and West Grand Lake strains is suggestive of local adaptations, which are difficult to prove in salmonids and are often indicated by circumstantial evidence (Taylor 1991). Rheotactic response meets the criteria proposed by Taylor (1991) by virtue of (1) its genetic basis as demonstrated in numerous other studies and (2) the fact that directional water flow serves as a selective pressure that logically should confer differential survival or reproduction on individual salmon with different rheotactic responses. For example, a positive rheotactic response should increase the survival rates of Sebago Lake fry because the fish are less likely to prematurely move downstream into Sebago Lake. The correlation of rheotactic responses with wild survival rates would provide further evidence that rheotactic behaviors are local adaptations caused by natural selection.

Several aspects of the study design support the conclusion that the observed movement differences between strains were genetic and not environmental. First, both strains were tested under identical conditions within each trial. Second, the salmon were tested within the ranges of density, velocity, and temperature found in natural environments to minimize the potential effects of anomalous environmental conditions. Third, environmental effects would have had to act differently on each strain to cause the observed movement differences. No statistically significant interactions occurred between strain and density or velocity, and the velocity and density manipulations affected all fry similarly. Fourth, the smolt movements were consistent with a priori expectations based on previous studies that compared juvenile salmonids from inlets and outlets. In addition, upstream movement was chosen as the only response variable in comparing the strains because it is more energetically costly than downstream movement and should, therefore, be a less probable choice of direction for fish that are simply attempting to escape unfavorable test conditions. Downstream movement may be less representative of innate rheotactic behavior because downstream is also the direction that fish unable to maintain their position in the currents would move, and it would be the easiest route that fish would choose to escape from unfavorable conditions. For all these reasons, innate differences appear to be the most plausible cause of the differences observed between the two strains.

Several elements of the artificial stream channels were designed to mimic natural stream conditions. Water velocity and crepuscular transition can affect rheotactic response and were kept representative of natural stream conditions. Substrate size, instream cover, and water depth were provided to give fish the opportunity to hold in the channels instead of migrating. Despite these elements, the proportions of fish moving upstream in this study were probably inaccurate estimates of upstream movement by wild salmon in natural environments. The environmental cues that influence rheotactic responses are difficult to identify in the wild, let alone duplicate in the laboratory. The important result of our laboratory tests was that differences between the strains were detected even in artificial environments that may have been suboptimal for salmon movement. Natural settings should provide a more optimal set of stimuli, thereby increasing directional movements and magnifying strain differences. Raleigh (1967) provided anecdotal evidence that laboratory tests underestimated upstream movement, noting that wild sockeye salmon fry in the Karluk Lake, Alaska, watershed move upstream in greater numbers than fry tested in laboratory trials.

The effects of density and water velocity on fry were consistent with those reported in the literature. Available space can regulate the density of stream-dwelling salmonid populations (Chapman 1966) and may explain the increased downstream movement of fry with density in this study (Table 4). Atlantic salmon fry are territorial in moving water and will defend stream stations soon after hatching (Saunders and Gee 1964; Gibson 1993). The low-density treatment of 1 fry/m^2 was roughly the average density reported for wild landlocked Atlantic salmon fry in Maine, whereas the high-density treatment of 2 fry/m^2 exceeded published reports of wild fry densities (Warner and Havey 1985). The fry that left the release section in search of space may have chosen to move in the easiest direction—downstream (Table 4).

The fry in this study were more likely to disperse at low velocities (90% left release chamber) than at high velocities (74% left release chamber). This difference was significant only in older fry (Table 4). Crisp and Hurley (1991) also noted that the dispersal rates of anadromous Atlantic salmon fry were lower at high than at low velocities. The gravel and instream cover in this experiment may have given fry a shelter from high velocities; if so, the older fry appeared more likely than the younger fry to use this shelter. The managers of regulated rivers may need to consider the effects of water velocity on newly hatched Atlantic salmon fry if instream dispersal affects their early survival.

Matching rheotactic response with environmental characteristics could improve the management of Atlantic salmon for restoration or put–grow–take fisheries. When two strains are available for stocking, the one whose rheotactic behavior best matches the habitat should be chosen. Stocking upstream-migrating juveniles in lake outlets and downstream-migrating juveniles in tributaries may increase the proportion of fish accessing the lake and subsequently reaching maturity. For example, outlet-spawning adults that migrate downstream from the lake may drop over barriers (such as waterfalls and dams) and be lost from the fishery. In contrast, inlet-spawning adults that move upstream would return downstream over any impediments they navigated on the way upstream, and not be lost from the system during spawning migrations. In Lake Ontario, where outlet-spawning habitat is nonexistent, the stocking of the inlet spawning Sebago Lake strain should provide salmon that will use tributary streams for spawning and juvenile rearing, and thus hasten the restoration of the species.

Acknowledgments

Financial support for this project was provided by the New York State Department of Environmental Conservation, the Adirondack Fishery Research Program (Department of Natural Resources, Cornell University), and by the Adirondack League Club. Laboratory and field assistance was provided by Peter Brown, Brian Weidel, and Kipp Powell. Heather Barker-Baird provided critical assistance with raceway construction and laboratory design. Charles McCullough, Cornell University, provided advice regarding the study design throughout the experiment, and Francois Vermeylen and Evan Cooch, Cornell University, helped with SAS modeling and analysis. Four anonymous reviewers provided valuable comments on an earlier draft.

References

AuClair, R. P. 1982. Moosehead Lake fishery management. Maine Department of Inland Fisheries and Wildlife, Fisheries Research Bulletin 11, Augusta.

Bams, R. A. 1976. Survival and propensity for homing as affected by presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (*Oncorhynchus gorbuscha*). Journal of the Fisheries Research Board of Canada 33: 2716–2725.

Beacham, T. D., and C. B. Murray. 1987. Adaptive variation in body size, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 44:244–261.

Bjornn, T. C. 1971. Trout and salmon movement in two Idaho streams, as related to temperature, food, stream flow, cover, and population density. Transactions of the American Fisheries Society 100:423–437.

Bowler, B. 1975. Factors influencing genetic control in lakeward migrations of cutthroat trout fry. Transactions of the American Fisheries Society 104:474–482.

Brannon, E. L. 1967. Genetic control of migrating behavior of newly emerged sockeye salmon fry. International Pacific Salmon Fisheries Commission Progress Report 16.

Brannon, E. L. 1972. Mechanisms controlling the migration of sockeye salmon fry. International Pacific Salmon Fisheries Commission Bulletin 21.

Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. American Naturalist 100:345–356.

Crisp, D. T., and M. A. Hurley. 1991. Stream channel experiments on downstream movement of recently emerged trout, *Salmo trutta* L. and salmon, *S. salar* L.—I. Effect of four different water velocity treatments upon dispersal rates. Journal of Fish Biology 39:347–361.

Gibson, R. J. 1993. The Atlantic salmon in fresh water; spawning, rearing, and production. Reviews in Fish Biology and Fisheries 3:39–73.

Healey, M. C., and W. R. Heard. 1984. Inter- and intrapopulation variation in the fecundity of chinook salmon (*Oncorhynchus tshawytscha*) and its relevance to life history theory. Canadian Journal of Fisheries and Aquatic Sciences 41:476–483.

Hemmingsen, A. R., R. A. Holt, R. D. Ewing, and J. D. McIntyre. 1986. Susceptibility of progeny from crosses among three stocks of coho salmon to infection by *Ceratomyza shasta*. Transactions of the American Fisheries Society 115:492–495.

Hensleigh, J. E., and A. P. Hendry. 1998. Rheotactic response of fry from beach-spawning populations of sockeye salmon: evolution after selection is relaxed. Canadian Journal of Zoology 76:2186–2193.

Jennings, M. J., J. E. Claussen, and D. P. Philipp. 1996. Evidence for heritable preferences for spawning habitat between two walleye populations. Transactions of the American Fisheries Society 125:978–982.

Kaya, C. M. 1989. Rheotaxis of young Arctic grayling from populations that spawn in inlet or outlet streams of a lake. Transactions of the American Fisheries Society 118:474–481.

Kaya, C. M., and E. D. Jeanes. 1995. Retention of adaptive rheotactic behavior by F_1 fluvial Arctic grayling. Transactions of the American Fisheries Society 124:453–457.

Kelso, B. W., T. G. Northcote, and C. F. Wehrahn. 1981. Genetic and environmental aspects of the response to water current by rainbow trout (*Salmo gairdneri*) originating from inlet and outlet streams of two lakes. Canadian Journal of Zoology 59:2177–2185.

Krueger, C. C., A. J. Gharrett, T. R. Dehring, and F. W. Allendorf. 1981. Genetic aspects of fisheries rehabilitation programs. Canadian Journal of Fisheries and Aquatic Sciences 38:1877–1881.

Montalvo, A. M., S. L. Williams, K. J. Rice, S. L. Buchmann, C. Cory, S. N. Handel, G. P. Nabhan, R. Primack, and R. H. Robichaux. 1997. Restoration biology: a population biology perspective. Restoration Ecology 5:277–290.

Raleigh, R. F. 1967. Genetic control in the lakeward migrations of sockeye salmon (*Oncorhynchus nerka*) fry. Journal of the Fisheries Research Board of Canada 24:2613–2621.

Raleigh, R. F., and D. W. Chapman. 1971. Genetic control in lakeward migrations of cutthroat trout fry. Transactions of the American Fisheries Society 98: 33–40.

Saunders, R. L., and J. H. Gee. 1964. Movement of young Atlantic salmon in a small stream. Journal of the Fisheries Research Board of Canada 21:27–36.

SAS Institute. 1990. The MIXED Procedure. Pages 533–651 *in* SAS procedures guide, version 6. SAS Institute, Cary, North Carolina.

Snedecor, G. W., and W. G. Cochran. 1989. Statistical methods, 8th edition. Iowa State University Press, Ames.

Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98:185–207.

Van Offelen, H. K., C. C. Krueger, and C. L. Schofield. 1993. Survival, growth, and distribution of two brook trout strains stocked into small Adirondack streams. North American Journal of Fisheries Management 13:86–95.

Warner, K. 1965. Fishery management in the Fish River drainage. Maine Department of Inland Fisheries and Wildlife, Fishery Research Bulletin 6, Augusta.

Warner, K., and K. A. Havey. 1985. Life history, ecology, and management of Maine landlocked salmon (*Salmo salar*). Maine Department of Inland Fisheries and Wildlife, Augusta.

Webster, D. A. 1982. Early history of Atlantic salmon in New York. New York Fish and Game Journal 29: 26–44.