North American Journal of Fisheries Management 42:438–446, 2022

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1002/nafm.10759

ARTICLE

Upstream and Downstream Dispersal Behavior of Hard- and Soft-Released Juvenile Atlantic Salmon

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Abstract

Failure of reintroduction efforts of extirpated populations is thought to be linked to maladaptive behaviors exhibited by captive-bred individuals in the environment where they are released. Soft-release conditioning tactics attempt to reduce maladaptive behaviors by providing reintroduced animals an acclimatization period prior to release. We used implanted passive integrated transponder tags and antennae to monitor the spatial and temporal dispersal behavior of captive-bred Atlantic Salmon *Salmo salar* that were acclimatized for 6 d prior to release (soft-release), with fish that were directly released (hard-release) into East Duffins Creek in Ajax, Ontario, Canada. In total, 232 of the 610 tagged fish (38%) dispersed from the release site. Downstream spatial dispersal did not differ significantly between the hard-release (32%, $n = 98$ of 310) and soft-release fish (30%, $n = 91$ of 300), but the hard-release fish were significantly more likely to move upstream (11%) than were the soft-release fish (3%). Timing of dispersal also significantly differed between the two groups: soft-release fish were detected dispersing, on average, approximately 15 d earlier than hard-release fish. These results suggest that soft-release tactics do affect dispersal behavior, and the findings will be of particular interest to fisheries management agencies that are charged with improving the success for stocking salmonids as part of reintroduction efforts.

The success of reintroduction efforts is generally measured in terms of the establishment and persistence of a self-sustaining population (Dickens et al. 2010), but successful outcomes are limited in number and scope (reviewed in Fischer and Lindenmayer 2000; Seddon et al. 2007). The period immediately following release of reintroduced animals—the establishment phase—is a precarious and sensitive period for survival (Dickens et al. 2010). The failure of reintroduced animals to survive and persist in the wild is thought to be linked to maladaptive behaviors that captively reared animals exhibit during this phase (Einum and Fleming 2001; Jule et al. 2008). These maladaptive behaviors include poor foraging (Einum and Fleming 1997), reduced antipredator responses (de Mestral and Herbinger 2013), and atypical dispersal behavior (Swaisgood 2010). The rising number of unsuccessful reintroductions has been met with a set of approaches—what Tetzlaff et al. (2019) refer to as "conditioning"—directed

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Received November 4, 2021; accepted February 6, 2022

at countering the negative effects associated with captive-rearing and reintroduction events. Conditioning can be "animal-focused," which involves various forms of environmental enrichment while in the captive setting, or "environment-focused," which involves enriching the release environment (Tetzlaff et al. 2019). Conditioning may offset some of the detrimental effects experienced by captively reared organisms (Huntingford 2004; Jonsson and Jonsson 2014), with the goal of producing more "natural-like" behaviors (Hyvärinen and Rodewald 2013). These approaches have been gaining in popularity among wildlife managers as well as conservation biologists (Hutchison et al. 2012; Reading et al. 2013; Jonsson and Jonsson 2014).

Environment-focused conditioning tactics are those that seek to expose captive-bred organisms to wild or semiwild settings—the most common of these tactics being *soft-release* (Tetzlaff et al. 2019). Soft-release generally refers to the practice of providing reintroduced animals with an acclimatization period that is free of predators at or near the release site prior to release, as compared with conventional *hard-release*, where reintroduced organisms receive little to no acclimatization prior to being released into the wild (Brown and Day 2002). In their meta-analysis, Tetzlaff et al. (2019) found that soft-release, compared with other tactics (environmental enrichment and predator training), had the most significant influence on stress-related postrelease survival, dispersal, and site fidelity across the range of taxa studied.

Arguably one of the most important behavioral concepts in reintroduction programs is dispersal behavior—a topic that, until recently, has received little attention in reintroduction research. Swaisgood (2010) argues that a widespread problem with captive-release programs is rapid dispersal away from release sites, as increased dispersal is linked with increased mortality due to increased levels of predation risk and high energetic costs of dispersal. Dispersal rate and timing are commonly measured metrics for movement related to survival of reintroduced organisms (Tetzlaff et al. 2019). To date, studies of the effects of soft-release on survival and dispersal rate have shown inconsistent results. For example, no difference in dispersal rates was observed between age-2 European Grayling *Thymallus thymallus* that were directly released into streams and those that were acclimatized in fenced-in pools at the release site prior to release (Thorfve 2002). In contrast, soft-released Brown Trout *Salmo trutta* fingerlings showed a decrease in dispersal and a 10–18% higher level of survival compared with hard-release fish (Cresswell and Williams 1983). Similar effects—a decrease in dispersal from the release site and increased survival rates for soft-released fish—have been observed for other salmonids in early life (presmolt; e.g., Jonssonn et al. 1999; but see Rosenberger et al. 2013).

Along with rate of dispersal, other common measures of movement behavior are dispersal patterns and spatial distribution (Egglishaw and Shackley 1973, 1980; Beall et al. 1994; Crisp 1995; Teichert et al. 2011; Foldvik et al. 2012; Eisenhauer et al. 2021). Analyses of dispersal and spatial distribution can involve simply measuring movement in a single dimension (upstream and downstream; Eisenhauer et al. 2021). A study comparing the dispersal pattern of wild and hatchery-reared juvenile Masu Salmon *Oncorhynchus masou* showed that captive-bred fish were caught in upstream traps at a significantly higher proportion compared with their wild counterparts (Nagata et al. 1994). Those authors suggested that the difference in dispersal direction was due to differences in swimming behavior brought on by the environments in which the individuals develop (Nagata et al. 1994). Although the postrelease dispersal patterns for salmonids that are liberated to lotic habitats can be variable, most studies suggest that fish are more likely to disperse downstream than upstream (Peery and Bjornn 2000; Andrews et al. 2013), including studies of Atlantic Salmon *Salmo salar* (Eisenhauer et al. 2021). This downstream dispersal bias may be related to the water flow causing passive dispersal of fish in the downstream direction (Heggenes and Dokk 2001). The effects of soft-release on upstream and downstream dispersal patterns, however, have yet to be studied. Understanding dispersal rates and patterns is beneficial to reintroduction efforts in the context of salmonid growth and ultimately survival; for wild subyearling anadromous salmonids, time spent lingering in riverine feeding sites is thought to be crucial for maintaining high growth rates and survival prior to smolt and migration downstream (Connor et al. 2003).

Another important way in which movement behavior can be understood is through the daily cycle of diurnal and nocturnal activity (Metcalfe et al. 1998). Most animals are adapted to consistent diurnal activity patterns (Metcalfe et al. 1998). Adaptation to captive-rearing settings can alter the diurnal activity pattern of fishes. For example, Álvarez and Nicieza (2003) found that hatchery-reared Brown Trout were predominantly active during the day, whereas wild Brown Trout were predominantly active at night (see also Alioravainen et al. 2020 for seminatural conditions). For wild Atlantic Salmon, diel activity patterns are season- and age-dependent (Johnston et al. 2004). Young-of-year Atlantic Salmon were observed to be more active during the day in early summer and shifted to a more nocturnal activity in late summer and into the colder season—the opposite was found for older post-young-of-year salmon in the same study (Johnston et al. 2004). It remains unclear whether captive-rearing or soft-release affect the diurnal activity patterns of Atlantic Salmon that are released into the wild.

Atlantic Salmon were once an abundant top predator in Lake Ontario and the target of a valuable fishery until their extirpation in the late 19th century (Dunfield 1985; Hawkins et al. 2019). While the Lake Ontario habitat has been restored and many of the factors leading to extirpation have been alleviated (Beeton 2002), reintroduction efforts have yet to restore a self-sustaining population, possibly due to a failure of captive environments to prepare the fish for the natural environments in the tributaries where they are released (Stewart et al. 2014). In this study we introduced captive-bred Atlantic Salmon to a tributary of Lake Ontario using two tactics. The tactics included a conventional hard-release (direct release into the stream) and soft-release (where fish were allowed to acclimatize for 6 d in specially designed enclosures within the stream prior to release). We used passive integrated transponder (PIT) tags to monitor the dispersal patterns of the fish that underwent the hard- and soft-release tactics—specifically the timing of upstream and downstream dispersal and the diurnal activity patterns between the groups of fish.

METHODS

Fish stock and husbandry.— The Atlantic Salmon were from the Sebago Lake strain (Maine, USA; 43.9°N, 70.6°W), which has been maintained for two generations at the Ontario Ministry of Natural Resources and Forestry (OMNRF) Harwood Fish Culture Station (44.18.06°N, 78.14.73°W) specifically for reintroduction efforts to Lake Ontario (2019 Annual Report of the Lake Ontario Management Unit). In the fall of 2017, gametes were collected from adults that are housed at the Harwood Fish Culture Station and transported to a hatchery facility at Western University, London, Ontario. At the Western University facility, eggs and milt were crossed using a 2×2 design, wherein each block in the cross consists of two females, with half of each female's eggs fertilized by each of two males. A total of 14 blocks were created (28 females, 28 males). The fertilized eggs were incubated in vertical incubation stacks with a circulating water system that was maintained at 7 ± 1°C. After hatch, on February 18, 2018, the fry were moved to mixed-family tanks with a single layer of loose gravel at the bottom of each tank. The tank temperatures were maintained at 7 ± 1°C until March 7, 2018, at which point the temperature was transitioned over a 3-week period to 11 ± 1°C. The tanks were kept at this temperature until mid-April when the temperature was again increased over a 3-week period to 15 ± 1°C.

PIT tagging and measurements.— During the second week of September 2018, we haphazardly selected 610 fall fingerling Atlantic Salmon and individually marked them with a PIT tag (Biomark TX1411SST; 12.5×2.07 mm, 0.102 g). We followed Cook et al. (2014) for the PIT-tagging procedure—briefly, the fish were anesthetized in 50mg/L of MS-222 (tricaine methanesulfonate) and the tags were injected into the body cavity with preloaded syringes. A subset of the tagged fish (192 hard-release and 167 soft-release) were weighed for comparison between groups. Based on the subsample of fish that was measured ($n = 359$) at the time of tagging, the hard-release fish weighed 3.83 g (SD ± 1.27) and the soft-release fish weighed 3.84 g (SD ± 1.50), indicating that there was no significant difference in mass between the two groups ($t = -0.08$, df = 357, $P = 0.94$). The fish were monitored, in their home tank, for tag rejections, condition, and mortality for 1 month prior to release to ensure that the PIT tags had remained inside the body of the fish. All of the tagged fish in the study survived tagging, and no tags were rejected. Each fish was individually scanned with a PIT tag reader prior to transport.

Study site, enclosures, and PIT tag antennas.— Our hard- and soft-release experiment was conducted in the East Duffins Creek, Ajax, Ontario, Canada, within the Greenwood Conservation Area (43°53′55.9″N, 79°03′54.2″W). East Duffins Creek is a 32-km tributary that empties into Lake Ontario and is part of the larger Duffins Creek watershed with a drainage area of 283 km^2. Duffins Creek is host to approximately 50 species of cold water riverine fishes, including at least three species of introduced nonnative salmonids: Rainbow Trout *Oncorhynchus mykiss*, Chinook Salmon *Oncorhynchus tshawytscha*, and Brown Trout (OMNRF 2020). Although Rainbow Trout and Brown Trout juveniles have been shown to possess better competitive ability for territory acquisition and use compared with Atlantic Salmon (e.g., Houde et al. 2017), Duffins Creek has been chosen by the OMNRF as an important site for the release of hatchery-reared Atlantic Salmon juveniles that are produced within the context of the reintroduction efforts for Lake Ontario (see 2019 Annual Report of the Lake Ontario Management Unit).

To assess the upstream and downstream dispersal of the tagged fish, PIT tag antennas (1×3 m in length; Biomark, Boise, Idaho) were anchored at narrow chokepoints of the stream 350 m apart. The antennas were anchored parallel to and across the stream bed in the middle of the water column to detect the PIT-tagged fish that were swimming throughout the water column. The detection range of the antennas was set to 45 cm above and below them to maximize the detection of the fish passing across the antennae. To prevent fish from swimming around the arrays, avoiding detection, mesh panels were installed on either side of the arrays to cover the remaining width of the stream. The dominant substrate (>50%) as defined by grain size (Wentworth 1922) at each of the arrays was rubble (54–179 mm). The 350-m stretch of stream between the two arrays was the designated "release site"—this is

where the soft-release enclosures (see details below) were installed and where the fish from both the hard- and soft-released treatments were released. The fish that were detected at the upstream antenna were considered to be dispersing upstream, and the fish that were detected at the downstream antenna were considered to be dispersing downstream. Fish that were not detected on either of the antenna were considered to have not dispersed and remained at the release site.

In total, nine soft-release enclosures were anchored to the streambed within the release site in three sets of three at a depth of 0.30 m—each group 50 m apart starting 100 m downstream of the upstream PIT tag antenna. The three enclosures per set were arranged staggered downstream from one another (no more than 1 m distance apart) so as to prevent flow obstruction from one enclosure to the next. The enclosures were constructed by connecting four wooden frames (1 × 1 m) covered with a 5-mm mesh net to create a 1-m^3 enclosure with no top or bottom panel. Steel rods were anchored into the stream bed at each of the four corners of the enclosure to provide stability and prevent the enclosures from washing away. The top of each enclosure was then covered with a twine grid to prevent avian predators from feeding on the salmon within, and the bottom edges of the pen were buried with rubble to prevent fish from escaping the enclosures.

Transport and release.— On October 9, approximately half of the fish ($n = 300$, soft-release treatment) were transported to the release site in 100-L live-well coolers at a density of 11.5 g/L. The water temperature was continuously monitored during transport, and sealed bags of dechlorinated ice were added every half hour to the cooler to maintain water temperature within 2°C of the home tank temperature on the day of release (14.8°C). The overall trip duration was approximately 3 h. Upon arrival at Greenwood Conservation Area, at 1540 hours local time, the fish were transported to the release site from the cooler to the stream in 19-L plastic pails. The process of transporting all of the fish from the vehicle to the enclosures took a total of 30 min. The fish were haphazardly and evenly distributed between the nine possible soft-release enclosures. Approximately 33 fish were housed in each enclosure, resulting in a density of approximately 9 g/L. The water temperature at the middle three enclosures was 14.5°C at the time that the fish were placed in the enclosures. The outside of each enclosure was cleaned of debris and checked daily for mortalities. No mortalities were observed over the 6-d acclimatization period within the soft-release enclosures. On October 15, after 6 d of soft-release acclimatization, the remaining fish ($n = 310$; hard-release fish) were then transported to the release site in the same manner as was described previously for the soft-release fish. The fish arrived at Greenwood Conservation Area at 1515 hours local time. The hard-release fish were transported in 19-L plastic pails (approximately 33 per pail) next to each of the nine soft-release enclosures and released with the lifting of the enclosures such that the hard-release and soft-release groups were released simultaneously. Fish dispersal was then monitored for a total of 57 d postrelease, until the beginning of the river freeze-up stage.

Monitoring upstream and downstream dispersal.— To detect and log PIT tags passing the antennas, each antenna was connected to an individual PIT tag reader and data logger (Biomark IS1001 Data Logger Board). The scan time for each reader was set to 75 ms and idle time to 120 ms. A pilot study on detection was carried out to ensure the reliability and detectability of passing PIT-tagged fish. A "test fish" (i.e., a rectangular piece of foam the size of a typical juvenile that was injected with a PIT tag) was repeatedly floated in the stream past each antenna three times (in the morning, afternoon, and before sunset). The PIT tag reader recorded, with 100% detection efficiency, the test fish floating above the antenna. The readers ran continuously for all 57 d of the experiment. Once a week the readers were turned off briefly (<1 min) to allow for one of the experimenters to replace the batteries that powered the system.

Fish that were not detected were assumed to have not dispersed from the release site. For the fish that were detected on an antenna, multiple detections per fish were possible and logged; however, only unique first detections were used for the analyses in this study. Approximately 94% (232 of the 242 fish that were detected on the array) of the individuals were detected once, but only ~6% were detected more than once (all of these occurrences were of fish first detected on the upstream antenna and then subsequently detected on the downstream antenna. Our analyses included only first unique detections of fish, so only the upstream detections for these occurrences were used for them. Unique first detections on the upstream antenna were assumed to represent upstream dispersal, and unique first detections on the downstream antenna were assumed to represent downstream dispersal. Latency to detection was measured as time (in days) from the date of release (October 15, 2018) until each unique first detection was made. Latency to detection was assumed to represent latency to dispersal in this study.

Environmental data.— Water discharge data were obtained from the National Hydrological Service (https://wateroffice.ec.gc.ca/search/real_time_e.html, accessed April 4, 2019). Water discharge (m^3/s) was measured at 5-min intervals at Duffins Creek at Ajax hydrometric station (station number: 02HC049; 43°50′5″N, 79°03′22″W), 8.5 km downstream of the release site. During the experimental period (October 9, 2018 to December 11, 2018), mean discharge was 2.41 m^3/s (range = 1.88–35.5 m^3/s). Daily

averages were used for analysis. Daylight timings were obtained from the National Research Council Canada (https://nrc.canada.ca/en/research-development/products-services/software-applications/sun-calculator/).

Statistical analyses.—To examine whether our experimental treatment (soft- or hard-release) affected the likelihood of detection at either the upstream or downstream array, we fit our data to a generalized linear model, assuming our response variable (detection) to be binomially distributed and our predictor variable being experimental treatment (hard- or soft-release) to generate log odds ratios of detections for our predictor variable. We ran the model for upstream and downstream detections separately to examine the effect of experimental treatment on the likelihood of detection at each antenna.

The effect of treatment on latency to detection (measured as the time (in days) from the date of release that a fish was detected on either array) for the fish that were detected by the array was examined using an analysis of variance (ANOVA) model. Our ANOVA model was set up with latency to detection as the response variable and treatment (hard- and soft-release) as the predictor variable. We then ran the same ANOVA model separately for downstream and upstream data exclusively to examine the effects of treatment on latency for each direction of dispersal.

To test for the effect of water discharge rate (flow) on the daily number of detections, we fit the daily detection count data to a generalized linear model, assuming our response variable to be Poisson distributed and zero inflated (Vidal et al. 2018), using mean daily discharge rate and treatment as predictor variables and an interaction term between the two predictor variables.

The diurnal timing of dispersal across treatment was tested using a chi-square goodness-of-fit test for assessing frequency distributions, with expected frequencies for day and night set at 53% and 47%, respectively, as this ratio represented the average daylight and darkness hours throughout the study period (October 15 to December 11, 2018). Each detection was scored as either representing a daytime or nighttime detection, and the cumulative frequency of detections was used as observed frequency values for our analysis. A chi-square goodness-of-fit test was used to compare total observed day and night detections with the expected frequencies (Dodd et al. 2018). We then compared the observed frequencies of hard- and soft-release detections using a Pearson's chi-square test with a Yates's continuity correction to determine whether there is a relationship between hard- and soft-release and daytime and nighttime detections.

The data analyses were performed using R language for statistical computing (version 4.1.0; R Foundation for Statistical Computing) with RStudio version 1.4.1106 (RStudio Team 2021). The zero-inflated regression model used the *pscl* package for RStudio (Zeileis et al. 2008; available at http://www.jstatsoft.org/v27/i08/), and all of the other analyses were conducted with packages contained in The R Base Package (R Core Team 2021).

RESULTS

In total, 232 of the 610 tagged Atlantic salmon (38%) dispersed from the release site, as measured by detection at either antenna (189 were detected at the downstream antenna and 43 were detected at the upstream antenna). There was a significant difference in log-odds ratio of fish that were detected between the two treatment groups at the upstream antenna ($B = -1.30$, SE = 0.38, $P < 0.001$), meaning that the hard-release fish were significantly more likely to move upstream (11%, $n = 33$ of 310) than were the soft-release fish (3%, $n = 10$ of 300). Also, there was no significant difference in the log-odds ratio of fish detections between the two treatment groups at the downstream antenna ($B = -0.18$, SE = 0.18, $P = 0.31$), meaning that there was no difference in likelihood of detecting a hard- or soft-release fish at the downstream antenna.

Latency to disperse either upstream or downstream ranged from 0 to 56 d postrelease (see Figure 1). On average, the soft-release fish were detected ~15 d earlier (mean detection latency = 10.34 d) than were the hard-release fish (mean detection latency = 25.79 d; $F_{1, 230} = 113.1$, $P < 0.01$; Figure 1). Next, we ran the same analyses separately for downstream detections ($n = 189$) and upstream detections ($n = 43$). For the upstream detections, the soft-release fish were detected upstream significantly sooner, ~10 d earlier (mean detection latency = 6.6 d) than were the hard-release fish (mean detection latency = 16.61 d; $F_{1, 42} = 6.32$, $P = 0.016$; Figure 1A). On average, the soft-release fish were detected downstream significantly sooner (~18 d earlier: mean detection latency = 10.75 d) than were the hard-release fish (mean detection latency = 28.89 d; $F_{1, 187} = 154$, $P < 0.01$; Figure 1B).

The model we used to examine the effect of discharge in relation to our hard- and soft-release treatments found that daily detection count (for all of the fish that were detected) was not significantly affected by mean daily discharge rate ($B = -0.08$, SE = 0.14, $P = 0.57$) but was significantly affected by treatment group (hard- and soft-release) ($B = 1.45$, SE = 0.71, $P = 0.04$); however, no significant interaction between mean daily discharge rate and treatment group was found ($B = 0.095$, SE = 0.16, $P = 0.55$), meaning that daily detection count was not affected by daily discharge rate but a difference in daily detections was observed between treatment groups, consistent with the results without the effects of discharge (see above).

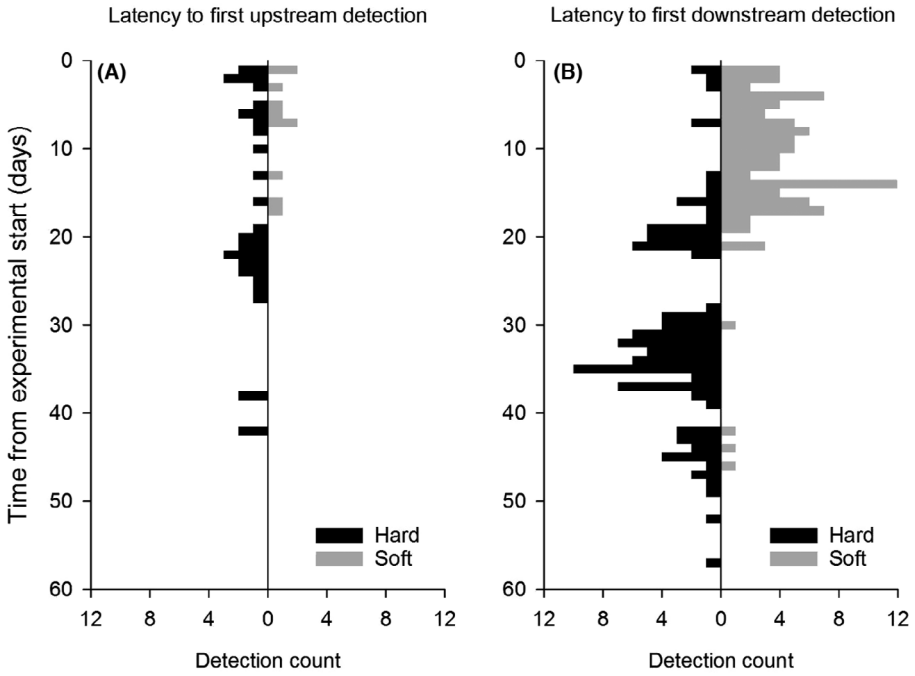

FIGURE 1. Plot of unique detection count (each count represents one unique fish detected) by latency (in days) of detection from time of release. Panel **(A)** shows the detection count at the upstream antenna, and panel **(B)** shows detection count at the downstream antenna. The hard-release detections are shown in black, and soft-release detections are shown in gray.

Overall, the Atlantic Salmon from both treatment groups were detected significantly more often during the night (73%, $n = 170$ of 232) than during the day (27%, $n = 62$ of 232), even when accounting for the proportion of daylight (47%) and darkness (53%) hours ($\chi^2 = 38.29$, df $= 1$, $n = 232$, $P < 0.001$, Figure 2). The hard-release fish dispersed at a higher proportion during the day (31%, $n = 40$ of 131) than did the soft-release fish (22%, 22 of 101), but the difference between daylight and darkness detections was not significant ($\chi^2 = 1.80$, df $= 1$, $n = 232$, $P = 0.18$, Figure 2).

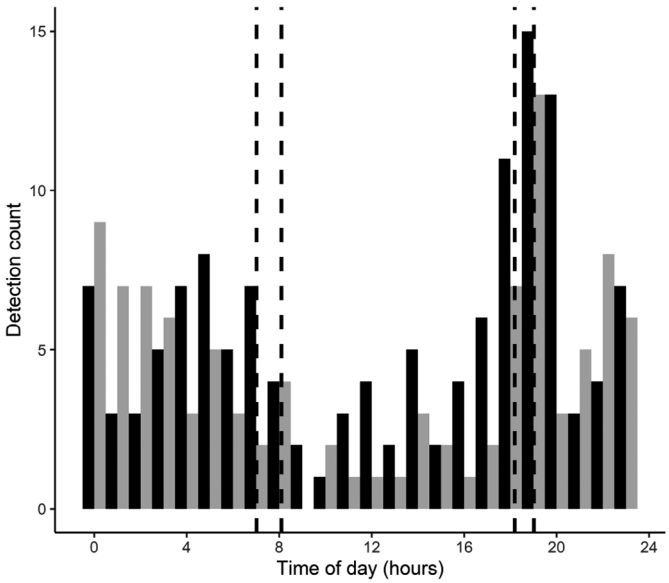

FIGURE 2. Histogram of unique dispersal detection count summed for each hour of the day across the study period. The black dashed lines represent the range of nautical twilight times across the study period (57 d). The black bars represent hard-release detections, and gray bars represent soft-release detections.

DISCUSSION

In this study we found that that the proportion of individuals dispersing upstream and the time to disperse after release for juvenile Atlantic Salmon were affected by release tactic. Soft-release fish were less likely to move away from the release site, and when they did move, they moved downstream earlier and were less likely to move upstream compared with hard-release fish. The hatchery-reared Atlantic Salmon in our study were more likely to disperse both up- and downstream during the night compared with during the day—we did not, however, find a significant difference between the two release groups in the time of day when they were detected dispersing. Taken together, these results suggest that the soft-release tactic does affect the short-term dispersal and potentially the spatial distribution of hatchery-reared Atlantic Salmon in the wild.

The observed stronger site fidelity—less dispersal away from release site—for acclimatized fish is in line with previous acclimatization studies in salmonids (Cresswell and Williams 1983; Kaya and Jeanes 1995; McCormick et al. 1998; Jonssonn et al. 1999; Eisenhauer et al. 2021). Previous studies have found that wild European Grayling are less likely to disperse from release sites than are their hatchery-reared conspecifics (Turek et al. 2010). Additionally, acclimatization prior to release was found to reduce dispersal rates for a number of salmonids (Kaya and Jeanes 1995; Jonssonn et al. 1999). The benefits of acclimatization have been attributed mainly to the recovery from stressful handling and transportation that can affect swimming performance (Maule et al. 1988), orientation (Kruzynski et al. 1994), predator avoidance (Gadomski et al. 1994; Olla et al. 1995), and feeding efficiency (Pickering et al. 1982). Recovery from stress depends on the type, intensity, and duration of the stressor (Olla et al. 1995; Zhang et al. 2020). Recovery from transport stress can take hours (Iversen et al. 1998) to weeks (Vieira Madureira et al. 2019). Enrichment can, however, reduce the stress response of fish (Näslund et al. 2013; Rosengren et al. 2017; Zhang et al. 2020) and time needed for recovery after stress in laboratory experiments. These effects, combined, could explain both the smaller number of soft-released fish moving away from the release site and the earlier downstream dispersal exhibited by soft-release fish in our study. It is possible that the soft-release fish in our study benefitted in terms of energy consumption and use from remaining at or near the release site, which could ultimately lead to greater survival, and the earlier downstream dispersal could be explained as an earlier dispersal to find more suitable habitat when faced with competition for territory near or at the release site (Höjesjö et al. 2016). More targeted studies should investigate growth rates, survival, microhabitat use, and competition between hard- and soft-release fish in the wild.

We found that hatchery juvenile Atlantic Salmon that were hard-released dispersed upstream more often than soft-release fish. The main direction of dispersal for wild Atlantic Salmon parr and smolts is naturally downstream (Foldvik et al. 2012), though parr can exhibit upstream dispersal in early summer to fill habitat that is voided by smolts beginning their downstream migration (Armstrong et al. 1997). The results of the latter study suggest that the early downstream dispersal of soft-release fish that we observed may have served as a stimulus for the hard-release fish to move upstream. Alternatively, stress-induced disorientation (Kruzynski et al. 1994) may have resulted in hard-release fish displaying an unnatural upstream dispersal tendency. Regardless of the mechanism, the results suggest that soft-release tactics may engender more appropriate movement behavior after release compared with conventional hard-release tactics.

The activity levels of salmonid fishes are highly responsive to predation risk and food availability (Metcalfe et al. 1999; Orpwood et al. 2006) and vary with season and water temperature (Roy et al. 2013). The findings from the current study support previous findings that during the autumn season, Atlantic Salmon parr were more active during the night than during the day (Roy et al. 2013; Dodd et al. 2018). Although Atlantic Salmon parr predominantly forage during daylight, relying heavily on vision to successfully forage on drifting prey (Keenleyside 1955), the autumnal nocturnal activity can be explained by reduced energy requirement and increased predation pressure (Roy et al. 2013). We predicted here that the hard-release fish, constrained to suboptimal habitat, would shift to daytime feeding to secure sufficient energy sources. However, we did not find any significant difference in activity levels relating to photoperiod between the two release groups. Although overall day/night activity levels did not differ between the release groups, further investigations with higher spatial acuity are required to more accurately address whether release tactic or stress levels affect foraging behavior in relation to photoperiod. Because a large portion of fish from both release groups remained at the release site, it is possible that the spatial distributions of feeding overlap but that the temporal aspect of feeding differs, benefitting one group over another.

Large-scale implementation of soft-release tactics (e.g., instream acclimatization prior to release) has yet to be fully adopted by fisheries management, partly because such methods require more effort than do traditional hard-release methods. However, a recent soft-release Chinook Salmon initiative, conducted by the OMNRF (2019 annual report of the Lake Ontario Management Unit), suggests that agencies may be willing to invest more into the release of hatchery-reared fish, provided that it improves survival. The OMNRF pilot project allows for hundreds of thousands of fish to be soft-released in stocking net pens at a time near the mouth of the river near Lake Ontario. Compared with hard-released fish, soft-released fish grow faster, survive better, and have a greater degree of site fidelity (Connerton et al. 2017). However, these studies observed only long-term straying (sampling occurred once per year over a 5-year period and included a large number of stocking events) but in some cases showed a 70-fold increase in straying of hard-release compared with soft-released Chinook Salmon. Still, this initiative demonstrates the capacity for management to implement soft-release tactics on a large scale. Based on the success of the Chinook Salmon soft-release program, OMNRF is now planning to test a soft-release strategy for stocking hatchery-released Atlantic Salmon that are destined for reintroduction to Lake Ontario. A longer-term comparison of lifetime reproductive success (survival and spawning success) among fish that are hard- and soft-released in the coming years will

undoubtedly determine the value of the additional effort that is required to conduct soft-release efforts.

ACKNOWLEDGMENTS

Funding for this research was provided through an NSERC Discovery Grant and NSERC Strategic Project Grant (to T.E.P. and B.D.N.). We are grateful for the assistance of Kevin Loftus (OMNRF Fish Culture), Jake Ruegg, and the rest of the staff at the Normandale Fish Culture Station, as well as William Sloan and the staff at the Codrington Fisheries Research Facility. We also would like to thank Ashley Watt, Ryland Corchis-Scott, Colin McFarlane, Mohamed ElShikh, and Colby Nolan for their help with PIT tagging, fish transport, and deploying the equipment used in this study. There is no conflict of interest declared in this article.

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