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Efficacy of releasing captive reared broodstock into an imperilled wild Atlantic salmon population as a recovery strategy

J. W. Carr*†, F. Whoriskey* and P. O'Reilly‡

**Atlantic Salmon Federation, P. O. Box 5200, St Andrews, New Brunswick, E5B 3S8, Canada and ‡Department of Fisheries & Oceans, Bedford Institute of Oceanography, 1 Challenger Drive, Dartmouth, NS, B2Y 4A2, Canada*

The strategy of releasing captive reared adult Atlantic salmon *Salmo salar* into the Magaguadavic River, New Brunswick, Canada, to spawn, was not an effective tool for rebuilding a seriously depressed wild population. The fish were first generation progeny from wild parents, and had spent their entire lives in captivity in either sea or fresh water. No differences in movement or behaviour patterns were observed between freshwater and seawater reared groups. Fish released in the lower river early (35 to 80 days prior to the natural spawning period) moved into a lake low in the system, and most stayed there near the commercial hatchery where they had been reared from egg to smolt. During the spawning season, none moved to the upper river reaches where most spawning habitat exists. Most broodstock released in the upper river reaches near the time of spawning stayed there during the spawning period. The following year few to no Atlantic salmon fry were found, and most appeared not to be offspring of released adults.

Key words: Atlantic salmon; captive-reared; microsatellite; restoration; sonic tracking.

INTRODUCTION

Atlantic salmon *Salmo salar* L. populations in the Bay of Fundy region have collapsed since the 1980s and many are now near the point of biological extinction (Amiro, 2003; DFO, 2003). Many factors could be contributing to their decline including increases in predator populations, changes in oceanographic conditions, freshwater habitat degradation (*e.g.* low pH, pollution, dams and introduced species), and impacts from the Bay of Fundy's commercial Atlantic salmon aquaculture industry, although the exact causes are not known at this time (O'Neil *et al.*, 2000; Cairns, 2001).

The Magaguadavic River's (Fig. 1) wild Atlantic salmon run has fallen from *c.* 1000 fish in the 1980s to <10 fish in 2002 and 2003. In response to the decline, stakeholders implemented a recovery programme for Atlantic salmon in the river in 1996. This group is composed of representatives from conservation and angling groups, the salmon aquaculture industry, and federal and provincial governments.

†Author to whom correspondence should be addressed. Tel.: +1 506 529 1385; fax: +1 506 529 4985; email: jonwcarr@nbnet.nb.ca

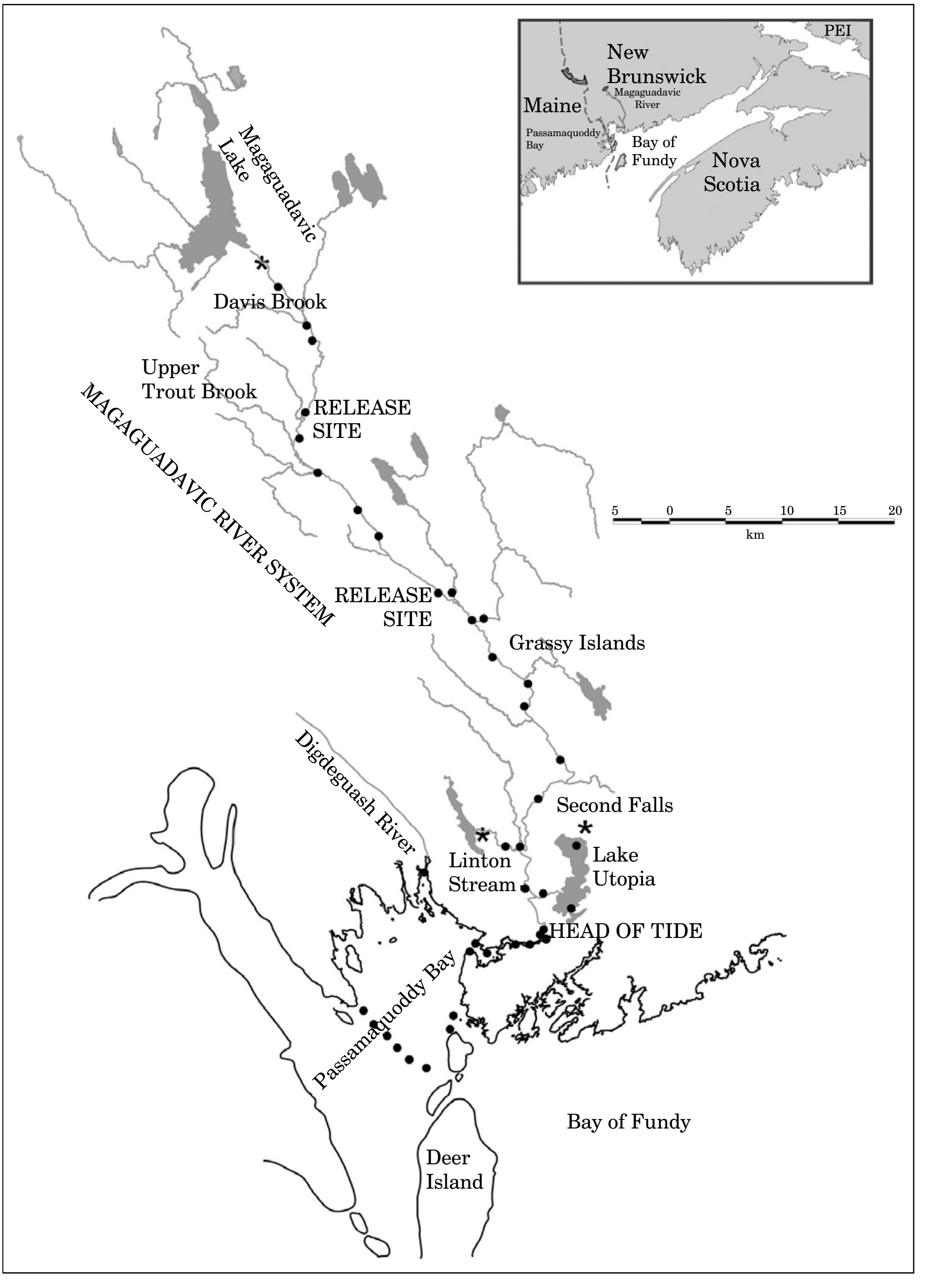

FIG. 1. Map of the Magaguadavic River showing the release sites (two in upper reaches of the river and one at head of tide), VR2 receiver locations (•), and the three commercial salmon hatcheries (*).

The immediate objective is to maintain the river's wild strain through live gene banking and supportive breeding, while research is conducted to identify, and if possible, mitigate principle factors in the decline.

The release of native animals from live gene banks to the wild is the core of the recovery programmes for many species (Griffith *et al.*, 1989), including salmonids (Kocik & Brown, 2002; Gibson *et al.*, 2003; Montgomery, 2003). While the efficacy of artificially reared salmonids in meeting conservation imperatives for wild populations has been questioned, it is clear that in some circumstances the use of these animals can be greatly beneficial (Utter, 1998; Levin *et al.*, 2001; Independent Scientific Advisory Board, 2002; Orr *et al.*, 2002; Miller & Kapuscinski, 2003).

The advantage of artificial rearing lies primarily in greatly minimizing juvenile mortality, which permits managers to rapidly develop a large pool of fishes for conservation uses. The risk is that they may become behaviourally and physiologically conditioned to captive conditions. Salmonids reared in captivity for several generations also become adapted to hatchery environments, and may be maladapted for survival and reproduction in the wild. Often, managers attempt to minimize adaptation to hatchery conditions by releasing fishes into the wild at an early life stage (Kapuscinski & Jacobson, 1987; Kincaid, 1993; Utter, 1998; E.T. Baum, T. King & J. Marancik, pers. comm.). The release of captive reared adult salmonids into river habitats to select their own mates and spawn naturally, however, is an alternative strategy.

Recent work with Atlantic salmon suggests that the release of mature adults may be an effective restoration strategy. In Newfoundland, the most successful introductions of self-sustaining runs of Atlantic salmon to previously unoccupied habitats were achieved by translocating mature adults and allowing them to spawn naturally in river habitats (Mullins *et al.*, 2003). Johnsen & Hvidsten (2002) similarly reported a high rate of spawning success from wild adult Atlantic salmon transplanted to a previously uninhabited Norwegian river. Dempson *et al.* (1999) captured ocean migrant smolts, reared them to the adult stage in sea cages, and released them back to the ocean just prior to spawning time at some distance from their home river. The fish survived well in the cages, and the majority homed back to their natal river, suggesting to the authors that the release of Atlantic salmon adults could be an attractive restoration tool. In the above examples, released fish spent much of their life cycle in the wild.

The Magaguadavic River is located near the heart of the North American east coast Atlantic salmon cage culture industry, and three commercial Atlantic salmon freshwater hatcheries are located in the river drainage (Fig. 1). Fish farmers have suitable culture facilities and considerable experience in rearing Atlantic salmon to the adult stage in sea cages. While translocation of wild adults does appear to successfully bolster spawning in Atlantic salmon populations, it is not known whether wild strain fish reared for their entire life cycle in captivity and released to spawn as adults, could do the same.

In collaboration with members of the New Brunswick Salmon Growers Association and the Department of Fisheries and Oceans, an experiment was conducted to evaluate the behaviour and spawning success of Magaguadavic origin Atlantic salmon reared in captivity through the majority of their life cycle, and then released to their native river just months prior to their normal spawning time. One experimental group was first reared in fresh water to the smolt stage, then transferred to sea cages where they matured in sea water, while the other group was reared entirely in fresh water.

Fish were reared in both fresh water and sea water because groundwater hatcheries are more secure from diseases than are marine facilities. Freshwater sites may be more desirable as gene banking facilities providing the freshwater reared animals behave as normal anadromous fish. The behaviour of gene-bank fish released to the river at the normal arrival time for wild fish was also documented. Early releases would reduce vulnerability to losses caused by hatchery failures, and synchronize the maturation cycle with temperature regimes in the river. These benefits, however, can only be realized if the fish show appropriate upstream migratory behaviour once released.

Thirty Atlantic salmon were fitted with sonic tags to document fish movements and any associations they might exhibit with the other fish. The specific objectives were to: (1) assess whether fish would travel together when released in small groups, (2) assess movement rates and destinations in the river of seawater *v.* freshwater reared fish, (3) compare movement and behaviour of early season *v.* late season releases, (4) determine if similar fractions of the fish released low or high in the river ended up on the spawning grounds at spawning time, (5) determine if members of the same family would end up on the same spawning grounds, possibly promoting inbreeding and (6) determine if spawning from the captive reared released adults increased juvenile Atlantic salmon densities in the river.

MATERIALS AND METHODS

STUDY AREA

The Magaguadavic River originates in Magaguadavic Lake in south-west New Brunswick, Canada, and flows south-easterly 111 km to Passamaquoddy Bay, an offshoot of the Bay of Fundy (Fig. 1). There are 103 named tributaries and >55 lakes within the 1812 km^2 river drainage. A 13·4 m high hydroelectric dam is located at the head of the tide. A pool and weir fishway bypasses the dam for upstream fish passage. All fish ascending the river from seawater must pass through a collection trap in the fishway. A downstream fish passage facility is also located at the dam. The river's headpond above the dam spans 18 km upstream to a small waterfall, which is accessible to upstream fish passage during most flows (Second Falls, Fig. 1). Lake Utopia empties into the lower part of the headpond *via* a natural canal (Fig. 1). The Magaguadavic system supports a sport fishery for landlocked Atlantic salmon, brook trout *Salvelinus fontinalis* (Mitchill) and introduced smallmouth bass *Micropterus dolomieui* Lacepède. The sport fishery for anadromous Atlantic salmon has been closed since 1992 because of the precipitous declines in the run.

Complete counts of the river's Atlantic salmon run are made in the fishway trap at the head of tide dam. Wild fish ascend the river from June to November. Spawning occurs in the river from late October to mid November. Most of the nursery habitat is located in the upper two-thirds of the drainage. Wild Atlantic salmon spend 2 to 4 years in the river before migrating to sea as smolts.

FISH ORIGIN

Atlantic salmon used in this study were first generation progeny of wild Magaguadavic parents (three females and four males) collected in 1998. The seven fish composed 23% of the total wild Atlantic salmon returns to the river in that year. Sperm of four males was used to fertilize the eggs from each of the three females. Thus the juveniles resulting from these matings were full sibs, half sibs or unrelated. Eggs were reared to the smolt stage at the Heritage Salmon commercial hatchery located near Lake Utopia (Fig. 1). Subsequently, the smolts were divided and fish were reared to adults in either fresh water or sea water. Freshwater rearing occurred at the Department of Fisheries and Oceans Mactaquac Biodiversity Facility. Seawater rearing occurred at two sites. Initially the fish were reared in commercial Atlantic salmon sea cages made available through the New Brunswick Salmon Growers Association in the Bay of Fundy for 6 months. Due to a disease outbreak in neighbouring areas, these fish had to be transferred to seawater tanks at the Huntsman Marine Science Center in St Andrews, New Brunswick, for the final months of rearing. All captive reared progeny were individually tagged (external Carlin or internal PIT), and a non-invasive tissue sample was extracted from the pelvic fin for DNA pedigree analysis.

SONIC TAGGING

V16-4H-R04K coded ultrasonic pingers (65 mm length × 15 mm diameter, and 26 g; produced by Vemco Limited, Shad Bay, Nova Scotia, Canada) were used to tag the Atlantic salmon. Pingers had a frequency of 69 kHz, minimum and maximum off delays of 20–69 s, and a minimum expected life of 570 days. Atlantic salmon were anaesthetized in clove oil ($40\,mg\,l^{-1}$). Fork lengths (L_F) were determined, and tags were surgically implanted in the peritoneal cavity. Germex was used to sterilize all surgical tools, sutures and pingers. Furacin was employed to clean the ventral surface of the fish prior to making a 25 mm mid-ventral incision beginning 15 mm anterior to the pelvic fins. Three to four sutures (4-0 Ethilon black monofilament nylon with FS-2 circular cutting needle) were applied to close the incision after tag insertion and a tissue cement (Vetbond) was used to seal the incision and stitches. Furacin was sprayed on the closed incision. Fish recovered in <10 min from the anaesthetic. The Atlantic salmon were monitored for a minimum of 7 days before being released.

RELEASE GROUPS

A total of 30 sonically tagged captive reared Atlantic salmon broodstock (15 each from freshwater and seawater sources) were released in 2002 into the Magaguadavic River during three stages. The first two stages were 'early releases' (stage one: 74–80 days, and stage two: 35–41 days in advance of the natural spawning period). The third stage was a 'late release' (near the time of the normal spawning period). Equal numbers of seawater and freshwater reared fish were released during each stage. Freshwater and seawater reared fish were randomly assigned to the designated release dates. All releases were separated by at least 2 days. In the early releases, a total of 20 sonic tagged fish were set free between 0800 and 1100 hours in fresh water at the head of tide dam (Fig. 1). These consisted of four (seawater reared) on 8 August, four (freshwater reared) on 10 August, one (seawater reared) on 12 August, one (freshwater reared) on 14 August, one (seawater reared) on 14 September, one (freshwater reared) on 16 September, four (freshwater reared) on 18 September, and four (seawater reared) on 20 September. The late stage consisted of five freshwater and five seawater reared sonic tagged Atlantic salmon released into the upper reaches (near spawning habitat) of the Magaguadavic River on 22 October (see Fig. 1).

In addition to the 30 sonic tagged fish, a total of 69 captive seawater reared fish were released in groups of five to 10 at eight different locations near spawning habitat in the Magaguadavic River drainage from 22 to 24 October 2002. The 69 Atlantic salmon were marked with Floy external tags (next to dorsal fin) that were colour coded for specific release locations. Seven wild anadromous Atlantic salmon had returned to the river in 2002 (26 July to 12 September). Before their release into the river, a non-invasive tissue sample was taken from each experimental and wild fish to permit later genetic profiling.

STATE OF SEXUAL MATURATION

The state of sexual maturation for the 20 sonic tagged Atlantic salmon released in the lower river reaches 35 to 80 days prior to the natural spawning period could not be determined by external features, as these had not yet developed. Of the 10 sonic tagged fish released in the upper reaches near the time of spawning, eight, four reared in fresh water and four reared in sea water, were sexually mature, as evidenced by obvious external secondary sex characteristics (*e.g.* hooked lower jaw in males and round ventral surface with swollen vent in females). At the time of release, only 45 of 69 Floy tagged fish reared in sea water exhibited obvious external signs of sexual maturation.

TRACKING

Movements of sonic tagged fish were monitored by positioning submersible receivers (VEMCO VR2 receiver) at strategic locations in the river (Fig. 1). Each receiver had a built-in omni directional hydrophone with data logging components programmed to decode pinger tag number and date and time of each detection. Weekly active searches for tagged fish was also performed (16 August to 12 November 2002) using boats equipped with VR60 receivers having either directional or omnidirectional hydrophones. The position of each Atlantic salmon on each date, detected from either active searches or fixed monitoring units, was plotted on National Topographical Series 1 : 50 000 maps (Department of Natural Resources, New Brunswick, Canada). Water temperatures (Vemco TR minilogs) were recorded in Lake Utopia and at the release sites during the study.

One freshwater reared (released 8 August) and one seawater reared (released 10 August) fish were not relocated following their release. These Atlantic salmon were omitted from the analysis. Lost signals may have been due to tag failure, mortality or predation.

Overall, the L_F of the sonic tagged seawater reared Atlantic salmon were significantly larger than the freshwater reared fish (Mann–Whitney *U*-test, $P < 0{\cdot}01$) (Table I). The L_F of the early released freshwater and seawater reared fish were similar (Mann–Whitney *U*-test, $P > 0{\cdot}12$) (Table I), however, late released freshwater reared fish were significantly smaller than the seawater reared fish (Mann–Whitney *U*-test, $P < 0{\cdot}01$) (Table I).

ASSESSMENT OF SPAWNING CONTRIBUTION

High water discharge prevented visual observations of sonic and Floy tagged Atlantic salmon during the natural spawning period in 2002 (Fig. 2). The natural spawning period for 2002, based on water temperature profiles, was estimated to be from 28 October to 24 November. In 2002, the mean water discharge near the later stages of the natural spawning period, and during post spawning times, was generally higher than the 10 year average for the river (Fig. 2). In 2003, electrofishing surveys for Atlantic salmon fry were conducted to evaluate the spawning contributions from stocked adults in 2002. Efforts were focussed in nursery areas to which sonic tagged fish were tracked, or those

TABLE I. Total numbers and median, minimum and maximum fork lengths of the sonic tagged seawater and freshwater reared captive Atlantic salmon broodstock for early, late and combined release groups that were actively tracked in the Magaguadavic River

			L_F (cm)		
Release group	Rearing source	*n*	Median	Minimum	Maximum
Early	Sea water	9	80·9	51·8	86·4
	Fresh water	9	75·0	64·0	82·3
Late	Sea water	5	79·5	73·0	85·2
	Fresh water	5	64·0	58·7	70·7
Combined	Sea water	14	79·7	51·8	86·4
	Fresh water	14	70·6	58·7	82·3

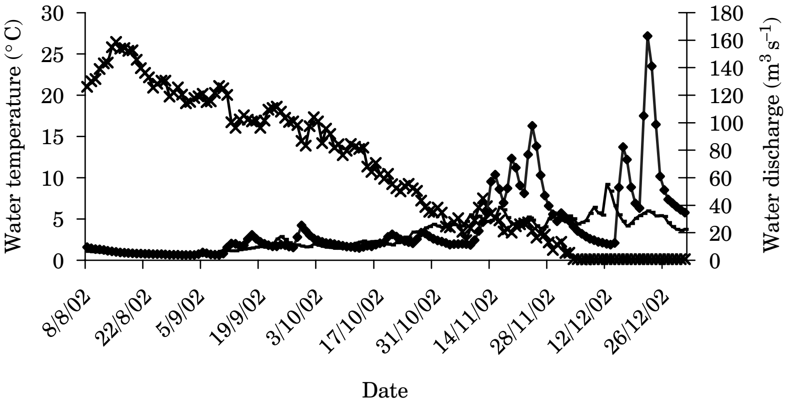

FIG. 2. Mean daily water temperature (✕) and discharge (◆, 2002; ■, 10 year mean) for the Magaguadavic River during the study period. The natural spawning period for 2002 was from 28 October to 24 November, based on water temperature profiles.

near the sites where the 69 additional Floy tagged fish were released near the time of spawning. One-pass electrofishing was done in various riffle habitats in the river's main stem from the mouth of Davis Brook to Grassy Islands (Fig. 1). A canoe was used to access most of these sites. As well, accessible riffle habitat sites were sampled in 10 different tributaries. Captured Atlantic salmon fry were anaesthetized, measured, and a sample of tissue taken before release for microsatellite and subsequent parentage analyses.

MICROSATELLITE ANALYSIS

Between 5 and 25 mg of tissue was sampled from each individual (captive reared broodstock, wild returning anadromous Atlantic salmon and wild captured juveniles), and preserved in 1 ml of 95% ethanol. Tissue was digested in a solution of 2 mg ml^{-1} of proteinase K, and purified using Qiagen DNeasy 96 well extraction plates under conditions specified by the manufacturer. Genetic variation was surveyed at six highly polymorphic microsatellite loci, *Ssa197*, *Ssa202* (O'Reilly *et al*., 1996), *SSspG7*, *SSsp1605*, *SSsp2215* and *SSsp 2210* (E. Verspoor, unpubl. data; genbank submission numbers AY081813, AY081812, AY081810, AY081806, respectively). Each locus was amplified individually using an MJ Research Engine Dyad Thermal Cycler. Reactions were carried out in 10 ul volumes, in 50 mM KCl, 20 mM Tris pH 8·4, 0·2 mM each dNTP, 0·5 units Taq DNA polymerase and a locus-specific concentration of labelled and unlabelled primer. For loci *Ssa197*, *SSspG7*, *SSsp1605*, *SSsp2215*, *SSsp 2210* and *Ssa 202*, labelled and unlabelled primer concentrations were 0·05, 0·05, 0·05, 0·05, 0·07 and 0·3 μM, respectively. Thermal cycling conditions were as follows: one cycle of 94° C for 2 min; three cycles of 94° C for 1 min, 58° C for 30 s, 72° C for 30 s; 35 cycles of 90° C for 30 s; 58° C for 30 s, 72° C for 30 s; one cycle of 72° C for 15 min. Following amplification, the PCR product for each locus was diluted with deionized formamide, and 0·9 ul from each combined with a further 2·3 ul of formamide and 0·05 ul of Amersham MegaBACE ET 400-R size standard. This cocktail was then denatured, and loaded onto a 96 lane MJ Base Station Fragment analyser (MJ Bioworks) for detection and sizing. Two identical samples were run on every gel, and *c*. 15% of all samples, from strategic locations, were run twice, to (1) quantify within and between gel variance in allele size estimates and (2) to detect the occurrence of most kinds of sample placement errors (*e.g*. duplications of individual samples and displacement of downstream samples, inversion of strip tubes and inversion of plates). Allele sizes were assigned to raw fragment length estimates using algorithms incorporated into an Oracle database programme and information on the distribution of raw allele sizes for each allele, at each loci, obtained from multiple previous runs.

PARENTAGE ANALYSIS

Microsatellite genotype profiles of the 32 0+ year juveniles captured in 2003 were compared to genotype profiles from all known putative parents, including the seven wild anadromous Atlantic salmon that ascended the river in 2002, and all captive reared adults that were released into the Magaguadavic River that year. Individual adults (wild or captive reared) that did not share at least one allele at two or more loci with a particular juvenile were automatically excluded as putative parents. In cases where individual adults shared one or more alleles at all but a single locus, the non-matching genotype was re-inspected in both the adult and the juvenile to confirm original allele assignments. Adults that had one or more alleles in common at all six loci with individual juveniles were considered to be potential parents, although this sharing of alleles may also occur by chance between unrelated adult-juvenile combinations.

RESULTS

LOWER RIVER (EARLY) RELEASES

Early release groups of sonic tagged Atlantic salmon did not travel together. Instead, they rapidly separated, and no patterns of synchronous receiver detections of two or more fish as they moved upstream to their resting point were recorded. In the subsequent analyses, all fish released in groups were treated as individuals.

None of the 18 sonic tagged Atlantic salmon from the early release groups moved upstream to the headwater spawning areas. Instead, all travelled to Lake Utopia (Fig. 1). It took sonic tagged fish 1 to 64 days to first enter the lake (Table II & Fig. 3). No significant differences were observed between the freshwater and seawater reared fish for both time to reach the lake and for residence time in the lake (Mann–Whitney *U*-test, $P > 0{\cdot}11$) (Table II). Movements of the tagged Atlantic salmon were, however, variable (Fig. 3). Some fish moved directly into the lake, whereas others moved throughout the headpond before entering the lake, with some of the latter fish travelling in and out of the lake (Fig. 3). Seawater tagged fish subsequently spent less time in the lake (median days = 84) compared to freshwater reared fish (median days = 171) (Table II).

After the tagged Atlantic salmon entered the lake, they congregated near the discharge pipe of a commercial Atlantic salmon hatchery where they had been reared from egg to smolt (Fig. 1). Residence time in the lake for sonic tagged fish ranged from 3 to 298 days (Table II). During the latter stages of the natural spawning period, three Atlantic salmon (two seawater and one freshwater reared) left the lake and were detected in a small tributary where some Atlantic salmon reproduction had been documented in the past (Linton Stream, Fig. 1).

TABLE II. Total fish numbers, and median, minimum and maximum number of days it took to enter the Lake Utopia, and the time spent in the lake, for sonic tagged seawater and freshwater reared captive Atlantic salmon broodstock from the early release groups

		Number of days to lake			Number of days in lake		
Rearing source	*n*	Median	Minimum	Maximum	Median	Minimum	Maximum
Sea water	9	9·0	2	64	84·0	12	228
Fresh water	9	5·0	1	34	171·0	3	298

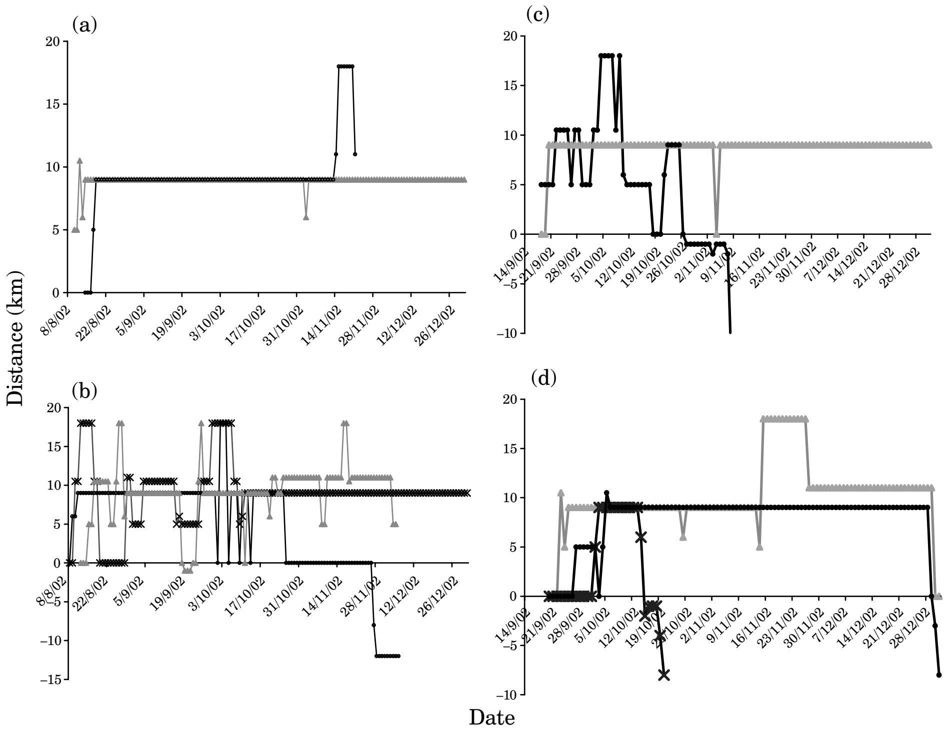

FIG. 3. Distances moved upstream from the head of tide (distance = 0 km) for the early releases of sonically tagged captive reared Atlantic salmon broodstock to the Magaguadavic River. Negative distances are measured into the estuary from the head of tide. Individual movements are given for (a) ($n = 2$) and (c) ($n = 2$) freshwater and (b) ($n = 3$) and (d) ($n = 3$) seawater reared fish. Movements of the tagged fish that stayed near the hatchery after entering the lake (during the 2002 tracking period) are not shown. Lake Utopia is 9 km upstream from the head of tide.

UPPER RIVER (LATE) RELEASE GROUP

No differences in movements were observed between the freshwater and seawater reared groups. Most (nine of 10) fish either held position or moved downstream from their respective release sites during the natural spawning period (Fig. 4). The only fish that moved >10 km upstream from its release site was a sexually immature freshwater reared fish (Fig. 3). The only sexually immature seawater reared fish remained near its release site throughout the study period.

Eighty per cent (eight of 10 fish) of the sonic tagged Atlantic salmon remained in the upper river reaches during most of the natural spawning period (28 October to 24 November 2002, based on water temperature profiles) (Fig. 2). Only two (20%) of the sonic tagged Atlantic salmon (one sexually mature individual from each rearing source) moved to the lower river reaches shortly after release (before the natural spawning period) (Fig. 4). No sonic tagged full or half siblings were detected in the same spawning habitat throughout the study period.

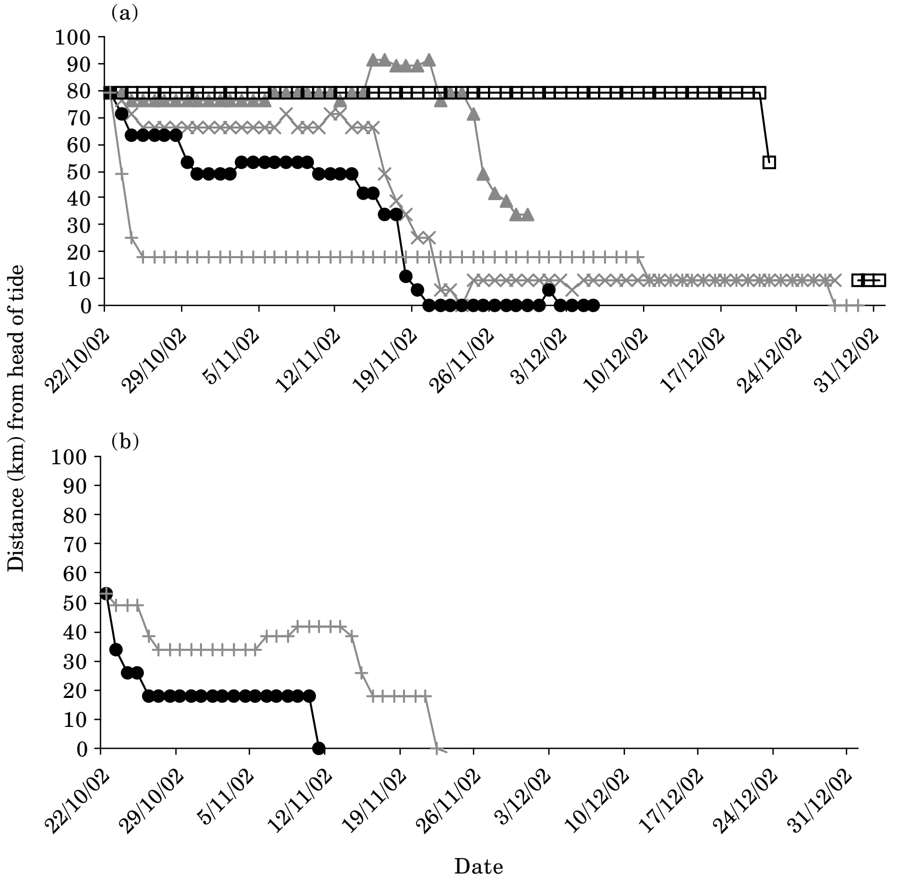

FIG. 4. Distances moved upstream from the head of tide (distance = 0 km) for the late releases of sonically tagged captive reared Atlantic salmon broodstock to the upper reaches of the Magaguadavic River. Individual movements are given for (a) freshwater and (b) seawater reared fish (▲, immature; ×, ▭, ●, +, mature). Movements of tagged fish that remained near their initial release sites are not shown.

FINAL TAGGED FISH POSITIONS

Fifty per cent of the sonic tagged Atlantic salmon eventually migrated to sea during the tracking period (Table III). Equal proportions left the river during autumn and spring (Table III). Seaward migrants were last detected either going over the dam, at the mouth of the Magaguadavic River, Passamaquoddy Bay, Digdeguash River estuary or in the Bay of Fundy (see receiver locations in Fig. 1). Only two fish (one each reared in sea water and fresh water) left the river prior to the natural spawning period (Fig. 3). One of those fish was detected at the mouth of the Digdeguash River during the latter stages of the spawning season (Fig. 1). Signals from the other 50% of sonic tagged Atlantic salmon were last detected in the river system (three in the upper river, three in the headpond and eight in Lake Utopia) (Table III). No additional signals were detected from the sonic tagged fish in the river system after June 2003.

TABLE III. The final positions (June 2003) of early, late and total releases of sonically tagged captive reared Atlantic salmon broodstock

Release group	Upper river	Lake Utopia	Head pond	Sea	
				Autumn	Winter–spring
Early	0	6	3	4	5
Late	3	2	0	3	2
Total	3	8	3	7	7

SPAWNING CONTRIBUTIONS OF CAPTIVE REARED ADULTS

High water discharge prevented visual observations of sonic and Floy tagged Atlantic salmon during the natural spawning period (Fig. 2). Extensive electrofishing surveys conducted in 2003 yielded few or no Atlantic salmon fry at all sites. Microsatellite genotype analyses of the 32 0+ year fry that were collected excluded nearly all captive reared and wild returning adults as possible parents. First, several common alleles at several microsatellite loci were present in the sample of juveniles but absent in all 99 captive reared adults (30 sonic and 69 Floy tagged fish) released into the river habitat. Second, genotype profiles of 29 of the 32 0+ year juveniles collected were not compatible (did not share at least one allele at all loci surveyed) with any of the sexually mature captive reared, or seven wild returning adults. Three juveniles collected from Linton Stream (Fig. 1) were compatible (did share one or more alleles at all loci surveyed) with Floy tagged captive reared released adults. One fry was compatible with a captive reared sexually mature female Atlantic salmon that had been released at a site 60 km away from Linton Stream (Upper Trout Brook, see Fig. 1). Another juvenile was compatible with a sexually mature male Atlantic salmon that was released in Upper Trout Brook (Fig. 1). The third fry was compatible with a captive reared mature male Atlantic salmon that had been released in the river at the head of tide (Fig. 1).

DISCUSSION

In this study none of the sonic tagged fish released in small groups prior to spawning travelled together, nor did any move to the upper river reaches. Shoaling and schooling in fishes have been shown to confer a number of advantages, including the reduction of individual and group predator vulnerability (Pitcher, 1986).

No behavioural or movement differences were found between sonically tagged Atlantic salmon reared to the adult stage in freshwater and seawater environments. Should this technique work for other populations or species, however, the results suggest there is no penalty associated with rearing fishes in secure freshwater sites. A freshwater rearing environment (*e.g.* groundwater) is more secure from parasites and diseases than seawater rearing facilities, reducing the risk of losing gene bank fishes to these agents (T.R. Goff, S.F. O'Neil & T.L. Marshall, pers. comm.).

By releasing fish early and low in the system it might have provided them with an opportunity to adjust to the river and allow time for sexual maturation. Releasing fish early also reduces rearing costs and the risks of potential disease transmission in their captive environment. The sonically tagged fish released early and low in the river all moved into a lake situated in the lower part of the river and congregated near a hatchery discharge pipe. Only 16% (three of 18 fish) of those fish were detected in a spawning tributary low in the river system during the natural spawning period. Microsatellite genetic analyses determined that no fry collected by electrofishing in the same tributary 9 months later were offspring from any of those three sonic tagged adults. Two other fish from the early releases left the lake and moved to sea prior to the natural spawning period. One of those two fish was subsequently detected at the mouth of a neighbouring river during the spawning season. A potential disadvantage of the release of mature adults is that unintended hybridizations with neighbouring populations may occur. Increased straying occurs frequently among salmonids reared in captivity (Hansen *et al*., 1991; Quinn, 1993).

Most of the sonic tagged Atlantic salmon released near spawning habitat in the upper reaches close to the onset of the natural spawning period, stayed in those areas during the natural spawning period. Only 20% (two fish) moved to the lower river, both shortly after being released. No upstream movements were observed for the sexually mature fish. Instead they either held position or had a tendency to move slightly downstream. Johnsen & Hvidsten (2002) reported that wild adult Atlantic salmon transplanted to a previously uninhabited Norwegian river near the time of spawning held position and spawned close to the release site in two of the four tracking years.

Few to no salmon fry were detected in the upper reaches near sites where both sonic and Floy tagged Atlantic salmon were released 9 months earlier. G. Mackey & N. Brown (pers. comm.) reported low densities of young-of-the-year Atlantic salmon in Maine rivers after the stocking of captive reared adults. Atlantic salmon fry tend to show a minimal dispersal from spawning sites during their first summer after hatch (Egglishaw & Shackley, 1973, 1977; Gee *et al*., 1978; Beall *et al*., 1994; Crisp, 1995; Johnsen & Hvidsten, 2002). It is also possible, however, that the low fry numbers detected were due at least in part to other post-spawning causes (*e.g*. episodic weather events and predation).

All sonic tagged fish had either left the river or had died by the first summer after release. Similarly, no captive reared adult Atlantic salmon released in the St Croix River were found in the river 1 year after release (L. Sochasky & R. Spencer, pers. comm.). Fifty per cent of the tagged fish in the present study survived to move to sea, with equal proportions leaving in the autumn and winter-spring. Only two fish left the river before the natural spawning period. Other studies report that wild Atlantic salmon begin migrating downstream after spawning and move to sea in the autumn or spring (Heggberget *et al*., 1988; Bagliniere *et al*., 1990).

The lack of juvenile experience in the river may have been one reason for the limited movements and exploratory behaviour of the sonic tagged fish. Site familiarity learned as a juvenile is important for the timing of both river ascent and homing of adults (Jonsson *et al*., 1990; Heggberget *et al*., 1993). Sonic tracking of escaped sea cage reared aquaculture Atlantic salmon in the

Magaguadavic River in 1993 and 1994 found the fish to hold positions and move only short distances within the headpond (Carr, 1995; Carr *et al*., 1997*a*). Power & McCleave (1980) reported similar behaviour for hatchery-reared adult Atlantic salmon in the Penobscot River, Maine.

Anadromous Atlantic salmon rely on imprinting in fresh water to return to their natal river to spawn (Heggberget *et al*., 1988). The migration into Lake Utopia of all sonically tagged fish released at the head of tide may have been due to a homing tendency to the hatchery where they had been reared to the smolt stage. Whoriskey & Carr (2001) transplanted escaped aquaculture Atlantic salmon that were captured attempting to enter the Magaguadavic River, back to sea up to 50 km from the river. They also noted a homing tendency for some of the escaped aquaculture Atlantic salmon, with up to 22% (31 of 144 fish) of the transplanted fish returning a second time to the river, and some fish returning a third and fourth time when they were moved to additional locations. Whoriskey & Carr (2001) suggested that the fish that did home might have originated from one of the three major commercial Atlantic salmon hatcheries located on the river system, and that they may have imprinted to the Magaguadavic water.

Another possible explanation for the lack of upstream movement is that the early released fish failed to mature. The maturity status of the individuals at the time of initial release could not be determined, although 71% (82 of 116) of their siblings that were kept in freshwater tanks at Mactaquac during the spawning period did mature (T. Goff, pers. comm.). Similarly, the rate of sexual maturity for the 69 seawater reared Floy tagged fish we released on the spawning grounds near the time of spawning was only 67%. Also, G. Mackey & N. Brown (pers. comm.) reported that the low reproductive success of seawater reared Atlantic salmon released in Maine rivers during 2000 and 2001 was in part a result of a low rate of sexual maturation. Carr *et al*. (1997*a*) reported that high fractions of the escaped aquaculture Atlantic salmon annually entering the Magaguadavic River were sexually immature. Why these fish entered the river remains unclear.

Microsatellite genetic analysis was used to determine that 9% (three of 32 fish) of the Atlantic salmon fry collected in Linton Stream were compatible with single (one maternal, two paternal) sexually mature Floy tagged captive reared parents released the previous autumn. Possibilities for the other parent for each of those fry include precocious male parr or landlocked Atlantic salmon. It is likely that the Atlantic salmon fry with no parental matches are escapes from commercial Atlantic salmon hatcheries located within this drainage area.

Juvenile Atlantic salmon leakage from the commercial hatcheries within the Magaguadavic River system may pose a threat to the ecological and genetic structure of the river's Atlantic salmon population, especially if they survive and interbreed with wild fish in the river. Several authors have reported genetic and ecological threats to wild populations from escaped aquaculture salmonids (Hansen *et al*., 1991; Hindar *et al*., 1991; Hutchinson, 1997; Carr *et al*., 1997*b*; Fleming *et al*., 2000; McGinnity *et al*., 2003), and the problem has become more pronounced with the global decline in wild salmonid populations (Parrish *et al*., 1998).

The findings from the present study suggest that a low rate of spawning may have occurred among the captive reared released fish. G. Mackey & N. Brown (pers. comm.) reported that the stocking of captive adults reared in marine net pens yielded little reproductive success in Maine rivers. Fleming *et al.* (2000) found aquaculture Atlantic salmon released to the wild had only 16% the lifetime reproductive success of wild Atlantic salmon. By contrast, a study in 1994 reported a high rate of spawning success for captive reared Atlantic salmon broodstock released into the Big Salmon River, New Brunswick, Canada (Bruce, 1995). Those fish were first generation progeny of wild Big Salmon River parents, and were reared from egg to smolt in a hatchery. Smolts were reared to sexually mature adults in sea cages before their release (>300 fish) into the river near the time of spawning. Occasional observations showed that the captive releases produced redds, and mated with each other as well as with wild Atlantic salmon. The Magaguadavic River failure may be due to factors such as the presence of a commercial hatchery, a low rate of sexual maturation, and the genetic health of the fish used.

The strategy of rearing Atlantic salmon entirely in captivity, and then releasing them as adults into the Magaguadavic River to spawn naturally, was not an effective tool for rebuilding this population. More effective restoration strategies may include the use of in river egg incubation devices, and the release of Atlantic salmon at juvenile life stages, with minimal time spent in hatcheries. The small founding population (seven wild Atlantic salmon) used to rebuild the Magaguadavic wild population could lead to inbreeding and the accumulation of deleterious alleles if new recruits are not included in the recovery programme. In order to increase levels of genetic variation in this river, introduction of anadromous Atlantic salmon from a geographically proximate river is being considered. Further analysis is needed to identify the most suitable donor stock so that the risks of outbreeding depression and loss of local adaptation can be minimized.

Finally, Atlantic salmon restoration strategies need to be assessed on a river-by-river basis. Reisenbichler *et al.* (2003) discuss the uncertainties and trade-offs in restoring fish populations. These include whether to allow natural colonization or to introduce fish, which populations are most suitable for reintroduction, adequate amount of gene flow from other populations, appropriate levels of artificial propagation, the most suitable life stages for releasing stocked fish, and the minimum numbers released to maintain the population.

A method that works at one site may fail at another. Rigorous evaluation is needed so that conservation and restoration activities can be more effective at restoring depressed Atlantic salmon populations in the future.

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