

Migratory patterns of hatchery and stream-reared Atlantic salmon *Salmo salar* smolts in the Connecticut River, U.S.A.

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The timing of downstream migration and detection rates of hatchery-reared Atlantic salmon *Salmo salar* smolts and stream-reared smolts (stocked 2 years earlier as fry) were examined in the Connecticut River (U.S.A.) using passive integrated transponder (PIT) tags implanted into fish and then detected at a downstream fish bypass collection facility at Turners Falls, MA (river length 192 km). In two successive years, hatchery-reared smolts were released in mid-April and early May at two sites: the West River (river length 241 km) or the Passumpsic (river length 450 km). Hatchery-reared smolts released higher in the catchment arrived 7 to 14 days later and had significantly lower detection rates than smolts stocked lower in the catchment. Hatchery-reared smolts released 3 weeks apart at the same location were detected downstream at similar times, indicating that early-release smolts had a lower average speed after release and longer residence time. The size and gill Na^+/K^+ -ATPase (NKA) activity of smolts at the time of release were significantly greater for detected fish (those that survived and migrated) than for those that were not detected. Stream-reared pre-smolts (>11.5 cm) from four tributaries (length 261–551 km) were tagged in autumn and detected during smolt migration the following spring. Stream-reared smolts higher in the catchment arrived later and had significantly lower detection rates. The results indicate that both hatchery and stream-reared smolts from the upper catchment will arrive at the mouth of the river later and experience higher overall mortality than fish from lower reaches, and that both size and gill NKA activity are related to survival during downstream migration.

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Key words: gill Na^+/K^+ -ATPase; juvenile; migration; size; survival.

INTRODUCTION

Downstream migration is a critical life-history stage for all anadromous fishes. In salmonids, it has been established that river migration and ocean entry of smolts imposes a high level of mortality that has significant influences on adult populations and overall sustainability (Williams *et al.*, 2001; Thorstad *et al.*, 2012). Predators, prey availability and a variety of abiotic factors influence the levels of mortality that occur during this stage. In addition to the influence of predators, anthropogenic factors such as dams, climate change and pollutants can negatively influence smolt survival (McCormick, 2009; Marschall *et al.*, 2011). Anthropogenic influences are the likely cause of loss of Atlantic salmon *Salmo salar* L. 1758 populations in the

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southern portion of their range in North America and Europe and may be significant impediments to their conservation and restoration (Parrish *et al.*, 1998).

In North America, the historic southern distribution of *S. salar* extended as far south as the Connecticut River, the largest river in New England, U.S.A. In the 1800s, dam construction and habitat loss led to the extirpation of *S. salar* from most of the rivers in southern New England, including the Connecticut River (Rideout & Stolte, 1988; Gephard & McMenemy, 2004). For the last 40 years, an active restoration programme has been conducted in the Connecticut River, and included construction of fish passage, habitat restoration and stocking of juvenile *S. salar*. The stocking programme consisted of two major strategies: rearing of smolts in hatcheries followed by release just prior to downstream migration and the release of unfed fry into streams and rivers where they rear naturally for 1–3 years before migrating downstream as smolts (Gephard & McMenemy, 2004). These two strategies have been adopted by a large number of *S. salar* restocking programmes, and their proper management and evaluation requires an understanding of their stage-specific survival and differences in migratory behaviour and survival during downstream migration.

Downstream migration of smolts is part of a series of behavioural, morphological and physiological changes that are known as the parr–smolt transformation. These changes are generally thought to be adaptive for survival in seawater and thus critical to successful migration and ocean entry (Hoar, 1988). The freshwater parr stage has poor salinity tolerance, and the development of a high degree of salinity tolerance during smolt development is thought to be especially critical to early ocean survival. The timing of downstream migration is critical to survival and adult return rates (Thorstad *et al.*, 2012). This period for high survival is thought to consist of two major components: an ‘ecological smolt window’ driven by the optimum levels of biotic and abiotic factors that determine survival and a ‘physiological smolt window’ determined by environmental factors such as photoperiod and temperature that cue the timing of smolt development that leads to migration and high levels of salinity tolerance (McCormick *et al.*, 1998). While some environmental factors such as temperature will contribute to both smolt windows, the factors regulating each window are not the same and their asynchrony will result in reduced survival (McCormick *et al.*, 1998). Many aspects of smolt development are reversible, so the ‘physiological smolt window’ will be driven by environmental factors that promote both the development and loss of smolt characteristics. Understanding the interaction of migration and physiological changes during smolting will be important for understanding how migration timing affects survival. Whether smolts achieve a high level of survival in accordance with the ecological smolt window will to a large extent be determined by the timing and speed of migration. Furthermore, measurement of the underlying traits of salinity tolerance such as gill Na^+/K^+ -ATPase (NKA) activity of fish migrating in the wild may be useful for determining the effects of environmental factors on the timing of smolt development (Zaugg & Wagner, 1973; McCormick *et al.*, 2003).

Adult return rates of *S. salar* reared in hatcheries and released as smolts are generally (although not universally) lower than those for wild fish (Jonsson *et al.*, 2003; Poole *et al.*, 2003; Kallio-Nyberg *et al.*, 2004; Saloniemi *et al.*, 2004; Chittenden *et al.*, 2008; Buchanan *et al.*, 2010; Theriault *et al.*, 2010). A number of factors have been implicated in this difference, although to date no single factor has been clearly demonstrated. Poor neurological development and the absence of predators and live prey in the hatchery environment may lead to a variety of behavioural deficiencies that are

especially acute when fish are released just prior to downstream migration (Kihlslinger & Nevitt, 2006). Development of salinity tolerance and its underlying physiological mechanisms may be incomplete in hatchery fish compared to fish in the wild (Shrimpton *et al.*, 1994; Sundell *et al.*, 1998; Chittenden *et al.*, 2008; Serrano *et al.*, 2009). This may be due to inappropriate photoperiod or temperature cues or the influence of poor nutrition, crowding, disease or other aspects of the hatchery environment that are absent in the wild or in fish that are released into the wild early in their development (Brockmark *et al.*, 2007). There has been increasing reliance on fish released soon after hatching to minimize the negative effects of hatcheries (Gephard & McMenemy, 2004; George *et al.*, 2009). Understanding the difference in migration timing and physiological development of hatchery and stream-reared fish will be a useful approach to determining the factors that influence the apparently lower survival of hatchery smolts and provide tools for resource managers to improve returns of all fish.

This study was undertaken to compare migratory timing of hatchery and stream-reared fish. Also examined was the effect of timing and location of release on migratory timing and downstream detection rates. In addition, size and gill NKA activity of hatchery fish at the time of release were measured as potential predictors of migratory timing and downstream detection rates.

MATERIALS AND METHODS

HATCHERY-REARED FISH

In 2000 and 2001, *S. salar* were obtained from the White River National Fish Hatchery, Bethel, VT. Fish used in this study were age-1+ year smolts from the Connecticut River strain and were the F1 progeny of sea-run returns. Fish were initially reared in indoor fibreglass tanks before being transferred in the autumn to outdoor circular tanks. At each release date [13 April 2000 ($n = 163$), 2 May 2000 ($n = 183$), 19 April 2001 ($n = 150$) and 7 May 2001 ($n = 154$)], smolts > 14 cm fork length (L_F) were tagged with passive integrated transponders (PITs). After PIT tagging, fish were placed in 200 l circular tanks and allowed to recover in aerated water maintained at raceway temperature for at least 30 min, and then placed in insulated 1 m diameter tanks for transport *via* trucks and then released. Travel time to each release site was similar (2 h). The northern release site into the Passumpsic River in East Barnet, VT, was 0.8 km from the confluence of the Connecticut River at river length 451 km. The southern release site into the West River in Dummerston, VT, was 5.8 km from the confluence with the Connecticut River at river length 240.6 km. Discharge data were obtained from the USGS North Walpole (NH) gauging station on the Connecticut River, as this station was between the two release sites and therefore deemed most appropriate for being representative of the overall conditions experienced by each group. Temperature data were obtained from a LICOR model 1100 temperature probe (www.licor.com) placed in the Connecticut River 200 m above the detection station in Turners Falls, MA.

STREAM-REARED FISH

As part of the restoration programme in the Connecticut River, the progeny of sea-run and F1 domestic *S. salar* are released as unfed fry into tributaries throughout the catchment. In October and November 2000, *S. salar* parr that had been previously stocked as fry were captured by electrofishing in four tributaries of the Connecticut River. Captured fish were held in perforated live cages ($L \times W \times H$: 64 cm \times 45 cm \times 41 cm, with 1 cm diameter perforations every 5 cm) directly in the stream flow for up to 1 h until they could be processed for PIT tagging and release. Only parr > 11.5 cm were used, as this is the size threshold for subsequent smolt development based on a long-term data set from Smith Brook, VT (S. D. McCormick, unpubl. data). Fish

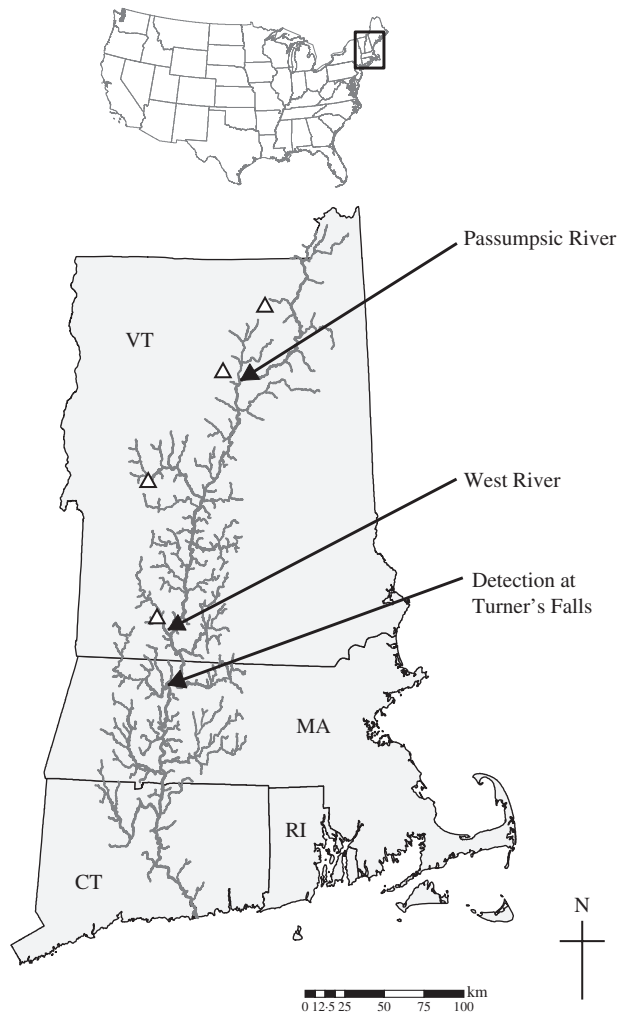


FIG. 1. Map of study areas in the Connecticut River catchment. \rightarrow , release sites of hatchery-reared *Salmo salar* at the West River (river km 240.6) and the Passumpsic River (river km 450.4) and the antenna location at the downstream bypass weir at Turners Falls, MA (river km 192.3). The tagging sites of stream-reared fish (Δ) in Vermont (autumn 2000) from north to south are: Paul's Stream, Joe's Brook, White River and Smith Brook. CT, Connecticut; MA, Massachusetts; RI, Rhode Island; VT, Vermont.

were held in live cages for at least 30 min to ensure complete recovery from the anaesthetic, and released throughout the electrofished area from which they were captured. Fish were captured within a 1 km stretch of each tributary, and the river km for each stream was calculated based on the lowest point of the capture area (Fig. 1): Paul's Stream (Maidstone, VT) at river length 551 km; Joes Brook (a tributary to the Passumpsic River in Barnet, VT) at river length 455 km, the White River (Bethel, VT) at river length 392 km and Smith Brook (Newfane, VT) at river length 261 km.

PIT TAGGING PROCEDURE AND DETECTION

Fish were anaesthetized using tricaine methanesulphonate (MS-222 at 100 mg l^{-1} , pH 7.0) buffered with NaHCO_3 . Body mass (M) to the nearest 0.1 g, L_F and total length (L_T) to the

nearest mm were recorded for each individual and PIT tags (Texas Instruments; www.ti.com; RI-TRP-WR3P glass-encapsulated tags; 3 mm diameter, 23 mm length) were inserted into the peritoneal cavity through a small (2–3 mm) incision made dorsally at the mid-line and just posterior to the pectoral-fin insertion. No stitches were required and antibiotic ointment was applied with a cotton-tipped swab to the incision after tag insertion. An external paint mark for each group was created using non-toxic acrylic paint injected between anal-fin rays with a 26 gauge needle and a 1 cc syringe in order to aid in their detection at the smolt collection facility in Turners Falls, MA. For hatchery-reared fish, biopsies of four to six primary gill filaments were placed into 100 μ l of ice-cold sucrose-EDTA-imidazole (SEI) buffer (250 mM sucrose, 10 mM EDTA and 50 mM imidazole, pH 7.3) and frozen at -80° C for later analysis (McCormick, 1993). Gill biopsies were taken from one fourth of the tagged individuals in 2000 ($n = 25$) per release location. This was determined to be too low to allow prediction of the influence of initial gill NKA activity at the individual level, so in 2001 all tagged fish were biopsied.

PIT TAG DETECTION SYSTEM

A TIRIS Series-2000 half duplex system was employed to detect PIT tags at Turners Falls, MA (Castro-Santos *et al.*, 1996; Zydlewski *et al.*, 2001). The TIRIS Series-2000 readers contain a radio frequency (RF) module that emits an electromagnetic energizing signal through a wire antenna. A PIT tag is detected when it enters the electromagnetic field generated by an antenna with the antenna acting as a receiver, then using the energy stored in the transponders' charge capacitor it is able to return the data (transmission). When a PIT tag enters this electromagnetic field, its individual code is transmitted back to the antenna and its code is sent to an attached personal computer with a date and time stamp for each individual read. A 2.44 m high \times 1.83 m wide antenna consisting of 12 gauge stranded copper wire was constructed on site and placed inside the downstream bypass entrance weir adjacent to the power generating station at Cabot Station, Turners Falls, MA, at river length 192.3 km. The antenna was tuned for maximal read rate (13 reads s^{-1}) and range (31–46 cm from the antenna plane). Tests of dummy tags indicated >90% detection efficiency at all flow conditions, with undetected tags being primarily those that went through parallel to the plane of the antenna. More than 100 smolts were observed passing through the antenna and the vast majority (>95%) were not parallel to the plane of the antenna. Fish whose PIT tag were read by the antenna system are referred to as detected, whereas those that were handled at Turners Falls for collection of a gill biopsy are referred to as recaptured.

Recapture of smolts occurred at the downstream bypass weir at Cabot Station, Turners Falls, MA, immediately below the antenna detection system. The bypass weir was operated daily during the migration period from 1600 to 2200 hours. Flow from the bypass weir was passed over a dewatering screen and fish were directed into sampling troughs where they could be easily counted and inspected. If any smolts entered the troughs with paint marks on their anal-fin, they were set aside in a secondary trough with flowing river water for no more than 2 h before they were sampled. The fish were anaesthetized, weighed, measured and a gill biopsy was collected as described above and the fish's individual PIT tag code was read. This allowed an opportunity to examine changes in gill NKA activity during migration.

GILL NKA ACTIVITY

Gill NKA activity was determined with a kinetic assay run in 96 well microplates at 25° C and read at a wavelength of 340 nm for 10 min as described previously (McCormick, 1993). Gill tissue was homogenized in 150 μ l of SEID (SEI buffer and 0.1% deoxycholic acid) and centrifuged at 5000 g for 30 s. Two sets of duplicate 10 μ l samples were run, one set containing assay mixture, and the other assay mixture and 0.5 mM ouabain. The resulting ouabain-sensitive ATPase activity is expressed as μ moles ADP mg^{-1} protein h^{-1} . Protein concentrations are determined using bicinchoninic acid (BCA) protein assay (Pierce; www.piercenet.com). Both assays were run on a THERMOMax microplate reader using SOFTmax software (Molecular Devices; www.moleculardevices.com).

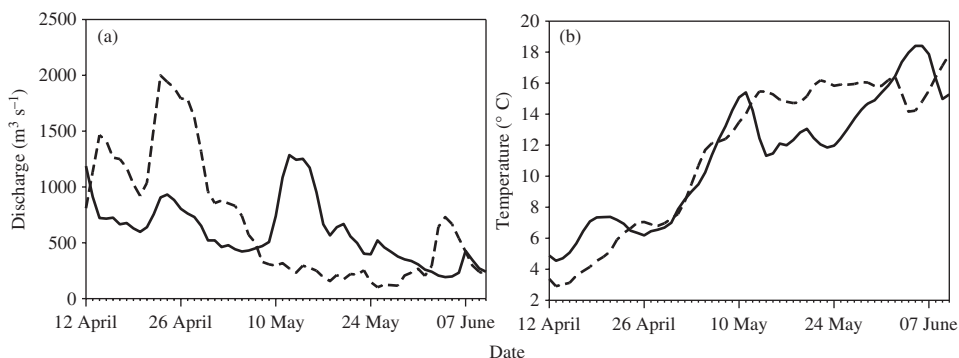


FIG. 2. Mean daily (a) discharge and (b) temperature of the Connecticut River in 2000 (—) and 2001 (---).

STATISTICAL ANALYSIS

Three or four-way analysis of variance (ANOVA) was used to determine whether gill NKA activity, L_F or Fulton's condition factor (K), where $K = 100 M L_F^{-3}$, at the time of release was different for fish that were subsequently detected compared to those that were not detected, with year (L_F and K only), site and time of release as covariates. If significant effects were determined ($P < 0.05$), Newman–Keuls test ($P < 0.05$) was used to compare detected *v.* undetected fish for each pair-wise comparison. Linear regression was used to examine the influence of L_F and gill NKA on migration speed, with separate analysis for each location and release date. Linear regression was also used to examine the influence of location (river km) on median time of arrival at Turners Falls. Pair-wise comparison of detection rates as a function of time or location of release was performed using Pearson's χ^2 test ($P < 0.05$). Akaike information criterion (AIC) analysis was used to evaluate competing logistic regression models examining the effect of year, release site, release date and their interaction on detection rates of hatchery-reared smolts.

RESULTS

Both 2000 and 2001 had increases in discharge in spring, with 2000 showing a later increase (mid-May) compared to 2001 (late-April) [Fig. 2(a)]. Mean discharge for the period 12 April to 10 June was slightly greater in 2001 ($684.7 \text{ m}^3 \text{ s}^{-1}$) than in 2000 ($601.7 \text{ m}^3 \text{ s}^{-1}$). Temperature increases were similar in the two years [Fig. 2(b)], with the minor exception of a decrease in temperature in mid-May 2000 associated with increased discharge. Mean temperature for the period 12 April to 10 June was also slightly greater in 2001 (11.6°C) compared to 2000 (11.2°C).

Hatchery-reared smolts released on 13 April 2000 at the West River were detected at the bypass weir over a 7 day period beginning 1 May with a median arrival date of 6 May [Fig. 3(a)], whereas fish released on the same day at the Passumpsic River were detected over a 9 day period beginning 11 May with a median arrival date of 13 May [Fig. 3(a)]. Hatchery-reared smolts released on 2 May 2000 at the West River were detected over a 4 day period beginning 5 May with a median arrival date of 6 May [Fig. 3(b)], whereas fish released on the same day at the Passumpsic River were detected over a 6 day period beginning 17 May with a median arrival date of 20 May [Fig. 3(b)]. Hatchery-reared smolts released on 19 April 2001 at the West River were detected over a 4 day period beginning 11 May with a median arrival date of 12 May [Fig. 3(c)], whereas fish released on the same day at the Passumpsic River were detected

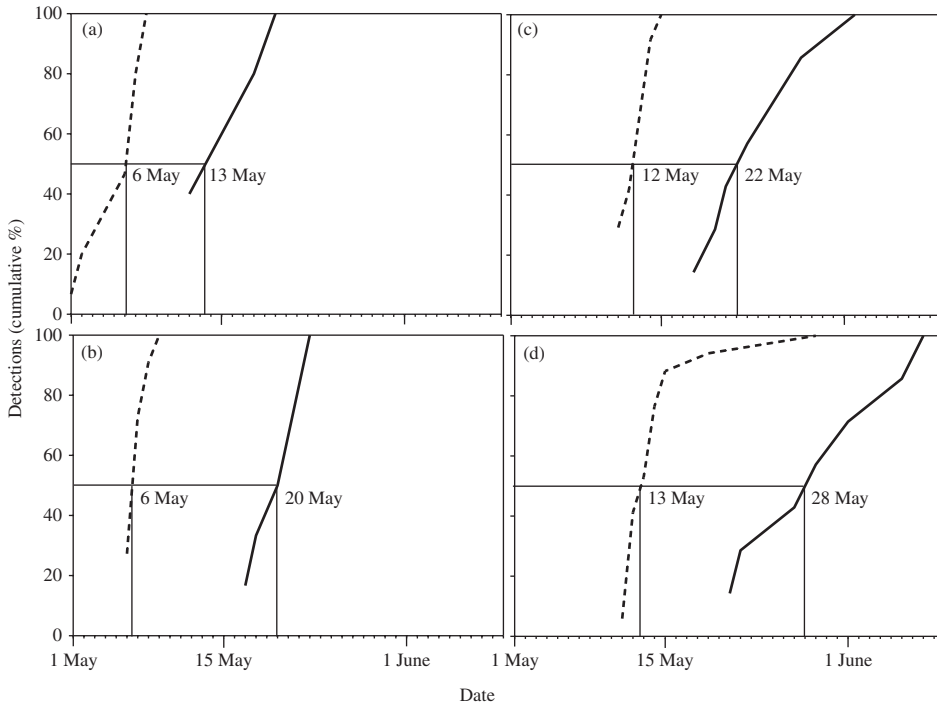


FIG. 3. Migration pattern of hatchery-reared *Salmo salar* smolts after release in spring of 2000 and 2001 showing release timing and location for West River (---), river km 240-6, and Passumpsic River (—), river km 450-4, and median arrival date: (a) 2000 release in mid-April, (b) 2000 release in early May, (c) 2001 release in mid-April and (d) 2001 release in early May. Sample sizes were 11–21 detections of fish released into the West River and five to seven detections of fish released into the Passumpsic River.

over a 15 day period beginning 18 May with a median arrival date of 22 May [Fig. 3(c)]. Hatchery-reared smolts released on 7 May 2001 at the West River were detected over an 18 day period beginning 11 May with a median arrival date of 13 May [Fig. 3(d)], whereas fish released on the same day at the Passumpsic River were detected over an 18 day period beginning 21 May with a median arrival date of 28 May [Fig. 3(d)].

For a given location, the mean apparent speed of hatchery-reared smolts was significantly less for hatchery-reared smolts released in mid-April compared to release in early May (Table I). Fish released in the Passumpsic River had significantly greater apparent speed than fish released in the West River at all release dates, although this difference was much smaller at the second release date (3.0-fold v. 1.2-fold). Although there was a significant effect of year (slightly slower in 2001), in each year, the pattern of migration speeds was similar for release date and location.

Detection rates (proportion of tagged fish detected at Turners Falls) of hatchery-reared smolts were higher for fish released at West River compared to those released farther upriver at the Passumpsic River, and these differences were significant for the mid-April release in 2000 and both releases in 2001 (Table II). For fish released into the West River, fish released in mid-April had higher detection rates compared to those released in early May (Table II). For fish released into the Passumpsic River, detection rates of fish released in mid-April and early May were similar. Logistic regression

TABLE I. Mean \pm S.E. apparent speed (km day^{-1}) of hatchery-reared *Salmo salar* smolts released in the West River (river km 240.6) and the Passumpsic River (river km 450.4) in 2000 and 2001 at two time points, the first in mid-April and the second in early May. Sample sizes for each release are shown in Fig. 2. There was a significant effect of year ($P < 0.05$), location ($P < 0.001$) and date of release ($P < 0.001$) on apparent speed, and a significant interaction between location and date [$P < 0.05$; three-way analysis of variance (ANOVA)]. Values with different lowercase letters within each year are significantly different from one another ($P < 0.001$, Newman–Keuls test)

Year	Mid-April release		Early May release	
	West River	Passumpsic River	West River	Passumpsic River
2000	2.4 ^a \pm 0.1	8.0 ^b \pm 0.4	11.3 ^c \pm 0.8	14.6 ^d \pm 0.8
2001	2.3 ^a \pm 0.1	7.5 ^b \pm 0.4	9.1 ^b \pm 0.7	12.6 ^c \pm 1.6

and AIC analysis of competing models that included year, release location and release date and their interactions indicated that the best model included year ($P < 0.01$) and site ($P < 0.001$). Odds ratio output of this model indicated that 2001 hatchery-reared smolts were 1.85 more likely to be detected as smolts released in 2000, and that fish released in the West River were 3.23 more likely to be detected as fish released into the Passumpsic River. The next competing model included year, release and site and had a ΔAIC of 0.69.

L_F , K and gill NKA activity immediately prior to release were analysed for their ability to predict subsequent downstream detection of hatchery-reared smolts. The L_F of detected fish at the time of release was consistently greater than those that were not recaptured and detection had a significant explanatory effect on size ($P < 0.001$; Fig. 4). K was also significantly different in detected fish, but there was no consistent difference between the detected and undetected fish (*i.e.* sometimes K was greater and sometimes lower). Gill NKA activity was analysed for 2001 when there were large numbers of fish biopsied prior to release. There were no differences as a function of detection for early released fish, but gill NKA activity at the time of release for late release fish was significantly higher for detected hatchery-reared smolts compared to those that were not detected (Fig. 5). In 2000, when only a portion of the fish was

TABLE II. Detection rates of hatchery-reared *Salmo salar* smolts on the Connecticut River after release at the West River and Passumpsic River tributaries in 2000 and 2001. Recapture rate is expressed as a per cent of total tagged and released fish that were later detected at the downstream bypass entrance weir in Turners Falls, MA (river km 192.3)

Year	Mid-April release		Early May release	
	West River (%)	Passumpsic River (%)	West River (%)	Passumpsic River (%)
2000	18.5	6.1*	13.4†	7.1
2001	32.0	9.9*	22.4†	9.5*

*A significant difference of the Passumpsic release from its paired West River release.

†A significant difference of the early May from the mid-April release at the same location (Pearson's χ^2 , $P < 0.05$).

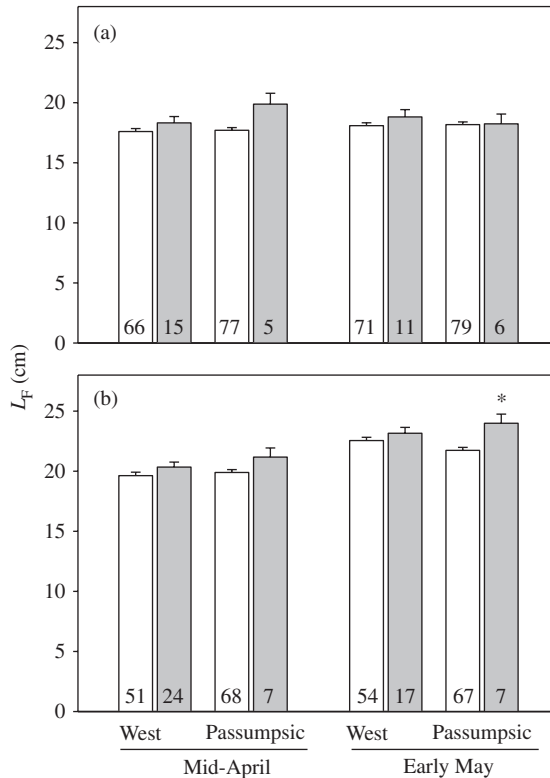


FIG. 4. Mean + s.e. fork length (L_F) at time of release for hatchery-reared *Salmo salar* smolts in (a) 2000 and (b) 2001 released in mid-April and early May at two locations (West River, river km 240.6, and Passumpsic River, river km 450.4). Four-way analysis of variance (ANOVA) indicated a significant effect of year, date, detection and a significant interaction between year and date ($P < 0.0001$). *, a significant difference between detected (□) and undetected (■) fish (Newman–Keuls *post hoc* test, $P < 0.05$). Numbers at the base of histograms are sample sizes.

biopsied, there were no significant differences in detection rates or migration times of biopsied and non-biopsied fish.

Gill NKA activity increased slightly during the 3 weeks of hatchery rearing between release dates of 13 April and 2 May (Fig. 6). Gill NKA activity of hatchery-reared smolts recaptured in Turners Falls was significantly greater than at the release dates, but similar to stream-reared smolts recaptured at the same locations.

Stream-reared smolts from Smith Brook (river km 260.7) were detected over a 22 day period beginning 9 May with a median arrival date of 15 May (Fig. 7) and a detection rate of 9.4% (Table III). It should be noted that this detection rate is not directly comparable to hatchery-reared smolts because stream-reared fish were tagged 6 months prior to detection and thus included over winter mortality. Stream-reared smolts from the West River (river km 392.2) were detected over a 24 day period beginning 12 May with a median arrival date of 17 May and a detection rate of 12.6%. Stream-reared smolts from Joe's Brook (river km 454.6) were detected over a 17 day period beginning 16 May with a median arrival date of 22 May and a detection rate of 2.8%. No stream-reared smolts from Paul's Stream (river km 550.8) were detected.

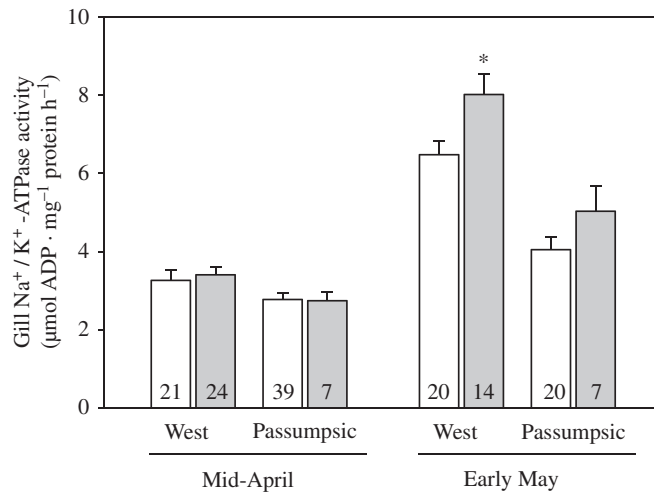


FIG. 5. Mean \pm s.e. gill Na^+/K^+ -ATPase (NKA) activity at time of release for hatchery-reared *Salmo salar* smolts in 2001 released in mid-April and early May at two sites (West River, river km 240-6, and Passumpsic River, river km 450-4). Three-way analysis of variance (ANOVA) indicated a significant effect of time and location of release and detection, and a significant interaction between detection and both time and location ($P < 0.05$). *, a significant difference between detected (□) and undetected (■) fish (Newman–Keuls *post hoc* test, $P < 0.05$). Numbers at the base of histograms are sample sizes.

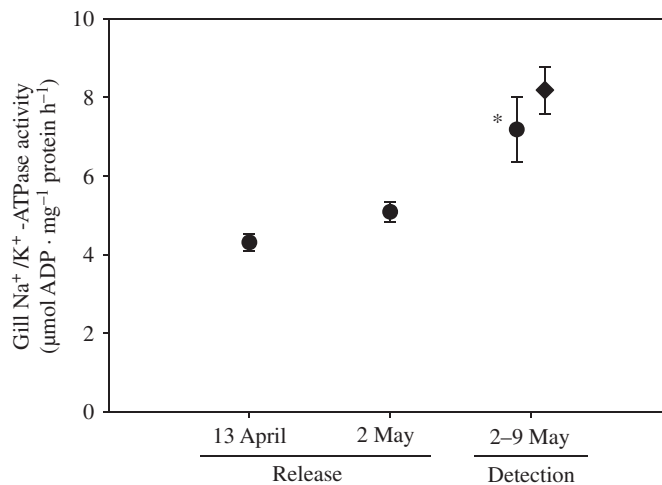


FIG. 6. Mean \pm s.e. gill Na^+/K^+ -ATPase (NKA) activity at time of release for hatchery and stream-reared *Salmo salar* smolts in 2000. Hatchery-reared fish (●) were sampled just prior to release in mid-April and early May (West River release site only) and after recapture at the Turners Falls facility between 2 and 9 May 2000. Stream-reared smolts (◆) were not part of the passive integrated transponder (PIT) tag study but were sampled in the same time interval as hatchery-reared smolts. *, significant difference from both of the released dates [one-way analysis of variance (ANOVA) followed by Student–Newman–Keuls test, $P < 0.05$]. Sample sizes were 25 at each release date and 9 and 12 for hatchery and stream-reared smolts captured at Turners Falls.

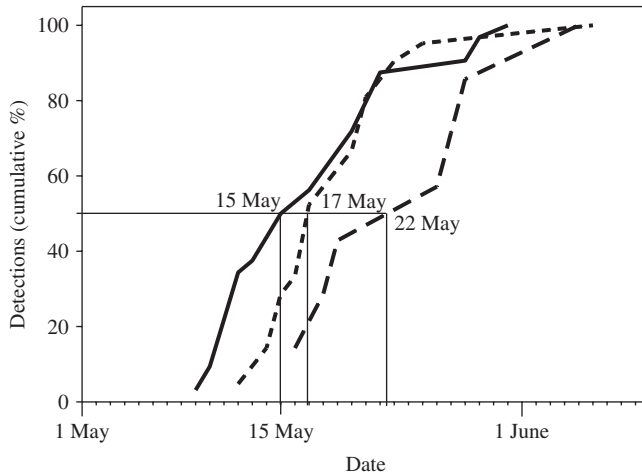


FIG. 7. Migratory pattern of stream-reared *Salmo salar* smolts tagged in the autumn of 2000 and detected during smolt migration in the spring of 2001 at the downstream bypass entrance weir in Turners Falls, MA (river km 192.3). Median spring arrival date at Turners Falls for fish tagged in the autumn at Smith Brook (—; $n = 32$), White River (---; $n = 21$) and Joes Brook (-.-.-; $n = 7$) are shown. There were no detections of fish from Paul's Stream.

Detection rates were significantly lower for the two most distant tributaries (Paul's Stream and Joe's Brook) compared to the two closest tributaries (White River and Smith Brook) (Table III). There was a significant relationship between the median arrival time at Turners Falls and distance from tagging (stream-reared smolts) or release (hatchery-reared smolts) of smolts (Fig. 8; $P < 0.05$, $r^2 = 0.90$).

DISCUSSION

In this study, the timing of downstream migration was similar for hatchery and stream-reared *S. salar* smolts that were released or tagged in the same areas. Both hatchery and stream-reared fish from upstream catchments arrived later and in few numbers than fish from more downstream catchments. Hatchery fish that were released

TABLE III. Detection rates and migration distance of stream-reared *Salmo salar* smolts passive integrated transponders (PIT) tagged in autumn of 2000 and later detected in the spring of 2001. River km to detection represents the distance from the tagging site to detection at the Connecticut River downstream bypass entrance weir in Turners Falls, MA (river km 192.3). Values with different lowercase letters were significantly different from one another (Pearson's χ^2 , $P < 0.05$)

Tagging site	River km to detection	Tagged	Detected	Detection (%)
Smith Brook	68	374	32	9.4 ^a
White River	200	167	21	12.6 ^a
Joe's Brook	262	246	7	2.8 ^b
Paul's Stream	358	91	0	0.0 ^c

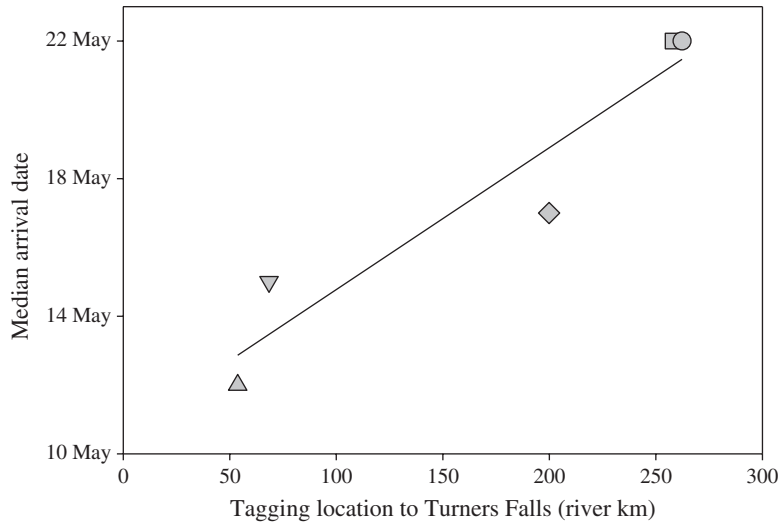


FIG. 8. Median arrival time at Turners Falls of hatchery-reared smolts from West River (△) and Passumpsic River (◻) and stream-reared smolts from Connecticut River tributaries; Smith Brook (▽), White River (◇) and Joe's Brook (○) during the 2001 smolt migration. Hatchery-reared smolts are those from the mid-April release date. The curve was fitted by $y = -9.070e + 5 + 2.191e + 1x$ ($r^2 = 0.90$).

3 weeks apart arrived downstream at similar times, indicating that time of release had only a minor effect on the timing of downstream migration. Finally, larger fish and those with greater gill NKA activity at the time of release were more likely to be detected downstream, suggesting that these factors are predictive of drive for downstream migration and survival.

Hatchery-reared fish released at river length 540.4 km arrived at river length 192 km between 7 and 15 days later than fish released on the same dates at river length 240.6 km. This later arrival would be expected based simply on the greater distance (204 km) that fish stocked upstream were required to travel. Stream-reared fish had a similar migratory pattern; fish released higher in the catchment arrived in Turners Falls later than fish from lower in the catchment. This difference has potential implications for the survival of fish from the upper catchment. It has been hypothesized that early arrival to the estuary is beneficial to smolt survival (Marschall *et al.*, 2011), and if this is the case then the later arrival of fish from farther north would likely mean lower overall survival. Fish migrating late in the season have lower levels of gill NKA activity and reduced seawater tolerance (McCormick *et al.*, 1999), probably due to exposure to higher temperature that occur late in the migratory period. In addition to the lower apparent in-river survival of fish from northern tributaries, late migrants from more northern tributaries may also have lower marine survival and contribute less to adult recruitment.

In spite of the later arrival times for smolts released in the upper river site, their apparent migration speed was greater than that for fish from the lower river site. This is especially interesting since smolts released upstream would have migrated past five dams (with possible delays at each dam) compared to only one for fish released into the lower river site. This effect, however, was relatively small (*c.* 25%) when fish were at their most active state after release in early May. Further studies will be required to determine what factors (such as difference in water velocity or initiation, speed or

periodicity of migration and effects of specific dams) may have contributed to this difference in migratory speed between upstream and downstream sites.

In addition to the effect of release location on arrival times, there was a clear effect of release location on detection rates. Hatchery-reared smolts released higher in the catchment had consistently lower detection rates than fish released higher in the catchment. Furthermore, logistic regression modelled an odds ratio of more than three-fold for detection rates of fish from the lower release site compared to those released at the upper release site. This difference is probably due to lower overall survival of fish released into the upper catchment. The distance travelled by fish released in the upper catchment was approximately five times greater, so the per km apparent survival may have been higher for fish in the upper catchment. It is important to exercise caution in equating detection rates with survival. There are other pathways for fish to pass the Turners Falls dam complex without necessarily passing through the bypass facility at Turners Falls, especially in high flow, so the detection rates represent a minimum survival estimate. The consistent pattern observed between years suggests that the overall patterns of detection, if not the absolute values, may indeed be related to survival. In contrast to the present results, release of hatchery-reared smolts 30–74 km above the recapture location on the River Simojoki in Finland did not result in detectable effects of release location on recapture rate (Jokikokko & Mantyniemi, 2003). In the Penobscot River, ME, which is similar in size to the Connecticut River, smolts had lower survival around dams and cumulative survival declined as fish moved downstream (Holbrook *et al.*, 2011).

There was a similar overall pattern of higher detection rates of stream-reared smolts from the lower catchment (Smith Brook and White River) compared to those released higher in the catchment (Joe's Brook and Paul's Stream). Although the initial tagging numbers were relatively small, the antennas did not detect a single fish from Paul's Stream, which is located 358 km above the detection facility. In addition to the longer distance, fish from Paul's Stream must traverse a large reservoir formed by the Moore Dam. While there are a number of dams on the mainstream of the Connecticut River, this dam is the highest and forms a much larger reservoir than any of the other dams. Migratory speed and survival of smolts through this reservoir are very low (Gephard & McMenemy, 2004), probably contributing to the absence of detection of fish from Paul's Stream. As a tributary of the Passumpsic, fish from Joe's Brook had a similar distance to travel as the hatchery-reared fish released into the Passumpsic, and the lower detection rates of Joe's Brook fish compared to fish at Smith Brook (a tributary of the West River) indicate higher in-stream mortality during downstream migration of both hatchery and stream-reared fish from the upper catchment. Consistent with the present results, modelling of smolt migration and survival predicts that survival of smolts from upstream tributaries will be more variable and often lower than those from downstream tributaries (Marschall *et al.*, 2011).

There was relatively little effect of timing of release on the migration pattern of hatchery-reared smolts. Fish released 3 weeks earlier were detected only slightly earlier, 1 day in the case of the lower release site and 1 week in the case of upper release site. Thus, the apparent migratory speed was greater for fish released in early May (Table II). These apparent migration speeds are calculated from the time of release to detection downstream at Turners Falls. The simplest explanation is that fish released in mid-April moved downstream at a lower speed than those released in May. It is also possible that early released fish spent some period of time in the release area

(staging) before they started downstream migration (Holbrook *et al.*, 2011), and therefore apparent migration speeds include both the delay prior to initiation of migration and the subsequent migration speed. This may in part be driven by the cooler temperatures in mid-April that may affect both of these components of migration (Zydlowski *et al.*, 2005; Sykes *et al.*, 2009). Greater apparent migration speeds were observed for Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) and steelhead trout *Oncorhynchus mykiss* (Walbaum 1792) captured in late spring compared to those captured earlier in migration (Smith *et al.*, 2002). The absolute magnitude of apparent migration speeds in this study is similar to that found for hatchery-reared *S. salar* at the Penobscot River, Maine (Spicer *et al.*, 1995).

For hatchery-reared smolts released into the lower river site, there were significantly higher detection rates in both years for fish released in mid-April compared to those released 3 weeks later. The effect of time of release was not apparent for fish released into the upper river site. Fish released early in the season may gain an advantage through acclimation to river conditions for some period of time before active migration begins. This result is consistent with higher adult return rates of hatchery smolts stocked in March in the Connecticut River relative to those stocked in late-April or May (Gephard & McMenemy, 2004). This stocking programme occurs primarily in the lower catchment. Stocking earlier in the season may reduce the stress of transport (and therefore increase survival) either through lower temperatures at this time or by avoiding the greater stress response that occurs at the peak of smolt development (Carey & McCormick, 1998). The basis for the apparent interaction between location and timing is not entirely clear, although it is possible that the lower survival of smolts released in the upper catchment masks or overwhelms any advantage of early release.

Although the effect of location and timing of release on detection rate was similar in each year, there was a significant difference between years, with fish released in 2001 having a three-fold greater rate of detection based on the logistic regression model. The reason for this difference in apparent survival between years is not immediately obvious, as the pattern and magnitude of flow and temperature did not differ substantially between the two years (Fig. 2). It has generally been found that higher river discharge levels are conducive to greater in-river survival of smolts (Lawson *et al.*, 2004). It is possible that high flows at a particular time during smolt migration was especially conducive to smolt survival in 2001, or that other factors such as increased numbers of predators were involved.

A consistent pattern of migration was found between hatchery and stream-reared smolts; fish that were tagged or released in a similar area arrived at similar times, and there was a consistent pattern of distance from the detection facility and arrival time (Fig. 8). This is consistent with long-term data at Turners Falls in which the timing of hatchery-reared smolts released upstream is similar to that for stream-reared fish (R. J. Stira, pers. comm.). Studies of radio-tagged *S. salar* and brown trout *Salmo trutta* L. 1758 in Denmark found similar migratory timing of hatchery-reared and wild smolts (Aarestrup *et al.*, 2002). In contrast, hatchery-reared coho salmon *Oncorhynchus kisutch* (Walbaum 1792) were slower to migrate than their wild counterparts and as a consequence arrived to the ocean later (Chittenden *et al.*, 2008), and were linked to lower levels of gill NKA activity in hatchery fish. Both migration speed and apparent survival were lower for hatchery-reared compared to wild anadromous *S. trutta* (sea trout) in the Baltic Sea, which was suggested to be due to the high lipid content of hatchery fish (Serrano *et al.*, 2009). In contrast, wild spring *O. tshawytscha*

in the Snake River (western U.S.A.) migrate earlier and for a longer period than hatchery-reared fish (Achord *et al.*, 1996).

The timing of arrival at Turners Falls (and by extension the ocean) was later for fish from both hatchery and stream-reared *S. salar* released higher in the catchment. In wild *S. salar* populations, there is evidence that smolts from more distant tributaries leave earlier and arrive at the ocean at the same time as fish lower in the catchment (Thorstad *et al.*, 2012). There is a known genetic component to migration timing (Orciari & Leonard, 1996), which could in part control tributary-specific migration patterns. In this study, there were no genetic differences among stream-reared fish in the upper and lower catchment since they were randomly chosen from the same genetic stock, and it is therefore possible that this genetic homogeneity is partly responsible for the difference in migration timing observed in stream-reared fish. The longer distance travelled and effects of barriers to migration (dams) probably also play a role, and a finer-scale analysis of the initiation of migration and movement speeds will be important in determining the relative contribution of these factors.

Larger hatchery-reared fish were more likely to be detected than smaller fish (Fig. 4), suggesting that size is a determinant of migratory urge and survival. Fish released at a later date were slightly larger than fish released earlier, but both detection and date were found to be significantly related to size of fish at the time of release and with no interaction, indicating that the effect of size on subsequent detection was not likely to have been driven by the impact of time of release. Indeed, fish that were released in April may have grown during the 3 weeks they were at large. The effects of size in this study are consistent with many studies that have found a positive effect of size of hatchery smolts on ocean fishery captures or adult return rates of *S. salar* (Bilton *et al.*, 1982; HENDERSON & CASS, 1991; Vehanen *et al.*, 1993; Lundqvist *et al.*, 1994; Miyakoshi *et al.*, 2001; Shimoda *et al.*, 2003; Saloniemi *et al.*, 2004). The present results indicate that higher in-river survival may also be a contributing factor to the survival of larger smolts to adulthood. There was a positive effect of size on in-river survival and migration speed of hatchery-reared spring *O. tshawytscha* (Monzyk *et al.*, 2009). Size effects on riverine, estuarine and ocean survival may all be related to the apparent size selectivity of smolt predators (Mather, 1998).

For fish released in early May, higher levels of gill NKA activity were observed at the time of release for fish that were subsequently detected compared to fish that were not detected (Fig. 4). The inability to detect an effect in mid-April is probably due to the overall lower levels at this early stage of smolt development, such that individual variation has not yet been expressed. The higher levels of gill NKA activity are unlikely to be directly related to higher in-river survival. Rather, they may be an indication of overall smolt development (including migratory urge) and overall health of the animals. Hatchery-reared *S. trutta* smolts with higher gill NKA activity were more likely to have migrated than those with lower gill NKA activity (Aarestrup *et al.*, 2000). In *O. mykiss* at the Columbia River, there was a positive relationship between gill NKA activity and avoidance of avian predation, although this may have included a salinity tolerance component as the study was primarily conducted in this river's large estuary (Kennedy *et al.*, 2007). It will be of interest to further examine the relationship of gill NKA activity to early ocean survival and adult return rates of *S. salar* smolts.

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References

- Aarestrup, K., Nielsen, C. & Madsen, S. S. (2000). Relationship between gill Na⁺,K⁺-ATPase activity and downstream movement in domesticated and first-generation offspring of wild anadromous brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 2086–2095.
- Aarestrup, K., Nielsen, C. & Koed, A. (2002). Net ground speed of downstream migrating radio-tagged Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) smolts in relation to environmental factors. *Hydrobiologia* **483**, 95–102.
- Achord, S., Matthews, G. M., Johnson, O. W. & Marsh, D. M. (1996). Use of passive integrated transponder (PIT) to monitor migration timing of Snake River chinook salmon smolts. *North American Journal of Fisheries Management* **16**, 302–313.
- Bilton, H. T., Alderdice, D. F. & Schnute, J. T. (1982). Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 426–447.
- Brockmark, S., Neregard, L., Bohlin, T., Björnsson, B. Th. & Johnsson, J. I. (2007). Effects of rearing density and structural complexity on the pre- and postrelease performance of Atlantic salmon. *Transactions of the American Fisheries Society* **136**, 1453–1462.
- Buchanan, R. A., Skalski, J. R. & Giorgi, A. E. (2010). Evaluating surrogacy of hatchery releases for the performance of wild yearling chinook salmon from the Snake River basin. *North American Journal of Fisheries Management* **30**, 1258–1269.
- Carey, J. B. & McCormick, S. D. (1998). Atlantic salmon smolts are more responsive to an acute handling and confinement stress than parr. *Aquaculture* **168**, 237–253.
- Castro-Santos, T., Haro, A. & Walk, S. (1996). A passive integrated transponder (PIT) tag system for monitoring fishways. *Fisheries Research* **28**, 253–261.
- Chittenden, C. M., Sura, S., Butterworth, K. G., Cubitt, K. F., Manel-La, N. P., Balfry, S., Okland, F. & McKinley, R. S. (2008). Riverine, estuarine and marine migratory behaviour and physiology of wild and hatchery-reared coho salmon *Oncorhynchus kisutch* (Walbaum) smolts descending the Campbell River, BC, Canada. *Journal of Fish Biology* **72**, 614–628.
- George, A. L., Kuhajda, B. R., Williams, J. D., Cantrell, M. A., Rakes, P. L. & Shute, J. R. (2009). Guidelines for propagation and translocation for freshwater fish conservation. *Fisheries* **34**, 529–545.
- Gephard, S. & McMenemy, J. (2004). An overview of the program to restore Atlantic salmon and other diadromous fishes to the Connecticut river with notes on the current status of these species in the river. *American Fisheries Society Monograph* **9**, 287–317.
- Henderson, M. A. & Cass, A. J. (1991). Effect of smolt size on smolt-to-adult survival for Chilko lake sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 988–994.
- Hoar, W. S. (1988). The physiology of smolting salmonids. *The Physiology of Developing Fish – Viviparity and Posthatching Juveniles: Fish Physiology 11* (Hoar, W. S. & Randall, D. J., eds), pp. 275–343. New York, NY: Academic Press.
- Holbrook, C. M., Kinnison, M. T. & Zydlewski, J. (2011). Survival of migrating Atlantic salmon smolts through the Penobscot River, Maine: a preresoration assessment. *Transactions of the American Fisheries Society* **140**, 1255–1268.
- Jokikokko, E. & Mantyniemi, S. (2003). The survival of stocked Atlantic salmon smolts during sea run and the timing of migration in the river Simojoki, northern Finland. *Aquaculture* **219**, 431–444.
- Jonsson, N., Jonsson, B. & Hansen, L. P. (2003). The marine survival and growth of wild and hatchery-reared Atlantic salmon. *Journal of Applied Ecology* **40**, 900–911.

- Kallio-Nyberg, I., Jutila, E., Saloniemi, I. & Jokikokko, E. (2004). Association between environmental factors, smolt size and the survival of wild and reared Atlantic salmon from the Simojoki River in the Baltic Sea. *Journal of Fish Biology* **65**, 122–134.
- Kennedy, B. M., Gale, W. L. & Ostrand, K. G. (2007). Relationship between smolt gill Na⁺, K⁺ ATPase activity and migration timing to avian predation risk of steelhead trout (*Oncorhynchus mykiss*) in a large estuary. *Canadian Journal of Fisheries and Aquatic Sciences* **64**, 1506–1516.
- Kihlslinger, R. L. & Nevitt, G. A. (2006). Early rearing environment impacts cerebellar growth in juvenile salmon. *Journal of Experimental Biology* **209**, 504–509.
- Lawson, P. W., Logerwell, E. A., Mantua, N. J., Francis, R. C. & Agostini, V. N. (2004). Environmental factors influencing freshwater survival and smolt production in Pacific Northwest coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 360–373.
- Lundqvist, H., Mckinnell, S., Fangstam, H. & Berglund, I. (1994). The effect of time, size and sex on recapture rates and yield after river releases of *Salmo salar* smolts. *Aquaculture* **121**, 245–257.
- Marschall, E. A., Mather, M. E., Parrish, D. L., Allison, G. W. & McMenemy, J. R. (2011). Migration delays caused by anthropogenic barriers: modeling dams, temperature, and success of migrating salmon smolts. *Ecological Applications* **21**, 3014–3031.
- Mather, M. E. (1998). The role of context-specific predation in understanding patterns exhibited by anadromous salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 232–246.
- McCormick, S. D. (1993). Methods for non-lethal gill biopsy and measurement of Na⁺,K⁺-ATPase activity. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 656–658.
- McCormick, S. D. (2009). Evolution of the hormonal control of animal performance: insights from the seaward migration of salmon. *Integrative and Comparative Biology* **49**, 408–422.
- McCormick, S. D., Hansen, L. P., Quinn, T. P. & Saunders, R. L. (1998). Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 77–92.
- McCormick, S. D., Cunjak, R. A., Dempson, B., O’Dea, M. F. & Carey, J. (1999). Temperature-related loss of smolt characteristics in Atlantic salmon in the wild. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 1649–1658.
- McCormick, S. D., O’Dea, M. F., Moeckel, A. M. & Björnsson, B. Th. (2003). Endocrine and physiological changes in Atlantic salmon smolts following hatchery release. *Aquaculture* **222**, 45–57.
- Miyakoshi, Y., Nagata, M. & Kitada, S. (2001). Effect of smolt size on postrelease survival of hatchery-reared masu salmon *Oncorhynchus masou*. *Fisheries Science* **67**, 134–137.
- Monzyk, F. R., Jonasson, B. C., Hoffnagle, T. L., Keniry, P. J., Carmichael, R. W. & Cleary, P. J. (2009). Migration characteristics of hatchery and natural spring Chinook salmon smolts from the Grande Ronde River basin, Oregon, to Lower Granite Dam on the Snake River. *Transactions of the American Fisheries Society* **138**, 1093–1108.
- Orciari, R. D. & Leonard, G. H. (1996). Length characteristics of smolts and timing of downstream migration among three strains of Atlantic salmon in a southern New England stream. *North American Journal of Fisheries Management* **16**, 851–860.
- Parrish, D. L., Behnke, R. J., Gephard, S. R., McCormick, S. D. & Reeves, G. H. (1998). Why aren’t there more Atlantic salmon (*Salmo salar*)? *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 281–287.
- Poole, W. R., Nolan, D. T., Wevers, T., Dillane, M., Cotter, D. & Tully, O. (2003). An ecophysiological comparison of wild and hatchery-raised Atlantic salmon (*Salmo salar* L.) smolts from the Burrishoole system, western Ireland. *Aquaculture* **222**, 301–314.
- Rideout, S. G. & Stolte, L. W. (1988). Restoration of Atlantic salmon to the Connecticut and Merrimack Rivers. In *Present and Future Atlantic Salmon Management* (Stroud, R. H., ed.), pp. 67–81. Ipswich, MA: Atlantic Salmon Federation.
- Saloniemi, I., Jokikokko, E., Kallio-Nyberg, I., Jutila, E. & Pasanen, P. (2004). Survival of reared and wild Atlantic salmon smolts: size matters more in bad years. *ICES Journal of Marine Science* **61**, 782–787.

- Serrano, I., Larsson, S. & Eriksson, L. O. (2009). Migration performance of wild and hatchery sea trout (*Salmo trutta* L.) smolts-implications for compensatory hatchery programs. *Fisheries Research* **99**, 210–215.
- Shimoda, K., Naito, K., Nakajima, M., Sasaki, Y., Misaka, N. & Imada, K. (2003). Marine survival and growth of masu salmon *Oncorhynchus masou*, in relation to smolt size [Japanese]. *Nippon Suisan Gakkaishi-Bulletin of the Japanese Society of Scientific Fisheries* **69**, 926–932.
- Shrimpton, J. M., Bernier, N. J., Iwama, G. K. & Randall, D. J. (1994). Differences in measurements of smolt development between wild and hatchery-reared juvenile coho salmon (*Oncorhynchus kisutch*) before and after saltwater exposure. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 2170–2178.
- Smith, S. G., Muir, W. D., Williams, J. G. & Skalski, J. R. (2002). Factors associated with travel time and survival of migrant yearling Chinook salmon and steelhead in the Lower Snake River. *North American Journal of Fisheries Management* **22**, 385–405.
- Spicer, A. V., Moring, J. R. & Trial, J. G. (1995). Downstream migratory behavior of hatchery-reared, radio-tagged Atlantic salmon (*Salmo salar*) smolts in the Penobscot River, Maine, USA. *Fisheries Research* **23**, 255–266.
- Sundell, K., Dellefors, C. & Björnsson, B. Th. (1998). Wild and hatchery-reared brown trout, *Salmo trutta*, differ in smolt related characteristics during parr-smolt transformation. *Aquaculture* **167**, 53–65.
- Sykes, G. E., Johnson, C. J. & Shrimpton, J. M. (2009). Temperature and flow effects on migration timing of Chinook salmon smolts. *Transactions of the American Fisheries Society* **138**, 1252–1265.
- Theriault, V., Moyer, G. R. & Banks, M. A. (2010). Survival and life history characteristics among wild and hatchery coho salmon (*Oncorhynchus kisutch*) returns: how do unfed fry differ from smolt releases? *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 486–497.
- Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H. & Finstad, B. (2012). A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology* **81**, 500–542.
- Vehanen, T., Aspi, J. & Pasanen, P. (1993). The effect of size, fin erosion, body silvering and precocious maturation on recaptures in Carlin-tagged Baltic salmon (*Salmo salar* L.). *Annales Zoologici Fennici* **30**, 277–285.
- Williams, J. G., Smith, S. G. & Muir, W. D. (2001). Survival estimates for downstream migrant yearling juvenile salmonids through the Snake and Columbia rivers hydropower system, 1966–1980 and 1993–1999. *North American Journal of Fisheries Management* **21**, 310–317.
- Zaugg, W. S. & Wagner, H. H. (1973). Gill ATPase activity related to parr-smolt transformation and migration in steelhead trout (*Salmo gairdneri*): influence of photoperiod and temperature. *Comparative Biochemistry and Physiology B* **45**, 955–965.
- Zydlewski, G. B., Haro, A., Whalen, K. G. & McCormick, S. D. (2001). Performance of stationary and portable passive transponder detection systems for monitoring of fish movements. *Journal of Fish Biology* **58**, 1471–1475.
- Zydlewski, G. B., Haro, A. & McCormick, S. D. (2005). Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behavior of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 68–78.