

## Seaward migrating Atlantic salmon smolts with low levels of gill Na<sup>+</sup>, K<sup>+</sup> -ATPase activity; is sea entry delayed?

Jo E. T. Strand · Jan G. Davidsen ·  
Even H. Jørgensen · Andun H. Rikardsen

Received: 14 April 2010 / Accepted: 27 October 2010 / Published online: 16 November 2010  
© The Author(s) 2010. This article is published with open access at Springerlink.com

**Abstract** Two groups of migrating wild Atlantic salmon (*Salmo salar*) smolts caught within a 1 week interval in the River Alta, northern Norway, were tagged with acoustic transmitters and measured for gill Na<sup>+</sup>, K<sup>+</sup> -ATPase activity in order to compare their smolt status with timing of sea entry. The first group of smolts had low levels of gill Na<sup>+</sup>, K<sup>+</sup> -ATPase activity and resided in the lower part of the river twice as long as the second group that had high levels of gill Na<sup>+</sup>, K<sup>+</sup> -ATPase activity. This indicates that early migrating smolts may not be completely physiologically adapted for salt water and delay their sea entry, thereby also synchronizing their seaward migration with the later migrating smolts.

**Keywords** Smoltification · Mortality · Anadromy · Survival · Telemetry · Salmonids

---

J. E. T. Strand (✉)  
Department of Natural Sciences,  
Finnmark University College,  
NO-9509 Alta, Norway  
e-mail: Jo.Strand@hifm.no

J. G. Davidsen · E. H. Jørgensen · A. H. Rikardsen  
Faculty of Biosciences, Fisheries and Economics,  
University of Tromsø,  
NO-9037 Tromsø, Norway

A. H. Rikardsen  
Norwegian Institute for Nature Research,  
Polar Environmental Centre,  
NO-9296 Tromsø, Norway

The period of sea entry and the first few months of marine life is a critical period in the life of the Atlantic salmon (*Salmo salar*) and occasionally characterised by very high mortality (Hvidsten and Møkkelgjerd 1987; Thorpe et al. 1994; Rikardsen et al. 2004; Davidsen et al. 2009). As a preparation for residency in the marine environment, juvenile Atlantic salmon undergo a parr-smolt transformation (termed smolting) before entering the sea (Hoar 1988; Boeuf 1993; McCormick et al. 1998). Among the biochemical, physiological and behavioural changes that comprise the smolting process, development of hypoosmoregulatory ability (seawater tolerance) is considered to be most critical for performance in seawater (McCormick and Saunders 1987). The development of seawater tolerance is associated with an increase in the number and size of the seawater chloride cell subtypes and a several-fold increase in gill Na<sup>+</sup>, K<sup>+</sup>-ATPase activity (Hoar 1988; Evans et al. 2005). Fish that have not completed their smolting process are subjected to osmotic stress when they enter seawater which can reduce swimming performance and thus make them more vulnerable to predators (Handeland et al. 1996), while individuals that are completely smoltified have been shown to have higher survival rates after sea entry (Moser et al. 1991).

The timing of the onset and completion of the smolting process is governed by photoperiod and water temperature, respectively (Solbakken et al. 1994; Handeland et al. 2003; Zydlewski et al. 2005), while water temperature and water flow are key

factors for the initiation of seaward migration (McCormick and Saunders 1987; McCormick et al. 1998). A successful sea entry presupposes that the completion of the smolt development is synchronised with the timing of migration. Stewart and co-workers (2006) found that smolts from upper tributaries generally begin migration earlier (one or several weeks) than those from lower tributaries, contributing to a more synchronized timing of sea entry of smolts from the entire watershed. It is believed that smolts use environmental cues in the rivers that are predictably correlated with favourable ocean conditions (e.g., temperature and food availability) to control movements in order to arrive at sea when growth and feeding condition is optimal (Hvidsten et al. 2009). However, there is little knowledge about if, and how, the timing of the seawater migration is synchronized with the development of seawater tolerance and to what extent there may be an asynchrony between smolt development and seawater entry within years in salmon populations. The main goal of the present study was therefore to examine the physiological smolt status (using gill  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase activity as an indicator of SW readiness) of two groups of smolts migrating at different times within the same year, and their subsequent migration timing to seawater.

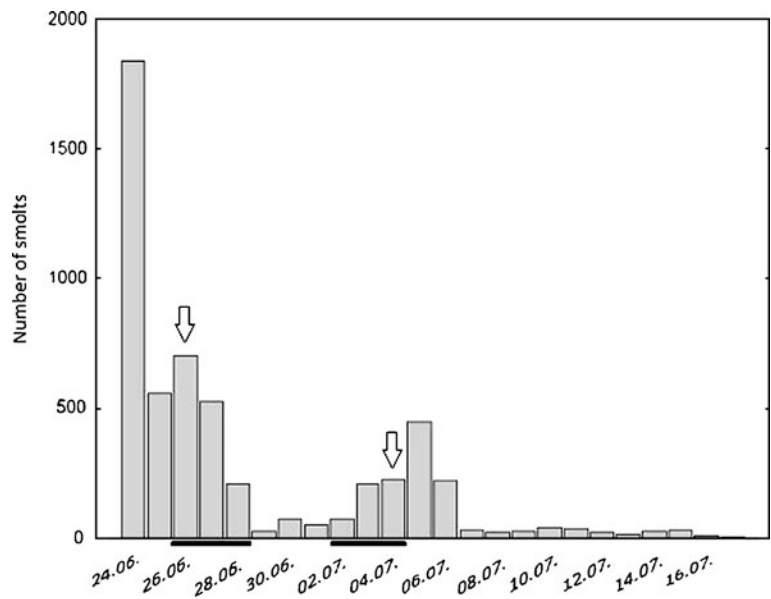
In River Alta, northern Norway (70°N 23°E), the main smolt migration occurs during a 2–3 week period in late June to mid-July (Hvidsten et al. 1998). During the smolt migration in this river in 2007, a total of 120 wild smolts were trapped during two periods (2×60 smolts) 11 km above the river mouth and tagged with acoustic tags (Thelma AS, Norway, model LP-7.3, diameter of 7.3 mm, length of 18 mm, mass in water/air of 1.2/1.9 g) using methods described in Davidsen et al. (2008). The smolts were released at the capture site 10 min after recovery. Due to an extraordinary high flow in June 2007, it was not possible to operate the trap in the river before 24 June. Based on earlier smolt migration observations in this river (Hvidsten et al. 1998) and the actual daily smolt catches in the present study (Fig. 1), it was assumed that the fish in the first group (26–28 June,  $n=60$ , mean  $L_F$  146 mm, S.E.=0.8; mean mass 28 g, S.E.=0.5) were tagged and released a few days after the assumed main peak of the smolt migration, while the fish in the second group (2–4 July,  $n=60$ , mean  $L_F$  147 mm, S.E.=1.1, mean mass 30 g, S.E.=0.7) probably represent the smaller second peak of

migrating smolts. River water temperature was 10–11°C during the first period and 13°C during the second period. In order to monitor the time of sea entry, two automatic listening stations (ALS) (Vemco INC, Canada, model VR2) were placed in the river mouth (detecting range 50–100 m). The last record of each smolt on the ALS's in the river mouth was used as the time of sea entry. In order to examine gill  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase activity of the smolts migrating in the two periods, a total of 20 additional smolts from the trap during each tagging period (sampled 26 June and 4 July) were sacrificed by a sharp blow to the head. Samples for measurements of gill  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase activity were taken, frozen in liquid nitrogen and later analyzed by the method described in McCormick (1993). Two-way ANCOVA was used to test for differences in gill  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase activity between the earlier and later smolt group and Mann-Whitney  $U$ -test to test for differences in migratory progress.

The results showed that smolts captured on 26 June had a four-fold lower gill  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase activity (Two-way ANCOVA,  $n=40$ ,  $P<0.001$ ) than the smolts captured a week later (Fig. 2). Further, the first group spent on average twice the amount of time in the lower part of the river before entering the sea than the second group (96 vs. 48 h, respectively, Mann-Whitney  $U$ -test,  $n=64$ ,  $P<0.001$ , Fig. 3). In total, a little more than half of the tagged smolts from each group (31 and 33, respectively) were recorded by the ALS's in the river mouth. The gill  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase activity of the smolts captured in the first period, close to the assumed peak of the smolt migration ( $3.3\pm 2.4 \mu\text{mol ADP mg protein}^{-1}\text{h}^{-1}$ ), was much lower than the activity normally found in fully smoltified Atlantic salmon from the River Alta ( $\geq 10 \mu\text{mol ADP mg protein}^{-1}\text{h}^{-1}$ ; Lysfjord and Staurnes 1998; Strand et al. 2007). This indicates that these fish were not fully smolted when passing the smolt trap 11 km upstream from the river mouth. In contrast, the mean activity in the second group ( $13.8\pm 4.4 \mu\text{mol ADP mg protein}^{-1}\text{h}^{-1}$ ) indicated that these fish had completed smolting. Therefore, there was a negative correlation between time spent by the smolts in the lower part of the river before sea entry and their gill  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase activity further up in the river (capture site).

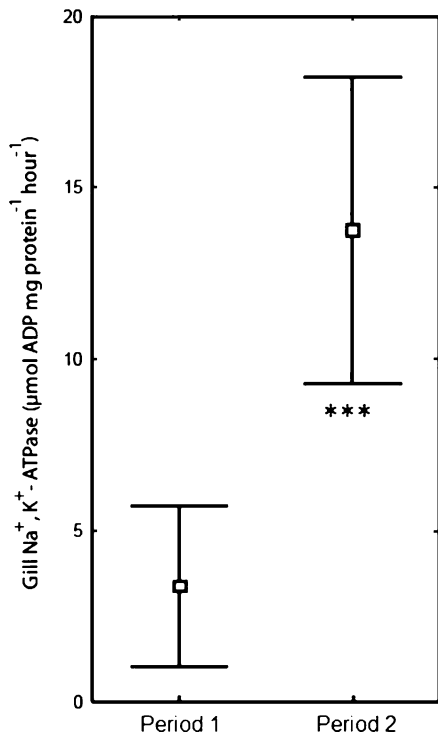
Several studies have shown that post-smolts are exposed to high predation immediately after sea entry (Reitan et al. 1987; Hvidsten and Lund 1988;

**Fig. 1** Total daily catch of smolts in the trap from 24 June to the smolt run had ended (18 July). Sampling was done consistently during the whole study period. The tagging periods are indicated by black lines at the x-axis and the dates at which gills were sampled for  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase activity with an arrow

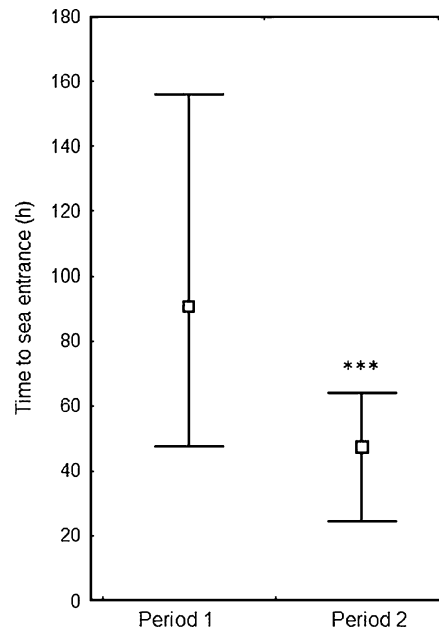


Dieperink et al. 2002) and that the risk of predation increases if fish suffers from osmotic stress (Järvi 1989; Handeland et al. 1996; Kennedy et al. 2007). It may therefore be suggested that the extended resi-

duency of the first smolt group in the lower part of the river was related to their low gill  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase activity and a need to improve seawater tolerance before entering seawater. The migration of Atlantic salmon smolts through estuaries is characterized by active swimming and is a continuous movement,



**Fig. 2** Gill  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase activity (mean  $\pm$  SE) of smolt sampled in period 1 (26 June;  $n=20$ ) and period 2 (4 July;  $n=20$ ). Asterisks denote significant difference between groups (\*\*\*,  $p<0,001$ )



**Fig. 3** Time from release to sea entry (median  $\pm$  Quartiles) of smolts tagged in period 1 (26–28 June;  $n=31$ ) and period 2 (2–4 July;  $n=33$ ). Asterisks denote significant difference between groups (\*\*\*,  $p<0,001$ )

usually with no apparent period of acclimatization to adjust to salt-water osmotic and ionic conditions (Lacroix and Knox 2005). Also smolts from the River Alta have a very short residence time in the estuary (Davidsen et al. 2009). The mean time from leaving the river mouth to pass an array of automatic listening stations four km outward in the Alta Fjord was 4 h in the present study. In this area, salinity varied from 10 to 20 at the surface to 30–35 at 4 m depth during the time of the migration (Davidsen et al. 2009), so the smolts entered full strength seawater already few hours after sea entry. It has been shown, however, that a thermal sum of approximately 350 d°C (i.e. the sum of daily mean temperatures) is needed for increasing the gill Na<sup>+</sup>, K<sup>+</sup>-ATPase activity from 6 to 12 μmol ADP mg protein<sup>-1</sup>h<sup>-1</sup> at the temperature (10–13°C) prevailing in the River Alta in late June/early July (Stefansson et al. 1998). The smolts in the first group experienced 40–60 d°C from when they were caught in the trap until entering the sea, which in the Alta Fjord is characterized by high salinity (>30) even during spring (Davidsen et al. 2009). Although the absolute values of gill Na<sup>+</sup>, K<sup>+</sup>-ATPase activity may vary between studies, partly due to analytical methods, 40–60 d°C seems to be too little for the first smolt group to complete their smolting process before they actually entered full strength sea water. Hence, if the low gill Na<sup>+</sup>, K<sup>+</sup>-ATPase activity of the 20 smolts sampled in the first smolt group is representative for the migrants in this period, a large number of smolts leaving the River Alta in 2007 possibly possessed a suboptimal smolt quality at the time of sea entry. Despite the possible suboptimal smolt quality of the first tagging group, a study on the survival of the corresponding two groups of tagged smolts during their first days as post-smolt in the Alta Fjord did not show any difference in survival (Davidsen et al. 2009). This finding is a paradox since earlier studies have revealed a strong, positive correlation between gill Na<sup>+</sup>, K<sup>+</sup>-ATPase activity and hypoosmoregulatory ability in Atlantic salmon (Strand et al. 2007) and further, that hypoosmoregulatory ability is predictive for survival in the sea (Virtanen et al. 1991; Staurnes et al. 1993). On the other hand we did not perform seawater challenge tests with these smolts in order to reveal their actual hypoosmoregulatory ability and the smolts were not tested for gill Na<sup>+</sup>/K<sup>+</sup>-ATPase activity at seawater entry. Therefore, categorical statements about smolt quality cannot be made at the current stage.

It is not known whether the difference in gill Na<sup>+</sup>, K<sup>+</sup>-ATPase activity found among migrating smolts in the present study represent a general trait among smolts in River Alta, or represents an occasional event. The result indicates that the quality of wild smolts may vary within smolt runs, but further studies are needed to reveal if this is a frequent event and if it is a general trend that earlier migrants are less prepared for seawater than later migrants. Several other factors may also influence the actual survival of early and late migrating smolts. For example, the risk of being severely infected with the parasitic salmon louse *Lepeophtheirus salmonis* (Krøyer) is shown to be higher for the latest migrating post-smolts in northern fjords (Bjørn et al. 2007), while the food availability often is best for early migrating smolts (Rikardsen et al. 2004; Hvidsten et al. 2009). Such factors may therefore select for early sea entry. The pronounced difference in gill Na<sup>+</sup>, K<sup>+</sup>-ATPase activity found between smolts about to enter sea in the River Alta emphasize the need for more knowledge about how physiological and ecological factors influence migration behaviour and survival of this species.

In conclusion, this study showed that smolts with low gill Na<sup>+</sup>, K<sup>+</sup>-ATPase activity aggregated in the lower part of the river and delayed their sea entry compared to later migrating smolts that appeared to be completely smoltified. Whether this behaviour is related to a need to improve seawater tolerance before sea entry, or an adaptation to synchronise sea entry in order to reduce the risk of predation, is an interesting question open to future research.

**Open Access** This article is distributed under the terms of the Creative Commons Attribution Noncommercial License which permits any noncommercial use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.

## References

- Bjørn PA, Finstad B, Kristoffersen R, Mckinley RS, Rikardsen AH (2007) Differences in risks and consequences of salmon louse, *Lepeophtheirus salmonis* (Krøyer), infestation on sympatric populations of Atlantic salmon, brown trout, and Arctic charr within northern fjords. ICES J Mar Sci 64:386–393
- Boeuf G (1993) Salmonid smolting: a pre-adaptation to the oceanic environment. In: Rankin JC, Jensen FB (eds) Fish ecophysiology. Chapman & Hall, London, pp 105–135

- Davidsen JG, Plantalech Manel-la N, Økland F, Diserud OH, Thorstad EB, Finstad B, Sivertsgård R, McKinley RS, Rikardsen AH (2008) Changes in swimming depths of Atlantic salmon *Salmo salar* post-smolts relative to light intensity. *J Fish Biol* 73:1065–1074. doi:10.1111/j.1095-8649.2008.02004.x
- Davidsen JG, Rikardsen AH, Halttunen E, Thorstad EB, Økland F, Letcher BH, Skarøhamar J, Næsje TF (2009) Migratory behaviour and survival rates of wild northern Atlantic salmon (*Salmo salar*) post-smolts: effects of environmental factors. *J Fish Biol* 75:1700–1718. doi:10.1111/j.1095-8649.2009.02423.x
- Dieperink C, Bak BD, Pedersen LF, Pedersen MI, Pedersen S (2002) Predation on Atlantic salmon and sea trout during their first days as postsmolts. *J Fish Biol* 61:848–852
- Evans DH, Piermarini PM, Choe KP (2005) The multifunctional fish gill: dominant site of gas exchange, osmoregulation, acid-base regulation, and excretion of nitrogenous waste. *Physiol Rev* 85:97–177. doi:10.1152/physrev.00050.2003
- Handeland SO, Järvi T, Fernö A, Stefánsson SO (1996) Osmotic stress, antipredator behaviour, and mortality of Atlantic salmon (*Salmo salar*) smolts. *Can J Fish Aquat Sci* 53:2673–2680
- Handeland SO, Björnsson BT, Arnesen AM, Stefánsson SO (2003) Seawater adaptation and growth of post-smolt Atlantic salmon (*Salmo salar*) of wild and farmed strains. *Aquaculture* 220:367–384. doi:10.1016/S0044-8486(02)00508-2
- Hoar WS (1988) The physiology of smolting salmonids. In: Hoar WS, Randall DJ (eds) *Fish physiology*, vol. XI B. Academic, New York, pp 275–343
- Hvidsten NA, Lund R (1988) Predation on hatchery-reared and wild smolts of Atlantic salmon, *Salmo salar* L., in the estuary of River Orkla. Norway *J Fish Biol* 33:121–126
- Hvidsten NA, Møkkelgjerd PI (1987) Predation on Salmon smolts, *Salmo-Salar* L., in the Estuary of the River Surna. Norway *J Fish Biol* 30:273–280
- Hvidsten NA, Heggberget TG, Jensen AJ (1998) Sea water temperature at Atlantic salmon smolt entrance. *Nordic J Freshw Res* 74:79–86
- Hvidsten NA, Jensen AJ, Rikardsen AH, Finstad B, Aure J, Stefánsson S, Fiske P, Johnsen BO (2009) Influence of sea temperature and initial marine feeding on survival of Atlantic salmon post-smolts. *J Fish Biol* 74:1532–1548. doi:10.1111/j.1095-8649.2009.02219.x
- Järvi T (1989) Synergistic effect on mortality in Atlantic salmon, *Salmo salar*, smolt caused by osmotic stress and presence of predators. *Env Biol Fish* 26:149–152
- Kennedy BM, Gale WL, Ostrand KG (2007) Relationship between smolt gill  $\text{Na}^+$ ,  $\text{K}^+$  ATPase activity and migration timing to avian predation risk of steelhead trout (*Oncorhynchus mykiss*) in a large estuary. *Can J Fish Aquat Sci* 64:1506–1516. doi:10.1139/F07-117
- Lacroix GL, Knox D (2005) Distribution of Atlantic salmon (*Salmo salar*) post-smolts of different origins in the Bay of Fundy and Gulf of Maine and evaluation of factors affecting migration, growth and survival. *Can J Fish Aquat Sci* 62:1363–1376
- Lysfjord G, Staurnes M (1998) Gill  $\text{Na}^+$ - $\text{K}^+$ -ATPase activity and hypoosmoregulatory ability of seaward migrating smolts of anadromous Atlantic salmon (*Salmo salar*), sea trout (*Salmo trutta*) and Arctic char (*Salvelinus alpinus*) in the Hals river, northern Norway. *Aquaculture* 168:279–288
- McCormick SD (1993) Methods for nonlethal gill biopsy and measurement of  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase activity. *Can J Fish Aquat Sci* 50:656–658
- McCormick SD, Saunders RL (1987) Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth and metabolism. *Am Fish Soc Symp* 1:211–229
- McCormick SD, Hansen LP, Quinn TP, Saunders RL (1998) Movement, migration and smolting of Atlantic salmon (*Salmo salar*). *Can J Fish Aquat Sci* 55:77–92
- Moser ML, Olson AF, Quinn TP (1991) Riverine and estuarine migratory behavior of Coho salmon (*Oncorhynchus kisutch*) smolts. *Can J Fish Aquat Sci* 48:1670–1678
- Reitan O, Hvidsten NA, Hansen LP (1987) Bird predation on hatchery reared Atlantic salmon smolts, *Salmo salar* L., released in the River Eira, Norway. *Fauna Norv Ser A* 8:35–38
- Rikardsen AH, Haugland M, Bjørn PA, Finstad B, Knudsen R, Dempson JB, Holst JC, Hvidsten NA, Holm M (2004) Geographical differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. *J Fish Biol* 64:1655–1679. doi:10.1111/j.1095-8649.2004.00425.x
- Solbakken VA, Hansen T, Stefánsson SO (1994) Effects of photoperiod and temperature on growth and parr-smolt transformation in Atlantic salmon (*Salmo salar* L.) and subsequent performance in seawater. *Aquaculture* 121:13–27. doi:10.1046/j.1365-2109.1999.00362.x
- Staurnes M, Lysfjord G, Hansen LP, Heggberget TG (1993) Recapture rates of hatchery-reared Atlantic salmon (*Salmo salar*) related to smolt development and time of release. *Aquaculture* 118:327–337
- Stefánsson SO, Berge AI, Gunnarsson GS (1998) Changes in seawater tolerance and gill  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase activity during desmoltification in Atlantic salmon kept in freshwater at different temperatures. *Aquaculture* 168:271–277
- Stewart DC, Middlemas SJ, Youngson AF (2006) Population structuring in Atlantic salmon (*Salmo salar*): evidence of genetic influence on the timing of smolt migration in sub-catchment stocks. *Ecol Freshw Fish* 15:552–558
- Strand JET, Johnsen HK, Arnesen AM (2007) Comparison of parr-smolt transformation in hatchery reared offspring of one domesticated and two wild populations of Atlantic salmon (*Salmo salar* L.). *Aquaculture* 273:250–256. doi:10.1016/j.aquaculture.2007.10.007
- Thorpe JE, Metcalfe NB, Fraser NHC (1994) Temperature dependence of switch between nocturnal and diurnal smolt migration in Atlantic salmon. In: MacKinlay D (ed) *High performance fish*. University of British Columbia, Vancouver, pp 83–86
- Virtanen E, Söderholm-Tana L, Soivio A, Forsman L, Muona M (1991) Effect of physiological condition and smoltification status at smolt release on subsequent catches of adult salmon. *Aquaculture* 97:231–257
- Zydlewski GB, Haro A, McCormick SD (2005) Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behavior of Atlantic salmon (*Salmo salar*) smolts. *Can J Fish Aquat Sci* 62:68–78. doi:10.1139/F04-179