Transactions of the American Fisheries Society 126:707–714, 1997
© Copyright by the American Fisheries Society 1997

Influence of Transmitter Attachment Procedures on Swimming Performance of Wild and Hatchery-Reared Atlantic Salmon Smolts

S. PEAKE AND R. S. MCKINLEY[1]

Department of Biology, University of Waterloo
Waterloo, Ontario N2L 3G1, Canada

D. A. SCRUTON

Science Branch, Habitat Research and Assessment, Department of Fisheries and Oceans
Post Office Box 5667, St. John's, Newfoundland A1C 5X1, Canada

R. MOCCIA

Department of Animal and Poultry Science, University of Guelph
Guelph, Ontario N1G 2W1, Canada

Abstract.—Effects of transmitter attachment procedures on smolts of Atlantic salmon *Salmo salar* have primarily been examined in the laboratory with hatchery-reared fish. Biotelemetry researchers must extrapolate findings of tagging studies to wild, migrating smolts. Because hatchery rearing can affect salmonid development and because field tagging procedures and environmental conditions can differ from those in the laboratory, we measured critical swimming speed of hatchery-reared Atlantic salmon smolts equipped with internal, external, or gastric dummy radio transmitters in the laboratory. We then repeated the experiment with wild, migrating fish in ambient environmental conditions. Swimming ability of hatchery smolts was not significantly affected by any attachment procedure, and no significant differences were found between fish tested 1 or 16 h after tagging. Similarly, wild smolts were not impaired by gastric transmitters; however, performance of wild fish tested 1 or 16 h after internal or external attachment was significantly lower than that of wild controls. Thus, reaction of hatchery-reared Atlantic salmon smolts to attachment procedures can differ from that of wild migrants. Biotelemetry researchers should exercise caution in interpreting data obtained from wild Atlantic salmon smolts equipped with internal or external radio transmitters during the first 16 h after tagging.

Recent technological advances in the design of radio and acoustic transmitters have allowed biotelemetry studies to be performed on increasingly smaller fish such as smolts of Atlantic salmon *Salmo salar*. Migratory behavior of tagged fish can represent that of the untagged population if transmitter attachment causes minimal physiological disturbance and no impairment of swimming. Currently used transmitters are surgically implanted into the body cavity (internal), inserted into the stomach (gastric), or fixed to the surface of the body (external; Mellas and Haynes 1985). Studies that have investigated the measurable effects of these procedures generally indicated that external tagging could significantly alter behavior or swimming ability of juvenile Atlantic salmon whereas gastric and internal tagging might not (McCleave and Stred 1975; Greenstreet and Morgan 1989; Moore et al. 1990).

The majority of studies investigating tagging effects on Atlantic salmon smolts has examined large hatchery-reared fish in the laboratory. The direct application of these results to biotelemetry studies in the field, however, may not be appropriate for several reasons. First, rearing conditions within hatcheries can cause alterations in growth (Boeuf and Gaignon 1989), development (Fleming et al. 1994), and smoltification (Kazakov and Kozlov 1985; Bjornsson et al. 1989; Farmer et al. 1989), all of which may affect swimming performance (Smith 1982) or tag-carrying ability.

Second, ratio of tag mass to fish mass (tag ratio) can affect the suitability of a particular attachment procedure (Marty and Summerfelt 1986). Because domestic stock tend to be more robust than fish from a wild population (Beamish 1978), large hatchery smolts, having low tag ratios, could possibly carry transmitters better than wild fish having higher tag ratios. Third, published studies have generally examined tagging effects in the sterile and stable conditions of the laboratory. Downstream migration of wild smolts often occurs after

[1] To whom correspondence should be addressed.

TABLE 1.—Mean fork length, mass, condition factor, range of tag ratios, and mean critical speed (Ucrit) of Atlantic salmon smolts within treatment groups. An asterisk (*) indicates a value for hatchery smolts that is significantly greater ($P < 0.05$) than the corresponding value for wild smolts.

Tag type	Treatment	N	Mean temperature (°C)	Fork length ± SD (cm)	Mass ± SD (g)	Condition factor[a]	Tag ratio (%)[b]	Ucrit ± SE (m/s)
				Hatchery smolts				
Internal	Tagged	12	12.0	20.0 ± 1.7*	106.9 ± 21.6*	1.336*	1.9–3.6	1.63 ± 0.02*
	Sham	12	12.0	19.4 ± 1.3	102.9 ± 17.4	1.409		1.68 ± 0.03
External	Tagged	12	12.0	20.2 ± 1.4*	112.5 ± 15.9*	1.365*	1.8–2.9	1.55 ± 0.02*
	Sham	12	12.0	19.1 ± 1.3	98.3 ± 16.6	1.411		1.62 ± 0.03
Gastric	Tagged	12	12.0	20.8 ± 1.3*	103.5 ± 12.7*	1.150*	2.1–3.0	1.52 ± 0.06*
	Sham	12	12.0	19.7 ± 1.1	103.5 ± 15.4	1.354		1.63 ± 0.03
Control		6	12.0	19.4 ± 0.8*	95.3 ± 10.5*	1.305*		1.61 ± 0.04*
				Wild smolts				
Internal	Tagged	12	16.3	18.7 ± 1.2	54.2 ± 11.4	0.829	3.0–6.0	1.14 ± 0.02
External	Tagged	12	15.4	18.6 ± 0.6	54.0 ± 5.9	0.839	4.0–5.9	1.15 ± 0.04
Gastric	Tagged	12	16.3	18.9 ± 1.2	59.0 ± 6.4	0.874	3.5–5.2	1.45 ± 0.02
Control		12	15.6	18.5 ± 1.0	55.4 ± 5.3	0.875		1.46 ± 0.03

[a] Condition factor = 100 × (mass, g)/(length, cm)^3.
[b] Tag ratio = 100 × (tag mass, g)/(fish mass, g).

heavy rains that cause fluctuations in discharge, turbidity, and water temperature (Solomon 1978). Therefore, laboratory studies, performed in the absence of environment, may underestimate responses of wild tagged fish to attachment procedures. Finally, previous studies have allowed tagged smolts to recover for periods of 24 h to several days before measuring swimming ability. In the field, fish are often released after recovery from anesthesia because timely release is particularly important if migration time and transmitter battery life are short.

These considerations suggest that responses by large, hatchery-reared Atlantic salmon smolts to tag attachment procedures under laboratory conditions may not be directly applicable to biotelemetry studies involving wild migrating smolts. To test this hypothesis, we measured critical swimming speeds of large hatchery smolts equipped with internal, external, and gastric tags in the laboratory. We then repeated the experiment with wild fish tagged and tested under field conditions. Groups were examined 1 or 16 h after transmitter attachment to determine if tagged smolts can be released soon after surgery.

Methods

Transmitters.—Dummy transmitters were identical to operational radio tags except that the battery and electronics were replaced with lead shot of equal mass. Tags were cylindrical, weighed 2.6 g in air, measured 22 mm in length, had a diameter of 7 mm, and were equipped with a 20-cm flexible wire antenna.

Hatchery smolts.—Hatchery-reared Atlantic salmon smolts were obtained from the Alma Aquaculture Station in Alma, Ontario, and all research on hatchery fish was conducted in a laboratory at this facility during the last 3 weeks of May 1995. Prior to this study, fish had been held for several months in a rectangular raceway (10 × 2 × 1 m) in which water was circulated at a rate of approximately 30 cm/s. Fish were fed commercial trout pellets from demand feeders and were exposed to the ambient photoperiod.

In all, 78 hatchery smolts were used. Three subgroups of 12 fish each were equipped with either internal, external, or gastric dummy transmitters; in each group, 6 fish were tested after 1 h, and 6 were tested 16 h after tagging. Three additional subgroups of 12 fish each were sham-tagged and tested in the same manner as tagged fish. A final group of 6 fish, tested 1 h after approximately 10 s of handling without anesthesia or surgery, served as controls. Mean lengths and masses of smolts within each treatment group are given in Table 1.

One day before experimentation, smolts were transferred to a 2,000-L circular holding tank and not fed, thus ensuring a postabsorptive state. The holding tank was aerated and supplied with freshwater (mean temperature, 12.0°C; range, 11.0–13.0°C). Water was circulated around the tank at approximately 20 cm/s. Fish to be examined 1 h after transmitter attachment were tagged late in the morning, placed in a 750-L recovery tank (aerated and supplied with freshwater circulated at approximately 20 cm/s) for 1 h, and then tested. Smolts

to be examined 16 h after attachment were tagged in the afternoon, placed in the recovery tank for 16 h, and then tested. After experimentation, fish were sacrificed by anesthetic overdose.

Hatchery smolts tagged with internal and external procedures were randomly selected from the 2,000-L holding tank and anesthetized by immersion in a MS-222 (tricaine methanesulfonate) bath (50 mg/L, buffered). Procedures used were similar to those of Mellas and Haynes (1985) with some minor exceptions. First, all fish were tagged in a V-shaped surgical tray. The tray contained freshwater for external tagging, whereas a diluted anesthetic solution (25 mg/L) was used for internal tagging. Second, for smolts equipped with internal tags, a small puncture was made in the body wall to one side of the initial incision, and the transmitter antenna was threaded through the puncture from inside the fish. All smolts were considered to have recovered from anesthesia when their buoyancy was regained and station was taken up in the current.

For gastric tagging, fish were placed in a gastric insertion chamber. The chamber was constructed from polyvinyl chloride (PVC) pipe (38 × 5 cm) with the top removed and the ends capped. A small hole was made in the front end cap and the apparatus was filled with freshwater. Fish were individually placed inside the chamber with the mouth against the front end cap. The transmitter was partly inserted into one end of a drinking straw (6-mm diameter), which was dipped into vegetable oil and inserted through the hole in the end cap, into the fish's mouth and into its stomach. A wire was pushed through the straw, injecting the dummy transmitter into the stomach. The wire and straw were then removed from the fish. The antenna exited via the mouth and was bent backwards to trail alongside the fish, which was then placed in the 750-L recovery tank.

Wild smolts.—Wild Atlantic salmon smolts were collected from a counting fence in Micmac Brook on the Indian River watershed in north central Newfoundland, Canada (approximately 49°N, 56°W). The counting fence was located approximately 45 km upstream from the estuary. Experiments occurred during the smolt migration (June 1995) at the Department of Fisheries and Oceans Indian River Research Station approximately 5 km from the collection site.

From the 48 wild smolts that were used, three subgroups of 12 fish each were equipped with internal, external, or gastric dummy transmitters; in each group, fish were tested after 1 h, and the remaining fish were tested 16 h after tag attachment. Because wild smolts of lengths similar to hatchery fish were scarce, not enough wild fish could be obtained to allow parallel sham tagging of similar groups. Instead, 6 fish were anesthetized for approximately 3 min before being revived and examined 1 h later. Another 6 smolts, tested 1 h after approximately 10 s of handling without anesthesia or surgery, served as controls. Mean lengths and masses of fish from each treatment group are given in Table 1.

Fish to be examined 1 h after attachment were captured in the morning, tagged, placed in a 750-L recovery tank containing Indian River water (mean temperature, 15.9°C; range, 14.8–18.3°C; circulated at approximately 20 cm/s) for 1 h, and then tested. Smolts to be examined 16 h after transmitter attachment were collected in the afternoon, tagged, placed in the 750-L tank for 16 h, and then tested. Control and gastric-tagged smolts were released after experimentation, while internally and externally tagged fish were sacrificed by anesthetic overdose.

Wild fish were subjected to the same surgical procedures described for hatchery smolts except for anesthetic used. Wild smolts were anesthetized with 2-phenoxyethanol diluted to 1 : 2,500 (volume : volume) due to regulations concerning anesthetic use in the field.

Swimming performance.—Swimming performance was evaluated by measuring critical swimming speed, a measure of prolonged swimming ability first described by Brett (1964). Experiments began by placing 3 smolts from the same treatment group in a 120-L Blazka-type swim speed chamber. Water was pumped from the 750-L recovery tanks, through the chamber, and back into the tanks. Fish were initially acclimated to a water velocity of 0.50 m/s for 2 h, after which velocity was increased by 0.13 m/s every 10 min until smolts were unable to leave the downstream retaining screen. Final swimming speed, time of fatigue, water temperature, and mass and fork length of each fish were recorded. Critical speed (U_{crit}) was determined by using the formula described by Beamish (1978).

One-way analysis of variance (ANOVA), linear regression analysis, and Bonferroni multiple comparisons were used to statistically examine the data. When equal variance tests failed, nonparametric tests were used (Kruskal–Wallis one-way ANOVA, Dunn's multiple comparison).

TABLE 2.—The P-values for linear regressions testing for correlations, within treatment groups, between critical swimming speed (Ucrit) of Atlantic salmon smolts and fork length, mass, and water temperature. No significant correlations were found (all Ps > 0.05).

Tag type	Treatment	P-values for: Fork length on Ucrit	Mass on Ucrit	Temperature on Ucrit
		Hatchery smolts		
Internal	Tagged	0.49	0.81	
	Sham	0.73	0.40	
External	Tagged	0.92	0.96	
	Sham	0.74	0.67	
Gastric	Tagged	0.87	0.44	
	Sham	0.49	0.26	
Control		0.22	0.57	
		Wild smolts		
Internal	Tagged	0.12	0.23	0.09
External	Tagged	0.35	0.34	0.26
Gastric	Tagged	0.17	0.08	0.73
Control		0.99	0.81	0.59

Results

No alterations in behavior among tagged wild and hatchery smolts were noticed and no mortalities occurred. Recovery of hatchery and wild smolts from anesthesia, after internal and external tag placement, occurred in 2–5 min. Both hatchery and wild fish equipped with gastric tags displayed a coughing-type behavior for a short time after tagging; however, this reaction was not observed in fish swimming in the flume.

Hatchery Smolts

Mean fork length (one-way ANOVA; $F = 1.55$; df = 12, 65; $P > 0.05$) and mass (one-way ANOVA; $F = 1.73$; df = 12, 65; $P > 0.05$) of hatchery Atlantic salmon smolts did not differ significantly among initial treatment groups. No significant differences in Ucrits occurred within treatment groups of fish tested 1 and 16 h after surgery (one-way ANOVA; $F = 1.35$; df = 11, 60; $P > 0.05$), so these data were pooled. Linear regression analysis showed that critical speeds of control fish, sham-tagged fish, and fish tagged with internal, external or gastric transmitters, were not significantly affected by fork length or mass (Table 2). No significant differences in critical swimming speed were found (Kruskal–Wallis one-way ANOVA; $H = 8.84$; $P > 0.05$) between tagged and sham-tagged groups (Table 1). Finally, mean critical swimming speeds among controls and smolts with gastric, internal, and external tags (Kruskal–Wallis one-way ANOVA; $H = 3.89$; $P > 0.05$) were not significantly different (Table 1).

Wild Smolts

Mean lengths of wild Atlantic salmon smolts, among initial treatment groups, were not significantly different (one-way ANOVA; $F = 0.296$; df = 7, 40; $P > 0.05$). Similarly, mean fish mass (Kruskal–Wallis one-way ANOVA; $H = 8.8$; $P > 0.05$) and water temperature (Kruskal–Wallis one-way ANOVA; $H = 10.9$; $P > 0.05$) did not differ significantly among treatment groups. No significant differences were found in Ucrits of fish tested 1 and 16 h after being equipped with gastric tags (Bonferroni multiple comparison; $t = 0.14$; $P > 0.05$), external tags (Bonferroni multiple comparison; $t = 1.57$; $P > 0.05$) or internal tags (Bonferroni multiple comparison; $t = -0.79$; $P > 0.05$), so these data were pooled. Swimming ability of controls and anesthetic sham controls was not significantly different (Bonferroni multiple comparison; $t = 0.67$; $P > 0.05$), so these data were also pooled. Linear regression analysis revealed that critical speeds of controls and tagged fish were not significantly affected by fork length, mass, or water temperature (Table 2). Significant differences were found in mean critical swimming speed among control smolts and those with gastric, internal, and external tags (one-way ANOVA; $F = 29.4$; df = 3, 44; $P < 0.05$). Controls and gastrically tagged fish did not differ significantly (Bonferroni multiple comparison; $t = 0.09$; $P > 0.05$), and fish with internal and external tags did not differ significantly (Bonferroni multiple comparison; $t = 0.08$; $P > 0.05$); however, smolts equipped with internal tags had a significantly lower mean Ucrit than control fish (Bonferroni multiple comparison; $t = 6.72$; $P < 0.05$) and gastrically tagged fish (Bonferroni multiple comparison; $t = 6.63$; $P < 0.05$). Similarly, smolts equipped with external tags had significantly lower mean critical speeds than gastrically tagged fish (Bonferroni multiple comparison; $t = 6.55$; $P < 0.05$) and control fish (Bonferroni multiple comparison; $t = 6.64$; $P < 0.05$) fish (Table 1).

Hatchery versus Wild Smolts

Because significant differences in length occurred between wild and hatchery smolts (Table 1), treatment effects on critical swimming speed relative to body length were compared (Figure 1). Mean relative Ucrit was found to differ significantly (Kruskal–Wallis one-way ANOVA; $H = 45$; $P < 0.05$) between similarly tagged hatchery and

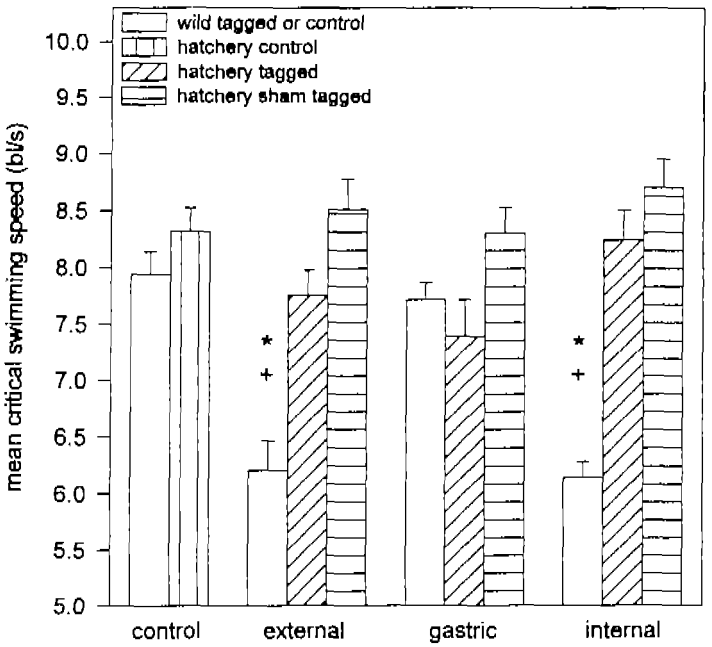

FIGURE 1.—Mean relative critical speeds (Ucrits) in body lengths per second (bl/s) of hatchery and wild Atlantic salmon smolts from the various tag treatments. An asterisk (*) indicates a significant difference between groups of similarly tagged wild and hatchery smolts. A plus (+) indicates a significant difference in mean relative Ucrit between a group of hatchery or wild fish and that of the corresponding hatchery or wild control group. Vertical line above bar indicates 1 SE.

wild fish. No significant difference was found in relative critical speed between hatchery and wild controls (Dunn's multiple comparison; $Q = 0.92$; $P > 0.05$) or between hatchery and wild gastrically tagged smolts (Dunn's multiple comparison; $Q = 0.82$; $P > 0.05$). Relative critical speed was, however, significantly reduced in wild smolts tagged with external (Dunn's multiple comparison; $Q = 3.19$; $P < 0.05$) and internal (Dunn's multiple comparison; $Q = 4.72$; $P < 0.05$) dummy transmitters relative to similarly tagged hatchery-reared smolts.

Discussion

In rivers, migrating Atlantic salmon smolts are thought to swim against but not faster than the flow rate, resulting in downstream movement at a speed slower than that of the current (Solomon 1978; Smith 1982). If the ability of a smolt to swim against the current is impaired by a particular transmitter attachment, the smolt's downstream travel rate will be faster than that of untagged fish, thus biasing telemetry data (Greenstreet and Morgan 1989). The present study indicates that, in the short term, prolonged swimming ability of hatchery-reared Atlantic salmon smolts is not affected by internal, external, or gastric dummy transmitter attachment. Critical speed of wild smolts is also not affected by gastric tags; however, wild fish equipped with external and internal tags showed 21.9% and 22.7% reductions in performance, respectively, relative to controls. Therefore, had these fish been used in a biotelemetry study, data collected for the first 16 h period might not have reflected the behavior of untagged migrants.

Mean Ucrits of wild fish equipped with external and internal dummy transmitters did not differ significantly, suggesting that drag due to external tags did not impair swimming ability. In addition, neither internal nor gastric tags contributed to drag; yet, performance was impaired by internal transmitters but not by gastric transmitters. These patterns suggest that the effect of the internal and external tags on swimming performance of wild smolts was physiological rather than mechanical. Internal and external procedures share one important characteristic: they both involve cutting or piercing of tissue. Although gastric tagging may cause fish some discomfort; little or no tissue damage occurs. Thus, stress caused by the surgical procedures probably contributed most to the reduced ability of wild smolts to carry internal and

external transmitters. That hatchery smolts were unaffected suggests they were not as stressed by the procedures or that their tolerance to stress was greater than that of wild fish.

Despite our attempts to treat hatchery and wild fish in as similar a manner as possible, some differences in methodology were unavoidable. These differences illustrate the need for caution in directly applying the results of laboratory tagging studies, performed on hatchery smolts, to field-based biotelemetry research. First, different anesthetics were used because environmental regulations did not permit us to use MS-222 in the field. Nevertheless, we believe that anesthetic use did not influence our results because no differences in recovery between anesthetized wild and hatchery fish were observed. Furthermore, swimming ability of wild fish was not affected by the use of 2-phenoxyethanol because no significant differences were observed between anesthetized and nonanesthetized controls; likewise, MS-222 did not affect swimming performance of hatchery smolts in similar comparisons.

Second, water temperatures during the time of the wild smolt migration were slightly higher than those at the hatchery. Although swimming ability of wild smolts, within treatment groups, was not altered significantly by fluctuations in water temperature (Table 2), wild fish possibly were affected by internal and external tagging because of the higher water temperatures. Also, although internal tags reduced swimming performance of wild fish, gastric tags did not, even though they both were tested at the same mean temperature (Table 1). Nevertheless, subsequent tagging studies should be carried out across a range of water temperatures that include all values that may be encountered in the field.

Third, hatchery fish might have been less stressed than wild stock prior to tagging because hatchery fish were probably more accustomed to handling and confinement. Capture and confinement of wild fish are inherent to most biotelemetry studies, and their effect on physiological condition cannot be properly simulated with hatchery fish. Fourth, because of differences in selective pressure, fish stocks may differ in terms of morphology, swimming ability, and stress tolerance. However, this possibility exists whenever findings from one fish population are extrapolated to another.

Finally, domestic fish tend to be more robust than wild stock (Beamish 1978). In the present study, mean length of hatchery fish was only slightly greater than that of wild smolts; however, hatchery fish were 43–52% heavier (Table 1). This phenomenon can have practical implications. Ratio of fish mass to transmitter mass, or tag ratio, has been shown to be an important consideration for the biotelemetry researcher, influencing the suitability of external (Greenstreet and Morgan 1989), internal (Marty and Summerfelt 1986), and gastric (Moser et al. 1990) attachments. In general, low tag ratios are considered to be more suitable than higher values. Tag ratios for hatchery smolts, in the present study, were lower than those of wild fish (Table 1), thus differences in tag-carrying ability might have resulted from inconsistencies in tag ratios.

The high condition factor of our hatchery smolts also suggests that they might have undergone a process called reverse smoltification. Normal smoltification involves a reduction in condition factor (Hoar 1988); however, Woo et al. (1978) reported that smolts of coho salmon *Oncorhynchus kisutch*, prevented from entering salt water, regained the high tissue fat and glycogen levels characteristic of parr. Other biochemical and behavioral factors associated with smoltification, such as salinity preference (McInerney 1964), glomerular filtration rate (Holmes and Stainer 1966), and branchial Na^+,K^+-ATPase activity (Zaugg and McLain 1970), have been shown to be reversible.

Smoltification of our hatchery stock also might have been incomplete or altered. Variables inherent to hatchery rearing that have been shown to affect development, smoltification, or levels of hormones involved in smoltification include size of holding tanks and rate of water flow (Boeuf and Gaignon 1989), type of artificial diet (Bergstrom 1989), water chemistry and pH (Farmer et al. 1989), photoperiod and temperature (Bjornsson et al. 1989), and illumination intensity (Kazakov and Kozlov 1985). If smoltification was altered, swimming performance of the hatchery stock might have been affected. Graham et al. (1996) found that station holding performance of juvenile Atlantic salmon, relative to body length, increased as fish became more silver in color. In addition, swimming ability among the hatchery and wild fish might have differed due to differences in body form. Taylor and McPhail (1985) found that fusiform juvenile coho salmon had greater swimming stamina than more robust fish of the same species. Thus, the possibility that wild-type development and smoltification of juvenile salmon can be altered or reversed by conditions in a hatchery makes it nearly impossible for researchers to ensure that morphology, physiology, behavior, and

swimming capability of hatchery-reared fish, at any given time or place, match those of wild smolts.

In conclusion, we report that, for a variety of possible reasons, wild Atlantic salmon smolts did not react to transmitter attachment procedures in the same way as hatchery-reared fish. Gastric tagging of wild and hatchery-reared Atlantic salmon smolts did not impair swimming ability and may be an appropriate attachment procedure in the short term. Problems associated with feeding, however, have been reported (Armstrong and Rawlings 1993) and may affect suitability for longer-term studies. Unlike hatchery fish, wild fish demonstrated significantly reduced prolonged swimming ability when tagged with external or internal transmitters, and performance did not improve after 16 h of recovery. Thus, results of laboratory tagging studies that use hatchery-reared smolts should be cautiously extrapolated to wild migrants. In addition, researchers should critically examine telemetry data from internally or externally tagged wild smolts if conditions such as water temperature or tag ratio differ from those in published tag studies. This cautionary action can be especially important if downstream migration rate is observed to be close to the speed of the current.

Acknowledgments

We thank T. Beddow, D. L. G. Noakes, G. Power, and G. Anderson for their critical reviews of the manuscript. We also wish to acknowledge the support provided by Lotek Engineering, Inc., for this study and the Canada Department of Fisheries and Oceans staff at Indian River (P. Rose, L. Cole, and T. Nicholls) for their technical assistance. Funding was provided to R.S.M. by the Department of Fisheries and Oceans and the Natural Sciences and Engineering Research Council of Canada.

References

Armstrong, J. D., and C. E. Rawlings. 1993. The effect of intragastric transmitters on feeding behaviour of Atlantic salmon, *Salmo salar*, parr during autumn. Journal of Fish Biology 43:646–648.

Beamish, F. W. H. 1978. Swimming capacity. Pages 101–187 *in* W. S. Hoar and D. J. Randall, editors. Fish physiology, volume 7. Academic Press, New York.

Bergstrom, E. 1989. Effect of natural and artificial diets on seasonal changes in fatty acid composition and total body lipid content of wild and hatchery-reared Atlantic salmon, *Salmo salar*, parr–smolt. Aquaculture 82:205–217.

Bjornsson, B., H. Thorarensen, T. Hirano, T. Ogasawara, and J. B. Kristinsson. 1989. Photoperiod and temperature affect plasma growth hormone levels, growth, condition factor, and hypoosmoregulatory ability of juvenile Atlantic salmon, *Salmo salar*, during parr–smolt transformation. Aquaculture 82: 77–91.

Boeuf, G., and J. L. Gaignon. 1989. Effects of rearing conditions on growth and thyroid hormones during smoltification of Atlantic salmon, *Salmo salar* L. Aquaculture 82:29–38.

Brett, J. R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. Journal of the Fisheries Research Board of Canada 21: 1183–1226.

Farmer, G. J., R. L. Saunders, T. R. Goff, C. E. Johnston, and E. B. Henderson. 1989. Some physiological responses of Atlantic salmon, *Salmo salar*, exposed to soft, acidic water during smolting. Aquaculture 82:229–244.

Fleming, I. A., B. Jonsson, and M. R. Gross. 1994. Phenotypic divergence of sea-ranched, farmed, and wild salmon. Canadian Journal of Fisheries and Aquatic Sciences 51:2808–2824.

Graham, W. D., J. E. Thorpe, and N. B. Metcalfe. 1996. Seasonal current holding performance of juvenile Atlantic salmon in relation to temperature and smolting. Canadian Journal of Fisheries and Aquatic Sciences 53:80–86.

Greenstreet, S. P. R., and R. I. G. Morgan. 1989. The effect of ultrasonic tags on the growth rates of Atlantic salmon, *Salmo salar*, parr of varying size just prior to smolting. Journal of Fish Biology 24:235–244.

Hoar, W. S. 1988. The physiology of smolting salmonids. Pages 275–343 *in* W. S. Hoar and D. J. Randall, editors. Fish physiology, volume 11B. Academic Press, New York.

Holmes, W. N., and I. M. Stainer. 1966. Studies on the renal excretion of electrolytes by the trout, *Salmo gairdneri*. Journal of Experimental Biology 44:33–46.

Kazakov, R. V., and V. V. Kozlov. 1985. Quantitative estimation of degree of silvering displayed by Atlantic salmon, *Salmo salar*, juveniles originating from natural populations and from fish-rearing farms. Aquaculture 44:213–220.

Marty, G. D., and R. C. Summerfelt. 1986. Pathways and mechanisms for expulsion of surgically implanted dummy transmitters from channel catfish. Transactions of the American Fisheries Society 115: 577–589.

McCleave, J. D., and K. A. Stred. 1975. Effect of dummy telemetry transmitters on the stamina of Atlantic salmon, *Salmo salar*, smolts. Journal of the Fisheries Research Board of Canada 32:559–563.

McInerney, J. E. 1964. Salinity preference: an orientation mechanism in salmon migration. Journal of the Fisheries Research Board of Canada 21:995–1018.

Mellas, E. J., and J. M. Haynes. 1985. Swimming performance and behaviour of rainbow trout, *Salmo gairdneri*, and white perch, *Morone americana*: effects of attaching telemetry transmitters. Canadian

Journal of Fisheries and Aquatic Sciences 42:488–493.

Moore, A., I. C. Russell, and E. C. E. Potter. 1990. The effects of intraperitoneally implanted dummy acoustic transmitters on the behaviour and biology of juvenile Atlantic salmon, *Salmo salar*. Journal of Fish Biology 37:713–721.

Moser, M. L., A. D. Olson, and T. P. Quinn. 1990. Effects of dummy ultrasonic transmitters on juvenile coho salmon. Pages 353–356 *in* N. C. Parker and five coeditors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Smith, L. S. 1982. Decreased swimming performance as a necessary component of the smolt migration in salmon in the Columbia River. Aquaculture 28:153–161.

Solomon, D. J. 1978. Some observations on salmon smolt migration in a chalk stream. Journal of Fish Biology 12:571–574.

Taylor, E. B., and J. D. McPhail. 1985. Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Canadian Journal of Fisheries and Aquatic Sciences 42:2029–2033.

Woo, N. Y. S., H. A. Bern, and N. S. Nishioka. 1978. Changes in body composition associated with smoltification and premature transfer to seawater in coho salmon, *Oncorhynchus kisutch*, and king salmon, *Oncorhynchus tshawytscha*. Journal of Fish Biology 13:420–428.

Zaugg, W. S., and L. R. McLain. 1970. Adenosine triphosphatase activity in gills of salmonids: seasonal variation and salt water influence in coho salmon, *Oncorhynchus kisutch*. Comparative Biochemistry and Physiology 35:587–596.

Received December 29, 1995
Accepted December 16, 1996