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Effects of Acoustic Transmitters on Swimming Performance and Predator Avoidance of Juvenile Chinook Salmon

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Abstract.—The objective of this study was to determine whether juvenile Chinook salmon *Oncorhynchus tshawytscha* are negatively influenced by the intraperitoneal implantation of acoustic transmitters. We evaluated swimming performance and predator avoidance of juvenile salmonids implanted with acoustic transmitters that weighed up to 6.7% of the fish's body weight in air. Critical swimming speeds (U_{crit}) of tagged, sham-tagged (surgery but no tag), and control fish were measured in a respirometer to determine tag effects on swimming performance. Swimming performance was similar among treatment groups at 1-d and 21-d postsurgery intervals. Predator avoidance of fish implanted with active tags was evaluated to determine whether tagged fish were impaired by the operation of the tags or predators were attracted to the signals emitted from the tags. Predator avoidance was evaluated by comparing the proportion of each treatment group consumed (active tag, inactive tag, sham, and control) during exposure to piscivorous adult rainbow trout *O. mykiss*. Surgical implantation of acoustic tags in juvenile fall Chinook salmon did not significantly affect swimming performance. Implantation of acoustic transmitters (active and inactive) did not result in greater predation susceptibility in tagged fish than in untagged fish.

Characterization of hydroelectric project impacts on migrating salmonids is a common component of current environmental impact statements and operational license applications. Biotelemetry is frequently used to characterize these impacts and provides biologists and managers with large- and fine-scale movement data from known individuals that can then be used to determine factors such as survival, travel rate, and passage routes through dams. Biotelemetry is currently used throughout the Columbia River basin to evaluate the survival and behavior of salmon *Oncorhynchus* spp. and steelhead *O. mykiss* as they pass hydroelectric projects. Juvenile salmonids in the basin are currently tracked with transmitters that emit a signal in either ultrasonic (69–307 kHz) or radio (27–300 MHz) frequency ranges.

Application of inferences from biotelemetry data to the population at large assumes that the movement, behavior, and survival of the tagged fish is unaffected by the tag implantation method, the mass of the antenna, or the drag created by the antenna (Schreck 1990). Results from studies designed to identify tag biases are mixed. Studies of juvenile Atlantic salmon *Salmo salar* (McCleave and Stred 1975), juvenile coho salmon *O. kisutch* (Moser et al. 1990), and juvenile rainbow trout (Brown et al. 1999) found no significant difference in short-term swimming performance between fish implanted with transmitters and controls. In the study conducted by Brown et al. (1999), transmitter antennas were trimmed to 2.5 cm, and the authors suggested that an antenna's length might have an additional impact on a fish's ability to swim and avoid predation. Therefore, a long, trailing antenna may constitute more of a burden to juvenile fishes than a large, internal transmitter. This idea is supported by the findings of Adams et al. (1998), who observed decreased swimming performance in fish implanted with transmitters weighing from 4.6% to 10.4% of a fish's body weight. The transmitters used in the Adams et al. (1998) study had external antennas that were 31 cm in length. Unfortunately, the fish used in most of these studies were larger than a typical outmigrating salmon smolt in the Columbia River; however, use of transmitters without external an-

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tennas may be one way to minimize any bias associated with biotelemetry studies of these small fish.

Ultrasonic transmitters, commonly referred to as acoustic transmitters, offer a viable alternative to radio transmitters; the two types are similar in size, but acoustic transmitters do not have external antennas. Acoustic transmitters do, however, have the potential for physical damage to hair cells arising from the acoustic output of the transmitter (Abbott 1973). Damage to the hair cells of a fish's lateral line could result in reduced short-distance detection of predators and prey (Popper and Carlson 1998). Denton and Gray (1993) demonstrated damage to the sensory hair cells of clupeid fishes as the result of intense sound stimulation. The review of studies presented in Popper and Carlson (1998) demonstrate that sound can be used to alter salmonid behavior. However, the frequency of sound used in these studies was typically less than 300 Hz, and the source was external to the fish. We are unaware of any studies that have implicitly investigated the effect of an implanted ultrasonic source on juvenile salmonid behavior or swimming performance.

Despite the importance of understanding the effects of acoustic transmitters on the behavior of downstream-migrating juvenile salmon, no studies have been conducted on juvenile presmolt Chinook salmon *O. tshawytscha* tagged with acoustic transmitters. Our objective was to determine the effect of surgically implanted acoustic transmitters on the swimming performance and predator avoidance of juvenile Chinook salmon. The study was designed to answer two questions: (1) is swimming performance influenced by the tagging process or the presence of an acoustic transmitter?; and (2) is predation on tagged fish higher than predation on untagged fish, and if so, is this due to impairment by the presence and operation of the tag or to the attraction of predators to the transmitter signal?

Methods

Fish acquisition, holding, and surgical protocols.—Juvenile fall Chinook salmon were acquired as eyed eggs from the Washington Department of Fish and Wildlife's Priest Rapids Hatchery on 4 December 2000. Fish were reared at an aquaculture facility (wet laboratory) at the Pacific Northwest National Laboratory in Richland, Washington. During the study period, the test population was held outside the wet laboratory in a circular tank (1,394 L, 1.83 m in diameter, 0.53 m deep). All holding tanks and test chambers were supplied with 16.8–17°C well water. Fish within the general population were fed daily ad libitum rations. Fish selected for a given test were not fed for 24 h before or 24 h after surgery.

Test fish ranged in length from 122 to 198 mm fork length (FL) and ranged in weight from 22.2 to 99.0 g. Test tags measured approximately 6 × 22 mm, and weighed 1.5 g in air and 1.0 g in water. Tag weights ranged from 1.4% to 6.7% of test fish weight in air. The only difference between the active and inactive tags was that the inactive tags were not programmed to transmit.

Surgical procedures followed those used by Brown and Mackay (1995). Each fish was anesthetized with a 50-mg/L solution of eugenol (clove oil) (Anderson et al. 1997; Keene et al. 1998). Fork lengths (nearest mm) and mass (g) for all treatment groups (including controls) were measured while fish were immobile. A small tube inserted in the fish's mouth during surgery provided a continuous solution of 10-mg/L eugenol. A 20-mm incision was made 3 mm from the midventral line, anterior to either of the pelvic fins. Incisions were closed with three simple, interrupted sutures (Ethicon absorbable 5–0 coated-vicryl, violet-braided sutures with taper-point SH needle). The daily order in which surgeries were performed (e.g., sham-tagged then tagged) was randomized. Following surgery, or handling for controls, fish recovered in a circular tank inside the wet laboratory (655 L, 1.22 m in diameter, 56 m deep) for a minimum of 24 h before they were exposed to a performance challenge or predator avoidance experiment. Lights inside the wet laboratory were automatically controlled to follow the natural photoperiod.

Swimming performance.—Juvenile fall Chinook salmon were randomly assigned to one of three treatment groups: tagged, sham-tagged (surgery, but no transmitter), and control. Sample size for each group was determined by assuming a standard deviation of 0.5 body lengths per second (BL/s) and a statistical power level of 90%. A minimum of 28 fish per group was estimated as necessary to allow detection of a 0.5-BL/s difference in critical swimming speed (U_{crit}) at the 95% confidence level. Actual sample sizes were 25 fish per group for fish tested 1 d after surgery (1-d fish) and 25–29 fish per group for fish tested 19–23 d after surgery (21-d fish). There was no significant difference in weight ($P = 0.919$) or length ($P = 0.277$) among groups (Table 1).

Critical swimming speed was measured by placing a fish in a clear, polyvinyl chloride (PVC) tube

TABLE 1.—Mean fork lengths (FLs) and weights (± SDs) of treatment groups used to assess the impact of implantation with an acoustic transmitter on swimming performance 1 and 21 d after surgery.

	FL (mm)		Weight (g)	
Group	1 d	21 d	1 d	21 d
Tag	142 ± 7	139 ± 8	36 ± 5	34 ± 6
Sham	143 ± 8	141 ± 8	37 ± 6	35 ± 5
Control	143 ± 8	143 ± 6	36 ± 6	37 ± 5

(90 cm long, 10 cm in diameter). A bundle of six tubes was constructed to allow simultaneous testing of six fish. The bundle was placed in the swimming chamber (1.76 × 0.54 × 0.57 m) of a Brett-type respirometer. The respirometer is capable of generating velocities from 0.07 m/s to over 2.1 m/s. The relationship between water velocity in the respirometer and motor speed was established with a flowmeter. An electrified grid containing separate circuits for each tube was secured to the downstream end of the tube bundle. A section of flow straightener/reducer (straws; 0.18 × 0.23 × 0.33 m) was placed at the upstream end of the tube bundle. A section of plastic grating was placed within each swim tube to prevent access to any low-velocity regions at the upstream ends of the swim tubes. A light was placed at the downstream end of the tubes to help the fish orient themselves, while a black cover was placed at the upstream end to provide cover and orientation.

Tests of 1-d swimming performance were conducted from 23 to 28 January and from 12 to 13 February 2002. Tests of 21-d swimming performance were conducted from 31 January to 7 February 2002. Critical swimming speed was calculated based on the formula of Brett (1964):

$$U_{crit} = u_1 + (t_i/t_{ii} \cdot u_{ii}),$$

where u_1 is the highest velocity maintained for the prescribed period (cm/s), u_{ii} is the velocity increment (cm/s), t_1 is time (min) fish swam at the ''fatigue'' velocity, and t_{ii} is prescribed period of swimming (min).

On the day of surgery, 1-d and 21-d fish were randomly assigned to one of the three treatment groups. All fish were anesthetized in 50-mg/L eugenol, and FLs and weights were taken. Those fish subjected to surgery were either tagged with an inactive transmitter or were not implanted with a transmitter (sham-tagged group). Following surgery, 1-d fish were placed into one of three recovery bins (0.43 × 0.30 × 0.30 m) by treatment (4 fish/bin) and given at least 24 h to recover before the swimming trial. All three bins were placed in the same circular tank during the recovery period. Fish in the 21-d group were placed in an outside raceway for 19–23 d following surgery or handling (controls). The raceway was partitioned into five treatment-specific compartments (235 L, 0.89 m long, 0.80 m wide, 0.33 m deep). Feeding of the 21-d fish resumed 24 h after surgery and continued until 24 h before the swimming trial. Individual 21-d test fish were removed from the outside raceway, brought into the wet laboratory, and placed into one of the treatment-specific bins at least 24 h before trial initiation.

Morning and afternoon trials were conducted on each test day. For each trial, two fish were randomly selected from each of the three treatment groups. The fish were again anesthetized in 50-mg/L eugenol. Fork lengths and weights were taken. After lengths and weights were recorded, fish were placed into the swimming chamber. Swimming trials began after a 15-min recovery period. Fish were given an acclimation period of 1 h with the respirometer speed set at 0.5 BL/s (Peake et al. 1997). The acclimation velocity was determined from the average FL of the six fish for a given trial. Thereafter, the speed was increased by 0.5 BL/s every 15 min.

When a fish stopped swimming and fell back to the downstream end of the tube, that segment of the shocking grid was activated to emit a 10-V shock. The fish received a 1-s shock at approximately 3-s intervals as long as it remained against the grid. If the fish did not swim away from the grid within 10 s (three consecutive shocks), the fish was considered to be fatigued and received no further shocks. The U_{crit} for that fish was then determined based on the speed at which the fish fatigued and the number of minutes the fish swam at that speed. If a fish began swimming again after fatigue, this was noted but was not incorporated into the U_{crit}. The trial was over when the last fish swimming remained against the shocking grid.

Predator avoidance.—Juvenile fall Chinook salmon were randomly assigned to one of four treatment groups for the predator avoidance studies. Treatment groups were active tag, inactive tag, sham, and control. Active tags were evaluated to determine if tagged fish were impaired by tag presence and operation or if predators were attracted to the signals emitted from tags. Sample size for each group was originally set at 30 fish in three trials, 10 fish from each group being used in each trial. The number of prey fish per group and the number of trials was based on a statistical power

TABLE 2.—Mean fork lengths (FLs) and weights (±SDs) of juvenile Chinook salmon overall and by treatment in the predator avoidance test.

	Mean FL (mm)					Mean weight (g)				
Group	Trial 1	Trial 2	Trial 3	Trial 4	Overall	Trial 1	Trial 2	Trial 3	Trial 4	Overall
Overall	138 ± 8	138 ± 7	138 ± 8	139 ± 7	138 ± 8	35 ± 6	35 ± 6	34 ± 6	36 ± 6	35 ± 6
Active tag	137 ± 10	138 ± 9	138 ± 8	139 ± 8	138 ± 8	33 ± 6	36 ± 8	34 ± 6	36 ± 7	35 ± 7
Inactive tag	140 ± 8	140 ± 5	139 ± 7	139 ± 6	140 ± 6	37 ± 7	36 ± 4	35 ± 5	35 ± 5	36 ± 5
Sham	138 ± 7	137 ± 8	138 ± 8	140 ± 7	138 ± 7	35 ± 6	34 ± 6	34 ± 6	36 ± 5	35 ± 6
Control	136 ± 7	138 ± 8	138 ± 10	140 ± 8	138 ± 8	33 ± 5	35 ± 6	34 ± 7	35 ± 5	34 ± 6

level of 90%, assuming a standard deviation of 0.2 (20%). Thirty fish per group was estimated to be adequate for detection of a 20% difference in predation rate at the 95% confidence level. A fourth trial of an additional 10 fish per group, was added following in-season analysis to increase sample size and power. There was no significant difference in FL among trials ($P = 0.755$) or treatments ($P = 0.417$) (Table 2). Additionally, there was no significant difference in fish weight among trials ($P = 0.825$) or treatments ($P = 0.437$) (Table 2).

Rainbow trout were selected as predators due to their availability, acclimatization to the test environment, and past performance as test predators (Neitzel et al. 2000). Twenty-five rainbow trout were placed in the test tank and acclimated for a period of approximately 4 weeks before introduction of juvenile fall Chinook salmon. During the acclimation period, predators were ''trained'' to eat live fish by presentation of juvenile rainbow trout. Flow at the upper end of the test tank was maintained at approximately 2.4 m/s between feeding periods. Flow through the tank was turned off just prior to prey fish introduction.

Predator avoidance tests were conducted in an uncovered, 9.14-m-long, 1.22-m-wide tank with a water depth of 0.76 m (8,475 L). Individual trials for the predator avoidance test were conducted on 30 November and on 3, 8, and 13 December 2001. Predator fish were fed pelletized food between trials.

At the beginning of a trial, all predator fish were crowded to one end of the tank with a moveable partition consisting of a PVC frame covered with mesh. After all predators were behind the barrier, the pump providing flow in the tank was turned off. Ten test fish from each treatment group (40 fish total) were then added simultaneously to the opposite end of the tank, behind another partition. After the prey had acclimated for 5 min, the partitions were simultaneously removed and the trial began. The trial continued until 50% of the prey had been consumed.

Observations were made at 15-min intervals during the first hour. After the first hour, observations were made as often as necessary to ensure that the trial could be stopped when 50% of the prey had been consumed. Prey fish that were seriously injured by a predation attempt (e.g., swimming upside down), were categorized as ''consumed'' for the purpose of terminating the trial, based on the assumption that those fish would die within the next 12 h. After 50% predation was achieved, the prey were crowded to one end of the tank and removed. Prey fishes were examined to assess the degree of predation (i.e., minor scratches to multiple deep bites or fatal wounds) and numbers from each treatment group that survived. All remaining fish, injured or healthy, were removed and placed in an inside circular tank for a period of 24 h for delayed mortality observation. Overall, no fish that were identified as healthy following a trial died during this recovery period, whereas all the fish that had been counted as consumed or dead at the end of the trial died within 12 h.

Data analysis.—Analysis of variance was used to test for differences among treatment groups when data were normally distributed; otherwise, data were analyzed with a Kruskal–Wallis test. A significance level of 0.05 was used for all tests. Critical swimming speed was compared among treatment groups to determine potential tag effects. The primary factor when testing for differences in U_{crit} was treatment group. Additional factors in the analyses included the post-surgery interval (1 d or 21 d), fish weight, fish length, tube assignment, and time of day (a.m. or p.m.) in which the trial was conducted. Analysis of variance with an assumed binomial error structure was used to determine whether significant differences existed in numbers of juvenile Chinook salmon consumed among the four treatment groups.

TABLE 3.—Mean relative critical swimming speeds (U_{crit}; body lengths per second) ± 95% confidence intervals (ranges in parentheses) for juvenile fall Chinook salmon 1 and 21 d posttreatment and for both times combined.

Treatment group	*N*	U_{crit}
1-d posttreatment		
Control	25	4.57 ± 0.35 (4.22–4.92)
Inactive tag	25	4.14 ± 0.47 (3.67–4.61)
Sham	25	4.21 ± 0.36 (3.85–4.57)
21-d posttreatment		
Control	29	4.51 ± 0.33 (4.18–4.84)
Inactive tag	27	4.24 ± 0.32 (3.92–4.56)
Sham	25	4.45 ± 0.41 (4.05–4.86)
Combined		
Control	54	4.53 ± 0.23 (4.30–4.77)
Inactive tag	52	4.19 ± 0.27 (3.92–4.46)
Sham	50	4.33 ± 0.26 (4.07–4.60)

TABLE 4.—Mean percentage of treatment fish consumed by rainbow trout (range in parentheses) by treatment for the four trials combined.

Treatment group	Percentage consumed
Control	40.0 (10–60%)
Sham surgeries	43.0 (22–70%)
Active tags	54.3 (30–70%)
Inactive tags	52.5 (40–70%)

Results

Swimming Performance

Of the 156 fish tagged or tested in the respirometer, none died; therefore, all fish were available for use in the analysis. A total of 54 control fish, 52 tagged fish, and 50 sham-tagged fish were included in the analysis (Table 3). There was no significant difference in U_{crit} among the three groups ($P = 0.142$; Table 3). Additionally, there was no significant difference in U_{crit} of fish tested at 1-d and 21-d posttreatment ($P = 0.567$), and there was no interaction between treatment group and day ($P = 0.873$). Therefore, to increase the probability of finding significant differences within a factor, the data from the two postsurgery interval groups were combined. Though not significantly different, U_{crit} point estimates for the 1-d and 21-d groups demonstrated that U_{crit} was highest for control fish and lowest for fish with tags (Table 3). Weight and FL were also analyzed to determine their influence on swimming speed. Weight did not have a significant effect ($P = 0.488$); however, FL did have a significant effect on swimming speed ($P = 0.001$).

The sample data showed a maximum difference in the sample means of 0.3 BL/s (Table 3). Based on a power analysis, our experiment would have had a 25% chance of detecting this as significant ($\alpha = 0.05$), assuming, of course, that a difference actually existed. Statistical power increased to 90% when detecting a difference of 0.73 BL/s, and to 95% when detecting a difference of 0.80 BL/s.

Predator Avoidance

Four trials consisting of 10 fish from each of the four treatment groups were conducted. All fish that underwent surgery swam actively following

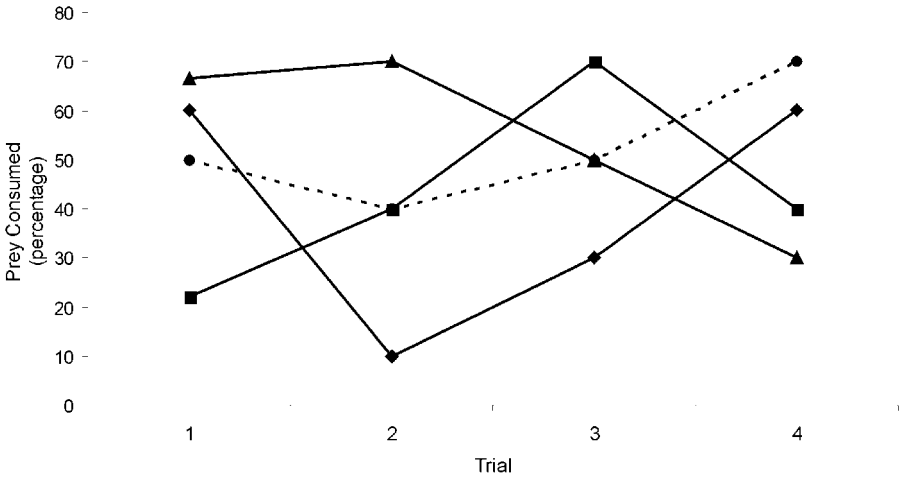

FIGURE 1.—Percentages of juvenile fall Chinook salmon consumed by rainbow trout during each of four predator avoidance trials for control (diamonds), active-tag (triangles), inactive-tag (circles), and sham-tagged (squares) treatment groups. Each point represents the percentage of fish consumed from a single treatment group ($N = 10$ fish per group for each trial); thus, the percentages within a given trial can exceed 100% when summed.

the 24-h recovery period. The percentage of fish consumed was highly variable by group and trial (Table 4; Figure 1). There was no significant interaction between trial and treatment group ($P = 0.136$), no significant differences in the percent consumed among the four trials ($P = 0.851$), and no significant difference in percent consumed among the four treatments ($P = 0.557$). This suggests that, given the sample sizes, there was not enough evidence to show a significant difference in predation among control fish, sham-tagged fish, and fish implanted with transmitters.

Weight and length also did not significantly affect the percentage of fish consumed ($P > 0.05$). Additional analyses that used weight and length as response variables were conducted to determine whether these factors varied among trials, among treatments, or between fish consumed or not consumed. This was done to ensure that predator avoidance was not a function of fish size. The results showed that there was no weight or length bias in the sampling among trials or treatments, and that predation did not depend on fish size ($P > 0.05$ for all factors).

An analysis was also performed that separated the treatment groups into those without transmitters (controls and sham-tagged fish) and those with transmitters (inactive and active tags). This was done based on the initial impression that fish with transmitters were consumed more often than fish without transmitters (Table 4). Combining the treatments resulted in an increased sample size per group, resulting in a decrease of the *P*-value; however, there was still not a significant difference in percent consumed between the two groups ($P = 0.172$).

Power analysis showed that high variability resulted in only a 14% power to detect a difference of 14% consumed (the maximum difference between the active-tag group and the control group). Additional analysis showed that sample sizes of almost 400 fish per treatment group would be necessary to significantly increase our ability to detect a 14% difference.

Discussion

Based on the results described here, surgically implanted acoustic transmitters representing from 1.6% to 6.7% of fish weight in air did not significantly affect swimming performance of juvenile Chinook salmon (124–154 mm FL) at 1 or 21 d postsurgery. Our research also demonstrated that fish with active acoustic transmitters were not more susceptible to predation than either fish with inactive transmitters or controls.

Mean U_{crit} (1-d and 21-d results combined) for controls appeared slightly higher (4.53 BL/s) than that of the sham-tagged (4.33 BL/s) and inactive-tag (4.19 BL/s) groups; however, no significant difference existed among the groups. Similarly, surgically implanted acoustic transmitters weighing up to 14.5% of fish body weight in air did not affect the swimming performance of control, sham-tagged, or tagged juvenile Atlantic salmon *Salmo salar* (>166 mm; Moore et al. 1990) or juvenile coho salmon (>150 mm TL; Moser et al. 1990). McCleave and Stred (1975) did report a significant decrease in swimming performance for juvenile Atlantic salmon (>200 mm total length) implanted with wide tags (19 mm long, 10 mm in diameter, 4.9% of body weight in air), but not for fish implanted with narrow tags (33 mm long, 8 mm in diameter, 6% of body weight in air). Juvenile Chinook salmon (>120 mm FL) that were surgically implanted with radio transmitters containing external antennas (2.2–5.6% of fish body weight in air) swam significantly more poorly than controls 1 d postsurgery (mean 3.45 BL/s versus 3.90 BL/s), but there was no difference 21 d postsurgery (mean 3.82 BL/s versus 3.97 BL/s; Adams et al. 1998). Our research and that of others demonstrate that placing a transmitter in a fish does not necessarily result in a ''tag effect''; rather, any bias associated with tagging is a function of several factors, such as fish size, tag size, antenna presence, and antenna length.

Critical swimming speeds achieved by tagged and untagged juvenile Chinook salmon in the present study were higher than the U_{crit} values for juvenile Chinook salmon reported by Adams et al. (1998). Radio transmitters used by Adams et al. (1998) had external, stainless steel antennas (31 cm long, 0.5 mm in diameter), whereas the acoustic transmitters we used lacked external antennas. Hydraulic drag on the antenna likely results in decreased swimming performance of tagged fish. It is important to note that Cooke and Bunt (2001) found no significant difference in the swimming performance or mobility rates of smallmouth bass *Micropterus dolomieu* when studying internal versus external antenna configurations. Differences in additional factors, such as training, rearing condition, muscle mass, muscle enzyme profiles, and water temperature, could also contribute to differences in observed U_{crit} values (Webb 1995). Swimming performance tests conducted for this study were done in 17°C water, compared to the

13°C water used by Adams et al. (1998). Water temperature used in our study may have been closer to the optimal temperature for juvenile Chinook salmon than that used by Adams et al. (1998). Davis et al. (1963) reported a first-failing swimming speed of 7.3 BL/s for yearling Chinook salmon tested at 11.5°C; this was the only water temperature at which fish were tested. Brett (1967) demonstrated that U_{crit} is related to test temperature, with U_{crit} increasing to an optimal temperature that coincides with maximal aerobic scope. Swimming speed of fingerling sockeye salmon *O. nerka* tested by Brett (1967) increased steadily up to 15°C, and then decreased as temperature increased further. This confirms the findings of Farrell (2002), who demonstrated that U_{crit} decreases beyond the optimal temperature.

The recovery period that occurs between tagging and fish release may affect long-term survival. In the present study, no statistically significant relationship between swimming performance and the duration of recovery (1 d versus 21 d) was documented, although there was a slight increase (0.10–0.20 BL/s) in mean U_{crit} values for the inactive-tag and sham-tagged groups during swimming tests conducted 21 d postsurgery versus 1 d postsurgery. This is consistent with the results of Moore et al. (1990), who also did not observe any long-term effects on the swimming performance of Atlantic salmon juveniles with surgically implanted transmitters.

Implantation of transmitters in fish results in an increase in fish density, which in turn can lead to a decrease in U_{crit} or an increase in energy expenditure (Lefrançois et al. 2001). When allowed access to air, juvenile salmon can increase the gas volume in their air bladders to compensate for the additional tag mass, thereby achieving a density similar to that of an untagged fish (Fried et al. 1976; Moser et al. 1990; Perry et al. 2001). Differences in swimming performance between tagged and untagged individuals are likely to be demonstrated when tags have external antennas, large volumes, or high fish-to-tag weight ratios (in water) or when the density of tagged fish differs from that of untagged fish (while fish are in deeper water). In the present study, tagged fish were given ample time to compensate for the excess tag mass and the tags lacked external antennas; these two factors have been shown to contribute to differential swimming performance in tagged and untagged salmonids.

In the present study, no difference in predation rates among treatment groups was observed; fish with and without tags were consumed in equal proportions. This is in contrast to the results of Adams et al. (1998), who reported juvenile Chinook salmon tagged with radio transmitters were consumed in higher proportions than control fish. The ability to avoid predation is partially a function of the swimming performance of prey because it affects the capture-to-attack ratio (Bams 1967). Therefore, in our study, because there were no statistical differences in swimming performance among prey groups, differential predation rates were less likely. This was not the case with the Adams et al. (1998) study, in which swimming performances differed among treatment groups depending on fish size and recovery time. In addition to achievement of upper U_{crit}, avoidance of predators also requires high acceleration and turning rates (Webb 1995), which may be inhibited by the drag associated with the external antennas of radio transmitters.

Factors other than swimming performance that may lead to differential predation include prey conspicuousness, failure to detect predators, and inability to shoal effectively (Mesa et al. 1994). As mentioned earlier, there was no significant difference in prey length among groups, suggesting little visible difference among prey. This differs from predation studies in which tags with external antennas are evaluated (Adams et al. 1998). Prey with external antennas are likely to be more conspicuous to predators, resulting in higher predation rates. Connors et al. (2002) observed intraspecific aggression toward the external antennas of juvenile wild Atlantic salmon (165 mm FL, 38.9 g mean weight) surgically implanted with dummy radio transmitters (2.0% of fish body weight in water). In addition to the aggressive behavior, Connors et al. (2002) also reported frequent depression of social rank following transmitter implantation that might have been facilitated by the use of externally trailing antennas. A long external antenna may provide an additional surface area for predators to strike and thereby secure their prey. In the present study, similar swimming performance among prey groups allowed prey to shoal effectively.

Prey with active transmitters were not more susceptible to predation than fish with inactive tags or untagged fish. In theory, increased susceptibility to predation may come from physiological changes to the test fish, such as damage to hair cells. However, the signal frequency of the transmitters (300 kHz) is beyond the auditory range described for salmonids (25–800 Hz; Abbott 1973; Popper and

Carlson 1998), indicating little potential for physical damage to hair cells or detection by predators.

Conclusions based on the movement, distribution, or behavior of tagged fish may provide results divergent from what occurs in the population of untagged fish. Thus, while our research shows no negative influence on juvenile salmon from tagging or the carrying of transmitters that represent 1.4–6.7% of fish weight in water, other factors should be examined, including growth and the behavior of fish swimming in deep water or under pressure.

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