

Growth, survival, and tag retention of steelhead trout (*O. mykiss*) surgically implanted with dummy acoustic tags

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Abstract Recent advances in micro-electronics make the study of the migration of even small marine animals (>12 cm) over many 1000s of kilometres a serious possibility. Important assumptions in long-term studies are that rates of tag loss caused by mortality or tag shedding are low, and that the tagging procedure does not have an unacceptable negative effect on the animal. This paper reports results from a study to examine the retention of relatively large (24 × 8 mm) surgically-implanted dummy acoustic tags over a 7-month period in steelhead pre-smolts (*O. mykiss*), and the effects of implantation on growth and survival. Although there was some influence on growth to week 12, survival was high for

animals > 13 cm FL. In the following 16-week period, growth of surgically implanted pre-smolts was the same as the control population and there was little tag loss from mortality or shedding. Currently available acoustic tags can be implanted in salmonid fish ≥12 cm FL, although combined losses from mortality and tag shedding were 33–40% for animals in the 12 and 13 cm FL size classes. By 14 cm FL, combined rates of tag loss (mortality plus tag shedding) for surgically implanted tags dropped to <15% and growth following surgery was close to that of the controls. Our results suggest that studies of ocean migration and survival over periods of many months are now feasible even for animals as small as salmon smolts. Surgically implanted salmon smolts are therefore good candidates for freshwater and coastal ocean-tracking studies on relatively long time scales (months). On such time scales, even relatively small salmon smolts may move thousands of kilometers in the ocean.

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Developments in Fish Telemetry

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Introduction

The potential for sea-floor observatories to dramatically increase our understanding of processes occurring within the ocean has recently been

reviewed (National Research Council, 2000); surprisingly, no mention was made of the ability of such observatories to potentially allow the tracking of marine animals during their extensive marine migrations. Recent developments in acoustic technology (Voegeli et al., 1998; Lacroix & Voegeli, 2000) offer the prospect of establishing extensive networks of underwater acoustic listening lines. Arrays formed of a series of such lines might eventually stretch the entire length of continents (e.g., Welch et al., 2003; see also www.postcoml.org). The development of continental-scale arrays would allow tracking the movements of even quite small animals for months or years over vast regions of the continental shelf. However, although important aspects of the technology needed to eventually allow the deployment of long-term monitoring posts on the seabed still need to be established and validated, an equally critical aspect of this work involves the question of how animals of different sizes recover from tagging with acoustic tags, and their rates of tag retention—the development of long-lived acoustic tags with operational lifetimes of months or years is meaningless if animals die from tagging or rates of tag loss are high.

This study was designed to examine the effect of tagging small salmon pre-smolts (steelhead trout; *Oncorhynchus mykiss*) with acoustic tags. The goals were: (1) to determine the appropriate size ranges and protocols for pre-smolt tagging, and (2) to establish rates of tag loss over time.

Materials and methods

Hatchery-reared steelhead trout were selected from part of a large-scale production within the British Columbia Fish Culture program, at the Vancouver Island Trout Hatchery in Duncan, B.C. Approximately 200 pre-smolts (Cowichan River stock) were selected and placed in a single rectangular fibreglass rearing tank several days before the start of the experiments at the end of February, 2001. At the end of the tagging procedure described below, all fish were transferred to a second fibreglass tank, which served to hold all of the control and tagged fish together in freshwater for the duration of the experiment. Feeding

and care of pre-smolts followed standard hatchery rearing procedures.

Dummy acoustic tags (8 mm diameter \times 24 mm long; 1.4 g) were cast from quick-setting epoxy resin with a 12 mm PIT tag embedded in the body of the tag to allow unique identification of each pre-smolt. The epoxy resin was mixed with a bright yellow colouring agent at the time the hardening agent was added to make it easier to see any tags shed onto the bottom of the hatchery raceway. Control fish also were implanted with a PIT tag, thereby ensuring that all fish used in the experiment were uniquely identified, and allowing the two groups to be placed in the same holding tank and eliminating possible tank effects on the results.

Treatment protocol was similar for the two groups of pre-smolts, but we made some slight modifications to our surgical procedure over the 3-day tagging period (19, 20, and 24 February, 2001). Two pre-smolts were netted from the initial holding tank and placed in a bucket of freshwater, into which had been added clove oil (80 ppm target strength). The clove oil was mixed 50:50 with ethanol and shaken, in order to improve the dispersion of the clove oil at the low temperature of the water (7°C). Once quiescent the first (control) pre-smolt was weighed, fork length recorded, and a PIT tag was injected into the abdominal cavity using a modified hypodermic syringe before placing the pre-smolt in the second fibreglass raceway. This process took approximately one minute to complete, allowing deeper anaesthesia to be induced in the second pre-smolt.

The second pre-smolt was handled identically except for the implantation process. After measuring and recording size, pre-smolts were placed ventral side up in a V-shaped trough formed from a sheet of acrylic plastic. The channel was partially filled with water to ensure that the head and gills remained submerged while the abdomen was exposed above the water line. A small amount of paper towelling was submerged in the trough, cushioning the fish and helping to prevent it from moving during surgery.

A fine-bladed scalpel was used to make an incision just large enough to allow passage of the dummy tag along the ventral midline anterior to the pelvic fins (11–12 mm), and the tag lightly

pushed through the incision and then forwards until the body of the tag lay fully within the abdominal cavity. The tag was then moved backwards using either the point of the scalpel or a pair of pointed forceps, so that the posterior end of the tag was located beyond the posterior end of the incision. In this way the two ends of the 24 mm long tag were both located under uncut abdominal musculature and the central section of the tag body lay under the incision. As monofilament suture material is generally viewed as preferable for use in fish (Gilliland, 1994; Wagner et al., 2000), the incision was closed with two simple interrupted sutures tied in Ethicon PDS-II 2-0 monofilament polydioxanone using a FS-1 cutting needle. The two stitches approximately trisected the incision, with the needle and suture passed fully through the abdominal wall on each side of the incision. The position of the tag acted as a shield, facilitating the completion of each suture without puncturing the internal organs or sewing them into the incision.

No major attempt was made to sterilise the working area other than to keep it clean and reasonably hygienic, as might be encountered in a field program. The surgeon (DWW) wore surgical gloves but did not change them between fish. The scalpel blade was dipped in betadine antiseptic at the start of each operation, but the blade was only changed when needed to ensure a sharp edge. The drop of betadine left on the tip of the blade was first placed on the abdomen of the fish and then spread out over the area to be incised with the tip of a gloved finger. Care needed to be used here because betadine in contact with the gills is lethal. (A second reason for the use of paper towelling, in addition to holding the anaesthetised fish in one position was to form a dam between the abdomen and the gills, minimising the chance of antiseptic-contaminated water reaching the gills). No antibiotics were used.

Some modifications to the surgical procedure were made during the course of the 2-day procedure. Oxygen was not initially used during surgery, but we found that the pre-smolts came out of their anaesthesia more rapidly with its use, and accordingly used oxygen bubbled into

the water using an airstone placed near the head thereafter. The water in the surgical table was still changed after every 2–3 fish to minimise the chance of the betadine antiseptic reaching the gills and to prevent thermal shock from the water in the surgical tray warming to air temperature.

Handling procedures were identical except for the surgery, since both the control and surgically implanted pre-smolts were held in the same tank. A record was kept during implantation of the relative size distributions for the two groups, and the tagging sequence was occasionally varied to ensure that the size distribution of pre-smolts tagged using the two procedures was similar. Pre-smolts were fed daily to satiation by an automatic feeder. Hatchery staff maintained the water temperature in the rearing trough at 7°C for the first 10 days after tagging, and then increased the temperature to 11°C for the duration of the experiment. We tried to ensure a similar size distribution of pre-smolts chosen for control and surgical implantation (Table 1), except that the smallest available pre-smolts were clearly too small to be implanted. Below ca. 11 cm FL, it was not possible to insert the tag into the body cavity and close the body wall. (There were significant fat bodies lying along the intestinal mesentery of these hatchery-reared fish, occupying space that in a lean wild pre-smolt might make it easier to place the tag in the body cavity).

Pre-smolts were netted in small batches from the indoor holding tank on 16 May, 2001, ~12 weeks after tagging, and lightly anaesthetised with clove oil. The PIT tag number for each animal was recorded and each animal measured for weight and length, and visually examined to assess the extent of healing. The same procedure was repeated again on 8 September 2001, ~16 weeks later (~29 weeks after implantation). During the holding period the tank was checked daily for dead fish or shed tags and the date of recovery was noted. The weight of the dummy tag was subtracted from the fish weights measured during the May and September evaluations. Statistical comparisons were based on an analysis of covariance.

Table 1 Rates of potential acoustic tag loss by size class to week 29

Fork Length (cm)	<11	11–12	12–13	13–14	14–15	15–16	16–17	Total
Mean Weight (g)	11.1	16.8	21.6	26.7	33.3	39.6	53.3	
<i>N</i>								
Dummy	1	6	15	20	15	15	11	83
PIT	7	15	7	16	18	16	6	85
<i>Mortality</i>								
Dummy	100.0%	50.0%	33.3%	10.0%	6.7%	6.7%	9.1%	15.7%
PIT	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
<i>Tag shedding</i>								
Dummy	–	16.7%	6.7%	30.0%	20.0%	6.7%	9.1%	13.3%
PIT	0.0%	0.0%	0.0%	6.3%	0.0%	0.0%	0.0%	1.2%
<i>Overall loss</i>								
Dummy	100.0%	66.7%	40.0%	40.0%	26.7%	13.3%	18.2%	28.9%
PIT	0.0%	0.0%	0.0%	6.3%	0.0%	0.0%	0.0%	1.2%

The initial number of fish (*N*) in each 1 cm size category is indicated, as is the mean weight of each length class. Mortality rates for fish surgically implanted with dummy acoustic tags dropped sharply for animals greater than 12 cm fork length. Although the rate of tag shedding (but not mortality) remained fairly high for the 13 cm size class, no dummy tags were lost before 39 days after implantation. Tag weight ranges from 15% of body weight in the <11 cm size class to 3.5% in the 15–16 cm size class

Results

Effect on survival

Some difficulty was initially encountered in the early stages of the surgery. It initially took considerable time to induce anaesthesia in the pre-smolts, so we replaced our standard stock solution of clove oil (which was several years old) with freshly purchased clove oil from a pharmacy, where it was sold as a toothache remedy. Use of the new stock resulted in 6 of the 13 subsequently implanted pre-smolts not recovering from the anaesthesia (including a run of five sequential deaths), and the death of the only PIT tagged pre-smolt associated with the tagging procedure. The problem appeared to be with the clove oil, as surgical times were low (~2 min). After switching back to the original stock solution of clove oil no further immediate mortalities were encountered.

These deaths were thus associated with a specific anaesthetic problem, and the animals surgically implanted under such conditions did not recover from the surgery. Implanted tags in such cases can be recovered and used in a different animal if animals are held for a brief period of observation post-surgery. We therefore excluded these cases from the analyses reported below, as it seems most relevant to examine what fraction of animals released into the environment would be expected to survive and retain their tags.

All but one mortality occurred during the initial 12-week period. Mortality was strongly associated with size, at least for the smallest animals examined (Table 1). For animals less than ca. 11.5 cm FL, it proved impossible to close the body cavity with the dummy acoustic tag inside, and the few animals that we attempted to surgically implant all died. However, although the dummy acoustic tag filled much of the body cavity, surgically implanted animals >11.5 cm FL (20 g) survived the surgery and mortality rates dropped sharply with increasing size over the interval 11–13 cm (Table 1). For animals ≥13 cm mortality remained low and constant at <10%. Mortality in the PIT-tagged control group was zero for the same size classes. Over the subsequent 16-week period (to week 29, 7 months post-implantation), only one additional dummy-tagged pre-smolt died (on 24 July). The surgical incision on this animal (12.1 cm at time of tagging) had not healed and mesenteric fat was protruding from the incision on both the May and September census. This animal had progressively lost weight between each examination.

Effect on growth

To examine the effect of surgical implantation on growth, we compared relative growth over the first (12 week) and second (16 week) study periods for the two groups (Fig. 1). Both controls and

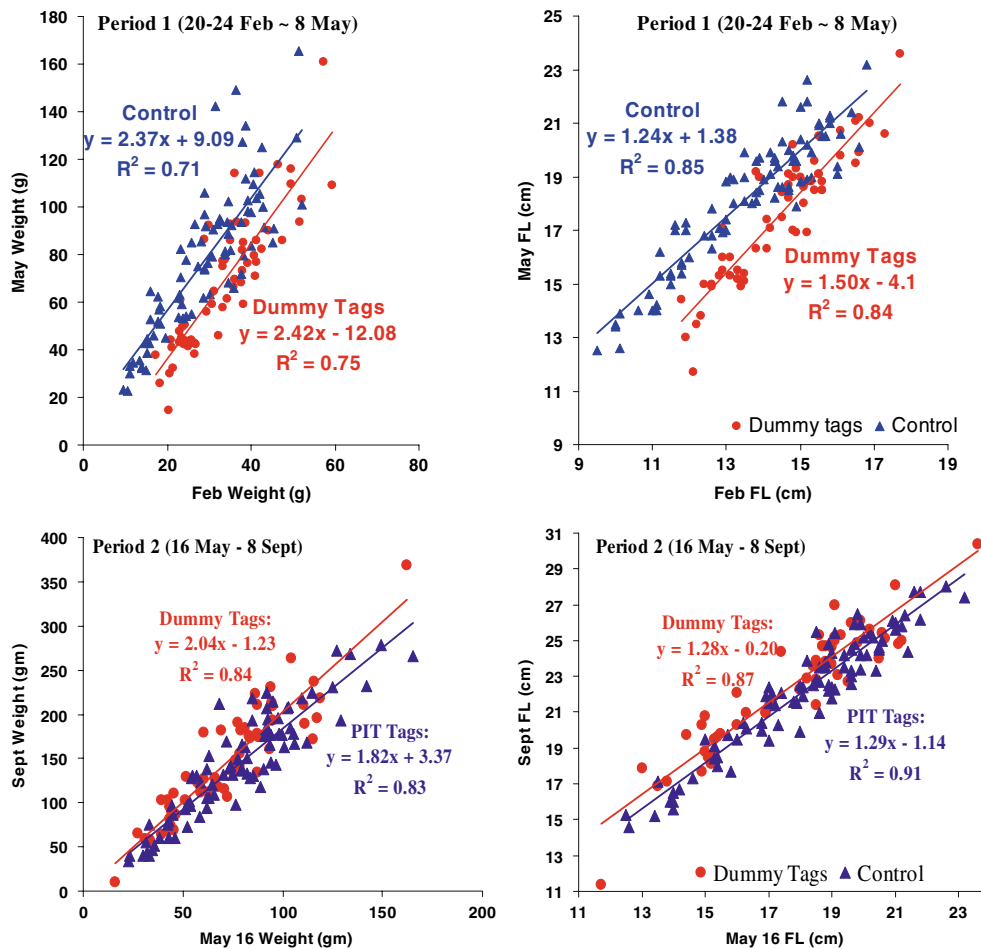


Fig. 1 Comparison of achieved growth for implanted pre-smolts over the first (12 week) and second (16 week) periods. Growth of surgically implanted pre-smolts was

implanted pre-smolts grew over the initial 12-week study period, although surgically implanted animals grew less for a given size than the controls (ANCOVA, $P < 0.05$). Linear regressions fitted to the data show that the growth patterns had nearly parallel slopes but different intercepts, suggesting that the effect of the surgical implantation was a reduction in growth that was similar for all size groups. Fitting a second model with a common slope but different intercepts supported this suggestion, as the fit was indistinguishable ($R^2 = 0.729$ for both). The difference in intercepts was 2.4 g, suggesting that animals of all sizes had reduced growth of roughly 2.4 g as a result of surgical implantation. For the smallest animals (~20 g or ~12 cm) this growth

reduced relative to the controls in the first period (top row), but not the second (lower row)

difference corresponds to a 35% reduction in achieved growth.

Closer examination of the residuals from the regression lines calculated using the data for the first period indicated that there was some tendency to heteroscedasticity, with the residuals tending to increase with increasing size. Log-transforming the size data and repeating the analysis resulted in a slight increase in R^2 (0.793) and a better residual fit, but showed a statistically significant difference in slopes (ANCOVA; $P < 0.05$), so that the difference in growth increment between implanted and control fish decreased even further at larger sizes. Although surgical implantation reduced growth at all sizes examined, the results indicate that

growth differences were progressively smaller and showed greater overlap between control and implanted pre-smolts when initial sizes were greater than 14 cm FL (roughly 30 g body mass; Fig. 1).

Comparison of growth increments for the second period (16 May to 8 Sept, 2001), indicates no statistically significant difference in growth increment for any size group (ANCOVA; $P < 0.05$; Fig. 1, lower row). On average, the surgically implanted animals grew slightly more than the controls.

Rates of tag loss

Tag loss (shedding) was also related to body size (Table 1; Fig. 2). By week 12 a total of 11 dummy acoustic tags (a 13% loss rate) were expelled from the body, apparently without damage to the pre-smolts. In the following 16-week period only two additional tags were shed, both animals in the 14 cm size class (a 16% loss rate). Pre-smolts recovered from the tank at week 12 that were no longer individually identifiable by the presence of a PIT tag in all cases appeared to be healthy and the surgical incision appeared to be fully healed. When shedding rates are compared for different size classes it is clear that tags were retained over the full size range examined, but that shedding

rates dropped from 16–30% in pre-smolts ≤ 13 cm to a low and stable rate of $\sim 7\%$ for animals ≥ 15 cm at implantation (Table 1). Tag shedding rates during the initial 12-week period were similarly low, but increased to 20% when the two shed tags found on 3 July and 18 August are included in the analysis (weeks 19 and 25; Fig. 3). The time course of tag losses (Fig. 3) shows that most tags were shed in a period around 4–12 weeks post-surgery, with only one tag shed >20 weeks post-surgery. The data thus suggests that the process is self-limiting and does not affect all tagged animals.

Some insight into the process of tag expulsion was obtained from examination of those tagged animals ($N = 18$; 22%) that initially appeared to be in the process of shedding the tag. These fish all had distended abdomens, apparently as a result of the tag being firmly pressed against the abdominal muscles from the inside (Fig. 4). (The remaining pre-smolts did not show evidence of the outline of the tag against the body wall). In each case the surgical incision was well-healed and showed no evidence of being likely to rupture. One pre-smolt was observed in the last stages of tag expulsion (Fig. 4). The abdomen was greatly distended around the tag and a “pore” had formed near the anterior end, through which the tag was completely exposed and clearly

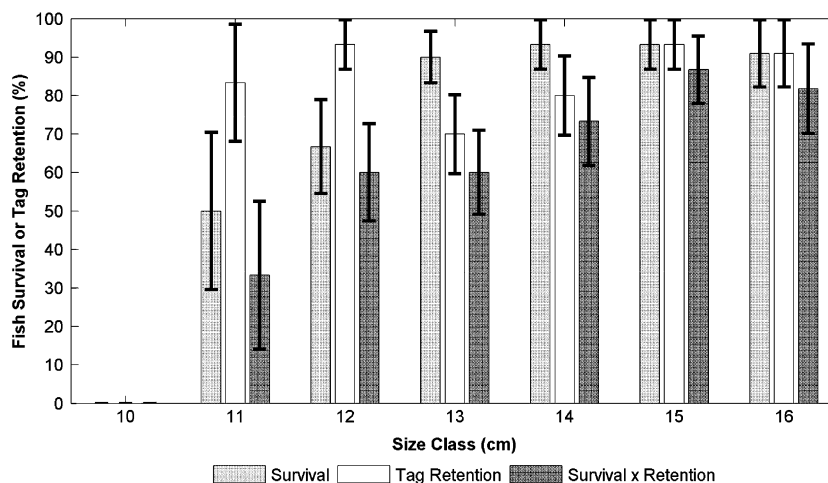


Fig. 2 Comparison of rates of pre-smolt survival, tag retention, and overall tagging success (survival \times retention) to 6 months post-implantation. Overall success increases rapidly with initial size at implantation from

33% for 11.5 cm pre-smolts to $>80\%$ of the surgically implanted pre-smolts. Error bars indicate ± 1 SE on the proportion

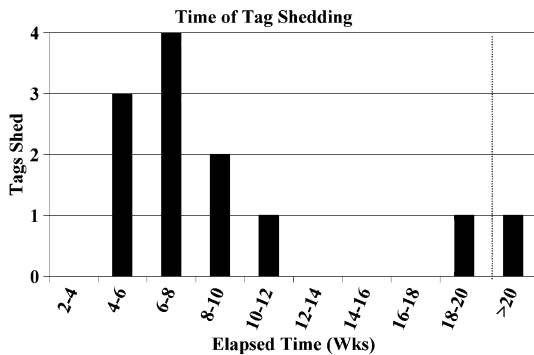


Fig. 3 Time course of tag shedding. Tag losses have been binned into consecutive 2-week periods. Median time to loss was 7.9 weeks, average time 9.8 weeks. A total of 13 tags were shed from a starting population of 90 implanted smolts

visible. The tissue forming the pore was remarkable for the absence of any evidence of trauma—the edge of the opening was smooth and neither the skin nor the underlying abdominal muscles showed any evidence of a ragged edge or infection, and there was no evidence of oozing from the wound. Rather than giving the impression of an ulcerated wound in the abdominal wall, the neatly rounded hole into the abdominal cavity seemed to cause little trouble for the fish and no evidence of significant trauma.

Discussion

Studies of the large scale movement patterns at sea of animals such as salmon pre-smolts will require monitoring their movements over thousands of kilometers and many months (or years) at sea. Newly-developed acoustic tracking technologies (e.g., Klimley et al., 1998; Voegeli et al., 1998; Lacroix & Voegeli, 2000; Lacroix et al., 2004; Welch et al., 2004; Lacroix & Knox, 2005) show great promise in revolutionising the study of the ocean migrations of these animals. An important aspect of such studies will involve the development of sampling protocols that will permit designing studies around animals of an appropriate size and age.

The purpose of the current study was to determine minimum size guidelines for applying the acoustic tags now commercially available to salmon pre-smolts. These tags have active

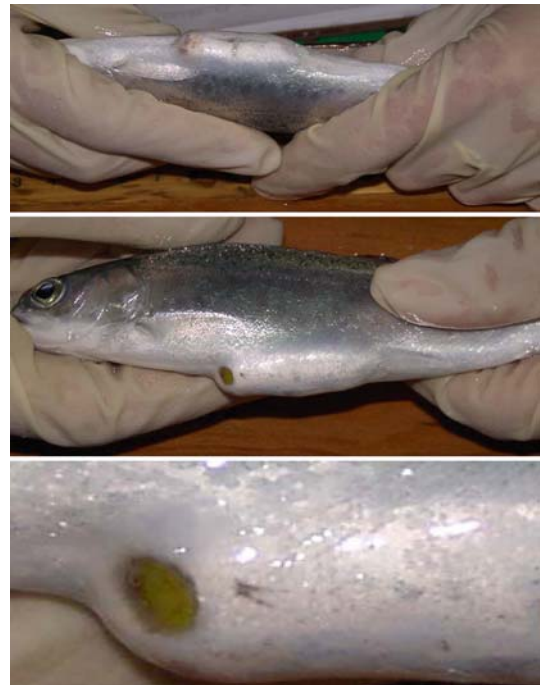


Fig. 4 Example of a pre-smolt in the process of extruding a tag. (Top) The abdomen is distended by the pressure of the tag against the abdominal wall. The right side of the abdomen shows some slight evidence of abrasion of the skin surface at the anterior end on the side facing the camera, presumably from contact with the tank wall. (Middle) The opposite (left) side of the pre-smolt shows a well-developed “pore”, through which the head of the dummy tag is clearly visible. (Bottom) Close-up view of the pore. Note the clean unulcerated edge of the pore; the skin and abdominal muscles have neatly drawn back, with no evidence of infection. This tag was shed 7 weeks after the photographs were taken and 19 weeks post-implantation

lifespans approaching 4–6 months. Two important aspects were initially identified during the planning phase: (a) to identify those sizes at which mortality is minimised and (b) the sizes at which growth is not seriously disrupted. In addition to these initial issues, we were surprised to discover that a significant proportion of pre-smolts appear to have a well-developed biological mechanism for eliminating these large tags from their body cavities, apparently with little trauma to the body. Tag shedding is a serious issue for long-term studies because either the death of the salmon pre-smolt or the shedding of the tag results in the loss of the tagged animal from the study population.

Although steelhead trout and Atlantic salmon pre-smolts can be quite large (often >16 cm), the other species of Pacific salmon seldom achieve that size in freshwater. As a result, we implanted the tags into animals as small as 10.8 cm. Our results indicate that for animals ≥ 14 cm fork length, overall rates of tag loss were relatively low and roughly constant (13%) over the initial 12 weeks of the study, and losses from mortality and tag shedding were equivalent contributors (Table 1; Fig. 2). Losses over the following 16 weeks were minor. At smaller sizes mortality and tag shedding rates both increased, but some tags were successfully retained to the end of the study even for animals in the 11 cm size range. At sizes less than 11 cm FL it was not possible to close the body cavity around these large tags. We suspect that mortality in the 11–12 cm size class might be lower for wild pre-smolts, because the hatchery fish used in this study had substantial mesenteric fat bodies that largely filled the abdominal cavity. This limited the amount of space available for accommodating an acoustic tag and would not be as large a problem in lean wild fish.

Several studies have examined the effect of surgical implantation of tags in small salmon. Lucas (1989) and Moore et al. (1990) noted no difference in growth between control and implanted groups of rainbow trout and Atlantic salmon, respectively. In contrast, Adams et al. (1998a, b) found initially reduced growth of surgically implanted chinook relative to control animals during the first 3 weeks post-surgery for animals of similar size (11.4–15.9 cm) to those used in the present study. They also noted that the growth rates and swimming capabilities of surgically implanted fish was superior to that of animals where the tag was placed in the stomach. Lacroix et al. (2004) used Atlantic salmon smolts and found similar results to our study, with an initial period of mortality followed several months later by a period of tag shedding.

Our results indicate that animals of all sizes examined grew after surgical implantation, but that there was some reduction in growth relative to controls over the initial 12 week period. For pre-smolts greater than 14 cm initial size (~30 g),

the growth depression was less evident and a substantial proportion of the surgically implanted animals achieved individual growth rates that were greater than the mean rate for the controls (Fig. 1). No difference in growth was evident after week 12.

Various studies have commented on the issue of determining an appropriate ratio of tag weight to fish weight, with several authors advocating a 2% rule. More recent studies suggest that a higher ratio may be reasonable. Zale et al., 2005 (review), suggested 4% was appropriate in at least some studies, while Lacroix et al. (2004) suggested that the ratio should not exceed 8% for Atlantic salmon smolts in the 25–45 g range. In our study, the tag to body weight ratio of the 14 cm size class (33 g) is 4.2%, close to Zale et al.'s suggestion.

Tag loss via extrusion directly through the body wall or passage into the intestine and then out the anus has been noted previously (Summerfelt & Mosier, 1984; Chisholm & Hubert, 1985; Marty & Summerfelt, 1986, 1990; Baras & Westerloppe, 1999; Lacroix et al., 2004). Shedding rates seem to be species-specific, ranging from 59% in a 24-week study of rainbow trout (Chisholm & Hubert, 1985), 49–59% over a 17-week study in channel catfish (*Ictalurus punctatus*; Marty & Summerfelt, 1990), and essentially zero in a 120 week study in tilapia (*Oreochromis aureus*; Thoreau & Baras, 1997). In our study, we observed an overall tag shedding rate of 13% to week 12, with the highest shedding rates in the smallest size classes, but with rates that then dropped quickly and stabilized at about 7% over 12 weeks in pre-smolts ≥ 14 cm. Two additional shed tags over the following 16-week period raised the shedding rate to 20% for the 14 cm size class (Table 1). This suggests that, as with mortality, the loss of animals from a tracking study are relatively small and occur over a relatively short duration early in the study period. Multi-year studies are likely to be feasible because tag-induced mortality and tag loss are transitory phenomenon, and not processes that persist over the long-term.

Tag shedding rates may be compared with the shedding rate for the PIT-tagged controls used in our study of 1%, similar to rates of tag loss

reported in other studies (ranging from 1% to 5% for coded wire tagged salmon (e.g., Eames & Hino, 1983; Blankenship, 1990) and 3% for PIT-tagged brown trout (Ombredane et al., 1998)). Thus rates of tag loss may be expected to be higher than for the simpler CWT or PIT tag technologies. Studies need to balance the additional information gain with the higher expected loss rates of these larger and more expensive tags.

The mechanism by which extrusion occurs appears to be similar to that of mammals (Lucas, 1989), with the tag first being completely encapsulated and adhesion of the capsule to either the coelomic wall or the intestines. Subsequent contraction of the myofibrils within the encapsulation tissue resulting in the tag being pressed in close contact with the intestine or the body wall. Contact necrosis then appears to result in the gradual passage of the tag through the wall of the intestine or abdomen, and then out of the body (Summerfelt & Mosier, 1984; Marty & Summerfelt, 1986).

We did not examine the detailed histological changes occurring within the body cavity. However, the lack of any visual evidence of disruption of the initial incision and the markedly distended shape of the abdominal wall around the tag in a number of cases (Fig. 3) strongly suggested that encapsulation of these tags was initially occurring and that the pressure from capsule contraction would eventually force these tags out of the body. Surprisingly, during the following 16 week period only two tags were shed, and all of the animals initially noted at week 12 to have significantly distended abdomens were categorized as nearly normal by week 29; abnormalities were restricted to minor lumps only slightly detectable by finger tip or eye.

Although this distension presumably has some effect on swimming ability, the lack of any ulceration evident in the tag extrusion process (Fig. 4) strongly suggests that the biological mechanism underlying the extrusion process is well-developed and does not appear to place great stress on the animal. Furthermore, the regression of many animals initially expected to shed their tags at week 12 suggests that most tag loss was over by the seventh month of this study.

The foreign body response (Coleman et al., 1974) is not unique to fish, and is found to frequently occur when implants are placed into humans. For example, encapsulation of artificial breast implants in women has been reported to occur at rates of 27–40% within the first year following surgery (Little & Baker, 1980; Moufarage et al., 1987) and is thought to represent a rejection mechanism expressed in these patients. As the reported rates of encapsulation in women are similar to those seen for the dummy acoustic tags used in the present study, this suggests that a broader biological mechanism is at work that determines the biological basis of the host response to the implant, since surgical implantation in humans occurs under highly sterile conditions with much more care taken in the choice of biomaterials. It is significant that in the case of breast implants, only a proportion of the patients developed a capsule around the breast implants, as was the case in the present study. In the majority of women, encapsulation of the breast implant seems to be uncommon if not expressed during the first year of implantation and surgical intervention to remove the implant and surrounding capsule was rarely needed past one year.

In tracking studies in fisheries, where tags with multi-year lifespans are now available, issues concerning long-term retention of the tags are just as important as direct effects of tagging on mortality. Tagging studies should be designed recognizing the potential for continued rates of loss of tags over the long-term from mortality or shedding to affect the goals of such studies. Ideally, protocols need to be developed to minimize long-term rates of tag loss.

Conclusions

In both the Atlantic and Pacific oceans there is growing recognition that marine survival has dropped sharply for many stocks of salmon, making formerly viable populations unsustainable even in the absence of exploitation. This phenomenon was unexpected and not consistent with standard fisheries models, which predict that populations recover rapidly when fishing pressure is relaxed. The increased mortality experienced at

sea has in many cases been greater than the combined influence of large-scale sport and commercial fisheries on some stocks, such as southern British Columbia coho or steelhead (e.g., Smith & Ward, 2000; Ward, 2000; Welch et al., 2000). In a large number of British Columbia salmon stocks ocean survival has dropped to one-tenth that of only 25 years ago. Such changes make it imperative that a better understanding be developed of where salmon go in the ocean, because other stocks of salmon whose rivers are in reasonable geographic proximity have much higher ocean survival. Large-scale telemetry studies offer great promise for answering a number of fundamental biological questions about the ocean life of salmon.

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