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The fate of intracoelomic acoustic transmitters in Atlantic salmon (*Salmo salar*) post-smolts and wider considerations for causal factors driving tag retention and mortality in fishes

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Abstract

Acoustic telemetry is a widely used method in assessing behavioural dynamics in fishes. Telemetry transmitters (tags) are often surgically implanted in the coelom of the animal with limited in situ testing and sometimes only assuming that they have minimal rates of post-release tag shedding and mortality. However, fish are capable of expelling tags and mortalities do occur following release, with the mechanism (s) underlying these effects not well-understood. The purpose of this research was to address causal factors underlying tag expulsion and tagging mortality in fishes. We conducted an empirical assessment of tag retention and post-surgical mortality rates in post-smolt Atlantic salmon (*Salmo salar*) fitted with dummy (non-transmitting) acoustic tags over a 92-day monitoring period. This was complemented with a meta-analysis of factors affecting tag retention and post-surgical mortality rates in the wider literature. Post-smolt salmon had high rates of tag expulsion (54.8%), impaired growth, and a foreign body response evident but exhibited low rates of mortality following tag implantation ($\leq 5.1\%$). The meta-analysis showed that mortality was generally low across all studies (12.4%) and was largely unaffected by model cofactors. Tag retention rates were high among the studies investigated here (86.7%) and had a weak negative relationship with tag:body mass ratios. Our results suggest that while mortality is often low among tagging studies, including this one, caution must be exercised in assessing stationary tag location data as they may represent an expelled tag rather than a mortality event. Our results also indicate that tag dimensions are not nearly as important as the tag:body mass ratio.

Keywords Meta-analysis, Tag:body mass ratio, 2% rule, Tag expulsion, Foreign body response

Introduction

Acoustic telemetry has become an increasingly popular method for assessing animal behaviour and spatial use patterns in contemporary aquatic biology [1, 2]. At its core, acoustic telemetry involves the use of acoustic transmitters (hereafter referred to as tags) that are externally attached to or internally implanted in an experimental animal, which relay position and can inform depth, acceleration, and/or environmental temperature

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of the focal organism to any receiver device in range [3]. The information provided by acoustic tags can be used to infer a wide range of life history characteristics and ecological interactions in aquatic organisms. These data can address specific questions pertaining to an animal's daily and seasonal movement patterns [4–6], habitat preferences [7–9], and predation [10, 11]. Overall, advances in acoustic telemetry have coincided with a renaissance in characterising animal behaviour and ecology, furthering our foundational understanding of the biology of aquatic organisms [3].

In a fisheries context, acoustic telemetry has proven to be an important tool for stock management through development of an improved understanding of managed species' biologies [1]. For example, telemetry has been used to assess rates of natural-, fisheries-, and predator-associated mortality in wild fishes [12–15], which can refine mortality model estimates in stock assessment profiles [1]. Furthermore, acoustic telemetry has provided great insight into the spatial use and migratory patterns of commercially important species. In the case of Pacific salmonids, factors underlying migration timing and fine-scale migration patterns have been elucidated using telemetry to better understand the spatial ecology of these fishes [16–19]. Given the flexibility of acoustic telemetry and the wealth of data it provides on numerous aspects of fish biology, it is well-suited for use in fisheries biology.

To characterize behaviours, fish are fitted with an acoustic tag, which is typically inserted into the coelomic cavity through a small midventral incision that is sutured closed, followed by recovery and release of the tagged fish [20]. The underlying assumption of such tagging procedures is that the tag is retained in the body cavity until the end of the tag's battery life and that the tag has a minimal effect on fish health and mortality. Indeed, there is support for this notion as, in a broad range of fish species, mortality and growth rates appear unaffected with tag retention levels being high [21–26]. Although prior work has established that monitoring durations following tag implantation is usually done over an acute duration (i.e., < 1 month [27]), longer-term impacts on tag retention, growth, and mortality are poorly understood. In addition, a comprehensive analysis of the effects of acoustic tags on animal recovery and tag fate (i.e., retention vs. expulsion) has yet to be performed on fishes. Such considerations could be useful in making predictions of tag effects and fate in understudied systems.

To date, acoustic telemetry has been used to track the movements of a wide range of aquatic animal species, including reptiles, invertebrates, and mammals [28]. Fishes, particularly the salmonids, remain the most studied taxa in this respect [28, 29]. Despite widespread use

of acoustic tags, there still exists a degree of uncertainty of how the tag may have adverse effects on the health and survival of the fish [30, 31]. Indeed, there appears to be a dearth of information relating to the effects of acoustic tags on juvenile Atlantic salmon. From what little has been addressed, Atlantic salmon have been documented to have abdominal tag expulsion and have had some basic characterisations of internal tag fate [26, 32, 33]. Indeed, tag expulsion through the abdominal wall has been documented in salmon smolts [26, 32, 33], with expulsion rates appearing to have a mass/size basis, such that larger tags, relative to the fish, have lower retention rates [32, 33]. Furthermore, Atlantic salmon appear to have high levels of survivorship following tag implantation (up to 100% [26, 32]), although studies using smaller sample sizes ($n=5$) have noted that mortality can be upwards of 60% [33]. Aside from these few works, virtually nothing is known about tagging-associated mortality and rates of tag retention in juvenile Atlantic salmon, hampering our ability to make interpretations surrounding the post-release fate of these fish in acoustic telemetry studies.

The purpose of this work is threefold: 1. assess the ultimate fate of an intracoelomically placed tag with respect to tag retention rates and anatomical responses to the tag, 2. characterise post-surgical mortality in Atlantic salmon post-smolts over a timeframe reflective of a typical tag's battery life (i.e., > 90 days), and 3. conduct a review of the literature to address the impacts and fate of acoustic tags in a broad range of fish species to help develop a predictive framework associated with tagging effects. This exploratory work was conducted using two sizes of acoustic tags, the Innovasea V7 and V8, which are often used in Atlantic salmon telemetry studies [14, 34, 35]. Fish were fitted with an acoustic tag through a midventral incision and were monitored for 92 days following the procedure. Instances of mortality and tag loss were recorded during this time. Necropsies were conducted to verify tag retention as well as to characterize the internal anatomical responses to the tag. A meta-analysis was used to determine the general effects of intraperitoneal tags on fish mortality and tag retention.

Materials and methods

Animal care and holding conditions

Atlantic salmon post-smolts ($n=180$; Body mass = 208.7 ± 3.0 g; Fork length = 269.7 ± 1.4 mm) were sourced from a commercial hatchery (Merlin Fish Farm Ltd., Wentworth, NS, Canada) in August of 2017. Fish were held as two shoals ($n=90$ tank⁻¹) in 3000 L circular tanks at the St. Andrews Biological Station (St. Andrews, New Brunswick, Canada). Tanks were maintained on a flow-through of filtered oceanic sea water (30 L min⁻¹) at 12 °C under a 12 h dark:12 h light photoperiod. Fish were

fed ad libitum daily on a diet of commercial salmon feed (Optiline MB 200, Skretting Canada, Vancouver, British Columbia, Canada). Animals were held for 2-week pre-surgery to acclimate to lab conditions.

Acoustic tag implantation procedures

Dummy tags provided by the manufacturer were made of the same material, weight, shape, and size without electronics were used for implantation into the test fish. Salmon were haphazardly assigned to one of three treatment groups ($n=60$ treatment⁻¹): a sham control, or the fish was fitted with either a V7 tag (V7TP-2L; 22 mm length \times 3.5 mm radius; weight = 1.7 g in air; Innovasea Systems Inc., Bedford, Nova Scotia, Canada), or a V8 tag (V8-4L; 21 mm length \times 4 mm radius; weight = 2 g in air). In the case of sham controls, animals underwent anaesthetization and the handling aspects of the surgical procedure; however, a tag was not implanted in the animal. Each dummy tag had a unique serial number to help in identifying an individual fish. Each fish was fitted, intramuscularly, with a small Passive Integrated Transponder (PIT) tag while under anaesthetic to positively identify each fish.

Prior to surgical manipulations, all fish were fasted for at least 24 h. On the day of the tagging, individual fish were netted from the holding tank and immediately transferred to a bath containing Syncaïne (aka tricaine methanesulfonate [MS222]; 100 mg L⁻¹; Syndel; Nanaimo, BC, Canada) to sedate the animal. Once fish had been visibly sedated (i.e., lack of reactivity, low opercular rate), fork length and body mass were quickly measured, and the animal was promptly transferred to a soft-foam V-trough. Restrained post-smolts had their gills continuously irrigated with aerated saltwater recirculated over their gills using a small hobby pump and a tube. This water contained a lower strength maintenance dose of Syncaïne (50 mg L⁻¹) to ensure that animals remained sedated throughout the entirety of the procedure. A small incision (~20 mm) was then made on the ventral midline of the fish, and the tag gently inserted into the celomic cavity. The incision was then closed using up to three independent sutures (at 0.5 mm intervals) at the middle and ends of the wound (4–0 Vicryl sutures; Ethicon Inc., Raritan, New Jersey, USA). The fish recovered in a bath of raw saltwater until their righting reflex and opercular movements returned to normal. Recovered fish were then moved to and held in one of two large circular tanks (~1000 L), each containing an equal proportion of fish that underwent one of the three treatments ($n=90$ fish tank⁻¹). Surgeries were performed by one of three persons in a haphazard manner and their contributions were recorded throughout the procedure.

Monitoring of chronic tag effects

Tagged fish were monitored daily over a total of 92-day period for any tag expulsions or mortalities. The former was determined based on acoustic tag IDs and matched to an individual by PIT tag at the end of the experiment. However, not all instances of dummy tag expulsion were immediately recognized as they were occasionally consumed upon deposition in the tank. In such instances, tags were discovered in necropsies and thus had no exact time associated with expulsion. At the cessation of the monitoring period, each fish was euthanized using a lethal dose of Syncaïne (150 mg L⁻¹). Fish length and weight were taken for determinations of growth-related indices and length–weight relationships (see below). External abnormalities related to the tagging procedure were also characterized. This included if there was tag protrusion of the body wall, if sutures were missing, or if the incision had fully healed. Post-smolts were then dissected to confirm the presence of the tag within the coelom and to characterize how the internal structures had reacted to the tag. In the case of the former, this was noted as one of three outcomes: retained, expelled, or in progress of expulsion, meaning that the tag was encapsulated in the body wall of the fish. With respect to the reaction of the internal structures, this included characterization of any organs or tissues that the tag had become lodged in or incorporated into. Any signs of abnormalities such as infection or tissue damage were also noted. The fish's sex was also determined during dissections.

Calculations and statistical analyses

All statistical analyses were made using the R programming language (v 4.1.1) using R Studio [v 1.4.1717; [36]]. For all statistical models, significance was accepted at $\alpha=0.05$ with all values being mean \pm SEM, unless otherwise noted. Survival analyses were conducted using the package 'survival' [37, 38]. Specifically, we used a Cox proportional-hazards model to ascertain the effects of tagging treatment (i.e., sham, V7, or V8) on the time to tag expulsion and mortality. In the case of the latter, sham fish were not included in the model as there was no tag to expel. It is worth noting that no loss of PIT tags was documented in any of the fish. In both models, fish that did not expel their tags or that survived the entire experimental series (i.e., 92 days) were censored from the analysis. Survival plots were made using the R package 'survminer' [39]. Comparisons of tag expulsion status between V7 and V8 fish were made using a Chi-square test of independence. Due to low sample sizes, the anatomical responses to each of the tags was not evaluated using statistical analyses and remain qualitative.

Instantaneous growth rate (g) was determined as follows, where Δt is the change in time in days, and w_1 and w_2 are the initial and final body masses of the fish (in grams), respectively [40].

$$g = \frac{\log_e(w_2) - \log_e(w_1)}{\Delta t} \quad (1)$$

Specific growth rate (G) was calculated as follows using the fish's instantaneous growth rate (g) [40]:

$$G = 100 \cdot (e^g - 1) \quad (2)$$

Specific growth rate (SGR) was then analysed for tagging-related effects using a linear mixed model using the package 'lme4' [41], which included SGR as the response variable with the main effects of tagging treatment (i.e., sham, V7, or V8), surgeon, and sex, and the random effect of holding tank. We also characterized the relationship between the change in absolute body mass in relation to the absolute change in length as a measure of condition of the fish (i.e., a larger increase in body mass relative to a given change of length was indicated that the condition of the fish increased during the study period) using the same linear mixed model. This model also included the covariates tagging treatment, surgeon, and sex as main effects with holding tank as a random effect. In both models, pairwise comparisons were made between the tagging treatments (sham, V7, or V8) were made using a Tukey test [42] using the R package 'emmeans' [43]. To ensure that model assumptions were met, growth data were visually inspected for adherence to normality and equal variance using a Q-Q plot and a residuals vs. fit plot, respectively.

Literature search and meta-analysis procedures

Literature searches were made using both Google Scholar (November 25 2021) and Web of Science (December 1 2022) with the following search terms: {[fish*] AND ("acoustic telemetry" OR acoustic*) AND (tag shedding* OR tag expulsion* OR tag shedding* OR retention* OR expulsion* OR tag loss*) OR (tag* mortality OR survival OR death OR mortality)}. For the Google Scholar results, we downloaded all publications from the first seven results pages constituting a total of 119 entries. For the Web of Science results, we selected the first 100 search results. Resulting lists were then first screened for their relevance by skimming the title and abstract to determine if it involved fish and tagging-based projects. From this preliminary list of papers, the specific details were extracted, which included the relevant citation information, taxa, species/common names, habitat (fresh, brackish, or saltwater), tag dimensions, type, and weight, incision location and size, and group sample

sizes. We further refined this list to only include works that were using intracoelomic tags that did not extend outside the body cavity (e.g., radio tags with antennae) or gastric tags. Consequently, our results consisted of studies using intracoelomic dummy tags, acoustic tags, and PIT tags and were limited to only those reporting tag loss and/or tag-associated mortality (See supplementary materials for full list of references not provided here; Additional file 1: Table S1 provides a list of the articles used in the meta-analysis). To determine tag:body mass ratio, reported values were used, if available. Otherwise, tag:body mass ratio was determined using the reported average body and tag mass. In instances, where only a range of tag:body mass ratios were presented, we opted to extract the higher end of the range as a more conservative measure of this metric (i.e., if effects do exist, this should produce the largest effect size), which was applied to all fish from the respective study source. We always used the upper range of incision size if these data were provided. Each experimental treatment was considered as an independent estimate and in some cases studies had multiple estimates from either testing multiple tag types or having multiple experimental species. Each of these individual estimates was coded with a unique experimental number and nested within the paper ID to ensure that model estimates were not producing pseudoreplication (see below). Experimental duration consisted of the maximum monitoring duration of a particular trial, if indicated.

Statistical meta-analysis procedures were conducted using the R package 'metafor' (V 3.4.0; [44]). Effect sizes and the corresponding variance for both mortality and number of tags retained were determined using the 'escalc' function. This involved expressing effect sizes as a proportional value, which were transformed using a Freeman–Tukey double-arcsine transform to meet model assumptions [45]. Transformed data were then analysed using a multivariate/multilevel linear (mixed-effects) model fit using a restricted maximum likelihood approach (REML; [46]). For both tag retention and mortality estimates, we treated our models in a stepwise fashion by first assessing a complete model with all fixed effects (tag length, tag diameter, incision size, experiment duration, and tag:body mass ratio) and then assessing each fixed effect individually against the response variable. This was done as some articles did not include all of the fixed-effects metrics and thus may not have been represented in the full model. To ensure that we accurately portrayed these metrics on affecting response variables, we opted to use the individual models as well. For all models, we also included paper ID as a random effect, which had a nested term of experimental number included for each work thereby accounting for any repeated sampling that may have occurred. P values

for all model terms were also corrected for false discovery rates using a Benjamini–Hochberg correction [47]. All model estimates/outputs are presented in the transformed data. Models were visually inspected using profile likelihood plots [44, 48].

Results

Tag retention

Rates of tag retention were poor among Atlantic salmon post-smolts. Overall, 54.8% of fish had either shed their tag already or were in the process of expelling their tag over the 92-day monitoring period. A total of 34.8% of all tagged fish had their tag fully expelled from the body cavity. Of those that fully expelled their tag and that had a recorded expulsion date, the overall mean time to tag expulsion was 33.3 ± 1.1 days ($n=20$). On a tag-treatment basis, V7 and V8 tags had comparable times to tag expulsions (likelihood ratio test = 1; $df=1$; $P=0.3$; Fig. 1) suggesting that tag size may not be a factor of importance. This is further supported by comparisons of the observed status of the tags at the termination of the experiment (i.e., retained, expelled, or in progress expulsion) being similar between fish fitted with V7 and V8 tag ($\chi^2=1.99$; $df=2$; $P=0.4$; Fig. 1). More specifically, only 48% and 42% of post-smolts fully retained their tags by the end of

the 92-day monitoring period for V7- and V8-fitted fish, respectively. Although tagging group had no effect on tag expulsion, it did appear that V8-fitted fish had a greater percent of fully expelled tags when compared to V7-fitted fish (41% vs. 29%).

Figure 2 exemplifies the differences between a tag that was retained and a tag in progress of expulsion. In fish that retained their tag, there was no external signs of the tag being forced from the body (Fig. 2A). Alternatively, the start of expulsion appeared to result from tag encapsulation by body wall mesentery (Fig. 2B) and then becoming lodged in the dorsal musculature (Fig. 2C). Typically, this was away from the incision site and occurred on the lateral surface of the fish. From an external view, an ‘in progress’ tag expulsion was demonstrated by a slight bulge in the skin (Fig. 2D) with gradual thinning and eventual rupture through the skin into the external environment (Fig. 2E). Fish that retained the tag completely often had the tag encapsulated by the mesentery (Fig. 2B) or lodged into one of the internal organs, such as the pyloric caeca (Fig. 2F).

We also quantified the fate of the tags within the body cavity of the fish. While this analysis was not statistical, most of the tags that were retained within the body cavity were encapsulated by the mesentery for both treatment groups (Fig. 3). These retained tags were largely concentrated to the right lateral of the left–right axis and the medial of the antero–posterior axis. The other most common response in fish that retained tags was that the tag was not encapsulated by any internal organs or structures (Fig. 3). In V7-fitted fish, one tag was found to be embedded in the pyloric caeca, while a singular fish with a V8 tag had the surrounding tissues adhering around the tag (Fig. 3). 0

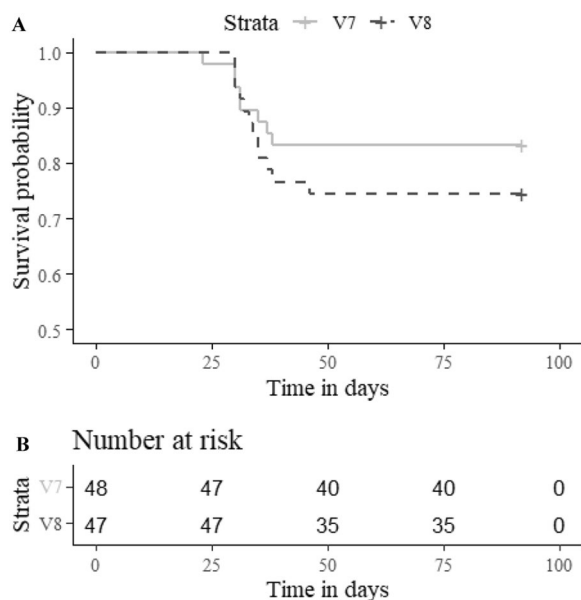


Fig. 1 Plot representing the number of days that an intracoelomic acoustic tag was retained inside the body cavity of an Atlantic salmon (*Salmo salar*) post-smolt following the insertion of either V7 (black, dashed line) or V8 (grey, solid line) acoustic tag. The corresponding risk table is presented below this plot. Fish were monitored over a 92-day time frame for tag expulsion through daily checks, with fish retaining the tag until the end of the experiment censored from the analysis (denoted by a ‘+’ shape)

Growth and condition outcomes

Tagging treatments impacted the growth indices investigated. There was a significant positive relationship between the change in a fish’s body weight and the change in the fish’s fork length ($df=165.40$; $t=18.79$; $P<0.001$), such that individuals that had larger changes in body mass also had larger length changes (Fig. 4). There was also a significant effect of surgeon on the change in the fish’s fork length ($df=165.10$; $t=2.51$; $P=0.013$; Table 1). There was no effect of either tagging type or sex on this relationship (Table 1). The use of the V7 tags resulted in lower SGR ($P=0.002$; Fig. 5) compared to sham controls by 14% (Table 1). In contrast, fish tagged with V8 tags were comparable to both shams and the V7 tagged fish (Fig. 5; Table 1).



Fig. 2 Images depicting the fates of acoustic tags in Atlantic salmon (*Salmo salar*) post-smolts following a 92-day monitoring period. **A** Incision from tag insertion (with retained sutures) has completely healed and there is no external sign of tag rejection. **B** Example of a tag that has been encapsulated by mesentery in the coelom of the fish. **C** Tag is starting to be expelled through the lateral surface of the dorsal musculature away from the incision. **D** Expulsion of the tag can be seen first as a bulge on the lateral surface of the fish, **E** culminating in it rupturing through the skin. **F** In the case of fish that did retain their tags, the tag was often seen lodged in one of the organ structures, such as in the pyloric ceca as depicted here

Post-tagging mortality

Mortality associated with the surgical procedures and implantation of acoustic tags was minimal across all treatment groups ($\leq 5.1\%$; Fig. 6). Interestingly, of the six post-smolts that died, two appeared to be quite thin and small suggesting some underlying physiological/anatomical issues. The remainder of these fish did not have any other obvious symptoms or signs that may have explained their mortality.

Meta-analysis summary and metaregression statistics

Across all studies, tag retention in fishes averaged 86.7%, ranging from 20 to 100%. In the full model, tag

retention was only affected by tag:body mass ratios (Estimate = -0.061 ; 95% $CI_L = -0.101$, 95% $CI_U = -0.021$; $P = 0.003$; Table 2), such that increased tag:body mass ratios are associated with a decrease in the likelihood of tag retention (Fig. 7). No other fixed effect had a statistically significant effect on tag retention in the full model, which was a pattern also shared by the individual models (Table 2). Point estimates and the corresponding confidence intervals as well as the models' meta-regression variance components for all the tag retention and mortality values used here can be found in the supplementary materials.

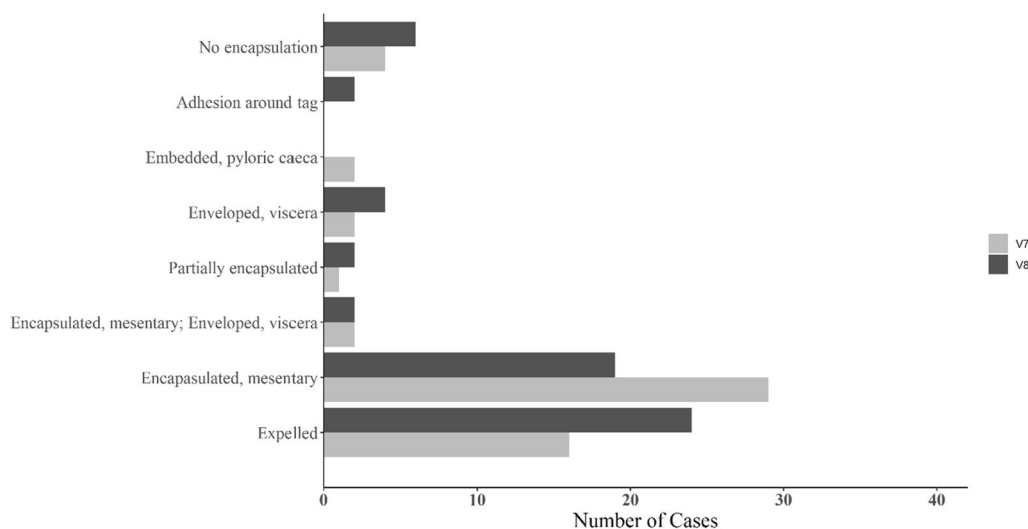


Fig. 3 Counts of the final anatomical location of an intracoelomic tag after 92 days being fit within an Atlantic salmon (*Salmo salar*) post-smolt fitted with either a V7 (light grey) or a V8 (dark grey) acoustic transmitter. These two treatment groups were not statistically compared against one another due to low sample sizes

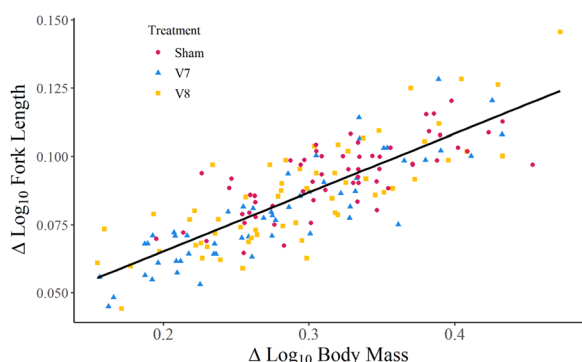


Fig. 4 Scatterplot representing a relationship between an individual Atlantic salmon (*Salmo salar*) post-smolt’s change in Log_{10} body mass with its change in Log_{10} fork length over a period of 92 days. Animals were treated as either a surgical sham or implanted with a V7 or V8 acoustic tag. A linear mixed effects model was fit to the data with the change in Log_{10} fork length as a product of the change in Log_{10} body mass, tag type, surgeon, and sex as the fixed effects, and holding tank as a random effect. Statistical significance was accepted at $\alpha=0.05$. Changes in Log_{10} fork length were found to be the product of changes in Log_{10} body mass ($P < 0.001$), whereas both tagging treatment and sex had no effect. The black line represents the overall relationship of the change in Log_{10} body mass with its change in Log_{10} fork length independent of tagging or sex effects

Collective mean mortality rate was 12.4% and ranged between 0 and 90%. In the full model, tag diameter was the only fixed effect found to influence tagging mortality across our studies via a positive relationship (Table 2). However, when looking at just tag diameter against mortality in the individual models, there was

no relationship between the two parameters (Estimate = 0.044; 95% $\text{CI}_L = -0.007$, 95% $\text{CI}_U = 0.021$; Adjusted $P = 0.346$; Table 2). None of the other fixed effect parameters exhibited statistically significant relationships with mortality in the individual models (Table 2).

Discussion

Possible causal factors driving tag expulsion in fishes

The immune system likely plays a key role in determining tag retention rates in fishes. While our understanding of how the immune system mediates the coordination, isolation, and expulsion of tags in fishes appears rather limited [46–52], there is a wealth of knowledge concerning the foreign body response in a clinical setting [53, 54]. Briefly, the response to a foreign object is coordinated by the immune system. The initial, acute phase of the foreign body response involves the release of proinflammatory factors that attracts neutrophils to the area, which further releases proinflammatory agents and increases localized vascularization. The neutrophils’ actions also attract monocytes to the area, which undergo differentiation to macrophages. The macrophages are the ‘workhorses’ of this system as they are responsible for enveloping the object and secreting degradatory compounds to eliminate the object while also further mediating the inflammatory response [53, 54]. However, if the object cannot be broken down, the actions of the macrophages switches to a chronic, fibrosis-generating role by activating fibroblasts to produce a proteinaceous, extracellular matrix (ECM) to encapsulate and isolate the foreign body from

Table 1 Statistical output for the effect of tag type (i.e., sham control, V7 or V8 acoustic tags) and sex on Δ length and specific growth rate (SGR) in Atlantic salmon (*Salmo salar*) post-smolts monitored over a 92-day holding period.

Response Variable	Term	Estimate	Standard error	df	t value	P value
Δ Length						
<i>Linear mixed model—fixed effects</i>						
	(Intercept)	0.019	0.004	92.35	4.36	<0.001
	Δ Weight	0.212	0.011	165.40	18.79	<0.001
	Tag type—V7	-0.004	0.002	165.00	-2.05	0.042
	Tag type—V8	-0.001	0.002	165.90	-0.56	0.580
	Sex—M	0.003	0.002	166.00	1.70	0.092
	Surgeon	0.002	0.001	165.10	2.51	0.013
<i>Pair wise contrasts</i>						
	Sham—V7	0.004	0.002	165	2.05	0.104
	Sham—V8	0.001	0.002	166	0.55	0.846
	V7—V8	-0.003	0.002	166	-1.55	0.271
SGR						
<i>Linear mixed model—fixed effects</i>						
	(Intercept)	0.783	0.048	10.12	16.47	<0.001
	Tag type—V7	-0.109	0.031	166.06	-3.48	<0.001
	Tag type—V8	-0.069	0.031	166.35	-2.24	0.026
	Sex—M	0.046	0.026	166.64	1.79	0.076
	Surgeon	-0.004	0.016	166.06	-0.25	0.800
<i>Pair wise contrasts</i>						
	Sham—V7	0.109	0.031	166	3.47	0.002
	Sham—V8	0.069	0.031	166	2.24	0.068
	V7—V8	-0.040	0.032	167	-1.27	0.415

A linear mixed effects model with the fixed effects of tag type, sex, surgeon, and Δ weight (Δ length model only), and a random effect of holding tank. Tag type effects were addressed using Tukey pairwise contrasts. Bolded rows represent statistically significant results ($\alpha=0.05$)

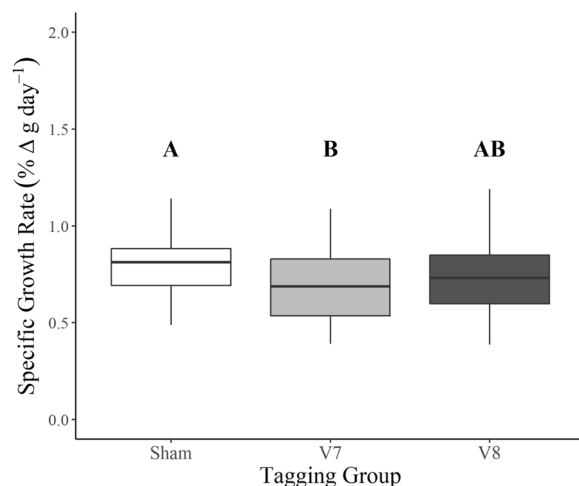


Fig. 5 Boxplot representing the effects effects of a sham control (white) or the insertion of either a V7 (light grey) or a V8 (dark grey) acoustic tag on the specific growth rate (SGR) of Atlantic salmon (*Salmo salar*) post-smolts. Statistical significance was accepted at $\alpha=0.05$. A linear mixed effects model (with treatment group, surgeon, and sex as fixed effects, and holding tank as a random effect) and Tukey pairwise comparisons were used to discern differences among treatment groups shown using letters

the surrounding tissues [53, 54]. This is preceded by vascularization of the capsule and an increased proliferation of the ECM until a steady state of growth is achieved. In the mammalian model, this process appears to largely result in the foreign body being retained and isolated as in the case of various biomaterials and implants [50–56] but in some rarer instances, these objects can be expelled from the body [57, 58].

In fishes, there is evidence that the foreign body response is important in mediating tag expulsion. One of the first works to address a causal mechanism underlying tag explosion found that in channel catfish (*Ictalurus punctatus*), like mammals, dummy acoustic tags were encapsulated in a layer of myofibroblasts and collagen tissue prior to expulsion [51]. Marty and Summerfelt's [51] proposed model of expulsion was similar to mammalian models at the time albeit with expulsion driven by the capsule's myofibroblasts contracting the tag against the body wall. Lucas [59] further elaborates on this model by suggesting that trans-body wall passage of encapsulated tags occurs through pressure necrosis at the exit point, which is supported by their histological characterisations therein. While our work did not address tissue histology

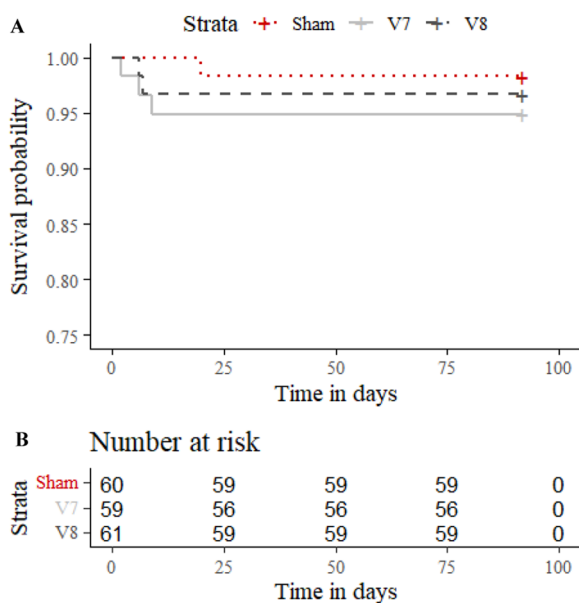


Fig. 6 Plot representing the survival of Atlantic salmon post-smolts following the sham surgery (red, dotted line), or the intracoelomic insertion of a V7 (black, dashed line) or V8 (grey, solid line) acoustic tag **A**. The corresponding risk table is presented below this plot **B**. Fish were monitored over a 92-day time period with survivors censored from the analysis (denoted by a '+' shape)

specifically, we did note that tags were often encapsulated by fibrous tissue in the body cavity of the fish and that expelled tags were encapsulated and superficially appeared to move through a site experiencing localized tissue necrosis (see Fig. 2) akin to what Lucas [59] had previously described. The greater body of literature also appears to support a role of the foreign body response in mediating tag retention/expulsion, as evidenced by tag encapsulation or tags translocating across body walls/organ structures [49, 50, 52, 60, 61]. While some of our salmon did have clear signs of body wall expulsion, we cannot rule out expulsion via the anus given that transintestinal movement of tags can occur in fishes [51]. Together, our results provide further evidence in support of the foreign body response in mediating tag expulsion.

The percentage of tags that were expelled or in the process of being expelled in our salmon was quite high. The 45% retention rate in these salmon was unexpected as prior work with salmonids demonstrates high retention rates (> 85% [30, 59–67]), which is further supported by our meta-analysis results of the wider fish literature (~87% retention). From an analytical perspective, low tag retention is problematic in a telemetry study as it may result in stationary tag location data being inferred as mortality, when in fact the tag has been expelled and the surviving fish remains active. Consequently, this high rate of tag shedding should be accounted for in acoustic

analyses when conducting trials with Atlantic salmon post-smolts. As with other works [32, 68, 69], we found that when shedding occurred, it was early in the monitoring period (~33 days) suggesting that losses are likely greater in the early stages following release. While we are unsure of the exact mechanism driving this effect in our salmon, tag expulsion rates can be modulated by several factors, including water temperature [50, 67, 70], large/heavy tag size [32, 51], and decreasing fish body size [63–68]. Our meta-analysis results also supported this to an extent, whereby we found a significant relationship between tag retention rates and tag:body mass ratios. However, we are sceptical that any of these factors are playing a role in the high rates of expulsion given that tag weights represented a small fraction of the fish's body mass (~1%), are a typical size for fish of this size class, and were reared in a 'normal' temperature range for this species [71]. In the clinical literature, the size, shape, location, and sterility of the object as well as any localized tissue damage can influence the magnitude of the foreign body response [54, 55, 72]. While entirely speculative, the area that the tag settled in as well as localized bacteria/tissue damage may have prompted a heightened immune reaction in response to the tag. Future works should address the role of the foreign body response in mediating tag retention dynamics in fishes as it could provide valuable insight in developing predictive models of tag expulsion likelihood in a field setting.

The results of the meta-analysis provided a great deal of insight to assess important factors related to enhancing tag retention in fishes. While tag dimensions and mass were shown to not affect tag retention rates in the meta-regression, tag:body mass ratio did positively scale with tag expulsion in the greater literature, indicating this as a key consideration in designing telemetry studies. Rather than a hard cutoff as proposed in the 2% rule [73], it suggests that this relationship exists along a continuum, where generally larger ratios correspond with a greater likelihood of expulsion, particularly at extreme tag:body weight ratios. In the context of the foreign body response, such comparatively large objects are likely to cause a greater immune response [54, 55, 72] and may result in earlier expulsion [51]. Our results also indicate that the absolute dimensions of the tag (length and mass) are not nearly important as the relative size of the tag to the size of the fish. Consequently, we would recommend using the smallest possible tag size that also meets the experimental goals of the project (i.e., maximizing the trade-off in tag size to battery life) to ensure a minimal loss from expulsion. Of additional interest is that monitoring duration did not affect tag expulsion rates in the present study. In some works, most tag loss appears to occur over the first few weeks of the monitoring period

Table 2 Meta-regression fixed effects model estimates comparing tagging and experimental parameters against tag retention and mortality rates in fishes.

Model (observations)	Parameter	Estimate	Standard error	z value	P value	CI—lower	CI—upper	Adjusted P value
Tag retention								
Full model (k = 42)	Tag length	-4.42E ⁻³	5.26E ⁻³	-0.84	0.40	-0.0147	0.0059	0.400
	Tag diameter	7.87E ⁻³	1.89E ⁻²	0.42	0.68	-0.0291	0.0449	0.939
	Incision size	6.81E ⁻³	9.72E ⁻³	0.70	0.48	-0.0122	0.0259	0.527
	Experimental duration	-5.08E ⁻⁴	5.56E ⁻⁴	-0.91	0.36	-0.0016	0.0006	0.362
	Tag:body mass ratio	-6.10E⁻²	2.03E⁻²	-3.00	0.00	-0.1009	-0.0212	0.003
Tag length (k = 71)	Tag length	-3.56E ⁻³	2.78E ⁻³	-1.28	0.20	-0.0090	0.0019	0.400
Tag diameter (k = 68)	Tag diameter	-7.63E ⁻⁴	9.91E ⁻³	-0.08	0.94	-0.0202	0.0187	0.939
Incision size (k = 57)	Incision size	4.02E ⁻³	6.35E ⁻³	0.63	0.53	-0.0084	0.0165	0.527
Experimental duration (k = 80)	Experimental duration	-3.34E ⁻⁴	3.28E ⁻⁴	-1.02	0.31	-0.0010	0.0003	0.362
Tag:body mass ratio (k = 62)	Tag:body mass ratio	-6.94E⁻²	1.70E⁻²	-4.08	0.00	-0.1028	-0.0360	<0.001
Mortality								
Full model (k = 43)	Tag length	-8.75E ⁻³	4.50E ⁻³	-1.94	0.05	-0.0176	0.0001	0.104
	Tag diameter	4.42E⁻²	1.61E⁻²	2.75	0.01	0.0127	0.0756	0.012
	Incision size	-1.53E ⁻³	8.02E ⁻³	-0.19	0.85	-0.0173	0.0142	0.849
	Experimental duration	-7.88E ⁻⁶	5.07E ⁻⁴	-0.02	0.99	-0.0010	0.0010	0.988
	Tag:body mass ratio	-2.29E ⁻³	2.18E ⁻²	-0.10	0.92	-0.0451	0.0405	0.917
Tag length (k = 80)	Tag length	-2.47E ⁻⁴	1.78E ⁻³	-0.14	0.89	-0.0037	0.0032	0.890
Tag diameter (k = 77)	Tag diameter	6.91E ⁻³	7.32E ⁻³	0.94	0.35	-0.0074	0.0213	0.346
Incision size (k = 60)	Incision size	-2.08E ⁻³	7.38E ⁻³	-0.28	0.78	-0.0165	0.0124	0.849
Experimental duration (k = 94)	Experimental duration	-1.83E ⁻⁵	2.13E ⁻⁴	-0.09	0.93	-0.0004	0.0004	0.988
Tag:body mass ratio (k = 67)	Tag:body mass ratio	3.56E ⁻³	1.49E ⁻²	0.24	0.81	-0.0256	0.0327	0.917

The term 'Full model' represents a meta-regression containing all fixed effects, while subsequent models examined a single fixed effect against the response variable. Meta-regressions were conducted using proportional data transformed using Freeman–Tukey double-arcsine transformations. Statistical significance was accepted at $\alpha = 0.05$ with P values being corrected for multiple comparisons using a Benjamini–Hochberg correction. Significant terms are bolded in the table. k values represent the number of observations for a specific model

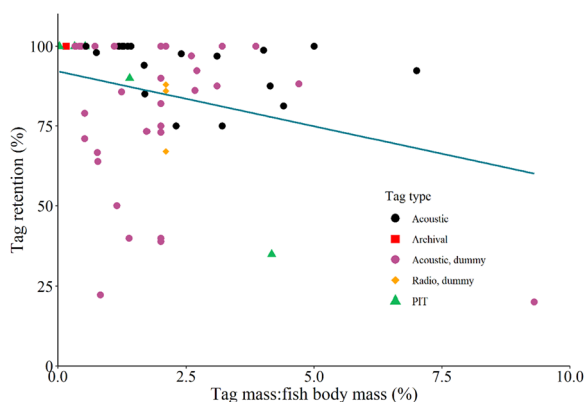


Fig. 7 Scatterplot representing the relationship between an intracoelomic tag being retained and the tag:body mass ratio of fishes. In the meta-regression, this relationship was statistically significant ($P < 0.05$) and is visually denoted by the blue line. Each point represents a unique experiment's tag retention rate across multiple studies and the type of tag is denoted by both colour and shape

with fewer losses happening over more chronic durations [32, 68, 69]. While this may be a trend in the literature, it is important to understand that our metric of time in the meta-regression represents an average tag loss over the monitoring duration rather than time to tag loss as this latter value was often not reported. As such, it is possible that tag loss may be greater in the initial weeks following implantation and should be considered when designing an experimental series.

Tag effects on growth rate

A key consideration when designing a telemetry study is avoiding adverse impacts of the tag itself on the behaviour and fitness of monitored fish [74, 75]. Effects on growth parameters are often used as a proxy for tag-related impacts on the fish and have been widely explored in tagged fishes [21, 24, 33, 59, 69, 73–78]. In the salmon investigated here, we found that tagging had a negative impact on SGR (14% lower for V7 tagged fish over a 92-day period), consistent with some of the literature [69, 77, 78]. Likely, tag burden or a stress effect related to

tag implantation is imparting a greater metabolic load on the animal resulting in reduced growth inputs. However, additional metabolic profiling would be needed to confirm such notions. Furthermore, tagging-related impacts on growth appear to be highly contextual and can have a strong temporal component. For example, Greenstreet and Morgan [78] found that while small size classes of salmon parr (<160 mm) had lost body weight, while larger conspecifics were still accruing body mass. Similarly, condition factor (K) of bloaters (*Coregonus hoyi* initially) decreased following tagging but recovered in the latter half of the experiment [24]. Indeed, we saw that Δ length was influenced by surgeon here suggesting that there can be variation stemming from slight differences in a person's surgical skills/approaches. As our monitoring of growth was based on initial and final changes in mass/length values, we may not be addressing some of the more nuanced changes in growth rates here. Overall, these results do suggest that tag burden is associated with impaired growth in post-smolt Atlantic salmon.

The effects of tagging in modulating mortality rates

Tag implantation appeared to have little impact on mortality of post-smolt salmon. This result is consistent with the literature, where the use of intraperitoneal tags is often associated with low rates of mortality (<10%) in salmonids [24, 26, 69, 79, 80] and, more broadly, teleost fishes [78–83]. Similarly, our meta-analysis concluded that mean post-release mortality rate was 12.4% across all studies examined, suggesting that the procedures used to implant tags appeared to have a minimal impact on post-release survival, all else being equal. However, caution must be exercised in this statement as tagging-mortality studies are often conducted in a controlled, laboratory-based environment, where the fish can recover under ideal environmental conditions and in the absence of predators [27]. It is entirely possible that the additional stress burden imparted by surgical procedures may increase susceptibility to mortality in the wild, especially if a fish is facing several energetically demanding processes simultaneously (e.g., temperature shifts, infection, sustained swimming, predator evasion). For Atlantic salmon post-smolts, tagging-associated mortality is expected to be fairly low based on our findings.

Tagging-mortality rates are not necessarily low across all settings and can be highly context-specific. While the experimental portion of this study demonstrated low tagging-associated mortality, there was considerable variation in study-specific mortality rates in the meta-analysis, ranging from 0 to 90% mortality. Several factors can exacerbate post-release mortality of tagged fish, including: fish length and body mass [69, 81–86], tag size [80, 84, 86], tag to body mass ratio [30, 32,

66, 87], and the source population of fish [80]. Based on our meta-regression results, these factors appear to have little influence on mortality, suggesting that responses are either highly context-specific (i.e., mortality arises under a specific set of conditions or in a specific species) or that there is largely a null effect. For example, the '2% rule' (i.e., tag mass remains under 2% of the fish's body mass [73]) was commonly believed to be an important consideration for minimizing tagging mortality and behavioural impairments in fishes [29, 88]. New evidence suggests that this effect is not ubiquitous; rather, contextual considerations should drive the appropriate tag size for the study in question [27, 74, 89]. Similarly, the general lack of effect of the model covariates in our meta-regression reflects an analogous situation, where context-specific effects of the experimental design are likely more important driving factors for tagging-related mortality. Together, our results suggest that there are no clear patterns related to tag parameters, incision size, or experimental duration affecting tagging-related mortality.

Despite the increasing popularity of acoustic tagging as a tool in fisheries science, we still lack a thorough understanding of the specific physiological mechanisms driving tagging-related mortality in fishes. Regardless of the specific methodology used, the process of tagging is generally considered to be stressful to fish. Capture [87–93], handling [91–96], and sedation/surgery [94–100] can all induce pronounced stress responses in fishes, which is often marked by elevations in metabolic rate and circulating levels of high energy substrates and cortisol as well as the development of acidosis, among a multitude of other effects. Indeed, stress biomarkers have been observed in fishes following the tagging procedure [101, 102], although reporting on tagging-specific responses are scant in the literature. At this time, we can only speculate that physiological perturbations associated with tagging are likely the main factor driving post-release mortality in tagged fish. Thus, we recommend that tagging be conducted in a manner that minimizes stress to the animal (i.e., minimize air exposure and handling, appropriate collection methods, minimizing captivity durations, ideal anaesthesia dosages [27, 100–105]) and that pilot trials be conducted to ensure that tagging conditions are optimized for fish welfare (i.e., appropriate training and expertise level of person performing surgery, selecting appropriate tag size, tag insertion location, and recovery periods [27, 103–108]). In addition, as survival/retention rates can differ between surgeons (reviewed in [109]), we also recommend that the person performing the tagging be recorded, which will permit for any tagger-related biases be addressed during the analysis phase of the study. While there remains uncertainty regarding the

physiological drivers surrounding post-tagging mortality, ensuring that stress is minimized should help enhance survival of tagged fish. We also recommend that all studies perform in situ testing when samples sizes allow.

Conclusions

This study attempted to characterise rates of tag retention and mortality in Atlantic salmon post-smolts fitted with dummy acoustic tags. Secondly, we conducted a formal meta-analysis of the literature to assess covariates that may influence tag loss and post-tagging mortality to discern how tagging procedures could be refined to minimize tag losses or mortality. Rates of tag loss were high in this study, in contrast to general findings in the literature, and may stem from a heightened foreign body response. Growth of tagged salmon post-smolts was also mildly impaired and may suggest increased metabolic loading associated with a tagged state. Mortality in experimental salmon was consistently low across treatment groups and was consistent with the literature at large. However, both the results of our experiment and of the meta-analysis are unable to address specific causal mechanisms underlying post-tagging mortality and suggest that context-specific effects, especially stress status, are likely the main driver of mortality. Together, we recommend that tagging be conducted in a manner that minimizes stress and that uses tag sizes that are appropriately scaled to the focal fish of interest (i.e., as small as possible). These factors would likely increase tag retention while minimising tag-related mortality to ensure that experimental series are reflective of fish behaviours and not misinterpreted as additional mortality (i.e., tag expelled, but fish survived).

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40317-023-00351-0>.

Additional file 1: Table S1. Paper identification key for the references used in the meta regression. **Table S2.** Meta-regression variance components for comparing tagging and experimental parameters against tag retention and mortality rates in fishes. Paper ID was treated as a random effect in the model, while experimental number was nested within this random effect. Meta-regressions were conducted using proportional data transformed using Freeman–Tukey double-arcsine transformations. **Figure S1.** Forest plot depicting point estimates and the corresponding 95% confidence intervals for mortality proportions in tagged fish from journal articles collected in the meta-analysis. Individual studies are represented by a coded number (Paper ID; see Additional file 1: Table S1 for references). In some cases studies collected multiple estimates of tagging-associated mortality which are represented by ticks following the study identifier. **Figure S2.** Forest plot depicting point estimates and the corresponding 95% confidence intervals for tag retention proportions in tagged fish from journal articles collected in the meta-analysis. Individual studies are represented by a coded number (Paper ID; see Additional file 1: Table S1 for references). In some cases studies collected multiple estimates of tagging-associated mortality which are represented by ticks following the study identifier.

Acknowledgements

The authors thank the Atlantic Salmon Federation for kindly supplying the dummy tags that were used as part of the experiments described in this study.

Author contributions

Experimental series were conceived by MT, SL, and GKR. Experimental series were run by MT, SL, GKR, BMW, and CH. Data analyses were conducted by MJL, with input from MT, BMW, CWM, and GE. The primary manuscript was written by MJL with all authors contributing to writing and editing subsequent drafts.

Funding

This study was supported from funding awarded by the Aquaculture Ecosystem Interactions Program at Fisheries and Oceans Canada.

Availability of data and materials

All raw data for both the experimental and meta-analysis portions of this project and R scripts used in this project can be found here: <https://github.com/mlaw27/Salmon-tag-retention-2023?search=1>

Declarations

Ethics approval and consent to participate

All experimental procedures were conducted in accordance with guidelines established by the Canadian Council for Animal Care (CCAC) under approval of the Fisheries and Oceans Regional Animal Care Committee (RACC; AUP #17–04).

Competing interests

Our paper has no competing interests to declare and has not been published/submitted elsewhere.

Received: 15 May 2023 Accepted: 26 October 2023

Published online: 22 November 2023

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