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Effects of intracoelomic transmitter implantation on metabolic rate, swimming performance, growth and survival in juveniles of two salmonids

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Abstract

In this study, we investigated the effects of acoustic tag implantation on standard and routine metabolic rate (SMR and RMR, estimated *via* oxygen consumption), critical swimming speed (U_{crit}), survival and growth in juveniles of rainbow trout *Oncorhynchus mykiss* and lake trout *Salvelinus namaycush*. Tag burdens ranged from 1.8% to 7.5% across the two species. Growth rates in acoustic-tagged fish were equal to or higher than those in other treatments. Acoustic-tagged *S. namaycush* had a marginally lower U_{crit} than controls but that effect was not replicated in the *O. mykiss* experiment. Tagging did not have clear effects on metabolic rate but there was an interaction whereby SMR and RMR tended to increase with time since surgery in tagged *O. mykiss* but not in other treatments (the same trend did not occur in *S. namaycush*). Survival was high across treatments (mean 98% survival among *O. mykiss*, 97.5% among *S. namaycush*). There were no statistically significant effects of tag burden (percentage of body mass) except for a weak negative relationship with growth rate (across species) and a weak positive relationship with U_{crit} but only in the *O. mykiss*. Collectively, our findings suggest there were minor, context-dependent effects of acoustic tagging in juvenile *S. namaycush* and *O. mykiss* during an eight-week laboratory experiment. Further research will be required to assess whether tagging can cause meaningful behavioural effects in these species in captivity or in the wild and whether there is a tag burden threshold above which deleterious effects consistently occur.

KEYWORDS
biotelemetry, conservation physiology, Great Lakes, respirometry, tagging effects

1 | INTRODUCTION

Acoustic telemetry is a powerful tool that fish biologists routinely use to study the behaviour and spatial ecology of fish in the wild and to assess rates of survival. Indeed, the use of telemetry in fish has rapidly grown over the past 10 years; it is now being applied to important problems in fisheries management such as invasive species monitoring, protected-area design and management and the survival of fish after catch-and-release (Cooke *et al*., 2013; Crossin *et al*., 2017; Hussey *et al*., 2015; Lennox *et al*., 2016). Studies using acoustic telemetry generally rely on an assumption that the methods used do not have systemic effects on the behaviour or survival of the study animals in ways that would bias findings. Unfortunately, in many such studies, that assumption is not supported by species-specific

experiments about the effects of tagging, in some cases because it would be impossible to do so (*i.e.*, for some species, it is not possible or practical to do long-term experiments in captivity). As a result, perceptions among fisheries managers about tagging effects can act as a barrier to research findings being used (Young *et al.*, 2013). The potential adverse effects of acoustic tagging include those caused by the capture and handling of the fish, the anaesthesia (if any) and surgical techniques used, the skill and experience of the surgeon and in the longer-term, the physical burden (usually permanent) of the transmitter (Methling *et al.*, 2011; Smircich and Kelly, 2014).

Even though many studies are not supported by empirical data on the effects of tagging, a significant amount of work has been done in this area, especially using juvenile salmonids. Surgically implanting a transmitter into the coelom of a fish creates a burden that could conceivably impair critical functions such as growth, survival, or swimming performance, depending on the size of the tag relative to the fish (Bridger and Booth, 2003; Cooke *et al.*, 2011). In general, larger transmitters have longer battery life and stronger signal transmissions (which increases detection range and efficiency); in most cases, therefore, it is desirable to use the largest tag possible, taking into consideration the study species. However, a widely cited rule of thumb in fish telemetry studies is that tag burden (the mass of the tag relative to the mass of the fish) should be less than 2% of body mass for intracoelomic implantation (Winter, 1983); consequently, many researchers seek to limit tag burden to 2% or less. However, this rule of thumb has been questioned for smaller fishes and there are likely to be species-specific variation in burden limits (Brown *et al.*, 1999; Smircich & Kelly, 2014; Winter, 1983). Moreover, if tagging small juvenile fishes that typically have high growth rates, tag burden should rapidly decrease with time since tagging if growth and survival are not meaningfully impaired by the tag. The 2% rule was based on early studies that described issues involving buoyancy in fishes (Brown *et al.*, 1999; Jepsen *et al.*, 2005). The swim bladder in freshwater fishes can change from *c.* 7% to 25% of the total body volume; the space taken up in the body cavity by a tag could restrict the fish's capacity to regulate its buoyancy (Alexander, 1966). In contrast, some evidence has emerged in tagging-effects studies that shows juvenile salmonids may be able to maintain growth, survival and swimming performance with tags that approach 10% of body mass (Collins *et al.*, 2013). Typical tag burden range in studies involving juvenile salmonids is 2%–10% (Brown *et al.*, 2010; Chisholm & Hubert, 1985; Ivasauskas *et al.*, 2012; Newton *et al.*, 2016).

The primary objective of this study was to assess the effects of surgical acoustic tag implantation on two juvenile salmonids: rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) and lake trout *Salvelinus namaycush* (Walbaum 1792). *Oncorhynchus mykiss* have been domesticated by the aquaculture industry and, as a result, are routinely used as a model for the study of fish behaviour and physiology, including some use in previous tag burden experiments (Chisholm and Hubert, 1985; Ivasauskas *et al.*, 2012; Sandstrom *et al.*, 2013). In *S. namaycush*, on the other hand, for which there have been telemetry studies in adult fish (Binder *et al.*, 2016; Cruz-Font *et al.*, 2016; Flavelle *et al.*, 2002), there has been no research to date on the effects of acoustic tagging. Both species are targeted by recreational fisheries (Brownscombe *et al.*, 2014) and *S. namaycush* are a native species in the Laurentian Great Lakes undergoing sustained restoration efforts (OMNRF, 2018). Acoustic telemetry has occasionally been applied to both species, but almost exclusively in adults (Binder *et al.*, 2016; Blanchfield *et al.*, 2009; Warner and Quinn, 1995).

For this study, transmitters of two different sizes were surgically implanted into fishes that spanned a range of sizes (all juveniles), such that we could evaluate tagging effects across a range of tag burdens (percentage of body mass). The variables measured included responses relevant to fitness: survival, growth, standard and routine oxygen consumption rate (SMR and RMR, respectively) and critical swimming speed (U_{crit}). U_{crit} is a measure of physiological capacity that approximates the speed at which fish can no longer swim aerobically and begin to rely on unsustainable, anaerobic burst-and-glide swimming and as such has some ecological relevance(Plaut, 2001). As far as we know, intermittent-flow respirometry, which we used here to estimate metabolic rate, has not previously been used to assess sub-lethal physiological effects of telemetry tags; past studies have sometimes looked at plasma cortisol as a sub-lethal indicator of stress (Smircich and Kelly, 2014). Metabolic rate could conceivably be responsive to telemetry tagging because of stress related to inflammation that could occur after surgery and during wound healing (Alsop & Wood, 1997; Allen *et al.*, 2016). We predicted that surgical implantation of transmitters would impair growth, survival and swimming performance relative to controls, increase standard metabolic rate because of stress and wound healing and that each of these effects would be stronger at higher tag burdens.

2 | MATERIALS AND METHODS

All fish transport, handling and experimental procedures were carried out in compliance with guidelines set by the Canadian Council on Animal Care and following approval by the University of Windsor Animal Care Committee (AUPP #17–19).

2.1 | Origin and housing of fish

Oncorhynchus mykiss (initially 13–36 g and 105–150 mm, in fork length (L_F), n = 120) were purchased from a nearby commercial aquaculture facility (Rainbow Springs, Thamesville, Ontario, Canada) while *S. namaycush* (initially 9–39 g and L_F 112–159 mm, n = 120) were donated by an Ontario Ministry of Natural Resources and Forestry fish culture facility in Chatsworth, Ontario. Trout were transported by road in 8–12°C continuously aerated water in an insulated transport tank to the Freshwater Restoration Ecology Center (FREC) in LaSalle, Ontario, for housing and experimental trials. While at FREC, the fishes were held in circular 850 l tanks connected to a recirculation system that continuously filtered, cleaned and aerated the water (dechlorinated municipal water source) whose temperature was also regulated by a thermostat-controlled chiller. *Oncorhynchus mykiss* were housed at 14.0 ± 1.0°C (mean ± SD), while *S. namaycush* were

housed at 11.0 ± 1.0°C; these temperatures approximate species-specific optima (Hokanson *et al*., 1977; McCauley & Tait, 1970) and prior acclimation temperatures for the animals we were using. Food was withheld for 24 h prior to use in respirometry trials or surgery but otherwise fish were fed *ad libitum* daily with EWOS 1.5 mm pellet (Cargill Inc.; www.cargill.com). The lighting in the building was automatically programmed to track the natural photoperiod and windows allowed some natural light to enter the room.

2.2 | Treatment groups and experimental design

All fishes except controls were individually tagged with a passive integrated transponder (PIT) so that individual fish identities could be tracked through time. PIT tags were inserted into the tissue surrounding the ventral fins on the left side of the fish using a sterilised Biomark MK165 injecting syringe with an N165 needle (Biomark mini HPT8 passive-integrated tags, 8.4 mm in length; 0.032 g in mass, Biomark,; www.biomark.com). Treatments were: (1) controls, which were not tagged in any way (n = 16 *O. mykiss*, n = 15 *S. namaycush*); (2) PIT-tagged fishes, referred to hereafter as the PIT group (n = 24 *O. mykiss*, n = 30 *S. namaycush*); (3) sham fish, which were PIT tagged and subjected to a standard surgery for intracoelomic transmitter implantation except that no tag was inserted (n = 25 *O. mykiss*, n = 30 *S. namaycush*); (4) acoustic-tagged fish, which were identical to the sham group except they received an acoustic transmitter (surgical methods described below; n = 25 *O. mykiss*, n = 30 *S. namaycush*). These treatments were designed to allow us to potentially differentiate the effects of the physical burden of acoustic tags from the effects of the surgery, while also controlling for the potential effects of the PIT tag. We used two sizes of acoustic tags to achieve a range of tag burdens: VEMCO (www.vemco.com) model V5 (12.7 mm long, 0.67 g in air) and model V6 (16.5 mm long and 0.97 g). Among tagged fishes, the tag burden ranged from 1.8%–6.0% of body mass (mass of tag as percentage of mass of fish) for the *O. mykiss* experiment and 2.5%–7.5% for *S. namaycush*.

Fish were held in a single tank divided into four sections with mesh screens (one for each treatment) to reduce the likelihood of tank effects. For *O. mykiss*, each treatment group was housed in the same section throughout the trials. For the second experiment (*S. namaycush*), each treatment group was moved to an adjacent section (*i.e*., clockwise) of the holding tank every 2 weeks in order to further minimise potential quadrant effects. Fork length and mass of all fish were measured every *c*. 2 weeks over the course of 2 months for both species (Figure 1), which involved brief handling (wet hands and smooth, wet surfaces only) and air exposure (<30 s). In addition to measuring growth and monitoring survival, subsets of fish were subjected to swimming performance tests in a swim tunnel (controls and acoustic-tagged fish only, further details below; Figure 1) and their metabolic rates were estimated *via c*., 20 h of automated measurements of oxygen consumption rate in intermittent-flow respirometers (all four treatment groups, details on respirometry below) at a range of times throughout experiments (Figure 1).

2.3 | Surgery

The methods used here are standard for insertion of acoustic transmitters into fish (Liedtke *et al*., 2012; Rub *et al*., 2014; Summerfelt & Smith, 1990; Wagner *et al*., 2011). Acoustic tags, PIT tags and surgical equipment were sterilised in betadine solution and rinsed with deionised water prior to use for each animal. All fish were

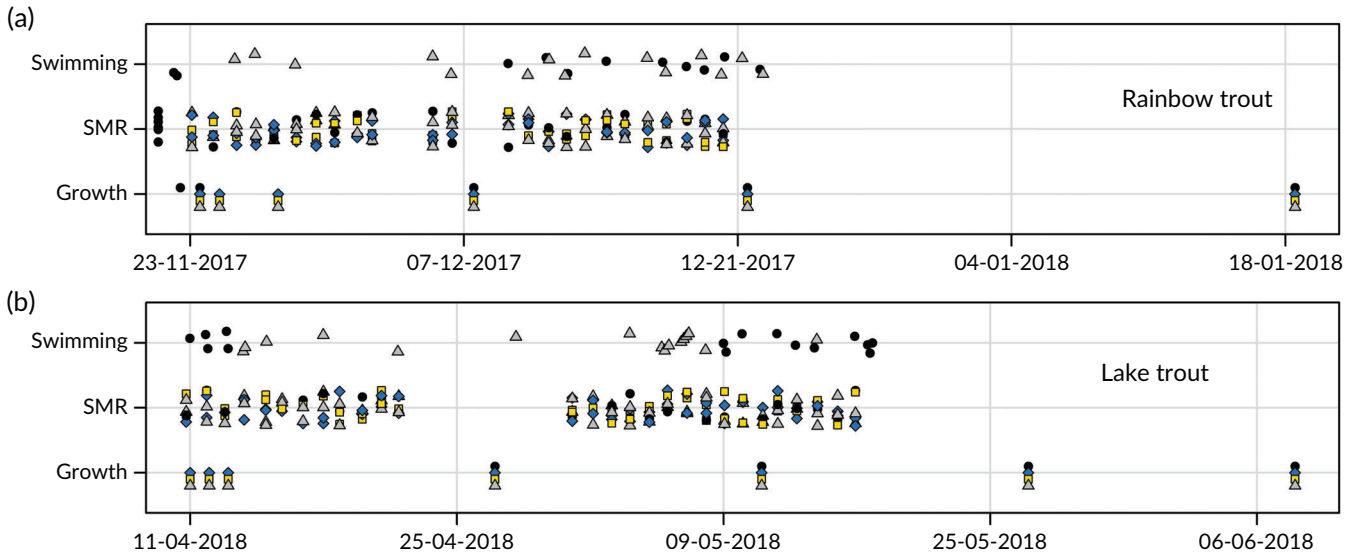

FIGURE 1 Timelines for the tagging effects experiment with (a) *Oncorhynchus mykiss* and (b) *Salvelinus namaycush*, indicating when data were collected relative to the start of experiments. ● represent controls, ◆ are fish from the PIT group, ■ are sham fish, and △ are acoustic-tagged fish. For swimming (U_{crit}) tests and measurements of SMR, each individual data point is shown, whereas we only include one symbol per treatment for the time point when mass (M_W) and fork length (L_F) measurements were taken (labelled as growth) for visual clarity (rather than showing individual points for L_F, n = 415 and M_W, n = 432 measurements for *O. mykiss* and *S. namaycush*, respectively)

anesthetised in a bath of 100 mg l^{-1} MS-222 (buffered with sodium bicarbonate at a ratio of 2:1) and monitored until opercular movements slowed and fish lost response to gentle physical stimuli (typically 3–4 min). Fish were then placed on their back in a V-shaped trough for surgery, during which their gills were irrigated with a continuously aerated maintenance dose of anaesthetic (buffered MS-222, 30 mg l^{-1}). A *c*. 1.5 cm incision was made at the abdominal midline towards the posterior of the fish, but anterior to the anus using a number 11 scalpel blade. The tag (transmitter) was then inserted into the abdominal cavity (in the case of the tagged treatment). The incision site was closed (for sham and tagged treatments) using two simple interrupted 5–0 Ethicon Vicryl Plus absorbable sutures (2–1–1-1 surgeon knot sequence) with an RB-1 tapered needle (Ethicon, Cincinnati; www.ethicon.com) at 0.5 cm intervals along the incision line. Fish were monitored in small, continuously aerated containers of water from the holding tank (same temperature) for post-surgical recovery for up to 1 h before being returned to their holding tank. Fish were on the surgery bench for 4.5 ± 0.3 min (mean ± SD). Fish were monitored daily for mortalities and tag loss throughout experiments. Growth measurements (mass and L_F) were taken every *c*. 2 weeks. We report and analyse tag burden here as the initial tag burden at time of surgery.

2.4 | Respirometry

The respirometry set-up consisted of eight custom-built polypropylene (clear) 3.1 l chambers that were submerged in a 200 l tank (Supporting Information Figure S1). The timing of respirometry trials ranged from 2 h to 35 days after the surgical procedure (*n.b.* time since surgery was a factor of interest in analyses). Each chamber had an external recirculation loop with an in-line pump that ensured the water in the chamber remained well mixed. Oxygen concentration was recorded for each chamber every 5 s with an optical sensor (OXROB10, PyroScience, Aachen, Germany; www.pyroscience.com) inserted into the recirculation line and connected *via* fibre-optic cables to one of two four-channel Firesting O_2 systems (PyroScience). A pump was connected to each chamber and flushed *c*. 12 l min^{-1} of aerated water from the surrounding water bath (emptying *via* a stand pipe). The flush pump was intermittently switched off (*c*. twice per hour) for 12–16 min (duration adjusted as needed to ensure dissolved oxygen remained >80% air saturation) to enable estimation of oxygen consumption rate. One chamber was always kept empty for measurement of background (microbial–algal) respiration (=seven fish per trial) and background respiration was also measured in each chamber before and after each trial. Respirometry trials were, 20–24 h in length, resulting in *c*. 40–50 measurements for each fish. At the end of the trial, each fish was weighed (wet mass, M_W, nearest 0.01 g), their PIT was confirmed (except for controls without PIT tags) with a tag reader and they were returned to their home tank. The blank (empty) chamber and location of treatment fish among the chambers were randomised for each trial. A temperature sensor for each Firesting O_2 system was inserted into the stand pipe of one of the chambers and used by the Firesting O_2 software (along with an atmospheric pressure sensor) to dynamically adjust the O_2 concentration measurements, which were continuously recorded throughout each trial (*i.e.*, not only when chambers were sealed).

Each fish's rate of oxygen consumption, $\dot{M}O_2$ (mg O_2 kg body $mass^{-1}$ min^{-1}), was calculated for each sealed cycle (flush pump off) with the following formula (Steffensen, 1989):

$$\dot{M}O_2 = \left(V_{RE}{M_W}^{-1}\right)\left(\delta CO_2 \delta t^{-1}\right)$$

where V_{RE} is the effective respirometer volume (l), M_W is the mass (kg) of the fish and $\delta CO_2 \delta t^{-1}$ is the slope of the linear decrease in oxygen content (measured in mg O_2 l^{-1} min^{-1}) when the chamber is sealed (Svendsen *et al*., 2016). Labchart reader 8.1.9 software (ADInstruments Inc.; www.adinstruments.com) was used to measure the rate (slope) at which oxygen decreased during each sealed cycle (mg O_2 min^{-1}), excluding the first 2 min at the start of each sealed cycle (typically referred to as the wait period in some respirometry protocols; Svendsen *et al*., 2016). The decline in oxygen content in the empty chamber during sealed cycles was used to dynamically adjust $\dot{M}O_2$ estimates for each fish (*i.e.*, by subtracting out background respiration). The respirometers were also sterilised with bleach, drained, rinsed and re-filled every 2 weeks to ensure background respiration remained low (<25% of the $\dot{M}O_2$ of the fishes). SMR was calculated by taking the 15th percentile of the entire set of $\dot{M}O_2$ values for each fish (referred to as $q_{0.15}$ in Chabot *et al*., 2016). SMR is defined as being analogous to the rate of oxygen consumption required for maintenance; *i.e.*, when the animal is not exhibiting any locomotory activity and no food is being digested or absorbed (Chabot *et al*., 2016). Routine metabolic rate (RMR) was calculated as the mean $\dot{M}O_2$ after discarding the first 8 h of measurements (*i.e.*, after allowing the fish to acclimate to the respirometer). Unlike SMR, RMR is meant to encapsulate minor variation in (unobserved) activity by the fish while in the respirometer. Because fish were randomly sampled from the holding tank for respirometry trials each day for *c*. 35 days, repeat sampling of the same individuals occurred. For all but the full control treatment, we used PIT tags to track individuals and avoided re-using the same individual twice for respirometry within a 1 week period. In total, we generated 172 estimates of SMR and RMR for *O. mykiss*: n = 47–48 per treatment (n = 24–25 unique individuals per treatment), plus n = 30 for full controls (*c*. 15 unique individuals). For the *S. namaycush* experiment, we collected 183 estimates of SMR and RMR: n = 50–54 per treatment (n = 27–28 unique individuals each), plus n = 26 full controls.

2.5 | Swimming performance

Swimming performance is an important trait and can be related to predator avoidance, foraging and migration (Anglea *et al*., 2004; Perry *et al*., 2013; Walker *et al*., 2016). U_{crit} is a standard and commonly used performance metric to evaluate aerobic swimming performance in fishes (Farrell, 2008; Jain & Farrell, 2003). In this study, we used a 30 l Brett-style swim-tunnel (Loligo Systems, Viborg, Denmark; www.

loligosystems.com) that was continuously flushed with fresh water at each fish's acclimation temperature (*i.e.*, we did not measure oxygen consumption). Fishes were transferred to the 46 cm long × 14 cm deep × 14 cm wide working section of the swim-tunnel and allowed to recover for 45 min at a water speed of *c.* 0.5 L_F s^{-1} (minimal effort required to hold position in swim-tunnel). Each fish then completed a practice swim during which the speed was gradually increased up to 40 cm s^{-1} (*c.* 3–4 L_F s^{-1}) over the course of 3 min and the fish was then encouraged to continue swimming at that speed for an additional 15 min (Lee *et al.*, 2003). After another 45 min rest period (Jain *et al.*, 1998), the U_{crit} swim was started. It involved gradually increasing the speed to *c.* 60% of species-specific expected U_{crit} (based on pilot tests before the experiment began) over the course of 10 min and using that speed for an initial 20 min conditioning interval. Speed was then ramped up in a sequential fashion in steps of *c.* 0.5 L_F s^{-1} every 20 min. The front of the working section of the swim-tunnel was darkened with black plastic and a light shone on the downstream end to encourage the fish to remain at the front. A metal grid at the downstream end of the working section was occasionally electrified for 1–2 s to motivate the fish to swim and prevent it from resting against it (a standard technique when using swim-tunnels; Clark *et al.*, 2011; Farrell *et al.*, 2003). If the fish remained on the back grid for more than 10 s (despite attempting to motivate the fish using electricity) or was only able to resume swimming for <30 s between bouts of resting on the downstream grid, the trial was ended and the time noted. U_{crit} (L_F s^{-1}) was estimated from: $U_{crit} = U_f + (T_f\, t^{-1})U_v$, where U_f is the speed (cm s^{-1}) of the last fully completed speed interval, T_f is the duration (s) the fish swam at the final speed interval before fatigue, t is the length of time (1200 s) at each speed increment at that velocity and U_v is the velocity increment (in cm s^{-1}; Brett, 1965; Tierney, 2011). Data were converted to L_F s^{-1} for analyses and data presentation.

2.6 | Growth measurements

PIT tagging enabled estimation of individual fish growth rates for fish in the PIT, sham and acoustic-tagged treatment groups. Specific growth rate (G_{SR}, percentage day^{-1}) was calculated as: $G_{SR} = (((M_{W2} - M_{W1})\, M_{W1}{}^{-1})100)\,(t_2 - t_1)^{-1}$, where M_{W2} and M_{W1} were the measurements (body mass in g, L_F in mm) of the fish at time t_2 and t_1 (days). A random subset of control fish (n = 15) was measured at each growth interval (Figure 1); these data were used to provide an estimate of the mean growth rate for control fish and are presented alongside the growth data for the other groups. Exploratory analyses revealed clear differences in growth between species and among time intervals, so to standardise growth rates and ensure variance was homogeneous across species–times, growth rates were converted to *Z*-scores for statistical analyses, based on the mean and SD for growth for that species and time interval (across the three tagging treatments: acoustic-tagged, sham, PIT). After the final length and mass measurements (at the end of each experiment), all experimental animals were euthanised with a lethal overdose of buffered MS-222 (1 mg l^{-1}).

2.7 | Statistics

To test for treatment effects on specific growth rate (M_W and L_F assessed in separate models), we used linear mixed effects models with species, treatment, time since the start of the experiment (=time since surgery for non-controls) and M_W as fixed effects, with individual fish ID as a random effect (using lme4 in R; Bates *et al.*, 2015). We used backwards model selection, beginning with a full model that included all one-way interactions. Likelihood ratio tests were used to assess the overall significance of each fixed effect to model fit, which work by comparing the Akaike information criterion (AIC) scores among nested models (*i.e.*, with and without each predictor variable using the drop1 function in R; www.r-project.org). *P*-values given (§3) for interaction terms arise from these likelihood ratio tests (*P*-values for each individual model parameter are given in Supporting Information Tables S1–S5). SMR and RMR were modelled separately with the same procedures described above for growth (initial candidate variables = body mass, time since the start of the experiment, tagging treatment and their one-way interactions), except that the SMR and RMR values were log-transformed (*i.e.*, to ensure model assumptions could be met).

For U_{crit}, we modelled the effect of treatment (full controls *v.* acoustic-tagged group), time since surgery and body condition as fixed effects. A species-specific condition index was used in place of body mass because the latter was strongly correlated with species (the *O. mykiss* had higher mass-at-length; *i.e.*, higher condition factor). To ensure standardisation across species, condition was calculated as the regression residual for each fish relative to the line of best fit for the species-specific relationship between L_F (mm) and M_W (g). Likelihood ratio tests were used to assess the overall significance of each fixed effect to model fit by comparing nested models (*i.e.*, with and without each predictor variable). Backwards model selection was used, starting with all variables and one-way interactions, with models built separately for each of the two species. We also tested for effects of tag burden, condition and time since surgery within the acoustic-tagged group (n = 15 *O. mykiss*, n = 16 *S. namaycush*) in the same way.

For all models, we checked whether they met assumptions (normality, homoscedasticity, independence, *etc.*) using *q*–*q* plots and by plotting model residuals against fitted values and all predictor variables including those not included the final model (Zuur & Ieno, 2016). All statistical analyses were conducted using R 3.0.1 (www.r-project.org). The type I error rate (α) was kept at 0.05. We refrained from using Bonferroni correction in order to avoid inflating the type II error rate (Nakagawa, 2004); one could argue that for our study questions, type I and II errors would be equally regrettable. However, acknowledging that *P*-values have limitations (Halsey *et al.*, 2015) we focus our interpretation on the strength and size of our effects and urge readers to do the same.

3 | RESULTS

3.1 | Survival and growth

Survival for both species was 100% in control fish and in the sham treatment. In the *O. mykiss* experiment, across treatments, two fish

died: both from the tagged treatment, for an 8 week survival rate of 92% (23/25) among fish implanted with transmitters (*i.e.*, survival in the other three groups was 100%). Among *S. namaycush*, three fish died: one from the tagged treatment (97% survival, 29/30) and two from the PIT treatment (93%, 28/30).

The PIT group ($P > 0.05$) and sham surgery groups ($P > 0.05$) did not differ from the acoustically tagged fish in L_F growth rate in either species (Figure 2 and Supporting Information Table S1). However, there was a main effect of species (higher growth in *O. mykiss*, $P < 0.01$) and an interaction with the PIT treatment whereby the PIT-tagged *O. mykiss* grew slower than did the other two treatments ($P < 0.001$; Figure 2). For growth of M_W, there was a similar treatment × species interaction (significant, $P < 0.05$) whereby the *O. mykiss* PIT group tended to grow at a lower relative rate than did other treatments across both species ($P < 0.01$; Figure 2 and Supporting Information Table S1). Fish in the control group were not individually marked so we could not estimate growth rates for those fish, but we did measure M_W and L_F of controls at each growth measurement interval. Raw M_W (g) and L_F (mm) in the other three treatments were not statistically different from controls at the start or end of experiments for *O. mykiss* (linear model with controls set as baseline factor level for treatment, all $P > 0.05$ for both mass and fork length). In *S. namaycush*, the first M_W and L_F measurements for the control group took place at 15 days, at which point there was a non-significant tendency for the PIT group to be smaller ($P < 0.05$ for both L_F and M_W). By the end of the experiment the PIT group were significantly smaller than controls for *S. namaycush* ($P < 0.01$ for both L_F and M_W). Other *S. namaycush* treatment groups (acoustic-tagged and sham surgery, both of which also had PIT tags) were not statistically different than controls at the first or final time points of measurement ($P > 0.05$ for both L_F and M_W).

We also examined whether there was an effect of tag burden (percentage) on growth rates within the tagged treatment. We found that, when combining both species (using *Z*-corrected growth data to control for among-species and time interval differences), for L_F growth there was a weak (model $R^2 = 0.079$) negative effect of tag burden ($P < 0.001$) in a linear mixed-effects model (Figure 3a; other variables were not significant; Supporting Information Table S2). For growth of M_W, there was an interaction between species and tag burden such that a weak negative effect of tag burden ($P < 0.05$) occurred in *O. mykiss* (model $R^2 = 0.075$) but not in *S. namaycush* (Figure 3b).

3.2 | Metabolic rate and swimming performance

For *O. mykiss*, there was no difference in SMR among treatments (Figure 4a and Supporting Information Table S3), but there was a treatment × time interaction ($P < 0.01$) that arose because of a tendency for SMR to increase with time since surgery ($P < 0.01$) in the acoustic-tagged fish (Figure 4a). In the sham, PIT and control groups the relationship with time since surgery was not significant (based on terms within the model, all $P > 0.05$; Figure 4a and Supporting Information Table S3). The results for RMR in *O. mykiss* were nearly identical to those for SMR (Figure 4b), except that the explanatory power of the model was lower ($R^2 = 0.12$; Supporting Information Table S4) than for the SMR model ($R^2 = 0.18$; Supporting Information Table S3). Focusing only on the acoustic-tagged group, tag burden had no effect on SMR or RMR (both $P > 0.05$) in mixed effect linear models that controlled for the effect of time.

In *S. namaycush*, there was an interaction between M_W and treatment (Figure 5 and Supporting Information Table S5). Specifically, there were significantly different relationships between M_W and SMR among treatments driven by a negative trend among controls ($P < 0.001$; Figure 5 and Supporting Information Table S5), such that the slope for PIT group differed significantly (Supporting Information Table S5). However, linear regressions within each treatment group suggested the only SMR– M_W relationships that were significant were for controls ($P < 0.01$) and for the sham treatment ($P < 0.01$) and the latter relationship was weak ($R^2 = 0.10$; Figure 5 and Supporting Information Table S5). Our model also included an intercept for the PIT group that was significantly lower than for the other treatments (Figure 5 and Supporting Information Table S5). In addition, there was a weak interaction between treatment group and time ($P < 0.05$; Supporting Information Table S5) that was driven by a positive time × SMR relationship that occurred in controls (Supporting Information Figure S2) but not in other groups (*c.f. O. mykiss* where the positive effect of time was in acoustic-tagged fish). For RMR in *S. namaycush*, we did not find any effects of tagging treatment nor any interactions with other factors, though there was a weak positive effect of time since the start of the experiment (across treatments; $P < 0.001$, $R^2 = 0.06$; Supporting Information Figure S3). Within the acoustic-tagged group ($n = 28$ unique individuals, $n = 53$ respirometry trials), tag burden had no effect on SMR or RMR (both $P > 0.05$).

Every *O. mykiss* we tested had a higher U_{crit} than every *S. namaycush* (Figure 6) and we found a subtle negative effect of our tagging treatment on U_{crit} in *S. namaycush* but not in *O. mykiss*. In *S. namaycush* U_{crit} ($R^2 = 0.30$, $n = 31$) there was a model-estimated 0.41 L_F s^{-1} decrease in U_{crit} (*c.* 11%) in the acoustic-tagged group relative to controls ($P < 0.05$) after controlling for an effect of time. The effect of time consisted of a tendency for higher U_{crit} values with increasing days elapsed since the beginning of the experiment (mean ± SD model estimate = 0.023 ± 0.008 L_F s^{-1} day^{-1}, $P < 0.01$). There was no interaction between time and tagging treatment in *S. namaycush* ($P > 0.05$). When solely examining the acoustic-tagged *S. namaycush* ($n = 16$), there was no effect of tag burden ($P > 0.05$). In *O. mykiss*, there was a weak effect of tag burden whereby acoustic-tagged fish with higher tag burden tended to reach higher U_{crit} (mean ± SD = 0.44 ± 0.20 L_F s^{-1} increase per 1% increase in tag burden, $P < 0.05$, $R^2 = 0.22$, $n = 16$). In addition, there was an effect of time since the start of the experiment in *O. mykiss* that was the reverse of what occurred for *S. namaycush*; *i.e.*, U_{crit} decreased with time elapsed from the start of the experiment (mean ± SD = −0.03 ± 0.01 L_F s^{-1} day^{-1}, $P < 0.01$, $R^2 = 0.21$), but there was no interaction between time and treatment (*i.e.*, acoustic-tagged *v.* controls, $P > 0.05$). There was no main effect of tagging treatment on U_{crit} in *O. mykiss* ($P > 0.05$), despite a small numerical difference between the median values of the two groups (Figure 6). In sum, we did not find any

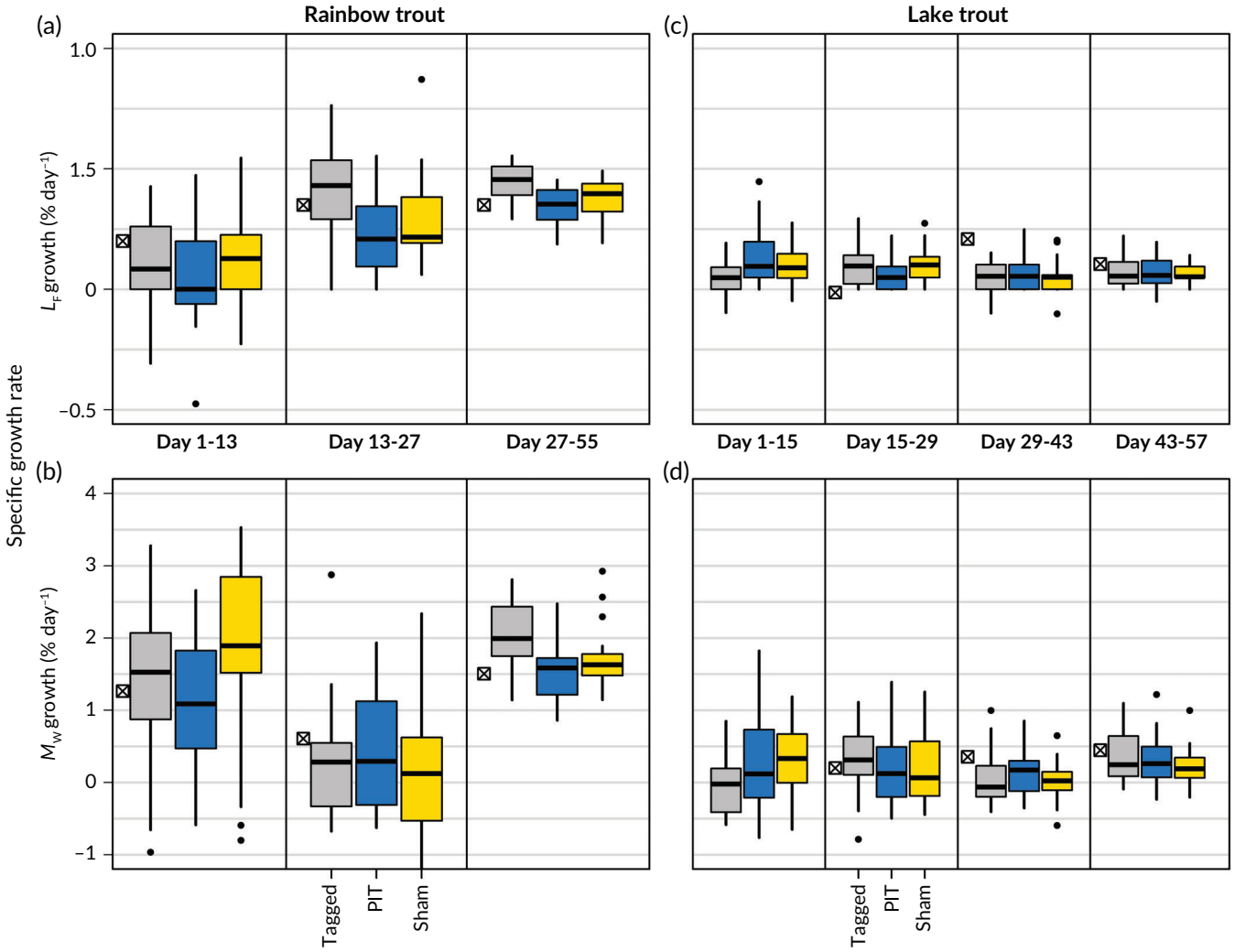

FIGURE 2 Boxplots (——, median; □, 25–75 percentiles; |, 1.5x the interquartile range; ●, outliers) showing (a), (c) fork length (L_F) and (b), (d) body mass (M_W) specific growth rates for the three treatments (▨, acoustic-tagged; ■, PIT-tagged only; ■, sham surgery) for which we could track individual (a), (c) *Oncorhynchus mykiss* and (b), (d) *Salvelinus namaycush* through time using PIT tags. ⊠, Estimate of growth rate in control fish based on group means taken at each time point; control fish were not PIT-tagged so we could not calculate specific growth rate for individuals

consistent predictors of swimming performance across the two species and the species-specific effects we did see were generally small.

4 | DISCUSSION

We investigated the effects of acoustic transmitter implantation on growth rate, survival, swimming performance and standard metabolic rate, replicating our experiment in two species. We did find a modest effect of acoustic tagging on swimming performance in *S. namaycush*, but the same effect did not occur in the *O. mykiss* experiment. There was a weak increase in metabolic rate (SMR and RMR) with increasing time since surgery in acoustic-tagged *O. mykiss* (and not in other treatment groups), but that effect could not be replicated in the *S. namaycush* experiment. Among acoustic-tagged fish, tag burden had no effect on SMR or RMR in either species. Survival and growth were not affected by acoustic tagging, but there was a subtle trend towards lower growth rates within the acoustic-tagged group that appeared to be driven by the individuals with the highest relative tag burdens (percentage of body mass, across both species). However, we did not have sufficient sample sizes, especially at higher tag burdens (*e.g.*, >5%), to be able to pinpoint a tag-burden threshold at which a growth impediment might occur.

To summarise, while we did find some species- and context-specific effects of our treatments, none of the effects were strong, nor were they consistent across our two experiments despite the use of the same methods, closely related species and similar water temperatures. Collectively, our findings suggest that tagging effects for juvenile *O. mykiss* and *S. namaycush*, at the tag burdens we used (notably, almost exclusively above 2%), are likely to be minor, particularly when set in the context of the substantial existing literature on tagging effects in these and other salmonids. Nevertheless, the subtle effects we did observe highlight the value in doing further tagging effects research on these species. Our findings also serve as a reminder that researchers using acoustic telemetry should ensure they minimise tag burden to the extent possible and maximise fish welfare by using best practices for fish handling and surgery (*e.g.*, Rub *et al.*, 2014).

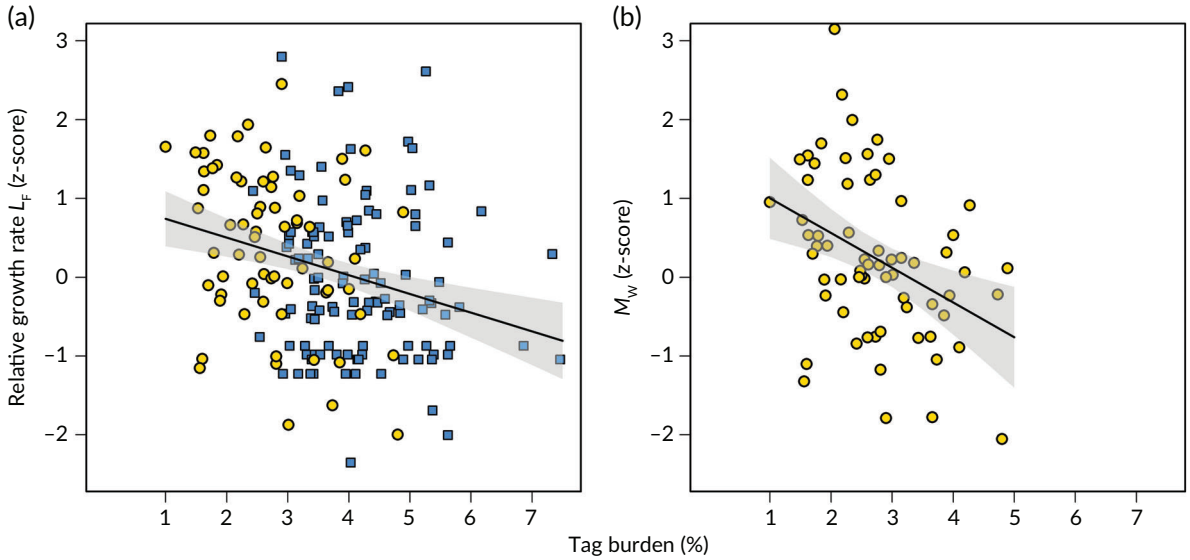

FIGURE 3 Standardised, relative growth rate (z-scores) for (a) fork length (L_F, R^2 = 0.079) and (b) body mass (M_W, R^2 = 0.075) as a function of initial tag burden for *Oncorhynchus mykiss* (●) and *Salvelinus namaycush* (■); there was no relationship between tag burden and growth rate for M_W in *S. namaycush*. Individual points represent all raw data (including repeated measures) of growth rate. ——, The linear mixed effects model ±95% CI

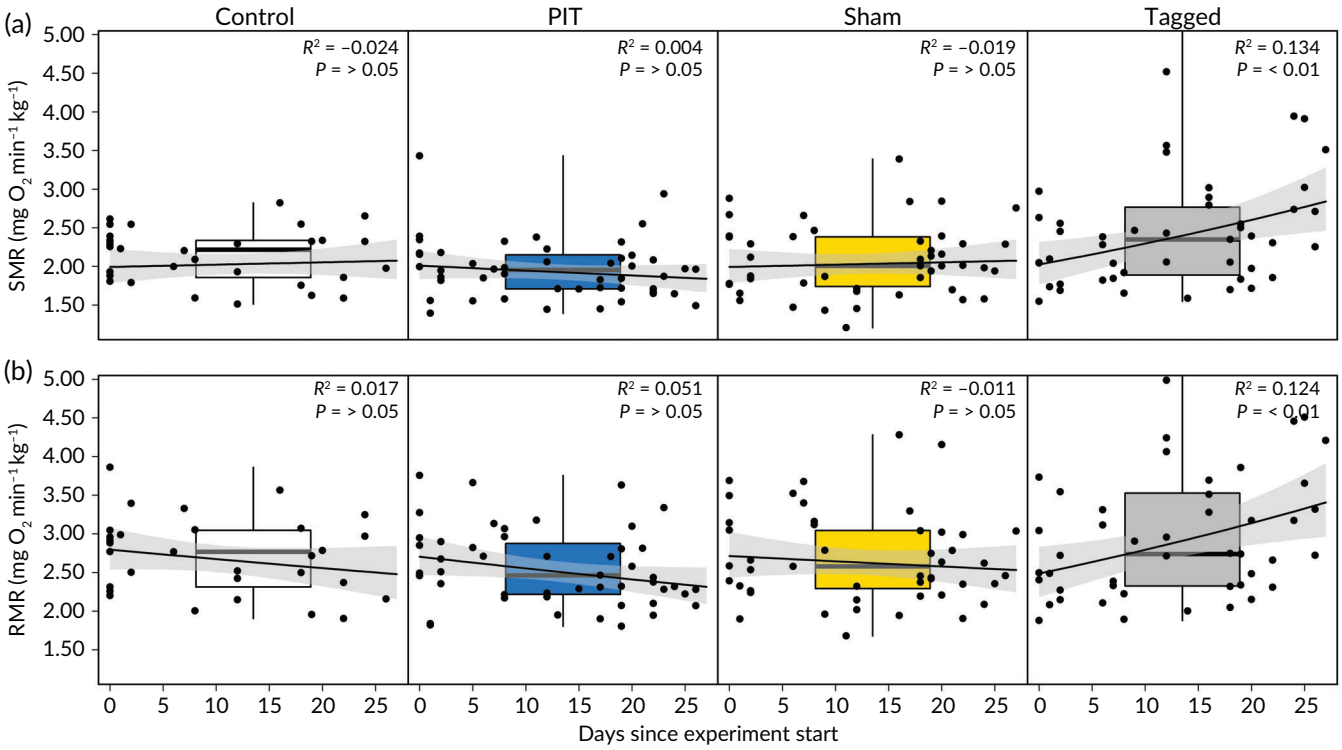

FIGURE 4 Boxplots (——, median; □, 25–75 percentiles; |, 1.5x the interquartile range; ●, outliers) of (a) standard metabolic rate (SMR) and (b) routine metabolic rate (RMR) in *Oncorhynchus mykiss*, estimated as a rate of oxygen consumption; separated by treatment group as a function of days since start of the experiment (*i.e.*, time of surgery). There was no main effect of treatment group (*i.e.*, differences among the boxplots). Days since the start of the experiment had a significant interaction with treatment group (SMR P < 0.01; RMR P < 0.001) in our models describing the data (*i.e.*, significantly different slopes among treatments; overall model marginal: SMR R^2 = 0.18; RMR R^2 = 0.12 (full model terms given in Supporting Information Tables S3, S4). ——, The simple linear regression ± SD of the data in each panel (associated R^2 and P values given in each panel)

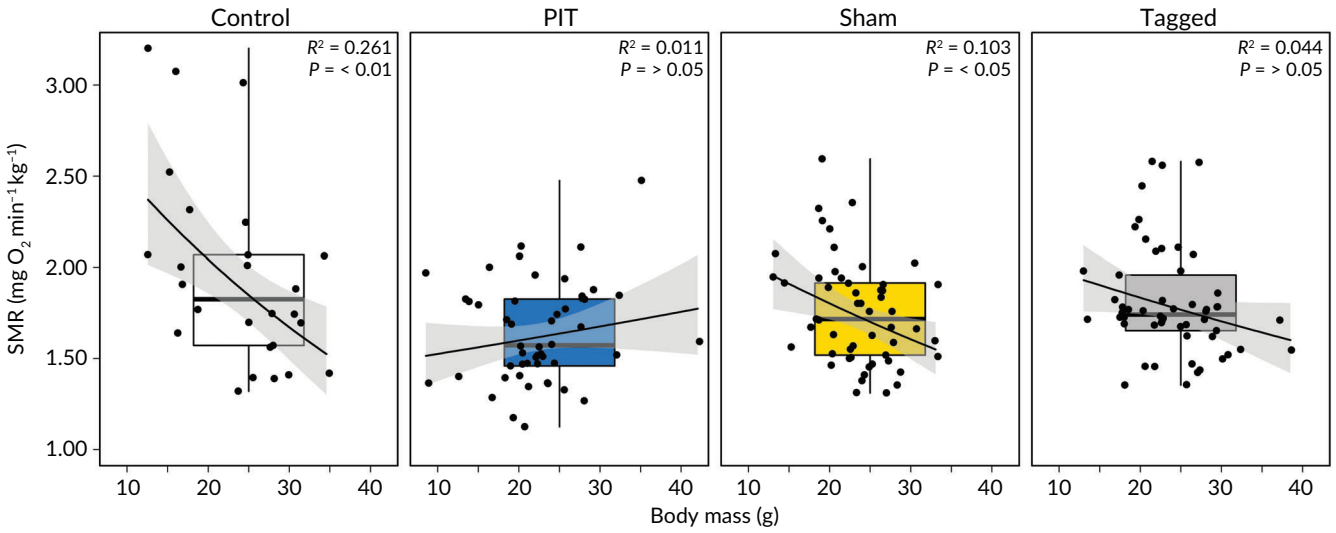

FIGURE 5 Boxplots (——, median; □, 25–75 percentiles; ├, 1.5x the interquartile range; ●, outliers) of standard metabolic rate (SMR) for *Salvelinus namaycush* estimated as a rate of oxygen consumption, separated by treatment group as a function of body mass, which had a significant interaction with treatment group in our model describing the data ($P < 0.01$, $R^2 = 0.25$; full model terms given in Supporting Information Table S5). There was also a main effect of treatment whereby SMR was marginally lower in the PIT group than in controls ($P < 0.001$). The same model ($R^2 = 0.25$; Supporting Information Table S5) included a weak interaction between time since the start of the experiment and treatment group ($P < 0.05$, Supporting Information Table S3 and Figure S1). ——, The simple linear regression ± SD of the data in each panel (associated R^2 and P values given in each panel)

4.1 | Tag burden, growth and survival

We found no overall differences in survival or growth in the acoustic-tagged group relative to the other treatments in either species. There was, however, a weak tendency for lower growth rate at higher tag burdens in both species. The *O. mykiss* and *S. namaycush* in this study experienced tag burdens of between 1.8% to 6.0% and 2.5% to 7.5%, respectively, which fall into the typical range used in previous studies of tagging effects, most of which aimed to challenge the 2% rule (Ivasauskas *et al*., 2012; Makiguchi & Kojima, 2017; Sandstrom *et al*., 2013). There have been no studies to date on the effects of tag burden on juvenile *S. namaycush*, but given the similar body shape, effects are likely to be comparable and generally were the same in this study. Previous studies using juvenile *O. mykiss*, housed at 10–15°C with a tag burden of 1.1%–3.4%, generally experienced no mortalities or significant effects on growth, although acoustic-tagged fish did exhibit slower growth than control fish in one experiment (Ivasauskas *et al*., 2012). Sandstrom *et al*. (2013) reported no significant differences in growth of juvenile *O. mykiss* (L_F 180–225 mm and 71.0–141.0 g) among their control and tagged treatment groups using similar tags to our study (*i.e*., VEMCO V7, 1.3%–2.3% tag burden, or V9, 3.4%–6.6% tag burden), nor did they find differences in tag retention rate.

There has been some evidence of negative effects of tag burden on growth, feeding and survival in juvenile *O. mykiss*. Makiguchi & Kojima (2017) suggested that tag burdens of >3% in juvenile and adult *O. mykiss* had short-term negative effects on feeding behaviour and that fish with a tag burden of *c*. 6.0% had a 10% poorer survival rate than controls with survival rate being negatively correlated with tag burden. They also reported no effects on physiological indicators of stress (*i.e*., plasma lactate levels) and concluded that a tag burden of 2% is probably conservative and suitable for adult and juvenile *O. mykiss* (Makiguchi & Kojima, 2017). Reduced growth has also been seen in *O. mykiss* with much higher tag burdens (>12%, Welch *et al*., 2007).

Importantly, the growth rates for juveniles of both species in our study were comparable with those reported in the literature for similar sized fishes, water temperatures and food availability (Eschmeyer, 1964; Gregory & Wood, 1999; Stewart *et al*., 1983); growth rates of *O. mykiss* and *S. namaycush* in our study were *c*. 0.4–2.0 and *c*. 0.1–0.4 (percentage body mass day^{-1}), respectively. The higher growth rates in *O. mykiss* can probably be attributed to a combination of warmer water (14 *v*. 11°C), natural differences in life history compared to *S. namaycush* and the fact that they came from an aquaculture population where selection for rapid growth has probably occurred. The experimental temperatures were close to the preferred range for each species (McCauley & Tait, 1970; Hokanson *et al*., 1977). We did observe a significant tendency for lower growth rates in the PIT-tagged *O. mykiss* group; an effect without an obvious explanation other than the potential for unwanted tank effects (lack of replicate tanks for each treatment). Taken together, our study suggests that tag burdens <6% and potentially as high as 7.5%, have minimal effect on juvenile *S. namaycush* and *O. mykiss* growth. Although this study only ran for eight weeks and effects may have been observed if the experiment ran longer, or had multiple replicate tanks per treatment, tag burdens would have decreased with continued growth and so the slight effect we observed in higher-burden fish would have probably disappeared over time.

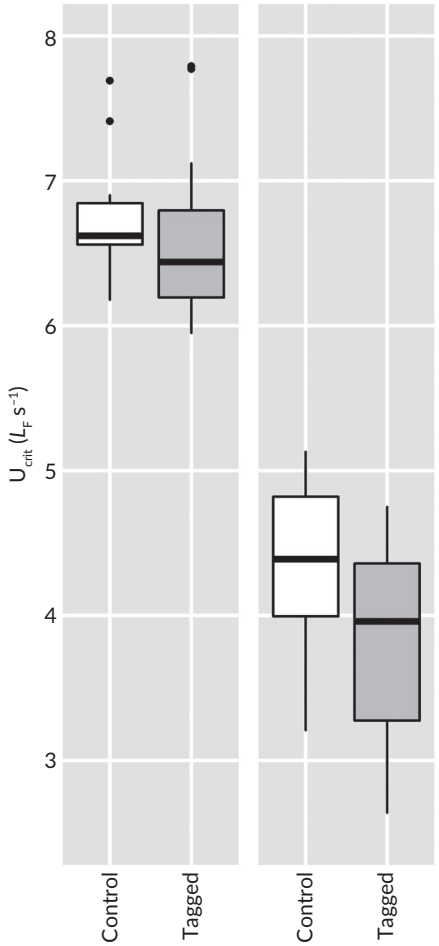

FIGURE 6 Boxplots (——, median; □, 25–75 percentiles; ⟊, 1.5x the interquartile range; ●, outliers) of critical swimming speed (U_{crit}) in (a) *Oncorhynchus mykiss* (n = 11 controls, n = 15 tagged; $P > 0.05$) and (b) *Salvelinus namaycush* (n = 15 controls, n = 16 tagged; $P < 0.05$). L_F, Fork length

4.2 | Metabolic rate

In this study, we were looking for potential changes in SMR and RMR arising from recovery from anaesthesia or inflammation, stress, infection, or wound healing associated with our tagging treatments. In the case of RMR, differences could have arisen among treatments had there been differences in activities levels of the fish while in respirometers. In *S. namaycush*, there was an interaction between treatment and M_W that was driven by a decrease in SMR in the control group with increasing M_W (the same did not occur for RMR). In the context of that result, however, there was no effect of tag burden (within the tagged group) and we have no explanation for the weak differences among treatments in terms of the effect of body mass, which did not occur in the *O. mykiss* experiment that involved the same methods. Instead, in the *O. mykiss* experiment, we saw a trend of increasing SMR and RMR with time since surgery among acoustically tagged fish, which suggests a possible effect of stress, infection, or inflammation caused by pressure from the transmitter applied to the sutures and incision in ways that worsened over time. However, we did not observe any macroscopically obvious signs of infection or inflammation in the acoustic-tagged group relative to the sham group, the effect of time since surgery was small (R^2 = 0.16) and it was largely driven by a few fish with high estimates of SMR and RMR. Moreover, in the *S. namaycush* experiment, it was the controls rather than the acoustic-tagged fish that exhibited a tendency for increasing SMR with time since the start of the experiment (Supporting Information Figure S3).

The absolute rates of oxygen consumption in this study were consistent with values from the literature for both species. Alsop & Wood (1997), found that juvenile *O. mykiss* (*i.e.*, 6–12 g M_W) fed to satiation (which would be expected to elevate $\dot{M}O_2$ significantly because of specific dynamic action) consumed oxygen at a rate of 2.1–3.7 mg O_2 kg^{-1} min^{-1}. A similar study reported that juvenile *O. mykiss* (*c.* 23–196 g) housed at 5–15°C and fasted for <30 h prior to measurements, had resting oxygen consumption rates of 0.95 mg O_2 kg^{-1} min^{-1} at 5°C and 1.9 mg O_2 kg^{-1} min^{-1} at 15°C (Rao, 1968). In juvenile *S. namaycush*, a study by Beamish *et al.* (1989), estimated average resting oxygen consumption (10–20 g fish at 10 ± 1°C) was *c.* 1.8 mg O_2 kg^{-1} min^{-1}. Gibson and Fry (1954) reported a lower SMR of 0.78 mg O_2 kg^{-1} min^{-1} for *S. namaycush* at 10°C. Meanwhile, a higher value for SMR of *S. namaycush* (*i.e.*, 2.3 mg O_2 kg^{-1} min^{-1}) was predicted from a regression relating metabolism, body weight, temperature and swimming speed (Stewart *et al.*, 1983).

4.3 | Swimming performance

We found that surgically implanted acoustic transmitters were associated with a reduction in U_{crit} in *S. namaycush* in this study (*c.* 11% reduction when controlling for an increase in U_{crit} with time elapsed in the experiment). However, among the 16 acoustic-tagged *S. namaycush* we swam in the swim-tunnel, there was no effect of tag burden across a range of 3.3%–7.4%. In *O. mykiss*, U_{crit} in acoustic-tagged fish was statistically indistinguishable from controls. Because of the intense effort required to conduct U_{crit} trials, our sample sizes were relatively small, meaning the small effect we observed in *S. namaycush* should be interpreted with caution. Unfortunately, there are no published data or well-developed quantitative or conceptual frameworks with which to interpret whether the small reduction in U_{crit} we observed in *S. namaycush* would be likely to have fitness consequences for these fish in the wild. U_{crit} is a measurement of the maximum aerobic swimming speed fish can maintain over an extended period. A small reduction in U_{crit} could therefore have negative effects on a fish's ability to migrate long distances. We would predict that predator evasion in these species would typically rely more heavily on burst-swimming capacity and maximum swimming speed (U_{max} rather than U_{crit}), in addition to visual and chemosensory acuity, neither of which were measured here but would be worthwhile indices of performance in future tagging effects studies.

The U_{crit} values for both species and treatments in this study were comparable with those found in the literature (Alsop and Wood, 1997; Burden *et al.*, 1998; Gregory and Wood, 1999; Katopodis and

Gervais, 2016; Rao, 1968). Based on a review of fish swimming performance by Katopodis and Gervais (2016), the average U_{crit} for *O. mykiss* (average total length, L_T = 116 mm, range: 22–420 mm) at *c.* 11.8°C is 43.6 cm s^{-1} or 3.8 body lengths (L_B) s^{-1}. However, there has been substantial variation among studies for *O. mykiss*, partly driven by body size: one study using 2.59 g fish with L_T *c.* 59.7 mm found fish reached a U_{crit} value of *c.* 71.1 cm s^{-1} or 11.9 L_B s^{-1} (Burden *et al.*, 1998). Gregory and Wood (1999), estimated *O. mykiss* (5.23–5.73 g) U_{crit} to be 3.42–4.23 L_B s^{-1}. Alsop and Wood (1997) obtained *O. mykiss* (6–12 g) from the same source as in the present study and found U_{crit} ranged from 3–10 L_B s^{-1}. An earlier study (Rao, 1968) reported that fish 30–150 g in size could maintain swimming speeds of *c.* 3.3–5.3 L_B s^{-1}.

For juvenile *S. namaycush* (122–129 mm L_T), Beamish *et al.* (1989), reported U_{crit} values of *c.* 76.5–95.4 cm s^{-1} (*c.* 6.0–7.5 L_B s^{-1}). Based on a review of fish swimming performance by Katopodis and Gervais (2016), the average U_{crit} for *S. namaycush* (average L_T = 181 mm, range 115–225 mm L_T) at *c.* 12.1°C is 4.7 L_B s^{-1} These critical swimming speeds are slightly higher than the U_{crit} values for *S. namaycush* in our study, but the fish we used were larger.

Studies comparable to ours (salmonids in similar size range) have often failed to find effects of tag burden on swimming performance, especially in the burden range used in our study. Brown *et al.* (1999) reported that a tag burden of 6%–12% in juvenile *O. mykiss* (5–10 g) did not alter swimming performance. Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) (6.7–23.1 g) with a tag burden of 3.1%–10.7% had U_{crit} of 4.3–4.7 L_B s^{-1} (47.5–51.2 cm s^{-1}) and no difference was found in swimming performance or growth rates between control, sham and acoustic-tagged fish (Brown *et al.*, 2006). In 12–87 g sockeye salmon *Oncorhynchus nerka* (Walbaum 1792) smolts, tag burdens >8% were associated with reduced performance in a swimming endurance test (Collins *et al.*, 2013), whereas fish with tag burdens <8% were indistinguishable from controls. In *c.* 131 g brook trout *Salvelinus fontinalis* with mean tag burdens of 9.3%, there was no difference in U_{crit} compared with sham controls (Smircich and Kelly, 2014). Pre-smolt coho salmon with similar tag burdens (up to 8%) as the present study experienced no adverse effects on swimming performance (or growth or survival, Chittenden *et al.*, 2009). Thus, when combining the weak effect on U_{crit} we observed with the previous literature, it seems unlikely that acoustic tagging, especially at lower burdens (*e.g.*, <8%), is likely to have ecologically meaningful effects on aerobic swimming capacity. Further experiments would be required to assess whether the presence of an acoustic-tag burden could affect the anaerobic swimming characteristic of predator evasion (*e.g.*, c-starts; Domenici and Blake, 1997).

4.4 | Significance and future directions

There are many reasons to continue to pursue and advance telemetry techniques. Identifying ideal fish sizes and release locations and times for native species restoration programmes that rely on releasing hatchery-grown fish provides a challenge for fishery management agencies and fish hatcheries (Ogburn *et al.*, 2017; Seddon *et al.*, 2007). Juvenile mortality and lack of natural reproduction are considered major impediments to fish stocking programmes oriented towards restoration (Ersbak & Haase, 1983). Measuring the success or survival of the juveniles involved in these stocking programmes is one of many examples in which acoustic telemetry could provide data useful to fisheries management (Pincock *et al.*, 2010). The data present in this study can help underlie such acoustic telemetry studies. Stocking programmes continue to be the most common strategy for restoring and rehabilitating native fish populations (U.S. Fish and Wildlife Service and Great Lakes Fishery Commission, 2010; Wehse *et al.*, 2017).

Along with previous literature in other salmonids, the results from the present acoustic-tagging study suggest juvenile salmonids can be implanted with acoustic transmitters (*c.* 2%–7% tag burden) with negligible effects on survival, growth, metabolic rate and swimming performance (U_{crit}). Nevertheless, we recommend that the research done here be replicated in other juvenile salmonids relevant to fisheries management, especially hatchery stocking programmes (*e.g.*, *O. tshawytscha*, Atlantic salmon *Salmo salar* L. 1758). Further research could examine fine-scale behaviours (*e.g.*, activity in an open field test, feeding rate, c-starts) and include higher tag burdens (as in some previous studies, *e.g.*, up to 12%) to identify burden thresholds at which lethal or sub-lethal effects begin to occur.

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AUTHOR CONTRIBUTIONS

All authors contributed to study design. A.P.D. and G.D.R. carried out the experiments using equipment, facilities and funding provided by T.E.P. and A.T.F. G.D.R. analysed the data and created the Figures. AD.P. and G.D.R. wrote the paper, which received input from all co-authors.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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