NRC Research Press

ARTICLE

No long-term effect of intracoelomic acoustic transmitter implantation on survival, growth, and body condition of a long-lived stenotherm in the wild

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Abstract: A fundamental assumption of biotelemetry studies is that there are no adverse consequences from the surgical implantation or presence of the acoustic transmitter. In fisheries, most studies have evaluated this assumption over only short time periods (<2 years) in a laboratory setting. Here we compared the survival, growth, and body condition of populations of lake trout (*Salvelinus namaycush*) in three lakes containing tagged and untagged individuals over a 12-year period (2002–2013). We found no significant negative effects of acoustic telemetry tagging on the long-term survival of fish (estimates of combined annual survival ranged from 67% to 91%) and no negative effect of surgical implantation on growth or body condition for fish of either sex. Additionally, we found no significant effect of transmitter:fish mass ratio on fish survival, growth (with the exception of smaller-bodied fish in one lake), or condition. Our results indicate the use of transmitters weighing <1.25% (in water) of fish mass is a desirable criterion for larger-bodied adult lake trout. Our findings support the assumption that long-lived fish species tagged with acoustic transmitters via intracoelomic surgery survive, grow, and maintain body condition similar to untagged conspecifics over the long term in the wild.

Résumé : Une hypothèse fondamentale des études de biotélémétrie est que l'implantation chirurgicale ou la présence d'un émetteur acoustique n'a pas de conséquences néfastes. Dans les pêches, la plupart des études n'évaluent cette hypothèse que sur de courtes périodes (<2 ans) et en laboratoire. Nous avons comparé la survie, la croissance et l'embonpoint de populations de truites de lac (*Salvelinus namaycush*) dans trois lacs renfermant des spécimens étiquetés et non étiquetés, sur une période de 12 ans (2002–2013). Nous n'avons relevé aucun effet négatif significatif de l'étiquetage à des fins de télémétrie acoustique sur la survie à long terme des poissons (taux de survie annuelle combinés estimés de 67 % à 91 %) ni aucun effet négatif de l'implantation chirurgicale sur la croissance ou l'embonpoint des poissons des deux sexes. Nous n'avons en outre relevé aucun effet significatif du rapport des masses de l'émetteur et du poisson sur la survie, la croissance (à l'exception des petits poissons dans un lac) ou l'embonpoint des poissons. Nos résultats indiquent que l'utilisation d'émetteurs dont la masse est <1,25 % (dans l'eau) de celle des poissons est un critère souhaitable pour les grandes truites de lac adultes. Nos constatations appuient l'hypothèse selon laquelle des poissons d'espèces longévives dans lesquels sont implantés des émetteurs acoustiques par chirurgie intracœlomique ont, sur le long terme et à l'état sauvage, des taux de survie et de croissance et un embonpoint semblables à ceux de leurs conspécifiques non étiquetés. [Traduit par la Rédaction]

Introduction

Biotelemetry can provide novel insights into the spatial ecology and survival rates of aquatic animal populations that were previously impossible to observe in the wild (Hussey et al. 2015). Biotelemetry has many uses in fisheries research, including applications in studies of fish movement and migration (Keefer et al. 2008; Fielder et al. 2020), anthropogenic impacts on survival and mortality rates in exploited stocks (Donaldson et al. 2008), spatial and temporal habitat use (Charles et al. 2017), and fish behaviour (Johnson et al. 2010). Application of biotelemetry to fisheries research has been occurring for more than half a century (Baras 1991; Cooke et al. 2013), but in recent decades, there has been a dramatic increase in the use of acoustic telemetry in fisheries research due to the technological advancements (e.g., increased battery life, signal strength, and miniaturization) and increasing affordability of the equipment (Kessel et al. 2014). Acoustic telemetry transmitters (hereinafter tags) are typically

Received 30 March 2020. Accepted 4 October 2020.

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externally attached or internally implanted, although intracoelomic surgical implantation is the most common approach (Jepsen et al. 2002; Bridger and Booth 2003; Brown et al. 2011).

A critical assumption of biotelemetry studies is that tagged (i.e., fish implanted with an acoustic tag in the coelom) fish are representative of their populations (Rogers and White 2007). Violations of this assumption could lead to spurious findings that are not representative of the studied fish populations but rather associated with the impacts of tagging. Documented negative impacts of capture, handling, and surgical implantation of tags include inflammation (Thorstad et al. 2000), reduced growth over short periods (~5 months; Jepsen et al. 2008), decreased swimming ability, altered behaviour (Zale et al. 2005), and increased mortality rates (Brown et al. 2013; Jepsen et al. 2015). Larger tag:fish mass ratios have been shown to amplify the effects of tagging (Jepsen et al. 2005). The general rule of using a tag weight no larger than 1.25% of the fish weight in water (or 2% for tag weight in air; Winter 1983) was largely accepted among researchers, but recent studies have indicated more species- and context-specific approaches to tag size should be considered (Brown et al. 1999; Jepsen et al. 2002; McCabe et al. 2019). By tailoring the most suitable procedures to the specific fish species and research project objectives, many of these impacts can be mitigated over short time scales (Jepsen et al. 2002).

A challenge for fisheries research remains in understanding the long-term effects of intracoelomic tag implantation (Cooke et al. 2011). Tags are routinely surgically implanted in species known to live for years (e.g., smallmouth bass, *Micropterus dolomieu*), decades (e.g., lake trout, *Salvelinus namaycush*), or more than a century (e.g., lake sturgeon, *Acipenser fulvescens*). Thus, the life-span of many freshwater fishes is well beyond the battery life of a tag or the duration of a given telemetry study, yet an implanted tag will remain with a fish for its entire life. Lake trout are a long-lived (50+ years; Schram and Fabrizio 1998), cold-water species that is sensitive to human disturbances for which telemetry studies have played an important role in conservation efforts for decades, especially in the Laurentian Great Lakes (Riley et al. 2014; Binder et al. 2017, 2018). As for other fish species, acoustic telemetry studies have been instrumental in improving our understanding of the ecology, life history, and habitat use of lake trout (Guzzo et al. 2016; Gallagher et al. 2019; Klinard et al. 2019), and in some smaller inland lakes, monitoring of telemetry-tagged lake trout has been ongoing for almost two decades (Blanchfield et al. 2005; Guzzo et al. 2017). However, more important than study duration (i.e., period when tags are active) is the consideration of long-term fish welfare, given that fish will carry implanted tags for the rest of their lives. Despite this, most tagging effects studies occur in laboratory settings and last for short durations of several weeks to months (e.g., Thorstad et al. 2000; Berejikian et al. 2007; Darcy et al. 2019). Potential long-term effects of tags could negatively impact estimates of growth, survival, movement, and behaviour from study populations and are thus important to quantify but are currently unknown.

The objective of our study was to assess the long-term lethal or sublethal effects of surgically implanted acoustic telemetry tags on adult lake trout within their natural habitat. Here we compare data from two complementary long-term studies of lake trout populations ongoing in several small boreal lakes. Data from an annual population monitoring program were used to compare survival, growth, and condition of lake trout that only experienced handling in this standard mark–recapture program with lake trout that were acoustically tagged in these same lakes (Guzzo et al. 2017). We also examined the effects of tag:fish mass ratio on growth and body condition. Given the documented potential for negative effects of acoustic telemetry tagging on fish survival (Brown et al. 2013) and growth (Jepsen et al. 2008) over short time periods, we considered that similar effects might be possible in tagged lake trout over longer (multiple-year) time periods. Because most lake trout were implanted with tags (weight in water) <1.25% of their mass, which is below the threshold at which negative effects have typically been observed, we predicted no relationship between tag burden and growth, condition, or survival. Support for this prediction would suggest that using tags <1.25% of fish mass is effective at mitigating tagging effects on adult lake trout, but not necessarily for other species.

Table 1. The number of lake trout surgically implanted with acoustic telemetry tags by year in three lakes at the experimental lakes area.

Year	Lake 373	Lake 375	Lake 626
2002	10	11	0
2003	0	3	0
2004	0	0	0
2005	7	8	0
2006	5	5	0
2007	3	3	0
2008	7	4	13
2009	7	5	7
2010	10	0	10
2011	6	0	5
2012	3	0	3
2013	0	0	0
Total	58	39	38

Methods

Study area and field data collection

Field research took place at the International Institute for Sustainable Development Experimental Lakes Area (IISD-ELA), a remote area of northwestern Ontario where 58 small lakes and their catchments have been set aside for research purposes and where long-term monitoring and manipulation of lakes has been occurring since 1968 (Blanchfield et al. 2009). Data collection took place within Lakes 373, 375, and 626 between 2002 and 2013 (12 years), which have a long historical record of fish population data, having been monitored annually for 34, 32, and 14 years, respectively. Lake 373 is a long-term reference lake that has not been manipulated (Guzzo et al. 2017). A whole-lake aquaculture study occurred in Lake 375 for a period of 5 years (2003–2007; Blanchfield et al. 2009; Rennie et al. 2019), and a whole-catchment water diversion experiment has disconnected Lake 626 from its upstream watershed since 2011 (Spence et al. 2018). Because these ecosystem manipulations have the potential to affect lake trout growth, condition, and survival (either positively or negatively), we conducted separate analyses for all lakes (see below). All lakes are closed to fishing by the public. All tagging and handling of fish was approved by the Freshwater Institute Animal Care Committee (Fisheries and Oceans Canada, Winnipeg, Canada).

Tagged lake trout

Between May 2002 and May 2012, a total of 135 lake trout underwent intracoelomic surgical implantation of an acoustic telemetry tag (hereinafter tagged fish; Table 1) as part of a long-term behavioural monitoring program at IISD-ELA. Fish were typically caught via angling in spring when water temperatures were below 11 °C. Fish were immediately brought to shore and anaesthetized with a sodium bicarbonate-buffered solution (120 $mg \cdot L^{-1}$) of tricaine methanesulfonate (MS-222; 60 $mg \cdot L^{-1}$) in lake water, with the exception of lake trout tagged in 2002, when clove oil was used as an anaesthetic (see Blanchfield et al. 2005). Once anaesthetized, fish were measured for fork length in millimetres (mm), weighed in grams (g), and received a passive integrated transponder (PIT) tag (Biomark, Inc.) in the dorsal musculature below the dorsal fin and above the lateral line if they did not already have one. Fish then underwent surgery for the implantation of a telemetry tag into their abdominal cavity, with the average surgery taking ~6.3 min (including measuring and weighing; a detailed description of surgical methods can be found in Blanchfield et al. 2005). Over the duration of this study, one of three different models of acoustic tags (that transmit acoustic signals during their battery life), all with pressure (depth) sensors, were surgically implanted into lake trout (V9AP-2 L, 3.6 g in water, ~90 days of battery life, turned on 45 days after implantation, n = 32; or V13P-1 L, 6.9 g in water, ~1300 days of battery life, n = 79; or V16P-4 L, 11.7 g in water, 987–1337 days of battery life, n = 24; VEMCO Ltd.). The mean body weight of this group of lake trout was 825 g (range: 487–1848 g). Tag weight in water averaged 0.86% of the fishes' bodyweight (in air) and was never greater than 1.80% (Blanchfield et al. 2005; Guzzo et al. 2017). A total of 58, 39, and 38 lake trout were implanted with acoustic tags in Lakes 373, 375, and 626, respectively. There was some evidence of possible tag expulsion (i.e., the tag being expelled from the body cavity of a fish through the incision), where the telemetry data satisfied the analysis criteria to declare the fish "dead" but the fish was later recaptured, but this phenomenon was uncommon (n = 2; see Results).

Untagged lake trout

In each spring and fall of monitoring, lake trout were captured using trap nets and in the fall were additionally captured with short-set gill nets set in the evening on spawning shoals (Mills et al. 1987, 2002). Fish were anaesthetized with a sodium bicarbonate-buffered solution of MS-222 in lake water and then weighed, measured for fork and total length, and given a batch-mark on their dorsal fin by fin-ray scarring (Welch and Mills 1981) to indicate the season of capture. Prior to 2008, all captured lake trout received both a visual implant tag behind the left eye and a Carlin-style sew-on tag just below the dorsal fin. In 2008, these tagging methods were replaced with the implantation of a PIT tag as described above. Fish recovered in a large tub of lake water before being released back into the lake. These handling methods are assumed to have no impacts on survival, mortality, or condition of the lake trout (Zydlewski et al. 2001). Lake trout captured and released in these lakes that did not receive acoustic tag implants represented a control group in the current study (hereinafter untagged fish). Data for untagged fish that were outside of the recorded length and weight measurements of the tagged group at the time of surgery were removed from all statistical analyses to account for the size selection of tagged fish.

Statistical analyses

Several types of data were collected over the study period for tagged and untagged fish, including (*i*) mark and recapture, (*ii*) known fate (fish known to have died based on telemetry; tagged fish only), and (*iii*) fish length and weight measurements. We employed several methods for determining and comparing survival and mortality estimates and examining sublethal effects, including (*a*) an estimation of instantaneous mortality via catch-curve analysis (Robson and Chapman 1960), (*b*) survival estimates from mark–recapture data using Cormack–Jolly–Seber (CJS) analysis (Cormack 1989), (*c*) Kaplan–Meier (KM) analysis using the Cox proportional hazard model (Pollock et al. 1989), and (*d*) regression analysis of the change in growth and body condition over time and tag burden.

Fates of tagged fish were determined using telemetry data for each day postsurgery during the life-span of the tag: (*i*) mortality (fish death), determined through the observation of no movement horizontally or vertically (if both were available; in some instances depth alone was used) from a tag over an extended period of time; (*ii*) survival (fish alive), when the tag moved around in all three spatial planes (*XYZ*); (*iii*) the fish was right-censored, meaning the animal was removed from the analysis for one of three reasons: tag failed prematurely (pressure sensor failed), tag disappeared (tag stopped pinging abruptly well before battery life was projected to run out, or fish was predated and removed from the lake), or the tag turned off (lasted for the full duration of battery life). In all cases, right-censored fish appeared to be alive when they were removed from the analysis, so right-censoring does not represent mortality. After right-censoring, the fate of a fish can no longer be determined using acoustic telemetry, but it may still be recaptured and identified via PIT tags.

A significance level of 0.05 was used for all statistical analyses where relevant. We used the statistical program R version 3.6.1 for all analyses (R Core Team 2020).

Survivorship and mortality

Catch-curve analysis (also known as the Ricker curve method) is a well-established stock recruitment and mortality calculation method (Robson and Chapman 1960; Smith et al. 2012). This method typically fits a linear regression to log-transformed catch-at-age data from age at peak catch and all older fish (Smith et al. 2012). The slope of this line represents the instantaneous mortality rate. We used a modified version of catch-curve methods by examining the number of individual fish recaptured over time (spring and fall, 6-month intervals) from time zero for each fish (first capture for nontagged fish, surgery date for tagged fish) rather than catch-at-age of a population from a single sampling event. The slopes were fit to catch-curves of both tagged and untagged lake trout and compared with a test for heterogeneity of slopes (i.e., whether there was a significant interaction between the grouping factor of tag status and the covariate of capture period, indicating different slopes between tagged and untagged fish). To achieve sufficient sample sizes, catch-curves were fit to lake trout within all three lakes combined, as the catch-curve method requires $n > 100$ to provide reasonable estimates (Smith et al. 2012).

We then applied a CJS model to mark–recapture data (Cormack 1964; Seber 1965; Jolly 1965) for tagged and untagged fish to determine survival estimates over the 12-year time period (24 intervals, representing every spring and fall modelled on equal separation of 6 months between sampling events). The CJS heterogeneous models we applied assume capture events are independent between animals and between sampling events (Pledger et al. 2003), which our data satisfy. Over the study period, 29 lake trout mortalities occurred postsurgery (n = 4, tagged fish) or after initial handling (n = 25, untagged fish) out of 1588 captured during recapture or handling, (i.e., death due to stress from capture in gill nets or angling). These deaths were not associated with intracoelomic surgery, and these fish were excluded from the CJS analysis at time of death. We considered 14 candidate models (see Table 2) with the model parameters survivorship (φ) and capture probability (i.e., the likelihood a fish would be captured; p) each either varying over time (varying estimates at each interval) or constant over time (the same for all time intervals) and possible interactions with tag group as an additional main effect. The data were tested for overdispersion on the full model; all subsequent models were given a $\hat{c}$ correction of 1.81. These models were evaluated for parsimony using second-order quasi-Aikike's information criterion ($QAIC_c$). We used the package "RMark" for the CJS analysis (Laake 2013).

We used a Cox proportional hazards (PH) analysis on known-fate data to examine potential effects of tag burden, tag model type, and lake on the probability of survivorship, which we define (see above) as the detection of regular acoustic telemetry signals of tagged lake trout (Kawabata et al. 2011). The PH model calculates the hazard ratio in relation to the instantaneous rate of an event occurrence (death of the fish) to explanatory variables. The hazard ratio represents the difference in likelihood of mortality event occurrence between two groups, one being a "reference" group (in this case Lake 373 for the lake variable and V13-1PL for the tag variable), where a ratio of 1 indicates no difference and a ratio of 10 indicates one group having 10 times the

Table 2. Candidate models from Cormack–Jolly–Seber analysis.

Model	No. of parameters	$QAIC_c$	$\Delta QAIC_c$	Akaike weight
$\varphi(t)p(t \times \text{tag})$	69	4401.89	0.00	1.00
$\varphi(t \times \text{tag})p(t \times \text{tag})$	92	4431.10	29.21	0.00
$\varphi(t)p(t + \text{tag})$	47	4446.26	44.37	0.00
$\varphi(t + \text{tag})p(t + \text{tag})$	48	4452.45	50.56	0.00
$\varphi(t + \text{tag})p(t)$	47	4454.83	52.94	0.00
$\varphi(t)p(t)$	46	4459.01	57.12	0.00
$\varphi(t \times \text{tag})p(t)$	69	4476.07	74.18	0.00
$\varphi(c + \text{tag})p(c + t)$	4	5289.81	887.92	0.00
$\varphi(c)p(c + \text{tag})$	3	5290.81	888.92	0.00
$\varphi(c + \text{tag})p(c)$	3	5296.97	895.08	0.00
$\varphi(c)p(c)$	2	5305.44	903.55	0.00
$\varphi(c \times \text{tag})p(c \times \text{tag})$	2	5305.44	903.55	0.00
$\varphi(c \times \text{tag})p(c)$	2	5305.44	903.55	0.00
$\varphi(c)p(c \times \text{tag})$	2	5305.44	903.55	0.00

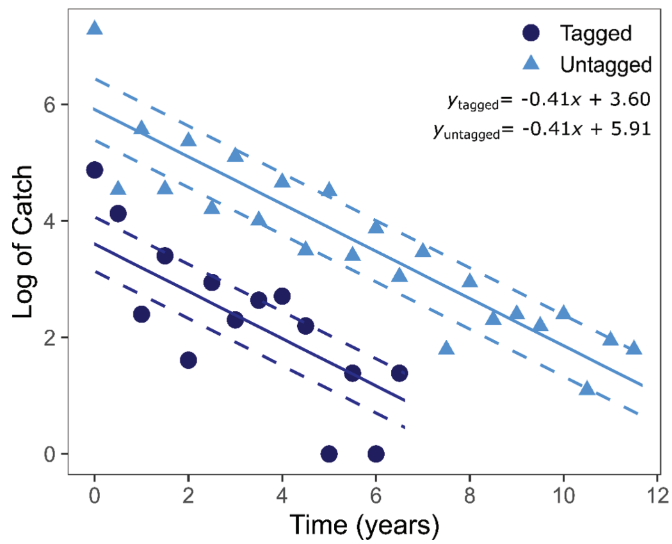
Note: *c*, constant time parameter; *t*, time-varying parameter; tag, effect of tag group. Model parameters are survivorship (φ) and capture probability (p). Models were evaluated using second-order quasi-Aikike's information criterion ($QAIC_c$). Lower $QAIC_c$ values indicate a stronger support for the model. $QAIC_c$ values were adjusted using $\hat{c} = 1.81$.

likelihood of event occurrence than the other (reference) group. We used a KM analysis for survival rate estimates, which has been shown to estimate accurate survival rates using known-fate data in telemetry studies, and is particularly useful in that it allows for the staggered entry of animals into the study (Pollock et al. 1989; Heupel and Simpfendorfer 2011). We defined the time of origin of the study to be at the time of surgery, where survival estimates were calculated daily from the time origin (Pollock et al. 1989). Assumptions of the PH and KM procedures are as follows: survival times are independent for individual animals; a random sample of animals of particular age, sex, and size class was sampled; and censoring was random (Pollock et al. 1989). We used the R package "survival" for these analyses (Therneau 2015).

Sublethal effects

Lake trout growth and body condition (general measures of fish health; Cade et al. 2008) were analysed using mark–recapture data. Annual change (i.e., change per year) in mass (g) was used as a measure of growth, and annual change in body condition was estimated from the residuals generated from a log-transformed fork length and weight linear regression (Meka and McCormick 2005; Dale et al. 2017). Fish with positive residuals were considered to be in better condition than those with negative residuals. Separate length–weight regressions were developed for each lake to support this analysis. Change in condition was tracked over the course of the study period for all fish with multiple catches. Linear mixed models (LMMs) were fitted separately for each lake using the annual change in growth and annual change in body condition as dependent variables and tagging group (tagged and untagged), time since intracoelomic surgery for tagged fish (continuous covariate), and time since first capture for untagged fish (continuous covariate) as fixed effects in the models. The individual fish identifier (which tracked fish over time through multiple capture periods) was treated as a random effect. We tested for heterogeneity of slopes between groups, and if slopes were found to be similar, proceeded with a two-way analysis of covariance (ANCOVA) to determine whether there was a consistent difference in annual change in mass (g) or body condition between tagged and untagged fish from time of first capture or surgery. If there was no difference found, we then tested the significance of the relationship between time and the two measures (growth or body condition). Owing to high variability in change in growth and condition shortly after first capture and our interest being focused on long-term effects, we removed data less than 1 year

Fig. 1. Log-transformed catch of lake trout (tagged and untagged) over time relative to initial capture. Time was recorded as zero when fish were first caught. Dashed lines around fitted lines represent 95% confidence intervals.



from first capture (16.8% of tagged and untagged lake trout recaptures). Most lengths and weights for untagged lake trout in this study were recorded close to spawning, as most fish are captured during the fall (Rennie et al. 2019). Because male and female lake trout differ in their allocation to gonads (gonadosomatic index or GSI of males typically 4%–5%, and 10%–15% in females; M.D. Rennie, Lakehead University, unpublished data), and because previous effects of increased egg retention in tagged females has been documented (Berejikian et al. 2007), we repeated these analyses separately for male and female fish.

To test for the significance of the effects of tag burden (the percentage of tag mass in water to fish mass at the time of surgery), we performed a regression analysis of the relationship of tag burden and change in body condition or change in mass. We removed records of tagged fish that were recaptured <1 year postsurgery due to our focus on examining potential long-term effects and the limited amount of short-term data available.

We used the package "lme4" to fit LMMs (Bates et al. 2015). To determine significance of LMM fits between "nested" models (e.g., models of greater versus lesser complexity), we compared these using the "anova" function in R (Bates et al. 2015), which produces a log-likelihood ratio test of the models being compared and generates p values indicating whether the added term in the more complex model explains significantly more variation than the simpler model. Regression lines were only included where significant relationships were found. Data were examined to assess whether parametric assumptions were met, and where necessary, data were transformed to meet assumptions. Where data could not be transformed or transformations were insufficient in meeting parametric assumptions, a nonparametric randomization approach was used. Briefly, the test statistic of the original data was compared with that from the same data resampled without replacement, and this procedure was repeated 9999 times — a pseudo p value (p_p) was estimated as the number of test statistics greater than or equal to the original test statistic from resampled data.

Results

In total, 135 adult lake trout underwent surgical implantation of acoustic telemetry tags (Table 1). Four tagged lake trout were

Fig. 2. Forest plot of the Cox proportional hazards model for fish survival with tag burden, lake, and tag model as independent variables. Hazard ratios (HR) greater than 1 indicate increased risk of mortality. Reference variables are variables that other variables are modelled against. Error bars indicate the 95% confidence interval (CI) of the hazard ratio.

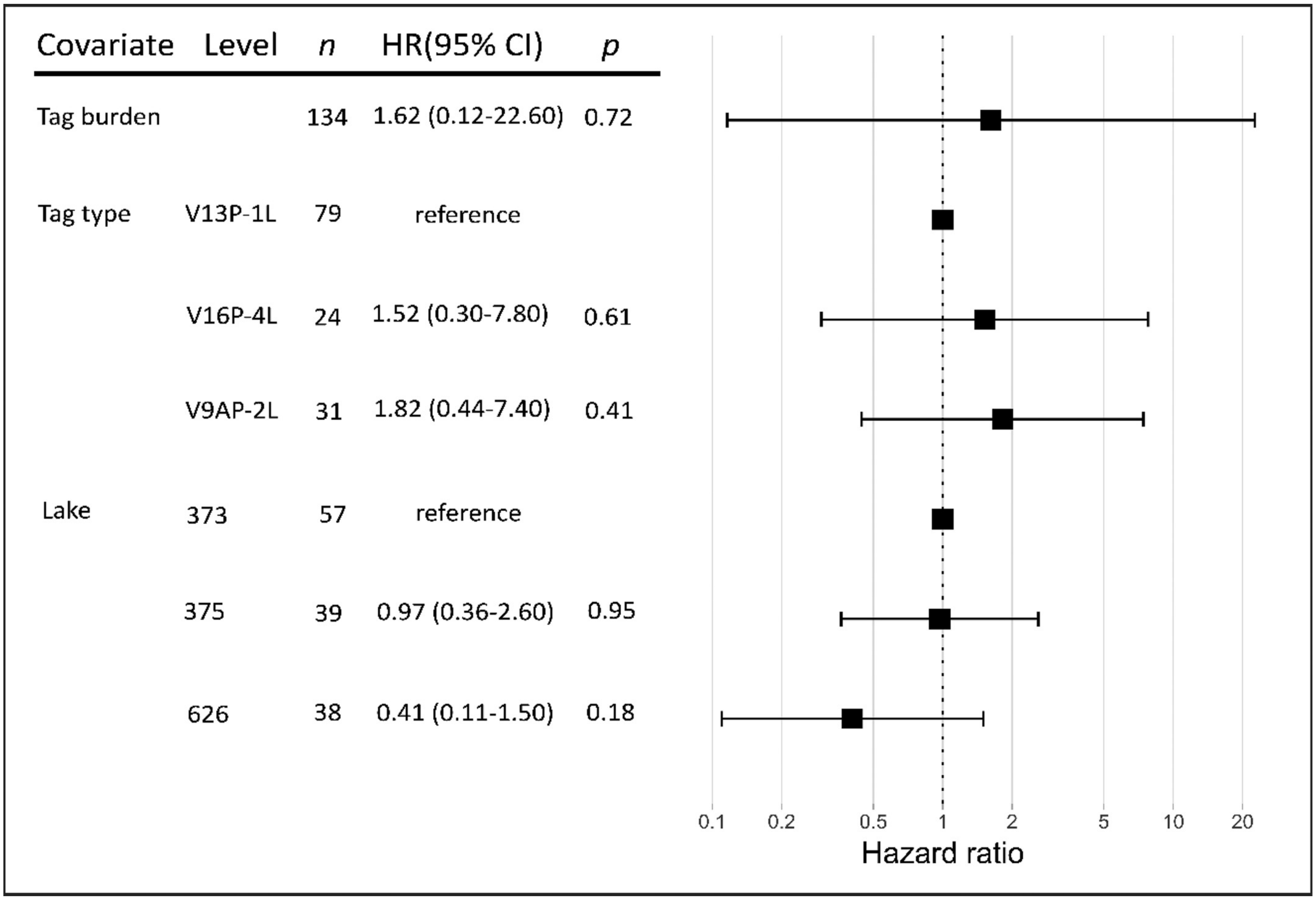


Fig. 3. Kaplan–Meier survival curve for all lake trout. Time was recorded as zero at date of surgery. Shaded areas represent 95% confidence intervals.

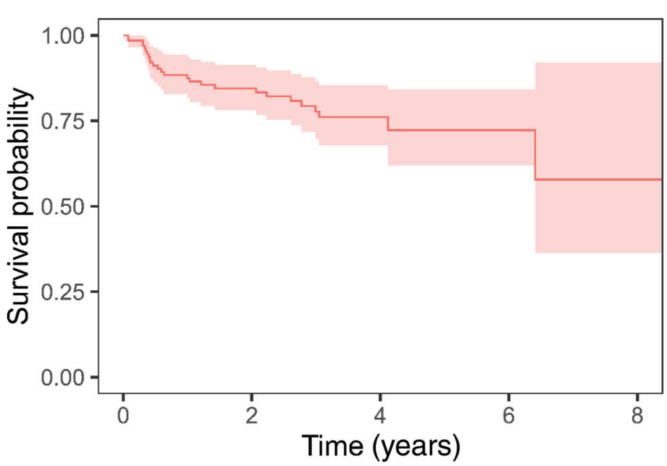
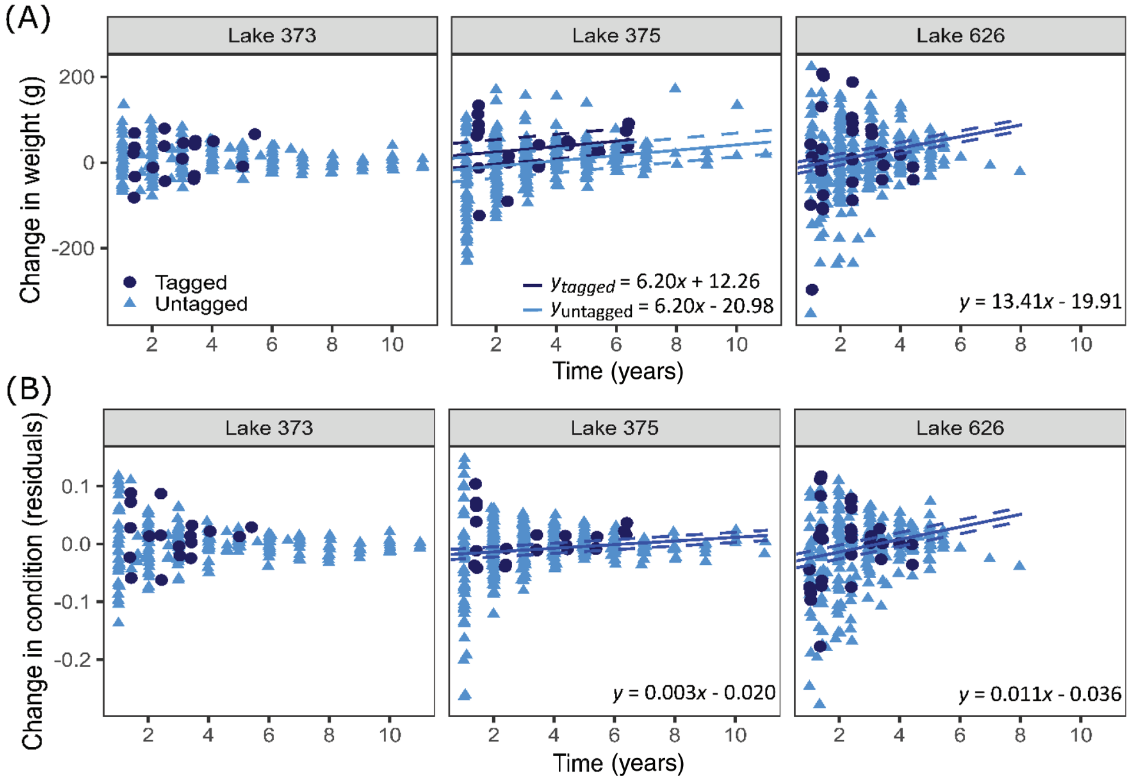


Table 3. Sample sizes and observations (recaptures) of lake trout within each lake for the growth and condition analyses.

				Untagged			
		Tagged		Condition		Growth	
Lake	Sex	*n* fish	*n* observ.	*n* fish	*n* observ.	*n* fish	*n* observ.
373	All	15	18	117	222	121	230
	Females	5	6	22	26	21	25
	Males	7	9	81	168	83	174
375	All	17	23	226	373	209	339
	Females	7	10	87	130	105	158
	Males	7	10	121	203	88	146
626	All	17	30	149	294	166	324
	Females	10	18	78	119	92	141
	Males	4	8	52	93	49	90

Note: The sample sizes of untagged lake trout differ between growth and condition analyses because they were included only if their length by weight relationship residuals (condition analysis) or weight (growth analysis) at the time of first capture fell within the range of the tagged lake trout. Samples sizes of all fish were greater than the sum of both sexes because sex was not determined for some fish.

Fig. 4. Annual change in weight (g) over time (A) and annual change in condition (log-transformed fork length and weight regression residuals) over time (B). Time is recorded as zero at date of surgery for tagged fish and date of first recording in capture history for untagged fish. Dashed lines represent 95% confidence intervals. [Colour online.]



never recaptured postsurgery, and one of these was never observed in the telemetry or mark–recapture data postsurgery. The longest a tagged fish was tracked for was 8.6 years (mean: 2.4 years, 95% CI: 2.1–2.7 years, using combined telemetry and recapture data), and the longest an untagged fish was tracked for was 11.5 years (mean: 3.4 years, 95% CI: 3.3–3.6 years, using recapture data). The first recorded postsurgery death of a tagged fish determined via acoustic telemetry data was after 27 days. There were two examples of possible tag expulsion by fish, but the results of statistical analyses were insensitive to the inclusion of these two fish. A total of 1455 untagged lake trout were included in this study, 379 of which were caught only once.

Mortality and survivorship

All recaptured tagged (n = 131) and untagged (n = 1455) fish were included in the catch-curve analysis. Instantaneous mortality rates were not significantly different between the groups (−0.41, 95% CI: −0.48 to −0.33), which translates to a combined annual survival rate of 0.76 (95% CI: 0.66–0.86). Likewise, there were no differences in mortality rates over time between tagged and untagged fish (since surgery for tagged fish and since first recorded capture for untagged fish; Fig. 1; test for heterogeneity of slopes $F_{[1,34]} = 2.20$, $p = 0.15$).

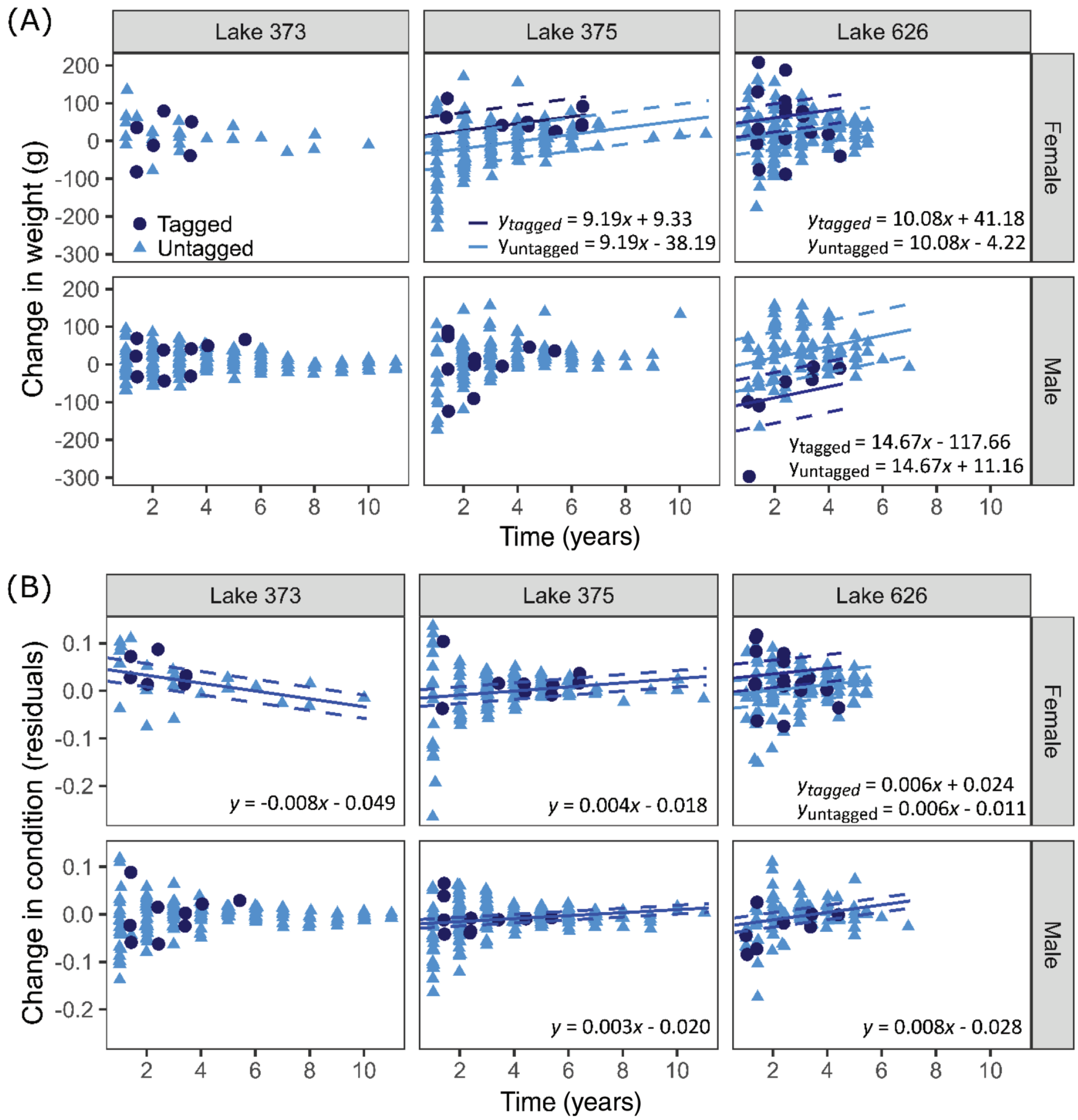
Of the 14 survival and capture probability models evaluated, only one model was strongly supported ($\Delta QAIC_c < 3$; Table 2). This model included survivorship under varying time (estimates made at each sampling interval) and capture probability under varying time with the interaction effect of tag group, $\varphi(t)p(t \times \text{tag})$. The most parsimonious model estimated a mean annual survival for both tag groups of 0.67 (95% CI: 0.50–0.86) and an interval capture probability for the tagged group of 0.25 (95% CI: 0.14–0.35) and for the untagged group of 0.18 (95% CI: 0.08–0.28).

The Cox PH model found no significant negative effect of tag burden, tag model, or lake (Fig. 2). The KM analysis estimated mean annual survival of all tagged lake trout to be 0.92 (95% CI: 0.89–0.97; Fig. 3) with 26 mortality events.

Growth and condition

Sample sizes of fish to assess impacts of telemetry tags on growth and condition were 496 untagged and 49 tagged fish, with similar numbers of fish sampled from each lake (Table 3). Log-likelihood ratio tests for heterogeneity of slopes (comparing models with an interaction between tagging group and time versus an additive model) found no significant interaction between tag group and time in any lake or for sex within each lake for either annual changes in growth or condition. We found a significant difference in the elevation of change in mass with time relationship between tag groups in several instances, indicating that larger fish on average received telemetry tags than those that did not. Within-lake comparisons showed significant differences in elevation between groups in Lake 375 among all fish (ANCOVA: $\chi^2 = 5.56$, df = 1, $p_p = 0.02$; tagged intercept = 12.26, untagged intercept = −20.98; Fig. 4A), whereas tagged females were significantly larger than untagged females in Lake 375 (ANCOVA: $\chi^2 = 4.50$, df = 1, $p_p = 0.04$; tagged intercept = 9.33, untagged intercept = −38.19; Fig. 5A) and in Lake 626 (ANCOVA: $\chi^2 = 5.53$, df = 1, $p = 0.02$; tagged intercept = 41.18, untagged intercept = −4.22; Fig. 5A). By contrast, tagged males in Lake 626 tended to be smaller than untagged fish (ANCOVA: $\chi^2 = 8.75$, df = 1, $p_p = < 0.01$; tagged intercept = −117.66, untagged intercept = 11.16). The same parameters analyzed for change in

Fig. 5. Annual change in weight (g) over time by sex and lake (A). Annual change in condition (log-transformed fork length and weight regression residuals) over time by sex and lake (B). Time is recorded as zero at date of surgery for tagged fish and date of first recording in capture history for untagged fish. Dashed lines represent 95% confidence intervals. [Colour online.]

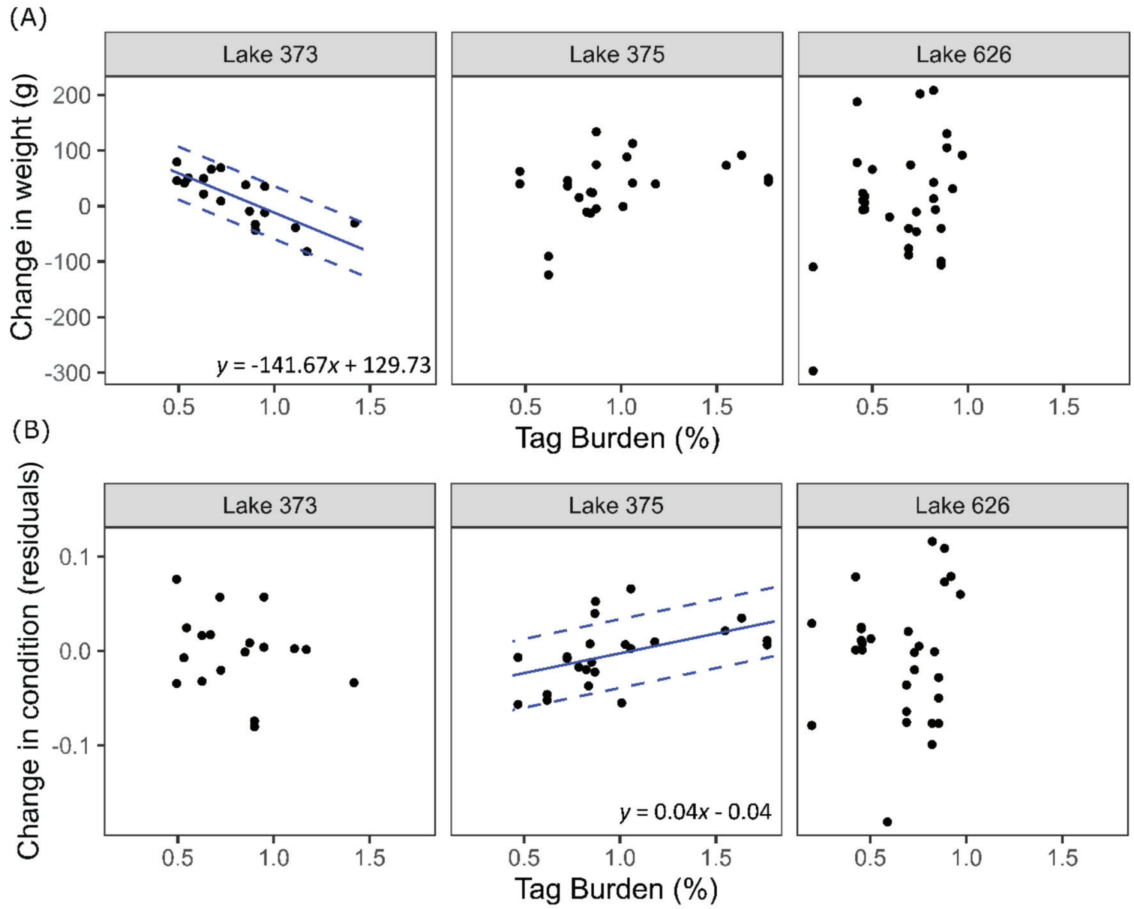


condition found a significant difference in elevation, suggesting higher body condition in tagged females in Lake 626 (ANCOVA: χ^2 = 5.59, df = 1, p_p = 0.02; tagged intercept = 0.024, untagged intercept = −0.011; Fig. 5B). Tests for the significance of the slope of the common regression line of both tag groups combined found a significant positive relationship between time and change in mass for fish in Lake 626 (χ^2 = 61.90, df = 1, $p < 0.001$, slope = 13.41; Fig. 4A). A significant common regression line for change in condition over time was also found in Lake 375 (χ^2 = 9.69, df = 1, $p = < 0.01$, slope = 0.003; Fig. 4B) and Lake 626 (χ^2 = 40.48, df = 1, $p < 0.001$, slope = 0.011; Fig. 4B). When data were analysed separately for each sex, significant positive relationships were found for females in Lake 375 (χ^2 = 4.07, df = 1, p = 0.04, slope = 0.004; Fig. 5B), males in Lake 375 (χ^2 = 8.67, df = 1, $p < 0.01$, slope = 0.003; Fig. 5B), and males in Lake 626 (χ^2 = 13.25, df = 1, $p = < 0.001$, slope = 0.008; Fig. 5B). Only females in Lake 373 demonstrated a slightly negative relationship with time for body condition when fish from both categories were considered (χ^2 = 7.24, df = 1, p = 0.01, slope = −0.008; Fig. 5B).

Tag burden

To be included in the tag burden analysis, lake trout had to be tagged and recaptured at least once after surgery. There were 12 fish with 16 total recaptures in Lake 373, 13 fish with 17 total recaptures in Lake 375, and 20 fish with 34 total recaptures in Lake 626. The mean tag burden (the percentage of tag mass in water to fish mass at surgery) for these fish was 0.86% (range: 0.19%–1.77%). Only lake trout in Lake 373 were found to have a negative relationship between tag burden and annual change in mass (χ^2 = 15.97, df = 1, $p = < 0.001$, slope = −141.67; Fig. 6A). We found a significant positive relationship of tag burden and annual change in condition only for lake trout in Lake 375 (χ^2 = 27.39, df = 1, p = 0.02, slope = 0.04; Fig. 6B).

Fig. 6. The relationship of tag burden (percent mass of tag to fish) and annual change in weight (g; A) or annual change in condition (residuals of log-transformed fish length and weight regression; B) by lake. Each point represents a single recapture of a fish. Dashed lines represent 95% confidence intervals. [Colour online.]



Discussion

We found no evidence of long-term negative impacts of intracoelomic surgeries and implantation of acoustic telemetry tags from three separate populations of tagged lake trout monitored for up to 8.5 years after surgery. Using multiple independent analyses, we found no differences in survival or mortality between tagged and untagged lake trout. Further, the hypothesis that body condition or growth would decline over time in tagged fish was not supported. Thus, even after the time when these tags stop transmitting (3 months to 6 years), they do not appear to negatively impact the survival, growth, or body condition of fish. We did observe that a higher tag burden resulted in greater than expected weight loss over time for one population. This population of lake trout tended to be smaller than those in the other two lakes, possibly making them slightly more susceptible to effects of tag burden. Regardless, by using several metrics (most importantly survival), the net result of our study strongly suggests minimal long-term effects of intracoelomic tagging on these fish populations.

Our finding of negligible long-term effects of intracoelomic tagging is particularly important for long-term investigations that can last a decade or more and for studies implanting tags in long-lived fish species. While only a small proportion of fish from study populations are typically implanted with acoustic tags, the potential for long-term impacts could negatively influence public or fisheries management perceptions (Young et al. 2013). Additionally, negative impacts could confound findings from long-term monitoring programs in which data from telemetry-tagged fish are used to inform fisheries management decisions. For example, if telemetry tag implantation led to lower growth and condition of fish, these individuals might not be representative of the larger population under study (Pine et al. 2003). Because the present study was conducted at IISD-ELA, a remote site where acoustic telemetry of a variety of long-lived fish species, including lake trout, has been underway continuously since 2001, the finding of no long-term impact of tag implantation is particularly relevant because any changes in the mortality, growth, and body condition should only be due to regional change or experimental manipulations. Our finding of no long-term impacts of intracoelomic implants suggests that telemetry-tagged lake trout are indeed representative of the populations they are drawn from and that this procedure has not influenced the results of past studies (e.g., Guzzo et al. 2017; Rennie et al. 2019).

Similar survival, growth, and body condition of tagged and untagged lake trout of both sexes strongly supports the continued use of telemetry as a tool to monitor fish populations. Because growth and body condition are often considered to be measures of the general well-being of a fish, the absence of a decline in these measures following surgical implantation provides strong support that intracoelomic tagging does not have a negative long-term influence on the health of tagged fish. Given that annual growth of lake trout in our study lakes is known to be variable and influenced by climate-mediated access to food resources (Plumb et al. 2014; Guzzo et al. 2017), this is an important finding. Moreover, the small lakes used in our study are ideal systems in which to examine the long-term effects of lake trout telemetry tagging because these small-bodied (usually <1 kg) populations, typical for lakes without pelagic prey fishes, are susceptible to impacts from disturbance (Plumb et al. 2014; Guzzo et al. 2017). The fact that we did not observe any negative effects of telemetry tag implantation among lake trout populations considered most likely to show such an impact is encouraging for future studies.

The similarity of condition and growth between tag groups regardless of sex is important, given previous work suggesting that egg retention in female fish receiving surgically implanted tags could increase, potentially impairing reproduction. Berejikian et al. (2007) documented an increase in egg retention in female steelhead trout (*Oncorhynchus mykiss*) with surgically implanted internal tags (although not intracoelomic) compared with an untagged control group. Greater egg retention could inadvertently inflate the long-term condition and growth of females through reabsorption of the retained eggs, but potentially negatively impact reproductive output. While we did not examine egg retention specifically, we do provide evidence that internal tagging does not have any potential knock-on effects of increased egg retention on female condition and growth over the long term. Additionally, the finding of some mass loss with increased tag burden, but not body condition, of the smaller lake trout of Lake 373 may suggest that targeting larger individuals that are closer to the tag:fish mass of <1.25% (in water) would be more generally suitable for telemetry involving adult lake trout. We encourage researchers studying other species to assess the ideal tag:body mass ratios to ensure the well-being of their study animals and the validity of their results.

As far as we are aware, this is the first study to assess the impacts of surgically implanted intracoelomic acoustic tags by comparing tagged and untagged fish in the wild, over such an extensive time period (comparison of tagged fish to untagged fish over 12 years; maximum tracking of tagged fish of 8.5 years). Our findings are based on a relatively large sample size of tagged fish ($n = 135$) in comparison with other studies evaluating survival of fish: lake trout, $n = 30$ (Muhlfeld and Syslo 2017); lake sturgeon, $n = 46$ (McCabe et al. 2019); brown trout (*Salmo trutta*), $n = 188$ (Jepsen et al. 2008). Studying the effects of tagging on fish is difficult in the natural environment; as such, previous research on the topic has largely taken place in lab settings over shorter periods of time (Koeck et al. 2013; Darcy et al. 2019). By comparison, the current study took place over more than a decade, and tagged fish were released and studied in their natural environment alongside untagged fish, thus eliminating any potential confounding stressors due to captivity. Though there are drawbacks to studies of this nature taking place in the wild, namely the difficulty in confirming mortality or tag expulsion (of which there were only two potential cases of 135 tagged fish in this study) via direct observation, the use of mark–recapture and telemetry data to investigate mortalities are common and robust methods for fisheries research. Further, the designated research lakes at IISD-ELA are closed to fishing and are not exploited; therefore, mortality and survival estimates are representative of natural rates, and any research-related mortality can be accounted for (e.g., Kidd et al. 2007).

Any evaluation of long-term survivorship and health of fish that receive intracoelomic implants for acoustic telemetry will greatly depend on the methods applied, including capture, surgical procedures, tag selection, and fish selection. Though different surgeons (<5) have been involved in studies at IISD-ELA, handling and surgical methods have been established with clear standard operating procedures (as described by Blanchfield et al. 2005) and extensive training of new staff and surgeons. The lack of difference between tagged and untagged fish provides a good independent assessment that training and surgical methods at this facility are sufficient to ensure good fish health after surgery. However, our study only includes adult lake trout, and the extension of our results for application to other life stages (e.g., juveniles) or other species may be limited. Further research involving younger life stages or other species over the long term is still required.

Given the increasing prevalence of telemetry studies, it is important to have a clear understanding of the potential impacts of tagging not only during the study, but also after the tags have stopped transmitting, to ensure that their survival rates, behaviour, and demographics are indeed representative of the populations from which they are drawn. This is especially relevant because many of the fishes that are currently the focus of acoustic telemetry studies (Stokesbury et al. 2005; Hayden et al. 2014; Guzzo et al. 2017; Kessel et al. 2018) are long-lived (i.e., walleye (*Sander vitreus*), 20 years; lake sturgeon, 80 years; Scott and Crossman 1973; Greenland sharks (*Somniosus microcephalus*), 270+ years; Nielsen et al. 2016). Furthermore, the rapid expansion of large-scale telemetry tracking networks in marine and freshwater ecosystems involves the release of thousands of tagged fish into the wild every year (Krueger et al. 2017). Yet, the fate of these tagged fish can be difficult to assess in these vast waterbodies when individuals are out of range of receivers (e.g., Patterson and Blanchfield 2013). As such, it is important to understand whether the presence of tags negatively impacts fishes even after they stop transmitting. Our findings of no long-term negative impacts are also encouraging for species that have special conservation status (e.g., lake sturgeon) where there is perhaps greater concern for the long-term survival and health of tagged fishes. Finally, knowledge regarding the long-term survival rates of tagged fish from surgery and (or) tag burden are useful for the planning and implementation of future studies, appropriate long-term consideration of animal welfare, and understanding potential impacts on smaller populations (Brown et al. 2011).

Acknowledgements

We thank the many Experimental Lakes Area researchers whose efforts contributed to this study, especially Lori Tate and Doug Guss, as well as several anonymous reviewers for constructive comments that improved this paper. Funding for this study was made available through Fisheries and Oceans Canada, the NSERC Strategic Grants program (PJB), the IISD-ELA, and a Canada Research Chair to MDR.

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