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Validation of a new acoustic telemetry transmitter for the study of predation events in small fishes

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Abstract

Acoustic telemetry has emerged as an important tool for studying the movement and behavior of aquatic animals. Predation-sensing acoustic transmitters combine the functions of typical acoustic transmitters with the added ability to identify the predation of tagged animals. The objective of this paper was to assess the performance of a newly miniaturized acid-based predation-sensing acoustic transmitter (Innovasea V3D; 0.33 g in air). We conducted staged predation events in the laboratory where acoustically tagged rainbow trout (*Oncorhynchus mykiss*) were fed to largemouth bass (*Micropterus nigricans*) at 3.3–7.0, 9.0–10.8, 16.0–20.0, and 22.0–25.8°C. We also conducted false-positive tests where tagged rainbow trout were held at 10.0 and 16.8°C without the risk of predation. Predation events were successfully identified in 92% of the staged predation trials. Signal lag (i.e., the time required for a predation tag to indicate that predation occurred) ranged from 0.11 to 6.29 days and decreased strongly with increasing water temperature and increased with increasing body mass of the tagged prey. Tag retention in the gut of the predator was much more variable than signal lag and was influenced by water temperature and individual predators but not by prey mass. No false positives were detected after 60 days at either temperature ($n = 27$ individuals). Although the relationships between water temperature, signal lag, and retention time are likely species-specific, the data reported here provide useful information for the use of these transmitters to study predation in wild fishes, especially for temperate, freshwater fish.

KEYWORDS
acoustic telemetry, freshwater, predation, signal lag, tag retention

1 | INTRODUCTION

Acoustic telemetry is widely used to study fish movement and behavior across ecologically meaningful spatial and temporal scales (Cooke et al., 2013; Hussey et al., 2015; Thorstad et al., 2013). Ongoing technological advancements, including increases in battery power and the miniaturization of acoustic tags, are broadening the scope of telemetry studies to smaller fish species and earlier life stages (e.g., Klinard et al., 2018; Matley et al., 2022; Szekeres et al., 2023). However, challenges still exist when interpreting telemetry data derived from smaller fishes. One key assumption is that telemetry data represent the movements, behaviors, and locations of the study animal originally tagged. When acoustically tagged fish are consumed by predators, their tags can continue to transmit while in the gastrointestinal tract of the predator, introducing a potential "predation bias" into telemetry data (Gibson et al., 2015). Small fishes can be consumed by predators at high rates (e.g., Daniels et al., 2019; Klinard et al., 2020; Rieman et al., 1991; Vogel, 2010; Weinz et al., 2020), making telemetry studies using small fishes particularly vulnerable to predation biases.

Several attempts have been made to identify predation events in telemetry studies. Predator and prey telemetry data have been compared to identify unusual prey behaviors indicative of probable predation events (e.g., Gibson et al., 2015; Romine et al., 2014) and on occasion such observations can be visually confirmed (e.g., Cooke & Philipp, 2004). However, identifying predation events via shifts in behavior relies on predators and prey exhibiting consistently distinct movement patterns, as well as statistical techniques that can be difficult to validate (Schultz et al., 2017). Temperature (Béguer-Pon et al., 2012) or depth (Thorstad et al., 2011; Thorstad et al., 2012) data from sensor tags have also been used to infer predation events. However, identifying predation events using data from sensor tags assumes different internal temperatures and/or depth usage between prey and predators.

To passively detect the predation of wild fishes, "tilt-based" and "acid-based" predation-sensing acoustic transmitters (hereafter "predation tags") have been developed. Tilt-based predation tags infer predation events by changes in an animal's orientation, whereas acid-based predation tags have a biopolymer coating that dissolves in the stomach acid of a predator, releasing a magnet that triggers a change in the identification number emitted by the tag to a new "post-predation" ID. The performance of a miniaturized acid-based predation tag (V5D) operating at 180 kHz was demonstrated in both laboratory (Halfyard et al., 2017) and field-based studies (Daniels et al., 2019; Hanssen et al., 2022; Lennox et al., 2021; Weinz et al., 2020). However as the minimum size of fish that can be tagged is influenced by the dimensions and weight of the transmitter (Jepsen et al., 2004), both the V5D predation tag (0.64 g in air; 4.3 × 5.7 mm diameter × 12.7 mm length) and the smallest available tilt-based predation tag (Thelma Biotel LP6; 1.2 g in air; 6.3 mm diameter × 14.5 mm length) are of sizes that preclude use in smaller species and life stages of prey fishes. Recently, Innovasea developed a smaller (0.33 g in air; 4.0 mm diameter × 15.5 mm length; 307-kHz V3D) iteration of the acid-based predation tag. These new, smaller tags offer the potential to provide precise behavioral data from many smaller species and life stages of prey fishes. They also identify when and where each fish has been eaten by a predator.

Prior to the field deployment of the new V3D predation tag, its performance and limitations need to be quantified. For example, there is a lag period between the time the tagged fish is consumed by a predator and the time the biopolymer is digested (hereafter "signal lag"). There is also a tag retention period, defined as the time between the consumption of tagged prey by a predator and the tag's excretion from the predator after traveling through the gastrointestinal tract. Research using larger predation tags provided evidence that signal lag and tag retention decrease with higher water temperatures (Halfyard et al., 2017), but the relationship between predation tag performance and water temperatures below 12°C is unknown. A trade-off between signal lag and false-positive rates (i.e., the rate at which tags switch to a post-predation ID without predation occurring) also occurred in earlier iterations; biopolymer properties that led to shorter signal lag also led to a higher rates of false positives (Halfyard et al., 2017).

The objective of this study was to assess the performance of Innovasea's V3D predation tags. We aimed to (i) evaluate if these predation tags accurately detect the occurrence of predation events, (ii) quantify predation tag signal lag and tag retention periods and examine the factors that influence them, and (iii) assess the false-positive rate for the predation tags as functions of water temperature. Water temperature is a strong driver of digestion intensity and gastric evacuation rates in fishes (e.g., Bromley, 1994; Volkoff & Rønnestad, 2020); therefore we predicted that signal lag and tag retention would decrease with warmer temperatures. As there is also evidence that meal size is linked to rates of digestion (e.g., Bromley, 1994; Legler et al., 2010), and because smaller prey would reduce the digestion needed to expose the biopolymer to a predator's stomach, we predicted that signal lag and tag retention would be higher in larger prey.

To achieve the first two objectives, we staged predation events in the laboratory using largemouth bass *Micropterus nigricans* (Cuvier 1828) as the model predator and juvenile rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) as the model prey species. To address the third objective, juvenile rainbow trout implanted with transmitters were held in the absence of predation at different water temperatures and assessed for false positives.

2 | METHODS

This research was conducted at Trent University (Ontario, Canada) between October 2022 and November 2023. All animal husbandry and experimental procedures were approved by the Trent University Animal Care Committee following guidance set by the Canadian Council on Animal Care (Trent University animal use protocol #28204).

2.1 | Fish collection and husbandry

Experimental trials were conducted across four ranges of water temperatures (3.3–7.0°C and 9.0–10.8°C [hereafter, "cold trials"], 16.0–20.0°C and 22.0–25.8°C [hereafter, "warm trials"]), with different groups of largemouth bass used in the cold and warm trials (Table 1). For use in the two cold-water predation trials, largemouth bass were collected from Rice Lake (Ontario, Canada) on October 26, 2022, using short-set trap nets and electrofishing. For use in the two warm-water predation trials, largemouth bass were also collected from Rice Lake via angling between June 20 and 23, 2023. All rainbow trout were obtained from a local hatchery and fed a maintenance ration of ~1% body weight daily.

All largemouth bass were acclimatized to the laboratory for a period of at least 1 month prior to the beginning of predation trials.

TABLE 1 Number of individuals, total length (in millimeters), and body mass (in grams) of largemouth bass (*Micropterus nigricans*) and rainbow trout (*Oncorhynchus mykiss*) used in different trial types and water temperatures.

Trial type	Water temperature (°C), mean ± SD (range)	Species	Total length (mm), mean ± SD (range)	Body mass (g), mean ± SD (range)	Number of individuals
Predation	4.6 ± 0.7 (3.3–7.0)	LMB[a]	413 ± 32 (391–460)	1050 ± 296 (628–1544)	5
		RT	151 ± 6 (146–166)	34 ± 4 (30–43)	15
	9.8 ± 0.2 (9.0–10.8)	LMB[a]	413 ± 32 (391–460)	1050 ± 296 (628–1544)	5
		RT	148 ± 12 (132–168)	35 ± 7 (25–46)	15
	18.0 ± 0.4 (16.0–20.0)	LMB[b]	392 ± 27 (365–430)	1070 ± 191 (826–1358)	5
		RT	140 ± 14 (121–173)	31 ± 9.0 (18–55)	15
	24.7 ± 0.4 (22.0–25.8)	LMB[b]	392 ± 27 (365–430)	1070 ± 191 (826–1358)	5
		RT	135 ± 10 (122–159)	28 ± 5 (21–41)	22
False positives	10.0 ± 0.2 (7.3–10.5)	RT	151 ± 7 (139–171)	37 ± 6 (30–47)	15
	16.8 ± 1.1 (13.6–18.6)	RT	134 ± 10 (123–162)	28 ± 7 (22–45)	15

Note: Superscript letters indicate the use of the same individual fish.
Abbreviations: LMB, largemouth bass; RT, rainbow trout.

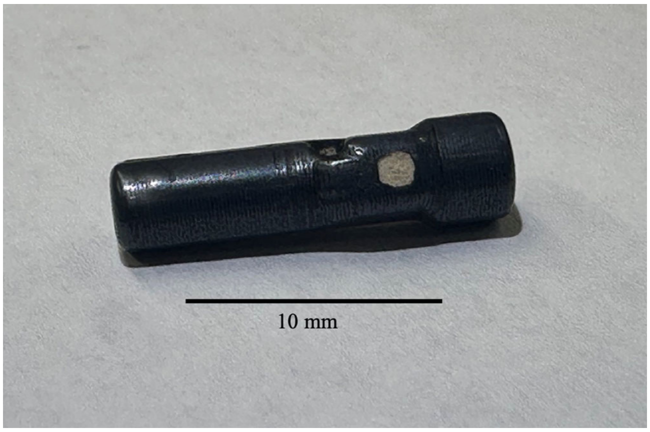

FIGURE 1 V3D predation tag with an intact biopolymer coating (white). This predation tag weighs 0.33 g in air, has a 141-dB acoustic power output at 307 kHz, and has dimensions of 4.0 mm diameter × 15.5 mm length.

During this period, they were trained to eat live hatchery-origin rainbow trout, although success was limited with fish held at the colder water temperatures. Throughout the acclimation and experimental periods, they were kept in large 395–724-L circular tanks (diameter = 1.2 m, water depth = 0.35–0.64 m), with recirculating filtration systems under lighting conditions that followed natural light regimes. The tanks were continuously flushed with fresh water from the adjacent Otonabee River. After experiments were complete, all fish were euthanized by immersion in a lethal dose of 500 mg L^{-1} buffered tricaine methanesulfonate (MS-222, Syndel, Nanaimo, B.C., Canada, https://syndel.com).

2.2 | Acoustic tag surgery

Surgical methods followed standard approaches in the field of fish telemetry (e.g., Wagner et al., 2011). The predation tags we used were Innovasea V3D-1x 307-kHz transmitters with a high residence transmission system (141 dB acoustic power output; 0.33 g weight in air; random delay of 10–14 s; estimated battery life 173 days; 4.0 mm diameter × 15.5 mm length; Figure 1). Prior to surgery, tags were tested to verify that the correct pre-predation ID codes were being transmitted and were sterilized via immersion in an iodine solution (as were all surgical instruments) before being rinsed with distilled water. For use in the false-positive and warm-water predation trials, rainbow trout were anaesthetized using an aerated knockout dose of 80 mg L^{-1} buffered MS-222; their gills were irrigated with a maintenance dose of 40 mg L^{-1} buffered MS-222 during surgery. Once a fish reached stage 5 anaesthesia (total loss of equilibrium, slow opercular rate, and no response to stimuli), body mass and total length were recorded (~15 s of air exposure). Once supine in the wetted surgical sling (Figure S1), a ~10-mm ventral incision was made ~10 mm anterior to the pelvic girdle and ~2 mm off the central midline. An acoustic transmitter was then inserted intraperitoneally, and the incision was closed with a single 5–0 monofilament absorbable suture (Ethicon PDS II Plus polydioxanone, Ethicon US, www.ethicon.com) using a 3-2-2 knot. Rainbow trout were permitted to recover from surgery in a small aerated water-bath, regaining equilibrium and normal ventilation patterns in 2–5 min (more quickly at higher temperatures). In the cold-water predation trials, fish were euthanized by immersion in a lethal dose of 500 mg L^{-1} buffered MS-222 immediately prior to surgery (because they were being force-fed to predators immediately post-surgery, see details below) and thus were not given a recovery period; their surgical procedures were otherwise the same as those described above.

2.3 | Predation trials

Largemouth bass were fed a total of 67 acoustically tagged rainbow trout across four water temperature treatments (Table 1). As largemouth bass were reluctant to actively feed on live rainbow trout in cold trials, we used force-feeding here (gavage). To do so, largemouth bass were anaesthetized in an aerated water-bath containing a 100 mg L^{-1} buffered solution of MS-222. A fish's mouth was held open and an euthanized acoustically tagged rainbow trout was gently pushed through the esophagus into the gut using rubber-tipped forceps. Force-feeding was also repeated five times in warm trials (one event of force-feeding for each predator) to compare with "natural" feeding events at those temperatures. Throughout the experimental period, bass used in warm trials were fed either acoustically tagged or untagged rainbow trout every 3 days. Bass used in cold trials were only force-fed acoustically tagged rainbow trout with a minimum of one week between trials. Cold trials occurred between December 1, 2022, and March 17, 2023, and warm trials occurred between July 24 and September 20, 2023.

Largemouth bass were kept separate in individual tanks, and an Innovasea 307-kHz HR3 acoustic receiver was placed at the center of each tank to log transmissions from the tags in the fish they were fed. Signal lag was calculated as the time between the predator ingesting the prey fish and the tag's first transmission of a post-predation ID. Tanks were inspected daily for egested tags; tag retention time was calculated to the nearest day as the time between the predator ingesting the prey fish and the observed time when the tag was evacuated from the predator.

2.4 | False-positive trials

To quantify the rate at which V3D predation tags changed to a post-predation ID without predation occurring, acoustically tagged rainbow trout were held for 60 days at two water temperatures. Rainbow trout ($n = 15$) were held at 10.0 ± 0.2°C (SD) between December 1, 2022, and February 2, 2023; additional rainbow trout ($n = 15$) were held at 16.8 ± 1.1°C between September 7 and November 8, 2023 (Table 1). Rainbow trout were fed ad libitum daily with 2-mm-size pellets (EWOS, Surrey, B.C., Canada, https://www.ewos.com/ca).

2.5 | Statistical analysis

All statistical analyses were conducted in R for Mac OS X (R Core Team, 2023, version 4.3.2). To investigate the drivers of signal lag, generalized linear mixed models (GLMMs) with varying fixed terms were fit by maximum likelihood and modeled with a gamma distribution and log link function. The fully parameterized model is expressed as:

$$\mathrm{Log}\,(S_t) = \beta_0 + \beta_1 T_t + \beta_2 P_t + r_t,$$

where signal lag S at time period t is a function of the fixed effects of water temperature (T; factor with four levels: 3.3–7.0, 9.0–10.8, 16.0–20.0, and 22.0–25.8°C) and prey mass (P; continuous variable) and the random effect of each individual predator ID (r; factor) (Table 2). Signal lag data were modeled using the "glmer" function in the package "lme4" (Bates et al., 2015). The proportion of variance explained by fixed and random effects (i.e., marginal and conditional R^2) was calculated using trigamma functions following the methods of Nakagawa et al. (2017). Models were assessed for best fit by sample-size adjusted AIC. Model assumptions were checked with visual inspections of a Q–Q plot and residuals against fitted values. Following model selection, pair-wise post hoc differences in signal lag between water temperatures were examined using the "emmeans" package, which computes and compares estimated marginal means of the best-fit model (Lenth, 2023). Prediction intervals for the best-fit model were produced using the "ggpredict" function from the package "ggeffects" (Lüdecke, 2018).

To investigate the drivers of tag retention, a mixed-effect Cox model was fit to tag retention times. This model is expressed as a hazard function $\lambda(t)$:

$$\lambda(t) = \lambda_0(t)\exp[\beta_1 T_t + \beta_2 P_t + r_t],$$

where λ_0 is the unspecified baseline hazard function; t is time; water temperature (T; factor with four levels: 3.3–7.0, 9.0–10.8, 16.0–20.0, and 22.0–25.8°C) and prey mass (P; continuous variable) are fixed effects; and individual predator ID (r; factor) is a random effect. As a test of the random effect of predator ID, the integrated log likelihood of the mixed-effect Cox model was compared to that of a Cox proportional hazard model with only the fixed effects of water temperature and prey mass using a χ^2 test. Cox models were used to right-censor tags that were retained in predators beyond 30 days (because tank temperatures were modified beyond this point) or if water temperatures varied beyond the accepted range within a 30-day trial period. The mixed-effect Cox model was fit using the "coxme" function in the package "coxme" (Therneau, 2022), and the Cox proportional hazard model was fit using the "coxph" function in the package "survival" (Therneau, 2023). Type-II ANOVA tables for model objects in the mixed-effect Cox model were calculated using the "Anova" function in the package "car" (Fox & Weisberg, 2019). Differences in retention times between water temperatures were also examined using the "emmeans" package. The probability of tag retention as a function of water temperature was visualized as a Kaplan–Meier survival curve using the "survfit" function in the package "survival." Coefficients of the mixed-effect Cox model were visualized with forest plots created using "ggplot2" (Wickham, 2016).

It has been proposed that the effectiveness of predation tags could conceivably be influenced by the force-feeding process (Lennox et al., 2021). Therefore, type-III ANOVA tables were calculated using the "Anova" function in the package "car" to test for differences in signal lag and tag retention times between tagged prey fish that had been force-fed and fish that had not. As all cold-water trials used force-feeding, these models were only fit to the warm-water predation trial data. In all statistical analyses, Holm-Bonferroni corrections

TABLE 2 Generalized linear mixed models evaluated based on Akaike's second order information criterion (AICc) for the signal lag of V3D predation tags.

Model	*K*	AICc	ΔAICc	W	Cum.*Wt*	LL	R^2
i. Lag ~1 + (1 | predator ID)	3	93.21	56.62	0.00	1.00	−43.39	0.42
ii. Lag ~ temperature + prey mass + (1 | predator ID)	7	36.59	0.00	0.73	0.73	−10.24	0.80
iii. Lag ~ temperature + (1 | Predator ID)	6	38.59	1.99	0.27	1.00	−12.52	0.78
iv. Lag ~ prey mass + (1 | predator ID)	4	90.02	53.42	0.00	1.00	−40.65	0.43

Note: The bolded model was best fit overall and selected for further analysis. Factors included in analysis: lag = signal lag (days); temperature = water temperature (°C); prey mass = prey body mass (g); predator ID = individual predator ID.
Abbreviations: *K*, number of parameters; LL, log likelihood; R^2, trigamma conditional R^2; *W*, AIC weight; ΔAICc, mean difference between a model's AICc and that of the best fit model.

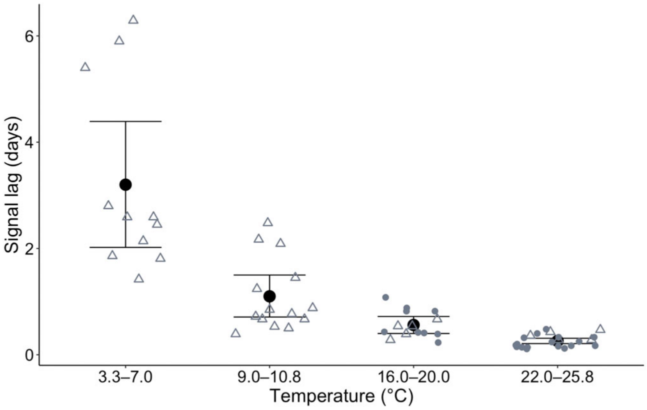

FIGURE 2 Signal lag time data of V3D predation tags at different water temperatures. Predation tags were surgically implanted in juvenile rainbow trout (*Oncorhynchus mykiss*), which were fed to largemouth bass (*Micropterus nigricans*). Small symbols represent individual signal lags. Large overlaid circles represent means of each treatment group, with 95% CI error bars. Triangular symbols represent trials where force-feeding was used; circular symbols represent trials where natural feeding was used. Significant differences in signal lag exist between all water temperatures ($p < 0.05$).

were applied to calculate *p*-values adjusted for multiple comparisons where needed.

3 | RESULTS

3.1 | Predation trials

A total of 66 predation trials were completed, with an additional trial being unsuccessful due to a prey fish being regurgitated by a predator. Overall, predation events were successfully identified in 92% (61/66) of trials. Signal lag time was inversely related to water temperature, increasing by a factor of 12.3 from the warmest trials to the coldest trials and by a factor of 2.2 between the two cold trials (Figure 2). Signal lag was best predicted by a combination of water temperature, prey mass, and predator ID (Model ii; Table 2). There was a positive effect of prey mass on signal lag ($p = 0.033$), and water temperature had a strong negative effect on signal lag as expected ($p < 0.001$, Table 3). Post hoc analyses revealed significant differences in signal lag ($p < 0.05$) in all pair-wise comparisons of our water temperature groups (Table S1). Trigamma conditional R^2 of the fully parameterized GLMM was 0.80, of which the random term of predator ID accounted for only 0.02 (Model ii; Table 2). Force-feeding did not significantly influence signal lag ($F_1 = 0.006$; $p = 0.939$) (Figure S2).

Tag retention times were also inversely related to water temperature, being shortest at 22.0–25.8°C (7 ± 5 days; mean ± 95% CI) and increasing to 13 ± 6 days at 16.0–20.0°C, 19 ± 13 days at 9.0–10.8°C, and 22 ± 11 days at 3.3–7.0°C. Tag retention was much more variable than was signal lag, with less clear differentiation among temperatures (Figure 3). The random effect of predator ID significantly improved model fits ($X^2 = 5.20$, $df = 1$, $p = 0.023$), highlighting differences in tag retention among the individual predators we used. Water temperature was also significant in the Cox mixed-effects model ($X^2 = 10.36$ $df = 3$, $p = 0.016$), but prey mass was not ($X^2 = 0.00$, $df = 1$, $p = 0.984$; coefficient estimates in Figure S3). Post hoc analyses only revealed statistical differences in tag retention periods between 16.0–20.0°C and 22.0–25.8°C trials ($p = 0.033$, Table S2). Force-feeding did not significantly influence tag retention periods ($F_1 = 0.71$; $p = 0.405$, Figure S4).

3.2 | False-positive trials

Of the 30 tagged fish used for false-positive trials, 3 fish held at 16.8°C failed to complete the 60-day trials: (i) a single rainbow trout died on September 9, 2023, and (ii) tag expulsions from two other rainbow trout occurred on September 25 and October 1, 2023. After 60 days, no tags in the remaining 27 fish had falsely triggered to indicate a predation event. Rainbow trout in the 10.0°C false-positive trial had grown an average of 26.4 ± 12.1 mm (SD) and 24.1 ± 13.0 g, representing a 17% length gain and a 66% mass gain (0.8% bw d^{-1}). Rainbow trout in the 16.8°C false-positive trial had grown an average of 49.8 ± 11.8 mm and 47.8 ± 18.5 g, representing a 37% length gain and a 170% mass gain (1.7% bw d^{-1}).

TABLE 3 Fixed effect terms of the best-fit model for signal lag (Model ii; Table 2).

Fixed effects	*E*	SE	*df*	*t*	*p*
3.3–7.0°C (baseline)	0.512	0.350	54	1.461	0.144
9.0–10.8°C	−1.147	0.180	54	−6.354	<0.001
16.0–20.0°C	−1.732	0.223	54	−7.765	<0.001
22.0–25.8°C	−2.419	0.217	54	−11.161	<0.001
Prey mass (g)	0.020	0.009	54	2.131	0.033

Note: Temperature effects are relative to baseline temperature category.
Abbreviations: *E*, estimated coefficients; *p*, *p*-value; *t*, *t* value.

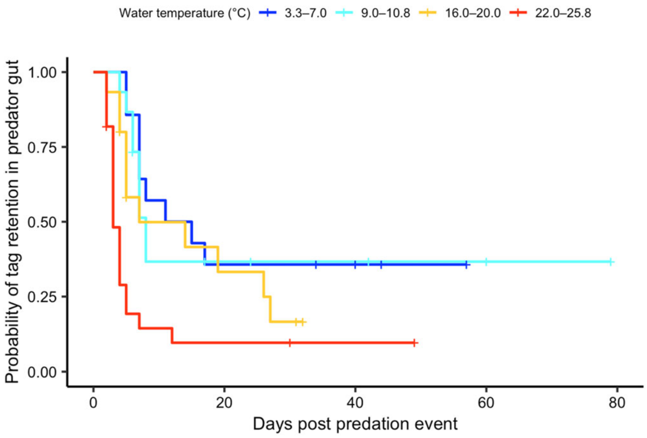

FIGURE 3 Kaplan–Meier survival curve of tag retention data from V3D predation tags. Predation tags were surgically implanted in juvenile rainbow trout (*Oncorhynchus mykiss*), which were fed to largemouth bass (*Micropterus nigricans*). There were statistical differences in tag retention periods between 16.0–20.0 and 22.0–25.8°C ($p < 0.05$).

4 | DISCUSSION

In this study, we assessed the performance of Innovasea's V3D predation tags, which are currently the smallest commercially available predation-sensing acoustic transmitters. The tags correctly identified the vast majority (92%) of predation events and appear unlikely to falsely identify predation events over short time scales (60 days, i.e., ~one-third of the maximum battery life of the tag). The signal lag time of V3D predation tags was strongly influenced by water temperature, being both longer and more variable at colder temperatures. Tag retention times were prolonged at colder temperatures but were much more variable within each temperature and among individual predators when compared against the signal lag response.

4.1 | Predation trials

The success of V3D predation tags in correctly identifying predation events is promising for field studies. Failure to identify predation events resulted from (i) tags being egested with their biopolymer coatings still intact ($n = 3$) or (ii) technical issues relating to tag deactivation during trials ($n = 2$). In the first scenario, all three failures occurred at either 3.3–7.0°C ($n = 2$) or 9.0–10.8°C ($n = 1$). As the success of acid-based predation tags relies on the gastric digestion of their biopolymer coatings, factors influencing the physiology of digestion are thus likely to influence their success in identifying predation events. Given that temperature is a strong driver of digestion speed in fishes (Bromley, 1994), it is likely that tags were egested with their biopolymer coatings intact at these colder temperatures due to reduced gastric activity. Although these relatively low failure rates are sufficient for most studies, additional exploration of the effects of temperature on predation tag performance would help further our understanding of this relationship. For example, a previous study using a cold-adapted model predator (brown trout *Salmo trutta*) found that V5D predation tags only identified 50% of predation events at a mean temperature of 11.8°C (Lennox et al., 2021). However, a study using the same predator and prey as we used here found that the same V5D predation tag successfully identified 94–95% of predation events at temperatures ranging from 12 to 22°C (Halfyard et al., 2017). Although these differences may be due, in part, to inconsistencies in study methodology or tag manufacturing, they highlight the importance of study replication at low temperatures, especially using species with different thermal performance curves for digestion than the warm-water predator we used here (e.g., salmonids that spend much of their lives at temperatures below 10°C; Brannon et al., 2004; Mulder et al., 2018). Lower rates of success can lead to uncertainties in interpreting field-derived predation data (e.g., Lennox et al., 2021). Therefore, we recommend that researchers validate the performance of V3D predation tags using their species of interest and relevant environmental conditions prior to field applications.

The importance of water temperature as a determinant of signal lag time is also reflective of its impacts on fish digestion. Our data on V3D signal lags closely reflected the relationship between largemouth bass gastric digestion intensity and temperature (Molnár & Tölg, 1962). Although evidence of inverse relationships between signal lag and water temperature was also found in other predation-sensing tags (Halfyard et al., 2017), the performance of predation tags at colder temperatures (<12°C) had not been previously assessed. Our results highlight that although the signal lags of V3D predation tags are suitable for most research applications greater than ~9°C, the large increase in both duration and variability in signal lag at colder temperatures, as well as the increased likelihood of failure described earlier, creates uncertainty for their use at the coldest temperatures. Performance of predation tags in cold water may be particularly relevant for some studies of juvenile salmonids given that their migrations can occur at water temperatures as low as ~4–5°C (Hartman et al., 1967; Whalen et al., 1999).

Prey body mass had a weak, positive effect on signal lag time. Although the effects of prey size on rates of digestion vary (Bromley, 1994), it is logical that smaller prey items would require less digestion to expose the transmitter to stomach acid, thus reducing signal lag. The relatively small effect size of prey mass compared to temperature in the GLMMs suggests that prey mass only had a minor influence on signal lag compared to temperature. Although we did use a wide range of prey body masses relevant to the type and size of tag we used (18.1–54.9 g; SD = 7.0 g), if researchers intend to deploy these tags into a wider range of prey sizes, they might need to consider further calibrations of the effect of prey body mass on signal lag.

Although we only found statistical differences in tag retention times between 16.0–20.0°C and 22.0–25.8°C, several tags were retained beyond the study period in cold trials. Therefore, the true tag retention times could not be determined for some of the cold temperature replicates and they were censored in the Cox models, thus reducing statistical power. Regardless, water temperature was important as an overall determinant of tag retention time, and there was an overall increase in retention time with decreasing water temperature, consistent with previous work (Halfyard et al., 2017; Schultz et al., 2015). However, retention times of the V3D predation tags we used here were several times longer and more variable than the larger V5D predation tag, which was assessed using staged predation trials with predators of the same species and size and similar prey body sizes, variables all thought to influence tag retention time (Gibson et al., 2015; Halfyard et al., 2017). Retention periods can be affected by a tag's size and shape (Klinard et al., 2019; Lennox et al., 2021), and so the long and variable retention times of V3D tags may be due to their small size helping them become lodged in the gastrointestinal tract of predators. Counter-intuitively, prolonged retention periods may decrease false negatives by providing more time in the gut, ensuring the biopolymer has a chance to be dissolved (which would be particularly relevant at lower temperatures).

Gastrically implanted tags may alter food passage and foraging patterns as has been documented for smaller salmon smolts in which tags likely occupied a large volume of the gastrointestinal tract (e.g., Armstrong & Rawlings, 1993; Hall et al., 2009). In the case of the largemouth bass we used as predators, the V3D tags were very small (1:2093–1:5147 ratio of tag:body mass). The predators we housed continued to eat and pass food regularly while V3D tags remained in their gastrointestinal tracts. In some cases, the order of tags being egested was different from the order in which the tags entered the predator, indicating that the tags did not create blockages. Although tags were retained longer by certain individuals (as reflected by the significance of individual predator ID when modeling tag retention), the reasons for this are unknown and may relate to variation in individual gastrointestinal tract morphology. Future studies could explore the drivers of V3D tag retention times (potentially using inexpensive "dummy" tags with individual IDs) and the potential detrimental effects of long-term tag retention on fish health.

The absence of false positives in our study suggests that V3D tags are likely to only indicate predation events when consumed by a predator. Although studies using predation tags in the field will likely exceed the duration of our false-positive trials, previous work examining false positives in a larger predation tag over a 120-day period found that false positives occurred on average at 47.0 ± 11.2 days post-tagging (mean ± SD) (Halfyard et al., 2017). Given that the predation tags dissected out of rainbow trout after our false-positive trials showed no visible evidence of biopolymer degradation, we believe that the 60-day study period was sufficient. With the most conservative tag programing settings, 60 days represent about one-third of the expected life span of these transmitters. Because chemical reactions are accelerated by higher temperatures (Stockbridge et al., 2010), it remains possible that false positives could occur at higher water temperatures and over longer time spans. The rate of V3D tag expulsion from prey fish was also relatively low compared to that of other salmonids and the broader literature (Lawrence et al., 2023), with expulsed tags not falsely triggering to indicate predation events. As tag expulsion rates from prey fish are thought to be correlated with the ratio of tag:body mass (Lawrence et al., 2023), our data suggest the small size of V3D predation tags makes them valuable for successful tagging of small prey fishes.

High tag burden (i.e., the ratio of tag:body mass) can impact the swimming performance, buoyancy, growth, or survival of tagged fish (Lacroix et al., 2004; Perry et al., 2001). Acceptable levels of tag burden vary by study objectives, tagging method, and study species (Jepsen et al., 2002, 2004). However in general, lower tag burdens reduce the likelihood that tagged individuals are affected by the presence of the transmitter and are thus more suitable than higher burdens (Brown et al., 2010). The reduced dimensions and weight of the V3D predation offer the possibility to study predation events in fish species and earlier life stages that may not have been possible before.

In summary, this study describes the performance of Innovasea's V3D predation tags. These predation tags successfully detected the majority of predation events and did not falsely identify predation events over several months. Being able to assess the spatial and temporal patterns in the predation of small fishes will provide key insights into the spatial ecology of fishes, helping refine fisheries management models and estimate the impacts of predators on target fish populations. Given that studies using predation tags will occur at a wide range of water temperatures, we recommend that researchers validate the performance of V3D predation tags using their specific species and environmental conditions prior to field applications.

AUTHOR CONTRIBUTIONS

Mitchell B. Shorgan: data generation, data analysis, and manuscript preparation. Heather Bauer Reid: data generation, manuscript revision, and editing. Silviya V. Ivanova: data generation, data analysis, manuscript revision, and editing. Aaron T. Fisk: study conceptualization, resources, manuscript revision, and editing. Steven J. Cooke: study conceptualization, resources, manuscript revision, and editing. Graham D. Raby: study conceptualization, resources, data generation, manuscript revision, and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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