Advancing the methodology used in fish telemetry tracking

A Thesis Submitted to the Committee on Graduate Studies in Partial Fulfillment of the Requirements for the Degree of Master of Science in the Faculty of Arts and Sciences

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ABSTRACT:

Advancing the methodology used in fish telemetry tracking. Mitchell Shorgan.

This thesis aimed to address potential sources of bias in electronic fish tagging studies in order to advance the methods used by future studies. I first provided a review and meta-analysis of intracoelomic tagging effects in fishes, summarizing the existing literature and assessing the extent to which previously identified research gaps have been filled. I also included the first large-scale meta-analysis on tagging effects, examining the 2% rule using empirical evidence from a broad representation of all published studies. I then assessed the performance of a newly miniaturized predation-sensing acoustic transmitter (Innovasea V3D), demonstrating that V3D transmitters can mitigate predation biases by correctly identifying most predation events without false positives. I finally examined if immobilization via MS-222 or TENS alters the behaviours of fishes in the wild following tagging, and identified the time required for fish to re-establish normal behaviour following transmitter implantation.

Keywords: Electronic tagging, acoustic telemetry, biotelemetry, fish ecology, tagging effects, sedation, electro-immobilization, MS-222, TENS, predation, signal lag, tag retention, meta-analysis, systematic review.

Preface

All research presented in this thesis was conducted in accordance with animal care protocols approved by the animal care committees of Trent University in accordance with guidelines set by the Canadian Council on Animal Care.

This thesis is written in a manuscript-based format. Acknowledgements from each chapter are provided at the start of the thesis, and references are combined at the end of the thesis. The three data chapters are ordered in a logical progression, and while an effort was made to reduce repetition within in each chapter, some redundancy does still occur. As I conducted this research with the support and guidance of several co-authors, the contribution of authors on each paper are compiled below.

Chapter 2: Shorgan, M.B., Raby, G.D., Fedus, A.L., Howell, B.E., Haniford, L.S.E., Howitt, L.C., Klinard, N.V., Matley, J.K., Brownscombe, J.W., Cooke, S.J., Fisk, A.T. (2025). Effects of surgical implantation of electronic tags in fishes: a review and meta-analysis. Submitted to Reviews in Fish Biology and Fisheries on January 17, 2025. Preprint: https://doi.org/10.21203/rs.3.rs-5851388/v1

Mitchell B. Shorgan: data generation, data analysis, manuscript preparation, manuscript revision and editing. Graham D. Raby: study conceptualization, manuscript preparation, manuscript revision. Amber L. Fedus: data generation, manuscript preparation, manuscript revision. Bradley E. Howell: data generation, data analysis, manuscript preparation, manuscript revision, and editing. Laura S.E. Haniford: data generation, manuscript preparation and manuscript revision.

Leah C. Howitt: data generation, manuscript preparation and manuscript revision. Natalie V. Klinard: study conceptualization, manuscript revision. Jordan K. Matley: study conceptualization, manuscript revision. Jacob W. Brownscombe: data analysis, manuscript revision. Steven J. Cooke: study conceptualization, manuscript revision. Aaron T. Fisk: manuscript revision.

Chapter 3: Shorgan, M.B., Reid, H.B., Ivanova, S.V., Fisk, A.T., Cooke, S.J., Raby, G.D. (2024). Validation of a new acoustic telemetry transmitter for the study of predation events in small fishes. *Journal of Fish Biology*, 104 (6). https://doi.org/10.1111/jfb.15827

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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Chapter 4: Shorgan, M.B., Howell, B.E., Larochelle, L., Cooke, S.J., Fisk, A.T., Raby, G.D., (2025). Behavioural impacts of MS-222 and electro-immobilization on wild fish assessed using a whole lake telemetry system.

Mitchell B. Shorgan: data generation, data analysis, and manuscript preparation. Bradley E. Howell: data generation, manuscript revision, and editing. Luc Larochelle: data generation, manuscript revision, and editing. Steven J. Cooke: study conceptualization, resources, manuscript revision, and editing. Aaron T. Fisk: study conceptualization, resources, manuscript revision, and editing. Christopher S. Vandergoot: study conceptualization, resources. Graham D. Raby: study conceptualization, resources, data generation, manuscript revision, and editing.

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Table of Contents

2.8 Endpoints

Chapter 3: Validation of a new acoustic telemetry transmitter for the study of predation events in small fishes………………………………………………………………………………

List of tables

List of figures

List of appendices

Chapter 1: General introduction

In recent decades, there has been a push for more holistic ecosystem approaches to fisheries management (EAFM) (Marshall et al. 2019; Skern-Mauritzen et al. 2016). Traditionally, fisheries have been managed by maximizing yields of individual fish stocks of commercial interest in isolation (Reeves et al. 2008). EAFM extend traditional management by recognizing the biological and physical complexities of aquatic resources, accounting for by-catch, habitat changes and ecosystem interactions (Foley et al. 2010; Morishita 2008). Underlying EAFM is data on life-stage specific habitat requirements and home ranges, interactions with different fish species (e.g., predator–prey dynamics), migratory timing and pathways, natural mortality, as well as by-catch and release mortality (Heenan et al. 2015; Lowerre-Barbieri et al. 2019; Ward et al. 2016). While typical methods of sampling fish distributions and abundance (e.g., catch records, trawling, seine netting, electrofishing) still play important roles in understanding these variables (Bonar and Hubert 2002), they often fail to capture temporal complexity, only providing a "snapshot" of the complex lives of fishes (Brownscombe et al. 2022).

Compared to conventional sampling techniques, acoustic telemetry offers the ability to continuously and passively track fishes of interest in their natural environment. Broadly, acoustic telemetry involves attaching electronic transmitters ("tags") to fishes, which record and transmit information via ultrasonic pulses that are detected and logged by hydrophones and receivers (Hussey et al. 2015; Thorstad et al. 2013). Acoustic telemetry has surged in popularity over the past two decades (Hussey et al. 2015; Matley et al. 2022). The advent of large collaborative research networks like the Ocean Tracking Network (Iverson et al. 2018) and regional or national networks like the Great Lakes Acoustic Telemetry Observation System in North America (Krueger et al. 2018), and the Acoustic Tracking Array Platform in South Africa (Cowley et al.

2017) has facilitated thousands of telemetry studies across hundreds of fish species and dozens of countries (Matley et al. 2024a).

Acoustic telemetry is now an important tool for studying habitat selection and use (e.g., Griffin et al. 2021; Rudolfsen et al. 2021), allowing the identification of reproductive, rearing and overwintering sites (critical habitats underlying effective fisheries management). The ability of acoustic telemetry to define spatial use in focused regions thus makes it key for planning and assessing the effectiveness of fishery boundaries and protected areas (Hussey et al. 2017; Kendall et al. 2017). Metrics underlying stock structure such as home ranges (e.g., Bradley et al. 2024), population connectivity (e.g., Hayden et al. 2018), migration timing and corridors (e.g., Brooks et al. 2019), and both natural (e.g., Bacheler et al. 2009) and by-catch and release mortality (e.g., Curtis et al. 2015) have all been extensively studied using acoustic telemetry. Telemetry tags can also be equipped with sensors measuring biotic variables (e.g., acceleration, tail-beat frequency, heart-rate, etc.) and abiotic variables (pressure/depth use, temperature, oxygen, etc.), helping understand individual and population level drivers of movement (Crossin et al. 2017; Payne et al. 2014). Acoustic telemetry is also relevant in understanding the movements of invasive species and their interactions with native species (reviewed by Lennox et al. 2016), a key component of EAFM.

Despite the clear use cases for acoustic telemetry in informing fisheries management, it still remains underutilized in this regard (Brownscombe et al. 2022; Crossin et al. 2017; Nguyen et al. 2018). The barriers limiting applications of acoustic telemetry to management have been discussed by several authors, who have raised concerns about the reliability and biases of telemetry findings (Brownscombe et al. 2019; Crossin et al. 2017; Young et al. 2018). One of the main assumptions of acoustic telemetry is that the behaviour and survival of tagged fish is representative of untagged conspecifics (Bridger and Booth 2003). However, fish need to be captured, handled, and implanted with tags, which has raised questions about how the tagging process may negatively impact fish health. Even minor surgeries can introduce infection, alter behaviours, disrupt physiological balance, and lead to mortality (both directly via surgical error or indirectly via infection or post-release predation) (Cooke et al. 2011).

Sedatives are often administered to fish in order to facilitate surgical procedures. Tricaine methanesulfonate ("MS-222") is one of the most widely-used sedatives for fishes worldwide and is capable of maintaining sedation for prolonged periods, allowing for complex surgical procedures (Topic Popovic et al. 2012). Currently, MS-222 is among few chemical sedatives approved for use in food fish in Canada and the United-States (Food and Drug Administration 2024; Health Canada 2010). However, due to its slow metabolic clearance, fish sedated with MS-222 cannot be consumed for a period of 5 days in Canada (Health Canada 2010) or 21 days in the United States (Food and Drug Administration 2024), making this sedative undesirable for field studies where tagged fish may be harvested by people and prolonged holding periods are not logistically feasible. As an alternative, electrical currents have been used to immobilize fish by generating electrotetany (muscle contraction) or electronarcosis (unconsciousness and muscle relaxation), collectively referred to as 'electro-immobilization' (Barham et al. 1987; Summerfelt and Smith 1990). Electro-immobilization has been demonstrated as an effective alternative for MS-222 in a number of studies (e.g., Bowzer et al. 2012; Durhack et al. 2020; Prystay et al. 2017; Trushenski and Bowker 2012; Trushenski et al. 2012a, 2012b) and offers the advantages of its ease of use, lack of chemical disposal, rapid induction and recovery times, as well as allowing fish to be released and consumed immediately (e.g., Chiba et al. 2006; Jennings and Looney 1998; Trushenski and Bowker 2012). However, vertebral column fractures and relatively high rates of mortality have been reported with electro-immobilization via alternating-current (AC) and pulsed-direct current (pDC) (e.g., Gaikowski et al. 2001; Redman et al. 1998; Walker et al. 1994), although the reported rates of injury from electro-immobilization are inconclusive and not fully understood (Reid et al. 2019). As such, some animal care committees have been reluctant to approve the use of electro-immobilization.

Surprisingly little is also known about the behavioural consequences of these techniques in wild fish and the time required for fishes to regain “normal” behaviour (Cooke et al. 2011), raising concerns that telemetry data collected in the days to weeks post-tagging is altered by tagging procedures. There are also concerns that the presence and size of the transmitter itself may cause injury, or impair movement and buoyancy control (Smircich and Kelly 2014). Although it has been traditionally accepted that the adverse effects of transmitter presence can be minimized with tag burdens (*i.e.,* transmitter mass as a percentage of fish mass) less than 2% (the “2% rule”; Winter 1983), little evidence exists to support this guideline. The 2% rule may be too conservative or liberal depending on the animal (Brownscombe et al. 2019; Thiem et al. 2011). Despite the ongoing miniaturization of acoustic transmitters, fish are still frequently implanted with tags that represent a substantial portion of their body weight (5-10% in some cases; e.g., Klinard et al. 2021; Rechisky et al. 2019), which could substantially bias study findings. When small fishes are tagged, it is often the case that they are consumed by other animals, with tags continuing to transmit in the gastrointestinal tract of the predator (e.g., Daniels et al. 2019). This introduces a “predation bias”, where the predator’s behaviour is recorded instead of that of the study subject. Unless accounted for, this clearly violates the assumption that telemetry data represent the movements, behaviours, and locations of the study animal originally tagged.

These potential sources of bias have raised questions about the reliability of telemetry data. For example, social science work revealed that many stakeholders and government employees involved in managing salmon fisheries in Canada's Fraser River were unsure if the handling involved with inserting or attaching telemetry transmitters made telemetry data unreliable (Young et al. 2018). If findings from acoustic telemetry studies are to be widely applied, evidence that the tagging process does not alter the behaviour or survival of tagged fishes should be readily available and interpretable for fishery managers and policy makers. Therefore, the overarching goal of this thesis is to address potential sources of bias in electronic tagging studies to inform the methods used by future studies.

Although there is a growing body of experimental evidence about tagging effects in fishes, there has been no published meta-analysis of tagging effects using a broad representation of all published studies. To address this, the second chapter of this thesis provides a comprehensive review and meta-analysis of tagging effects in fishes. In chapter 3, I demonstrate the performance of Innovasea's miniaturized V3D-1x 307-kHz transmitters. These tags combine the functions of typical acoustic transmitters with the ability to identify the predation of tagged animals, allowing researchers to study predation in wild fishes and assess the degree to which predation biases occur. In chapter 4, I use a whole lake acoustic positioning system to assess the effects of the tag implantation process on post-release behaviours in the wild, comparing fish sedated during surgery with MS-222 against those electro-immobilized using TENS. Collectively, the work presented in this thesis aims to provide useful contributions that advance the methodology used in fish telemetry.

Chapter 2: Effects of surgical implantation of electronic tags in fishes: a review and meta-analysis

2.1 Abstract

Electronic tags have been used for decades and continue to gain popularity. Tags are often implanted in the coelom of fishes, with a substantial body of experimental evidence now assessing the effects of those tags. We revisit a review of tagging effects (Cooke et al. 2011) to provide the most comprehensive review and meta-analysis of intracoelomic tagging effects in fishes to date. We reviewed 295 studies, yielding 226 laboratory trials reporting survival and 215 reporting tag retention. Mean survival in tagged fishes was 88.26% and tag retention was 87.05%. Both metrics were negatively related to tag:body mass ratios (i.e., tag burden), remaining above 90% on average with tag burdens below ~3–4%. Substantial heterogeneity existed among studies, with a modest portion of the variability in survival and tag retention explained by family, tag burden or trial duration. Across the tagging effects literature, 42% of papers documented negative effects of tagging on growth, and 34% found reduced critical swimming speeds relative to controls. Progress has been made in addressing some knowledge gaps, but biases in the tagging effects literature remain and only a small fraction of species used in electronic tagging studies are represented. Interest in understanding sublethal endpoints is growing, however, the importance of factors such as sex, reproductive status, sterility, and tag coatings remain poorly understood. Tag burdens of ~3–4% appear to balance tag size and unwanted tagging effects. More research is needed to better understand sublethal tagging effects and improve the inferences made from electronic tagging studies.

2.2 Introduction

Electronic tagging and tracking of fish has surged in popularity over the past several decades (Hussey et al. 2015; Matley et al. 2022). The advent of large collaborative research networks like the Ocean Tracking Network (Iverson et al. 2018) and regional or national networks like the Great Lakes Acoustic Telemetry Observation System in North America (Krueger et al. 2018), and the Acoustic Tracking Array Platform in South Africa (Cowley et al. 2017) has facilitated thousands of studies across hundreds of fish species and dozens of countries (Matley et al. 2024a). There is now an abundance of datasets on fish survival and behaviour that can and have been used to answer a range of fundamental and applied questions (Crossin et al. 2017; Matley et al. 2022; Jacoby and Piper 2023). Indeed, it is likely that most use cases of electronic tracking have relied on research funding tied, at least in part, to questions relevant to fisheries management and conservation (Krueger et al. 2018). Although there is widespread desire to use behavioural data to inform fishery management decisions, a key assumption in doing so is that the behaviour and survival of tagged fish is representative of a larger population of animals (e.g., Ross and McCormick 1981, Lewis and Muntz 1984, Brown et al. 2011). In addition, there is an expectation that research methods do not impair the welfare of tagged fishes (Cooke et al. 2013; Soulsbury et al. 2020).

What are the negative effects of implanting a small electronic device inside a fish? This question is reasonable and is often posed by members of the public, fishery managers, and other stakeholders concerned about the reliability of research findings (e.g., for management applications) and the ethical aspects of animal welfare. There is a growing body of experimental evidence about tagging effects, including the effects of tags on growth (Bégout Anras et al. 2003; Urbaniak et al. 2016), survival (Reubens et al. 2012; Bass et al. 2020), swimming performance (e.g., Murchie et al. 2004; Janak et al. 2012), and numerous other endpoints (e.g., Lower et al. 2005; Montoya et al. 2012; Moser et al. 2013). However, over 600 unique species have been tagged in acoustic telemetry studies alone (Matley et al. 2024a); tagging effects have been studied in only a small fraction of these species. Researchers may rationalize that tagging has limited long-term impacts based on a subset of tagged fish being tracked consistently or recaptured in good condition (e.g., Caputo et al. 2009; Schoonyan et al. 2017; Patel et al. 2019). Researchers may also explain that the best practices they follow to capture, handle, tag, and release fish align with approaches that maximize survival (Rub et al. 2014; Brownscombe et al. 2017, 2019; Clemens et al. 2023). While these justifications may be true in many instances, they do not always yield confidence across the tagged population because they do not represent empirically derived evidence (e.g., randomized control trials) relevant to species, life stage, and context. Realistically, we will never generate a robust evidence base about tagging effects for every species, life stage, and context. However, ample evidence has been generated for some species, and synthesizing existing data (both qualitatively and quantitatively) can provide information on the generalizability of different aspects of tagging and identify shortcomings in our current base of evidence. In either case, researchers need to be confident they are collecting accurate data to answer their research questions: ensuring tagging effects are not interfering with study goals is crucial (Bridger and Booth 2003).

Evidence syntheses, especially those that include meta-analyses, represent arguably the most rigorous form of scientific evidence (Gurevitch et al. 2018; Murad et al. 2016). In medicine, systematic reviews (which typically include meta-analyses where possible) have been the standard of evidence for decades. The environmental sciences have been slower to adopt the same standard of evidence, but momentum has grown over the last two decades (Cooke et al.

2017). Examples of high-quality evidence syntheses include the effects of windfarms on birds (Stewart et al. 2007), the role of wooded riparian areas in lowering stream temperatures (Bowler et al. 2012), and the efficacy of marine protected areas (Sciberras et al. 2015). As of 2009, 108 published studies quantified tagging effects across a range of tag types (mainly radio telemetry; Cooke et al. 2011). Many experiments on tagging effects have since been carried out amidst the broader rise of acoustic telemetry, leading to the opportunity for an updated evidence synthesis. Although a few meta-analyses have since been published on tagging effects in juvenile salmonids (Vollset et al. 2020) or using a small subset of data (Lawrence et al. 2023), there has been no published meta-analysis of tagging effects in fishes using a broad representation of all published studies.

Here, our goal was to provide a comprehensive, up-to-date review and meta-analysis of tagging effects in fishes. We focused on tags implanted into the coelom of fishes (i.e., intracoelomic tagging), which is the most common way fish are tagged with transmitters (Matley et al. 2024a). Indeed, intracoelomic tagging is likely the best option for most long-term studies mainly due to higher tag retention (i.e., likelihood of a tag remaining with the fish), a reduced chance of tissue damage/infection, and a lower impact on swimming performance compared to other tagging modalities (Jepsen et al. 2015; Matley et al. 2024b). We encourage readers interested in the effects of external tagging to read a review on the topic by Jepsen et al. (2015).

We conducted an exhaustive search of the English-language peer-reviewed literature and extracted details on methods and results from papers exploring various endpoints (e.g., growth, survival, tag retention, physiology, swimming performance) associated with tagging effects. Cooke et al. (2011) identified several knowledge gaps about tagging effects; we sought to assess the extent to which those gaps have been filled in the *ca*. 15 years since. Our hope is that this paper can serve as a useful base of evidence for researchers when addressing questions about tag burdens, tag retention, and tagging effects and will facilitate research that addresses remaining knowledge gaps.

2.3 Approach

Candidate papers were identified using several approaches. First, we performed a boolean search of the Web of Science Core Collection (April 15, 2024; Trent University login) using the search terms: (TS=(surg* AND (tag* OR transmit* OR archival OR telemetry OR logger) AND (fish* OR survival OR condition OR swim* OR retention OR growth)) AND WC=(Fisheries OR Water Resources OR Marine & Freshwater Biology OR Ecology OR Pathology OR Zoology OR Oceanography OR Biodiversity Conservation OR Veterinary Sciences OR Limnology OR Environmental Sciences OR Biochemistry & Molecular Biology OR Biology OR Behavioural Sciences OR Infectious Diseases OR Evolutionary Biology)), identifying 941 articles. To complement this search, we performed an additional search of the acoustic telemetry database "TrackdAT" (Matley et al. 2024a) on April 16, 2024 using the filter "tagging effects", which identified 183 articles (including duplicates). We also performed a cited reference search of Cooke et al. (2011) on Web of Science (April 16, 2024), yielding 179 articles (including duplicates). Finally, the reference lists of Cooke et al. (2011), Musselman et al. (2017) and Lawrence et al. (2023) were examined to further identify additional resources not identified by the previous searches, yielding 48 new articles.

After removing duplicate papers, the resulting list was filtered for peer-reviewed studies published in English that examined the effects of intracoelomic implantation of tags in fishes. We excluded studies examining aspects of surgical procedures in the absence of tag implantation, review papers not including new experimental trials, and studies focusing solely on anesthesia or immobilization. In total, we were able to identify and access 295 papers that evaluated the effects of intracoelomic implantation of tags in fishes.

All data extraction was conducted by a single individual (MBS) and verified by other authors. Data extracted included relevant citation information, the country in which the study was conducted, the number of species studied, the taxonomic family and species/common names, the location of the study (i.e., laboratory, field), the type of tags used (i.e., radio, acoustic, passive integrated transponders [“PIT”], archival, etc.), the life stages and sex of the animals, water temperatures, study duration (in days) and study design (i.e., if controls, shams or power analyses were used). In studies with experimental trials of varying durations, the study duration was defined as the duration of the longest trial. To evaluate trends in study objectives and how this has changed over the past ~15 years, each study was then categorized with respect to the same topics as those described in Cooke et al. (2011): Comparing tagging approaches (e.g., external, gastric), tag size (or manipulations in fish size to evaluate tag burden), biotic factors (e.g., sex, stage of maturation), environmental correlates (e.g., water temperature, salinity, etc.), tag coatings, antenna configurations, incision and wound closure, sterility and antibiotics, and surgeon characteristics. Papers examining tagging effects beyond these topics were included and classified as “others”. The endpoints measured in each study were also examined, which were based on those described in Cooke et al. (2011) but modified slightly to include other commonly studied endpoints. These included: mortality, incision healing and/or necropsy results, growth and feeding, surgery duration, behaviour, swimming performance, physiology, reproductive fitness, and tag and/or suture retention.

For use in the meta-analysis, data were further screened according to the following criteria:

- Only data from trials that occurred in controlled tank environments were used; data resulting from field or mesocosm (e.g., cage, pond) trials were excluded. This was done as conditions in these studies were not controlled. Mortality and tag retention were also typically inferred rather than directly observed in field studies.
- Only data from treatment groups where tags did not extend outside the body were used. Any trials with externally attached tags or radio/archival tags with external antennae or stalks were excluded.
- Only data from studies where either survival or tag retention could be determined were used.
- Studies without at least one control group were excluded.
- Studies in which mean tag burden was not provided or could not be determined were excluded.
- Studies that used experimental tag coatings were excluded.
- Studies were excluded if outcome data (i.e., survival, retention, growth) were pooled between controls and treatments in results, or if treatment groups were reported differently than how they were described in the methods (i.e., experimental groups were pooled together in results).

For studies that met these criteria, we then extracted where available: suture types used, tag dimensions and weight (in air), tag:fish mass ratios, initial and final fish weights and lengths, incision sizes, sample sizes, mortality, tag retention, growth rates and critical swimming speeds (U_{crit}). For our analyses, families with fewer than five observations were grouped as “others”. To standardize fish lengths, we used conversion factors from www.fishbase.org to convert all lengths to fork lengths. In cases where tag burden was not reported, we calculated tag burden as the combined mass in air of the tags used divided by the average mass of the fish used. If possible, we also verified reported tag burdens using the tag and fish mass provided in each paper; in cases where discrepancies occurred, our calculated values were used in analyses.

All statistical analyses were conducted in R for Mac OS X (R CoreTeam 2024, version 4.3.2). Effect sizes and corresponding sampling variances were calculated for survival and tag retention data using the “escalc” function in the “metafor” package (Viechtbauer 2010). Effect sizes were generated for each experimental treatment, with effect sizes calculated across 74 studies and 215 individual experimental trials for tag retention, and across 81 studies and 226 individual experimental trials for survival (Figure A1.1). Effect sizes for tag retention were transformed using an arcsine transformation to stabilize variances given the relatively high frequency of rare events (i.e., ~100% tag retention in many trials) and small sample sizes. Arcsine transformations were chosen over Freeman–Tukey double-arcsine transformations given the latter’s potential low accuracy at values close to its domain limits (Jeong 2018). Arcsine square root transformed risk differences were used for survival effect sizes given the high frequency of 100% survival in many trials and small sample sizes (Rücker et al. 2009).

Random forests and associated variable selection procedures are relatively robust against issues caused by collinearity, allowing the predictive power of these metrics to be compared (Lindner et al. 2022). Given the large number of potential predictor variables, we fit random forest algorithms to survival and tag retention effect sizes in order to identify potentially important predictors using the “randomForest” package (Liaw and Wiener 2002). Random forests were fit with 1000 trees and the default number of variables were tried at each split (the square root of the number of predictors). Predictors included were family, trial duration (days), temperature (°C), surgery type (i.e., if tags were inserted via incision or injection), mean incision size, simplified wound closure type (i.e., absorbable monofilament, non-absorbable monofilament, silk, absorbable braid, adhesive, or staples), as well as initial fish mass and fork length.

Relying on tag:fish mass relationships may be misleading in understanding tagging effects, as tag length or volume may be more important for fish with body cavities that are small relative to their body mass (e.g., Moser et al. 2007; Robinson et al. 2021). Therefore, we also included three measures of tag burden as predictors in random forests: tag:fish mass, tag:fish length, as well as tag:fish volume. Tag volumes were estimated based on the dimensions of each tag, with fish volumes estimated based on approximate mass:density relationships in fishes (~ 1060-1090 kg/m^3; Jones and Marshall 1953). Important predictor variables were identified using a combination of the mean square error (%IncMSE; the change in mean square error with randomly permuted variables) and the increase in Node Purity (IncNodePurity; the change in the homogeneity of the groups created) using unscaled *p* values from the package "rfPermute" (Archer 2011). To examine relationships between predictors and effect sizes, we also evaluated each variable's partial dependence plot using the "pdp" package (Greenwell 2017). Bivariate interaction plots were also examined to evaluate interactions among important predictor variables. Out-of-bag calculations were used to assess random forest fit in data left out of tree fitting, rather than a true independent test dataset, given the relatively small dataset used (n = 215 for tag retention; n = 226 for survival) (Breiman 2001). Given that tag burden as a function of length, mass and volume could not be estimated for all papers, we further explored the relative importance of each burden metric by producing a second random forest using only papers where all three metrics were available and examining %IncMSE, IncNodePurity and the partial dependency of each metric.

Using predictors identified as important ($p < 0.05$) in random forests (i.e., family [factor], tag burden [continuous variable], and trial duration [continuous variable]), we fit mixed effect models using the "rma.mv" function in the "metafor" package. This allowed for a variance structure accounting for pseudoreplication by fitting nested random effects for both paper ID and trial number. We fit separate mixed effect models for tag retention and survival using overall datasets and datasets containing only salmonids given the abundance of data for this family (n = 66 and n = 73 effect sizes for salmonid tag retention and survival, respectively). Each model was checked for collinearity using the "vif" function in the "metafor" package. Pseudo R^2 values for each model were calculated by examining the proportional reduction in the sum of the two variance components when compared to a reduced model. Associated bias-corrected and accelerated (BCa) confidence intervals were bootstrapped using the "boot" function with 1000 replicates (Davison and Hinkley 1997; Canty and Ripley 2024).

To examine the "2% rule" using the existing literature, a combination of partial dependencies for tag:fish mass and generalized additive models (GAM) fit to the overall survival and tag retention datasets with the package "mgcv" were used (Wood 2011). Although there does not appear to be a universally accepted standard for tagging success rates (Schumann et al. 2020), we aimed to identify tag burdens that achieved 90% survival and tag retention on average.

2.4 General characteristics of tagging studies

Since the publication of Cooke et al. (2011), there has been considerable progress made in understanding tagging effects in fishes. Of the 295 papers we reviewed, 182 (~ 62%) were published after 2009. In 2011, the journal *Reviews in Fish Biology and Fisheries* published a special issue titled "Advancing the science and practice of surgical implantation of electronic tags in fish" (Volume 21, Issue 1), which contributed 12 papers for that year. Since 2009, the most papers published in a single year (*n* = 24) was in 2013. However, since 2015, the annual number of studies appears to be in decline (Figure 2.1a). We speculate that this may be a result of a consensus in the academic community that the refinement of surgery methods and reductions in tag size have largely negated the negative impacts of intracoelomic tagging. Surveys of stakeholders in the academic community within the last decade have indicated minimal concerns related to the effects of the tagging process and presence of a tag on fish behaviour and welfare (Nguyen et al. 2021; Young et al. 2018), but it is unclear if those perspectives are widespread. A useful addition to the review presented here would be a focused survey on the current thoughts and attitudes of researchers and fishery managers regarding the effects of internal tagging on fish.

Tagging effects papers were published in a variety of formats, with the majority being academic journal articles (*n* = 216) or management briefs (*n* = 35). Similarly to what was found by Cooke et al. (2011), most papers were published in five journals: *North American Journal of Fisheries Management* (*n* = 55), *Transactions of the American Fisheries Society* (*n* = 42), *Journal of Fish Biology* (*n* = 37), *Fisheries Research* (*n* = 21), and *Animal Biotelemetry* (*n* = 18). The journals *Fisheries Research* and *Animal Biotelemetry* have replaced *Marine and Freshwater Research* and *Hydrobiologia* as the fourth and fifth most popular journals for this topic since 2009.

The 295 studies reviewed were conducted in 33 different countries, the majority occurring in the United States (*n* = 141), Canada (*n* = 44), Denmark (*n* = 12), France (*n* = 10), Norway (*n* = 10), and Australia (*n* = 8). The United States and Canada have seen the greatest increase in publications since 2009, increasing by 166% (*n* = 88) and 120% (*n* = 24), respectively. Most studies (*n* = 273) occurred in the northern hemisphere. Only 14 studies were conducted in developing countries (i.e., South Africa [Kerwath et al. 2005; Thorstad et al. 2009; Childs et al. 2011; Huchzermeyer et al. Cowley 2013; Hanzen et al. 2020; Trotter et al. 2024], Brazil [Schulz 2003; Lopes et al. 2016; Pinheiro et al. 2018; Peressin et al. 2021], Bahamas [Smukall et al. 2019], Laos [Grieve et al. 2018], Namibia [Økland et al. 2003], and Seychelles [Patel et al. 2019]), with South Africa and Brazil publishing 4 and 3 studies, respectively, since 2009.

One of the recommendations made by Cooke et al. (2011) was for "studies that transcend the laboratory and the field with more studies in marine waters and on a diversity of taxa". Most studies we reviewed (72%; *n* = 212) were conducted in freshwater, with only 19% (*n* = 57) in saltwater. Another 3% (*n* = 10) of studies conducted trials using both fresh and saltwater, and 2% (*n* = 5) had trials in brackish waters (all but one of these 15 studies were published since 2009). We were unable to definitively identify water types in eleven studies (4%) due to insufficient reporting of methods. Since 2009, there have been 120 new tagging effects studies in freshwater, 41 in saltwater, and seven that did not specify the water types used. Given that the majority (~76%) of studies conducted in marine or brackish waters were published since 2009, efforts have been made to address the lack of saltwater studies, but freshwater species remain dominant in the literature.

Most studies (67%) were completed in the laboratory (*n* = 198), with fewer in the field (*n* = 55). An additional 17 studies used mesocosms exclusively. Since 2009, there have been 122 new studies in the laboratory, 37 in the field, 13 in both, and 10 in mesocosms. Some advancements have been made in integrating laboratory and field trials, with 25 studies that combined laboratory and field trials (13 studies occurring since 2009). These integrated approaches can help assess the applicability of lab-based experiments to *in situ* conditions, combining the control of lab studies with the complexity of real-world environments (e.g., Le Pichon et al. 2015). However, few studies have done so, suggesting more work is needed (also see Matley et al. 2024b).

Another recommendation made by Cooke et al. (2011) was for comparative studies that evaluate the same surgical techniques on multiple species. Despite this, most tagging effects studies (90%, *n* = 262) have focused on a single species, with only 20 studies examining two species and 13 studies examining three or more species. Although some excellent comparative tagging effects studies have been published (e.g., Musselman et al. 2017; Schumann et al. 2020), there remains much work to be done to fill this gap, particularly in terms of comparative studies that also manipulate environmental conditions.

The families used in tagging effects research have remained fairly consistent since 2009, with salmonids remaining the dominant family in new tagging effects research (Figure 2.2). Centrarchids represent a decreasing portion of new tagging effects research compared to acipenserids and anguillids (Figure 2.2). Although elasmobranchs have been tagged in over 300 acoustic telemetry studies (Matley et al. 2022), we identified only three studies investigating the effect of tagging on elasmobranchs. Researchers can point to the fact that tag burdens are likely minimal in these large animals, however, many uncertainties remain regarding tag retention, inflammation, and wound closure rates. While we will never realistically generate direct evidence about tagging effects for every species, species-specific responses to tagging highlight the need for further research to support the growing use of electronic tagging across diverse environments and taxa.

There has been a considerable shift in the type of tags examined in tagging effects studies. Radio tags were predominant in the late 1990's and early 2000's, with over half of the studies included in Cooke et al. (2011) using radio tags. Since then, only 13 of 182 tagging effects studies published since 2009 have used radio tags. In contrast, tagging effects studies using acoustic tags were relatively sparse until 2005 ($n < 16$), after which their use greatly increased, surpassing radio tagging studies by 2010 (Figure 2.1b). Acoustic tags have since become the primary tag type used in tagging effects studies (118 studies since 2009). The use of PIT and radio frequency identification tags (RFID) tags followed a similar trend to acoustic tags, with studies rapidly increasing in number after 2005 and surpassing radio tag studies by 2010 (with 79 studies published since 2009). There have been consistently low numbers of tagging effects studies using other tag types (e.g., archival loggers) since 1975.

2.5 Trends in study design

Cooke et al. (2011) recommended that future studies should use rigorous controlled manipulations based on statistical designs that have adequate power, account for inter-individual variation, and include controls and shams. Of the 295 studies we reviewed, most new studies (67%) were conducted in a lab, where controlled manipulations can occur. However, 25% (n = 74) of all studies did not include controls and 77% (n = 226) did not include shams (i.e., fish undergoing surgery without tags being implanted). This trend has continued since 2009, with 24% (n = 44) of studies published since then not using controls and 76% (n = 138) of studies not using shams in their study design; only ~21% (n = 40) of studies since 2009 included both shams and controls in their study designs. Studies using both controls and sham surgeries have been effective in differentiating the effects of surgical procedures and environmental conditions from those of the tags themselves. For example, although mortality was high (~50%) in tagged groups of eulachon (*Thaleichthys pacificus*), similar mortality in control and sham groups allowed Hanson and Ostrand (2013) to conclude that tagging did not increase mortality. Although there are obvious challenges in using shams and controls in field studies, certain studies have used previously tagged fish (e.g., Wilson et al. 2017) as control groups. Mesocosm studies using small ponds (e.g., Jepsen et al. 2017) or cages (e.g., Warren-Myers et al. 2021) also provide the opportunity to couple the use of experimental controls with greater ecological realism.

Although we noted a general increase in sample sizes through time, small to moderate sample sizes (~3–15 replicates per trial) remain common (presumably due to high equipment costs or difficulty keeping certain species in captivity), with studies incorporating power analyses being very infrequent (n = 15; n = 9 since 2009). *A posteriori* “post-hoc” tests have received ample criticism (reviewed by Dziak et al. 2020), however, we find the limited use of *a priori* tests surprising given their ability to maximize the value of research using small sample sizes (e.g., Kyonka, 2018). Although flexible statistical techniques accounting for individual variation (i.e., random effects) have become increasingly popular, uncertainty in model estimates remains strongly influenced by sample size (Gomes, 2022). Likely, effects, or lack thereof, observed in some tagging studies can be attributed to inadequate sample sizes (i.e., type I and II errors). Therefore, we highly recommend the use (and reporting) of *a priori* analyses to understand the sample sizes required to detect an effect with the desired statistical power.

Where the study period could be determined, the most frequent study duration (n = 93) was less than one month (Figure A1.2), similar to the findings of Cooke et al. (2011). Since

2009, 64 studies assessed tagging effects over a period of up to one month, with only 19 studies exceeding one year. Tagging effects studies have now been conducted across a variety of time periods, although several of the longer-term studies were anecdotal reports of tagged fish being recaptured years to decades following release (e.g., Mangan 1998; Smukall et al. 2019). Although evidence of tag implantation negatively impacting fishes over the long term is limited (Matley et al. 2024b), one study discovered evidence of pressure necrosis nearly three years after tagging at the surgical site, with some dissolvable sutures still present (Caputo et al. 2009). We believe that collaborative acoustic tracking networks offer a practical way to enhance long-term tagging effects research in the wild. We also believe that exploring long-term tagging effects using controlled manipulations and less-understood endpoints is still needed. As reviewed elsewhere (see Matley et al. 2024b), exploring long-term immune responses in greater detail may help us understand what scenarios lead to mortality and tag expulsion, as well as addressing long-term welfare concerns.

2.6 Meta-analysis results

Across the 74 studies and 215 individual experimental trials included, mean tag retention was 87.05% (range: 0–100%; Figure 2.3). Mean survival was 88.26% (range: 0–100%) for treatment (i.e., tagged) fish, 94.96% for sham tagged fish (range: 58.0–100%), and 96.39% for controls (range: 53.33–100%) across the 81 studies and 226 individual experimental trials included (Figure 2.4).

The random forest fit to tag retention data explained 42.5% of the variation in the data, with family, trial duration, and tag:fish mass identified as significant ($p < 0.05$) predictors of tag retention (Table A1.2; Figure 2.5). Smaller effect sizes (i.e., higher tag losses) were predicted when tag:fish mass ratios were greater than ~4%, with smaller differences in predicted tag retention occurring in trials exceeding ~300 days (Figure 2.5). There were also relatively small differences in predicted tag retention among families, with Acipenseridae and families grouped under “others” having higher predicted tag retention, and Clariidae, Ictaluridae and Salmonidae having relatively low predicted tag retention (Figure 2.5). Tag:fish length was a relatively poor predictor of tag retention in the random forest, appearing to over-predict tag retention at the higher end of its range compared to both tag:fish mass and tag:fish volume (Figure 2.5; Figure 2.6). Tag:fish length also did not appear to interact with family in a way that would suggest superior predictive power for certain families (Figure 2.6). Although tag:fish volume significantly improved node purity (p = 0.020), a separate random forest suggested that tag:fish mass better predicted tag retention even when standardized for equal sample sizes (Figure 2.6).

When fitting mixed effect models with the predictors identified from the random forest (i.e., family, trial duration, and tag:fish mass), tag retention was not predicted by family or trial duration but was affected by tag:fish mass such that higher tag burdens led to lower retention (Table 2.1; Figure 2.3). However, the variance in tag retention was poorly explained by predictors (R^2 = 0.14, 95% CI [0.00, 0.29], Figure 2.3). Based on the available data and partial dependencies from random analysis, tag burdens of ~3–4% appear to be an approximate threshold above which tag retention decreases substantially (Figure 2.3; Figure 2.5). A GAM fit to the overall tag retention dataset indicated ~90% tag retention at a tag:fish mass ratio of 3.4. Fish implanted with tags ≤ 3.4% of their mass had a mean tag retention of 92.9%, whereas those implanted with tags > 3.4% of their mass had a mean tag retention of 73.8% (Figure 2.3).

When fitting mixed effect models for salmonids, tag retention was affected by both tag:fish mass and, to a lesser extent, trial duration (Table 2.1). Variation in tag retention was somewhat better explained in salmonids ($R^2 = 0.24$, 95% CI [0.00, 0.51]) than in the overall dataset, but there remained ample variation we were unable to model (Figure 2.7). Tag retention in salmonids was lower than the overall dataset at 77.7%. Tag:fish mass ratios also appear to impact tag retention in salmonids beyond ~3–4% (Figure 2.7). Salmonids implanted with tags ≤ 3.4% of their mass had a mean tag retention of 88.8%, whereas those implanted with tags > 3.4% of their mass had a mean tag retention of 68.7% (Figure 2.7).

The random forest fit to survival data also explained a small percentage of the variation in the data (26.3%), with only tag:fish mass and tag:fish volume identified as potentially important predictors of survival ($p < 0.05$); trial duration had a weak, non-significant effect ($p = 0.07$; Table A1.3; Figure 2.8). Similar to tag retention, there appeared to be an approximate threshold for the effects of tag burden on survival at ~3–4% (Figure 2.8). There were relatively small differences in predicted effect sizes as a function of other predictor variables, except for high predicted mortality in the family Sciaenidae (Figure 2.8). There was also slightly higher predicted mortality in studies with short durations (< 20 days; Figure 2.8). Tag:fish length was a relatively poor predictor of survival and did not appear to interact with family in a way that would suggest superior predictive power for certain families (Figure 2.9). Tag:fish volume appeared to perform similarly to tag:fish mass in terms of mean square-error and node purity (Figure 2.8). When standardized for unequal sample sizes, tag:fish volume led to slightly better mean square-error and node purity compared to tag:fish mass (Figure 2.9). However, given that more data was available for tag:fish mass compared to tag:fish volume ($n = 222$ and $n = 189$, respectively), and that tag burden is generally given as tag:fish mass, we decided to focus on tag:fish mass as our index of tag burden for further modeling of survival.

When fitting mixed effect models with the predictors identified from the random forest (i.e., family, trial duration, and tag:fish mass), survival was significantly affected by tag:fish mass such that increased tag:fish mass was associated with decreased survival (Table 2.2; Figure 2.4). Survival was also significantly lower in the family Sciaenidae ($p = 0.009$; Table 2.2). A modest portion of the variability in survival was explained by our suite of predictors ($R^2 = 0.32$, 95% [0.20, 0.53]), which included tag burden, trial duration, and family. Based on the GAM fit to survival data and partial dependencies from random forest analysis, tag:fish mass ratios appear to impact survival at ~3% (Figure 2.4; Figure 2.8). This GAM indicated ~90% survival at a tag burden of 2.7%; fish implanted with tags equal to or less than 2.7% of their mass had a mean survival of 92.3%, whereas those implanted with tags greater than 2.7% of their mass had a mean survival of 81.5% (Figure 2.4).

When a separate mixed effect model was fit to data from salmonids, survival was only affected by tag:fish mass (Table 2.2; $R^2 = 0.47$, 95% CI [0.31, 0.72]). Survival for salmonids was comparable to the overall dataset at 86.3%. Tag:fish mass ratios again appear to impact survival in salmonids beyond ~3% (Figure 2.10). Salmonids implanted with tags $\leq$ 2.7% of their mass had a mean survival of 93.6%, whereas those implanted with tags > 2.7% of their mass had a mean survival of 82.8% (Figure 2.10).

2.7 Trends in study objectives

Cooke et al. (2011) characterized tagging effects studies by their objectives and provided brief analyses where possible. Below, we revisit these objectives, updating analyses and discussing the extent to which they have been addressed in the *ca.* 15 years since using key papers as examples.

2.7.1 Comparisons with other tagging techniques

Different surgical approaches were compared in 73 of the 295 studies reviewed, with 59% (*n* = 43) published since 2009. Half of these studies (*n* = 35) focused on comparing intraceolomic tagging to external or gastric tagging. Similar to the findings of Cooke et al. (2011), tagging via internal surgical implantation generally had less negative consequences compared to external tagging (e.g., Bégout Anras et al. 2003; Mitamura et al. 2006; Kume et al. 2023) or gastric tagging (e.g., Hall et al. 2009; Neely et al. 2009). As the success of intracoelomic tag implantation can be influenced by a fish's dimensions (Jepsen et al. 2002), external tagging can be a viable option for certain juvenile fishes (e.g., age-0 pallid sturgeon *Scaphirhynchus albus*; Johnson et al. 2014) or fishes with compressed body cavities (e.g., European flounder *Platichthys flesus*; Neves et al. 2018).

Technological advancements have led to the miniaturization of acoustic tags that can be rapidly injected rather than surgically implanted through a sutured incision. This approach has the potential to minimize tagging effects through reduced handling time and wound size. The injection of tags was compared to surgical implantation in 10 studies, with the relative effectiveness of tag injection being study-specific (which is also reflected in the poor predictive power of "surgery type" in our meta-analysis). Two of the four studies evaluating tag injection in juvenile salmonids found that injection outperformed surgical implantation (Cook et al. 2014; Deng et al. 2017). However, other studies using non-salmonids have observed reduced healing and survival when tags are injected (Baras et al. 1999; Baras et al. 2000; Archdeacon et al. 2009; Kano et al. 2013). As the syringe may damage the internal organs of a fish (particularly by inexperienced surgeons), we recommend that researchers wishing to inject tags conduct pilot studies to minimize the likelihood of negative tagging effects.

2.7.2 Tag size

Of the 295 studies reviewed, we identified 91 studies that examined tag size as an objective, with 59 (65%) being published since 2009. Considering that many of these studies manipulated fish size to evaluate the effects of tag size, substantial work has been done to understand the relationships between fish size and tagging success. Although our analyses provided evidence that tag size significantly predicts both mortality and tag retention, there was substantial variability in the overall literature (Figure 2.3; Figure 2.4). Our analyses also revealed that fish implanted with tags weighing less than ~3–4% of their body weight had both a mean tag retention and survival above 90%, however, given the aforementioned variability, we caution against the use of a generalized tag burden limit. The appropriate tag size should be chosen based on the objectives, species, and life stages used in a study, with the use of the smallest tags possible being preferable to avoid unwanted tagging effects.

As described by others (e.g., Jepsen et al. 2004), larger tags can lead to a variety of acute and chronic effects beyond reduced survival and tag retention. There has been a growing interest in understanding these sublethal endpoints, including growth (e.g., Ashton et al. 2017), migration success (e.g., Brown et al. 2013a), swimming performance (e.g., Collins et al. 2013), metabolic rates (e.g., Darcy et al. 2019) and physiology (e.g., Makiguchi and Kojima 2017). An increasing number of studies are also recognizing the need to examine the effects of tag size using more complex environmental conditions. This includes 15 studies examining the impacts of tag size when environmental correlates were manipulated, including pressure changes (e.g., Carlson et al.

2012), water temperatures (e.g., Robinson et al. 2021), salinity changes (e.g., Brunsdon et al. 2019) and light levels (e.g., Ferrari et al. 2014). Ten of these 15 studies (~67%) were published since 2009. This also includes studies providing greater ecological realism by examining tag size in field settings, with ~70% of these studies being published since 2009. For example, tag:body mass ratios were negatively correlated with Pacific lamprey (*Lampetra tridentata*) dam passage success in the wild despite transmitters not influencing swimming performance in the laboratory (Moser et al. 2007). As fish behaviour is driven by complex environmental stimuli and social interactions that cannot be fully recreated in short-term laboratory studies (Magnhagen 2012; Fahlman et al. 2020), these field studies are particularly important for gaining a holistic understanding of the effects of tag size.

To effectively compare tagging effects to the broader literature, it is important that tag burden in air is provided for each experimental group. Across 295 studies, over 45% did not report mean tag burdens for each treatment group, and over half of these studies did not provide sufficient information for tag burdens to be calculated (e.g., tag or fish weight was missing). We also identified over a dozen studies with errors in tag burden calculations or reported tag specifications, as well as dozens more that failed to report other aspects of the surgical procedure (e.g., suture types used, duration or level of anesthesia). As discussed elsewhere (see Clemens et al. 2023; Thiem et al. 2011), several studies also cited other sources for their surgical methods, many of which themselves were not readily accessible or reported incomplete details. In many cases, we were left to make assumptions about the surgical methods used. Overall, the recommendation of Cooke et al. (2011) for studies to address all components of the surgical event has not been sufficiently met, which does not aid in addressing ongoing concerns about the reliability of electronic tagging study findings.

2.7.3 Biotic factors

Cooke et al. (2011) recommended that future studies consider how biotic factors, such as sex and stage of maturation, influence tagging outcomes. Despite this, biotic factors were only examined in 31 of the studies we reviewed, with 16 of them being published since Cooke et al. (2011). Most of these studies focused on biotic factors in adult fish (*n* = 18, 56%), with only a few studies (*n* = 7, 22%) using juvenile fish. Similarly, few studies (*n* = 7, 22%) examined biotic factors across multiple life stages.

Similar to the findings of Cooke et al. (2011), few studies have examined how sex influences tagging effects, likely because determining sex in fish often requires lethal examination of the gonads. Non-lethal methods such as ultrasound or genetic sampling are often expensive and require specialized equipment (Hulthén et al. 2014). Furthermore, sexual dimorphism or secondary sexual characteristics can be cryptic and are often only visible while spawning (Andersson 1994; Cott et al. 2013). In total, sex-specific survival was only examined in five studies with mixed results. For example, although higher male mortality has been observed in tagged spotted sea trout (*Cynoscion nebulosus*; Reese Robillard et al. 2015) and curimba (*Prochilodus lineatus*; Peressin et al. 2021), the opposite was observed in northern pike (*Esox lucius*; Winter et al. 2020). We only identified four studies examining sex-specific tag retention, generally finding lower tag retention in female fish, particularly in gravid individuals. Although pressure from the egg mass can increase the likelihood that transmitters are lost via the incision (Marty and Summerfelt 1986), two studies also found expelled tags in reds or spawning grounds (Bateman et al. 2009; Šmejkal et al. 2019), indicating that tags may also penetrate the gonads and leave the body during reproduction. Given that unequal sex-specific survival and tag retention could substantially bias data, further research on sex-related tagging effects is needed to avoid drawing inaccurate conclusions about survival and movement data in telemetry studies.

In our analysis, two studies quantified tagging effects using surrogate species to avoid experimentation with endangered or rare species. Tagging methods were tested on golden perch (*Macquaria ambigua*) before being applied to endangered Macquarie perch (*Macquaria australasica*; Ebner et al. 2009), and tagging effects were evaluated in blue catfish (*Ictalurus furcatus*) in the field and channel catfish (*Ictalurus punctatus*) in a hatchery (Gerber et al. 2019). Blue and channel catfish showed similar tag retention and survival rates in both hatchery and field settings. However, while golden perch exhibited high survival and tag retention, the endangered Macquarie perch had lower survival in the wild when the same techniques were applied. Although surrogate species can aid in surgeon training, we caution against their use when evaluating tagging effects given these examples along with the species- and study-specific variability in tagging effects seen in our analyses.

2.7.4 Environmental correlates

Cooke et al. (2011) recommended that more studies evaluate surgical outcomes as functions of different environmental variables. We found 37 studies investigating the effects of various environmental factors on tagging. Consistent with Cooke et al. (2011), water temperature remains the most studied environmental variable. Fourteen studies examined temperature as a factor, with nine of them published since 2009. Overall, survival rates were generally higher when fish were tagged in cooler water temperatures, but temperature thresholds for tagging will vary by species. A better understanding of optimal tagging temperatures would still be useful for developing tagging protocols and predictive models of tagging effects.

The second and third most common environmental factors pertained to migrating fishes, including the impacts of dam passage or salinity transitions. Some evidence of increased recovery times from tagging (Daniels et al. 2021) and reduced swimming speeds (Morrison et al. 2013) occurred during salinity transitions, possibly indicative of tagging effects being magnified by the added stress of homeostatic adjustments. Migrating fishes passing through turbines at hydroelectric dams can be exposed to rapid changes in pressure, causing barotrauma (Brown et al. 2013a). Barotrauma can lead to incision tearing and visceral expulsion, with evidence that mortality and/or tag loss relating to these injuries increases at higher tag burdens (Brown et al. 2009; Carlson et al. 2012). All studies examining salinity transitions and dam passage (*n* = 13) were conducted on salmonids and only two were conducted in 2009 or earlier. This is not surprising given the current efforts in rehabilitating salmon migrations, and that salmonid tagging often occurs during migrations from fresh to salt water (Brunsdon et al. 2019). Other commonly tagged anadromous fishes (e.g., acipenserids) have received very little attention in this regard.

Ferrari et al. (2014) examined how tagged and untagged fish reacted to a sudden shift from light to darkness, a common method for assessing stress responses through startle or escape behaviours, activity level changes, or changes in shelter-seeking. Although no impacts of tagging were found in fish tagged with micro-RFID tags, it is important to note that stress responses may vary with different tagging methods, species, or environmental conditions, and behaviours could differ over longer observation periods. Future studies examining how other stressors, such as sudden changes in temperature or water quality, impact the behaviour of tagged versus untagged fish could provide additional insights.

2.7.5 Tag coatings

Only eight of the 295 papers reviewed examined tag coatings, with just two published since 2009. A new PIT tag coated with food grade polymers was tested in largemouth bass (*Micropterus salmoides*), with similar survival and tag retention as traditional glass-encapsulated PIT tags (Siepker et al. 2012). Heath et al. (2023) examined the immune responses of dummy tagged rainbow trout (*Oncorhynchus mykiss*), observing altered immunogenic responses between different tag coatings despite similar wound healing and tag encapsulation. As these immune disruptions could impact the health and behaviour of these tagged animals (Heath et al. 2023), they demonstrated the importance of examining sublethal metrics beyond the typical endpoints included in tagging effects experiments.

Although typical epoxy coatings are likely appropriate for most species, several studies published prior to 2009 provided evidence of increased tag retention when other tag coatings were used (summarized in Cooke et al. 2011). We find it surprising that few studies have examined tag coatings in recent years given that experimental tag coatings could benefit commonly tagged species with low tag retention rates (e.g., ictalurids). Therefore, additional work on tag coatings and the associated immune responses could be valuable.

2.7.6 Antenna configurations

Ten of the 295 papers included examined antenna configurations, with just two of these studies being published since 2009. The most recent study (Jepsen et al. 2013) examined how the presence or absence of a trailing antenna and different aseptic conditions influenced tagged Atlantic salmon smolts (*Salmo salar*), with no detectable difference in survival, growth and healing between treatments. Although not technically antennae, the effects of protruding lightsensing stalks from archival tags were evaluated in Pacific halibut (*Hippoglossus stenolepis*), with few differences in long-term physiological responses identified between treatments (Loher and Rensmeyer 2011).

Although the research needs identified by Cooke et al. (2011) in understanding how antenna lengths and configurations impact fish health and signal reception range remain, the lack of new studies addressing such concerns is not surprising given that PIT tagging and acoustic telemetry have become the dominant forms of fish tracking (Figure 2.1).

2.7.7 Incision and wound closure

Forty-six of the 295 papers reviewed evaluated incision and wound closure, with approximately half of them being published since 2009. Different means of incision closure were examined in 28 papers, the use of sutures versus no sutures was examined in eight papers, incision locations were examined in seven papers, and the use of different suture numbers and/or knot patters was examined in seven papers.

Although sutures are often used to increase tag retention, their necessity has been debated in recent years as improved survival and healing have been reported for non-sutured incisions (Wagner et al. 2011; Deters et al. 2012). Of the eight studies that explicitly contrasted incisions that were closed versus left open, four studies observed higher tag retention when incisions were closed using sutures (Baras et al. 1999, 2000; Mueller et al. 2006; Schumann et al. 2020), and two studies observed better healing and/or survival in fish with non-sutured incisions (Liss et al. 2018; Schumann et al. 2020).

It appears that a greater focus has been placed on the different types of wound closure methods (e.g., different suture types, tissue adhesives), with 28 studies examining this (about half occurring since 2009). Despite suture type not being an important predictor in our random forest modelling, absorbable monofilament sutures either performed better (10/13) or similarly (3/13) to other closure methods, improving healing and reducing inflammation compared to non-absorbable monofilament (e.g., Ammann et al. 2013; Boone et al. 2013; Sandstrom et al. 2013; Miller et al. 2014), silk (e.g., Thoreau and Baras 1997; Wagner et al. 2000; Ivasauskas et al. 2012), absorbable braid (e.g., Boone et al. 2013) and tissue adhesives (e.g., Kaseloo et al. 1992). These sublethal effects often occurred in the absence of altered survival (e.g., Ivasauskas et al. 2012) or tag retention (e.g., Ammann et al. 2013). Therefore, it is likely that although our modelling was unable to find differences among wound closure types, important sublethal differences in fish health still occur between closure types. Monofilament appears to be the least reactive suture material (Wargo Rub et al. 2014) and although more work is merited on the necessity of sutures, absorbable monofilament sutures appear to be the most effective wound closure method based on the literature.

The effectiveness of other wound closure types besides absorbable monofilament sutures varied among studies and species. For example, silk sutures appeared to reduce healing times in *Piaractus brachypomus* compared to non-absorbable monofilament (Baras 2000), yet silk sutures led to greater inflammation than non-absorbable monofilament in rainbow trout (Wagner et al. 2000). Silk sutures also had better healing and tag retention compared to tissue adhesive in black crappie (*Pomoxis nigromaculatus*) (Petering and Johnson 1991), yet led to decreased healing rates in pikeperch (*Sander lucioperca*) compared to tissue adhesive (Rożyński et al. 2017). We recommend that researchers intending to use other wound closure types conduct pilot experiments and consult the literature.

Papers examining incision positions have primarily compared midline incisions (along the linea alba) with lateral incisions. Lateral incisions led to higher survival and tag retention in channel catfish (Gerber et al. 2019) and better healing characteristics in lake sturgeon (*Acipenser fulvescens*) (Hegna et al. 2019). Conversely, midventral incisions reduced the likelihood of injury in grass carp (*Ctenopharyngodon idella*) (Schramm and Black 1984) and increased movement in rainbow trout (Wagner and Stevens 2000). In general, the specifics of creating and closing an incision (i.e., the use of sutures, and where to place the incision) should be evaluated on a species-by-species basis. For example, benthic species may benefit from a lateral incision to avoid contact with bottom substrate, possibly avoiding wound and suture irritation (Wagner et al. 2011). However, minimizing tag size as well as incision size and depth using experienced surgeons is likely the best way to consistently minimize injury (Helfman et al. 2009; Rub et al. 2014; Brownscombe et al. 2019).

Cooke et al. (2011) identified the need for research on suture patterns, with only four such studies published since 2009. Both Boyd et al. (2011) and Brown et al. (2013b) examined single vs. double suturing on juvenile chinook salmonids in the context of simulated dam passage, with no differences in survival or tag retention occurring among treatments. Cooke et al. (2011) also recommended the incorporation of knowledge and techniques emerging from medical and veterinary disciplines. Some advancements in human medicine have focused on developing new wound closure methods that minimize surgery time while maximizing tissue healing. The suture materials discussed above require the use of knots to secure them in place, which can cause inflammation where they rub against the fish’s skin and lead to tag loss or wound dehiscence if they rupture or loosen over time (Nambi et al. 2023). Barbed sutures have been found to improve surgery time and tissue aggravation in human applications (e.g., Moran et al. 2007; Hashemi et al. 2012), but their use for intracelomically tagging fishes has only been assessed in two studies, with mixed success (Woodley et al. 2013; Patel et al. 2019).

A method used frequently in humans to reduce incision size, surgery time, and healing is laparoscopic or "keyhole" surgery, where surgery is performed internally through a small incision using a trocar to pass instruments into the body cavity. Laparoscopic tagging has been limited in fishes, but has been successfully used in sharks (Patel et al. 2019), striped marlin (*Kajikia audax*) (Domeier et al. 2019), and Atlantic bluefin tuna (*Thunnus thynnus*) (Rouyer et al. 2023). Clearly, there remains opportunity to further incorporate techniques, tools, and knowledge from the medical and veterinary disciplines.

2.7.8 Sterility and antibiotics

The roles of sterility and antibiotics in fish surgery remain poorly studied, as only four studies focused on sterility and/or antibiotics. Eleven studies used antibiotics while tagging fish, but only two of these studies manipulated antibiotic use as an experimental treatment. Although the role of antibiotics was inconclusive when tagging blue catfish (Gerber et al. 2019), they helped prevent post-surgical infection in hybrid striped bass (*Morone saxatilis* × *M. chrysops*; Isely et al. 2002). Only two studies assessed aseptic techniques. Chomyshyn et al. (2011) evaluated the importance of aseptic techniques when implanting electronic tags in fishes. No differences in physiological status or mortality were detected between sterility treatments, but handling times were longer when using aseptic techniques (Chomyshyn et al. 2011). Given the efficacy of antibiotics such as enrofloxacin in treating bacterial infections in fishes (e.g., de Oliveira et al. 2023; Rostang et al. 2021), we believe that antibiotics hold potential in reducing the risk of post-surgical infections. As discussed elsewhere (see Mulcahy, 2011), research on dosages, timing, therapeutic efficiencies, and administration routes is needed.

2.7.9 Surgeon characteristics

Two studies examined how surgeon characteristics affect the intracoelomic tagging of fishes prior to 2009, with an additional 13 published since. Interestingly, all but one of these studies found that surgeon experience had some effect on post-tagging outcomes, including mortality, suture retention, tag retention, wound inflammation, and surgery duration (Deters et al. 2012; Sandstrom et al. 2013; Hoyle et al. 2015; Lopes et al. 2016; Carrera-García et al. 2017; Brunsdon et al. 2019; Keller et al. 2021; Robinson et al. 2021; Heim et al. 2024). For example, Lopes et al. (2016) compared an experienced surgeon to a novice surgeon in their ability to implant telemetry tags into a neotropical fish (*Prochilodus lineatus*). On average, the novice surgeon took twice as long to complete the procedure, and recovery times for fish tagged by the novice surgeon were also longer. Fish tagged by the expert surgeon also exhibited a better overall appearance and had smaller wound areas one week after surgery (Lopes et al. 2016). Heim et al. (2024) also found differences in survival and in-river performance between fish tagged by two surgeons following the same surgical procedure. They noted that surgical skill, fish mass and the order of tagging session (morning or afternoon) impacted survival during tagging, suggesting that the inexperienced surgeon initially struggled with smaller fish but improved with practice throughout the day.

The existing literature supports that the experience of a surgeon plays an important role in managing the effects of the surgical implantation of electronic tags, with increased surgery times, tag placement, incision quality, and internal injuries all thought to have effects on tagging success (Cooke et al. 2011; Deters et al. 2012; Lopes et al. 2016; Carrera-García et al. 2017). We support previous suggestions that implementing training programs (including feedback training) for surgical tagging could help mitigate potential biases in the data (Cooke et al. 2011; Lopes et al. 2016).

2.7.10 Other objectives

An additional 78 papers could not be summarized using the objectives originally described by Cooke et al. (2011). These studies examined tagging effects without manipulating tag size or other elements of the surgical procedure, which included numerous feasibility studies using species (e.g., Gardunio and Myrick, 2012; Musselman et al. 2017) and life stages (e.g., Thompson et al. 2014; Walton-Rabideau et al. 2019) for which tagging effects had been understudied. Other studies included here examined the feasibility of using new technologies and procedures (e.g., Holland et al. 2006; Tuohy et al. 2015; Haulsee et al. 2016; Midwood et al. 2018). For example, tagging effects were documented in longnose gar (*Lepisosteus osseus*) when an electric rotary tool with a circular cutting blade was used to cut through this species' rigid ganoid scales during the surgical procedure (Midwood et al. 2018). Although almost 70% of the studies included in this section were published since 2009, tagging effects remain studied in only a small fraction of the hundreds of unique species tagged in acoustic telemetry studies.

Many studies included in this section also focused on applying new or uncommon endpoints to study tagging effects. This included immune responses (Semple et al. 2018), behaviours in response to novel environments (Singer et al. 2019), telemetry-based metrics (Gerber et al. 2017), social interactions (Swanberg and Geist 1997), school swimming metrics (Georgopoulou et al. 2022), and others. Additionally, six studies included in this section evaluated tagging effects on a temporal basis to establish post-surgical recovery times. For example, both lab trials and field telemetry data were used to provide evidence of temporary tagging effects in juvenile lingcod (*Ophiodon elongatus*) and a method for testing tagging effects in the wild (Lee et al. 2013).

An additional six studies also examined tagging effects by recapturing fish carrying transmitters for years after tag implantation, and greater than a decade in some cases (e.g., Mangan 1998; Mazel et al. 2013; Smukall et al. 2019). Although many of these studies only described tagging effects from a single recaptured individual, Caputo et al. (2009) examined the nutritional physiology and condition of 17 largemouth bass that carried tags in the wild for 335 to 1402 days. Physiological parameters were comparable between untagged and tagged largemouth bass, however incision inflammation and infection were still present in some tagged fishes (Caputo et al. 2009).

2.8 Endpoints

2.8.1 Mortality

Mortality is perhaps the most measurable and important endpoint when assessing tagging effects. Mortality was quantified in ~ 79% (*n* = 233) of the 295 studies we reviewed, and in ~ 80% (*n* = 145) of studies published since 2009.

Mortality continues to be measured across a wide array of time scales, ranging from hours (e.g., Luo et al. 2014) to years (e.g., Hühn et al. 2014) after tag implantation. Although estimating mortality is inherently easier in laboratory environments, several studies have provided greater ecological realism in mortality estimates by using mesocosms (e.g., Jepsen et al. 2022) or examining the expected return rates of tagged fishes in the wild (e.g., Hulthén et al.

2014). For example, using experimental lakes containing tagged and untagged lake trout (*Salvelinus namaycush*, a long-lived species), survival rates in the wild were assessed over a 12-year period (Hubbard et al. 2021). Since an implanted tag will presumably remain with a fish for its entire life, such approaches are particularly valuable for assessing survival in long-lived fishes.

The surge in popularity of acoustic telemetry over the past several decades provides an important method for quantifying survival rates in the wild. Although there are evident limitations with the use of shams and controls in telemetry studies, as well as difficulties separating mortality and tag loss via expulsion, several studies have demonstrated the utility of telemetry for assessing the survival of tagged fishes (e.g., Tuohy et al. 2015; Winter et al. 2020). Such approaches are particularly effective for providing ecological realism (i.e., assessing mortality where tracking occurs) in tagging mortality estimates for species where tag retention rates are known.

2.8.2 Tag retention

Tag retention remains one of the most common endpoints in tagging effects studies, with 192 of the 295 studies reviewed evaluating tag retention (116 of which were published since 2009). Although tag retention has been largely studied in laboratory environments (likely due to the ability to directly observe tag loss), it has also been quantified in a number of field studies. For example, mark-recapture and electrofishing surveys have been used to investigate the short-term (≤1 week), annual (1 year), and long-term (≥1 year) retention of PIT tags in resident rainbow trout across 11 study streams (Meyer et al. 2011). They found that short-term and annual retention rates for PIT tags were relatively high, averaging 96% and 81%, respectively. However, long-term retention rates were lower for larger females that had reached sexual maturity, with egg expulsion attributed as an important driver of tag loss (Meyer et al. 2011).

Other efforts have been made to understand the pathways underlying tag retention (summarized by Lawrence et al. 2023), with the literature supporting the role of the foreign body response in mediating tag expulsion. Much of this work has been done using catfishes (order Siluriformes), which can undergo transintestinal expulsion of acoustic tags. This process involves internally implanted transmitters, originally placed in the fish's abdominal cavity, becoming encapsulated in fibrous tissue. Over time, the encapsulated tags are absorbed into the intestinal tract and expelled from the anus (Baras and Westerloppe 1999; Holbrook et al. 2012; D'Amico et al. 2021; Durhack et al. 2024). Unsurprisingly, the effectiveness of tagging catfishes such as channel catfish, blue catfish, and African catfish (*Heterobranchus longifilis*) has had varying success (Baras and Westerloppe 1999; Holbrook et al. 2012; Durhack et al. 2024). There is also evidence of a foreign body response in post-smolt Atlantic salmon implanted with dummy acoustic tags, with high rates of tag expulsion (54.8%) despite low mortality ($\leq$ 5.1%; Lawrence et al. 2023).

Although tag expulsion rates can be influenced by water temperature (Deters et al. 2010; Robinson et al. 2021) and tag size (Brunsdon et al. 2019), there remains substantial variation in tag retention rates that is poorly understood (as summarized by the low R^2 derived from our meta-analysis of tag retention). As discussed by Lawrence et al. (2023), the size, sterility, and location of the object, as well as localized tissue damage, have been shown to influence the magnitude of the foreign body response in the clinical literature (Onuki et al. 2008; Anderson and Jiang 2017; Carnicer-Lombarte et al. 2021). More research focused on the role of the foreign body response and other drivers of variation in retention is still needed.

2.8.3 Incision healing and necropsy

Assessing incision healing and internal healing via necropsy remain among the most common endpoints in tagging effects research, with 159 studies examining either of these endpoints (over half of which were published since 2009). We grouped these endpoints together here due to the complementary nature in which they can be used to assess healing.

Although largely qualitative in nature, both methods are informative. For example, incision inflammation, infection, and the retention of absorbable sutures was identified in recaptured largemouth bass acoustically tagged years earlier (Caputo et al. 2009). By examining wound healing in photographs of acoustically tagged walleye (*Sander vitreus*) captured for fishery harvest, Schoonyan et al. (2017) also revealed long-term retention of absorbable sutures past the time when they would benefit incision healing. Since absorbable sutures are not typically designed for use in poikilotherms and aquatic environments, they likely do not perform in fish as they would in mammals (Rub et al. 2014). Removing sutures after the wound has healed is also impractical for many field applications. Suture materials that dissolve more readily at cold temperatures would be useful for fishes.

Necropsies can be useful for understanding tag retention. For example, necropsies were used to identify tag expulsion through the intestine and body wall of catfishes, providing evidence of poor long-term tag retention (e.g., Baras and Westerloppe 1999; Durhack et al. 2024). Other studies using necropsies have observed tag encapsulation and body cavity healing (e.g., Walton-Rabideau et al. 2019), predicting high long term tag retention. Although much work has been done using these endpoints, we encourage their use in future tagging effects studies given their simplicity and effectiveness.

2.8.4 Growth and feeding

Growth and feeding remain common sublethal measures of tagging effects, with 135 of the 295 studies reviewed including at least one of these endpoints (86 of these studies [~64%] published since 2009). Unfortunately, the diverse ways in which growth data were reported across these studies, as well as variations in experimental design, precluded meta-analysis of the effects of tagging on growth. Of the 135 papers that reported some data on growth, 124 compared growth between intracelomically tagged and untagged fishes, with 52 of them (~42%) finding statistical differences in growth rates. Interestingly, 20 of these 52 papers observed compensatory growth, characterized by an initial decline in growth after tag implantation followed by an eventual recovery of growth rates in which tagged fish 'catch up' to the body size of controls. For example, juvenile muskellunge (*Esox masquinongy*) exhibited a temporary delay in growth within the first month after implantation, but no significant differences in growth were detected after four months compared to controls (Walton-Rabideau et al. 2019). An explanation for this delay in growth is that tagged fishes may initially redirect more energy toward healing rather than feeding and growth (Walton-Rabideau et al. 2019). These delays seem highly variable between studies, ranging from the first 3–4 days after tagging (Baras et al. 1999; Ouedraogo et al. 2014) to up to 12 weeks after tagging (Welch et al. 2007). Although compensatory growth may not be particularly relevant for long-term field studies (i.e., studies using tags with years of battery life), studies examining fish behaviour during the initial days–weeks after tagging may capture behaviours characteristic of fish focused on wound healing. Therefore, continued studies of growth rates using long-term trials with frequent measurements are required to better account for potential behavioural biases in the weeks to months following tagging.

Although growth rates have typically been estimated in laboratory experiments (85.3% of studies), nine studies since 2009 evaluated how tagging affected growth in the wild. For instance, Hubbard et al. (2021) analyzed mark-recapture data for lake trout collected over a 12-year period and found that transmitter implantation with tag burdens ranging from 0.19–1.77% had no impacts on growth. While this long-term data provide valuable insights into how tags affect fish over several years, it does not show if initial reductions in growth occurred in the first few days or months after tagging.

In addition to directly measuring growth, 22 studies also evaluated feeding behaviours and gut fullness (*n* = 10 since 2009). Since changes in growth can take time to occur (especially in slow growing species), assessing feeding behaviours and gut fullness can be more sensitive short-term measures of tagging effects. For example, tagged juvenile lingcod (*Ophiodon elongatus*) initially reduced their feeding activity, but only for the first week after tagging (Lee et al. 2013). Tagged delta smelt (*Hypomesus transpacificus*) also had lower gut fullness compared to untagged controls after 28 days (Wilder et al. 2016). Although reduced feeding behaviours and gut fullness could be due to stress, it could also be due to tags occupying space in the body cavity that could otherwise be used for the gut to expand.

2.8.5 Physiology

Evaluating physiological metrics can provide insights into the mechanisms that affect the survival and behaviour of fishes. We noticed an increase in the use of physiological endpoints: while only 36 of the 295 studies reviewed (12%) included physiological endpoints, 25 of these studies were published since 2009.

The effects on tagging on physiology have been quantified via rates of oxygen consumption (Darcy et al. 2019; Arechavala-Lopez et al. 2021) and reflex action mortality predictors (RAMP scores; Tsitrin et al. 2020). The most common method of collecting physiological data remains via blood samples. For example, plasma lactate levels were collected in rainbow trout eight days after tagging, revealing a negative correlation between plasma lactate and body mass (Makiguchi and Kojima 2017). This suggests that smaller fish experienced greater stress for over a week after tagging (Makiguchi and Kojima 2017). Other means of sample collection, such as non-invasive cortisol determination, can be useful. Reemeyer et al. (2019) examined the effects of PIT tagging on cortisol release in Gulf killifish (*Fundulus grandis*) by assessing cortisol levels from tank water samples as an indirect estimate of plasma cortisol. They coupled this approach with blood sampling to evaluate a wide array of physiological stress indicators, including hematocrit levels, plasma cortisol concentrations, blood glucose, and lactate levels. An immediate stress response was induced in PIT-tagged individuals compared to similarly handled controls, which dissipated within one week of tagging (Reemeyer et al. 2019).

A few recent studies have investigated how the surgical implantation of transmitters alters immune responses in fishes. For example, Semple et al. (2018) examined inflammatory cytokine expression in rainbow trout following acoustic tag implantation. While no significant inflammation at the site of surgery or long-term behavioural effects occurred, tagged individuals exhibited an increase in pro-inflammatory cytokine gene expression 10 weeks after surgery, indicating that the fish may have been coping with chronic inflammation. They also noted encapsulation of transmitters within adipose tissue by day 15, indicative of a foreign body response. There is a need to better understand the infections and immune responses resulting from tag implantation. As discussed by Matley et al. (2024b), immune responses to tagging may be more common than presumed; exploring these responses would help elucidate what scenarios lead to infection, mortality, or changes in behaviour.

Although the process of intracoelomic tagging (i.e., fish capture, handling, air exposure, and tagging) can cause both acute and chronic stress, the duration and severity of these responses appears to be species-specific and influenced by various number of abiotic and biotic factors (Donaldson et al. 2008). Since these physiological disturbances can drive changes in behaviour or survival, continued study of physiological responses to intracoelomic tagging is needed to better understand the factors contributing to mortality and behavioural changes.

2.8.6 Swimming performance

Swimming performance was examined in 45 of the 295 papers included (*n* = 23 since 2009). Studies reporting haphazard observations of swimming behaviours or movements in the wild were not included here (as in Cooke et al. 2011). Swimming performance is closely related to fitness and is an integrative assessment of fish physiology and health (Plaut 2001; Yan et al. 2013), making it a useful sublethal metric in tagging effects studies.

Almost 80% (35/45) of papers assessing swimming performance did so by examining critical swimming speeds (U_{crit}), where fish are forced to swim against incrementally increasing water flow until fatigue (Downie and Kieffer 2017). Although there was insufficient data for a meta-analysis of the effects of tagging on U_{crit}, ten of these 35 papers found that U_{crit} was lower in tagged fish, with an additional two studies observing reduced U_{crit} only during the first hours following tagging. Excluding papers with trailing antennae, the lowest tag burden that led to significant differences in U_{crit} following recovery from intracoelomic tagging was 3.4% (Walker et al. 2016). Interestingly, this threshold is similar to the tag burden limits identified from our meta-analyses of survival and tag retention. Despite the popularity of U_{crit} in tagging effects research, over half of the papers included here studied salmonids, which is not surprising given the continued interest in rehabilitating salmon migrations (swimming performance has clear ecological relevance for long distance migrations; Plaut 2001; Downie and Kieffer 2017). A better understanding of how tagging influences U_{crit} in other taxonomic groups is still needed.

Other less common measures of examining swimming performance included prolonged swim tests (e.g., Close et al. 2003; Collins et al. 2013), studying swimming kinematics (Clark 2016), predator avoidance tests (e.g., Adams et al. 1998; Janak et al. 2012) and burst swim tests (e.g., Knaepkens et al. 2007; Haas et al. 2023). Interestingly, tagging resulted in slower burst speeds in juvenile sea lamprey (*Petromyzon marinus*), but did not manifest in altered swimming endurance (Haas et al. 2023). Burst swimming (e.g., C-starts) is a key part of predator avoidance (Domenici and Blake 1997); additional studies addressing the impacts of tagging on swimming performance beyond U_{crit} would be useful.

2.8.7 Behaviour

Of the 295 studies reviewed, 22% (n = 64) included behavioural metrics (n = 46 since 2009). Given the diversity in the behavioural measurements that were made, it was not possible to include behaviour as a response variable in our meta analyses.

Among these studies, 21 were conducted in the field, many of which assessed behaviour using acoustic telemetry. For example, the movements of newly tagged and previously tagged common bream (*Abramis brama*) were compared in a river system (Gardner et al. 2015). Newly tagged fish travelled significantly farther than previously tagged fish (i.e., controls) only in the first five days post-tagging, although both groups covered similar linear ranges. Many field studies also assessed how tagging affects migratory behaviour. For example, internal acoustic transmitters paired with external pop-off data storage tags did not alter residence time, departure direction, or migration speeds of European eels (*Anguilla anguilla*) (Verhelst et al. 2022).

Only two studies examined the behavioural impacts of tagging in mesocosms. The impacts of tags on Atlantic salmon were studied in aquaculture cages, revealing altered survival and depth use (Wright et al. 2019). Similarly, the effects of tagging on depth preferences and environmental adjustments in ballan wrasse (*Labrus bergylta*) and lumpfish (*Cyclopterus lumpus*) have been examined (Geitung et al. 2020). Both species initially remained in the lower sections of the cages but gradually adjusted to their preferred depths, suggesting that tagging did not impair their ability to adapt to temperature and salinity conditions. Arguably, the impacts of tagging on fish behaviour is likely the endpoint researchers are most interested in. Since fish behaviour cannot be fully replicated in short-term laboratory studies (Magnhagen 2012; Fahlman et al. 2020), field and mesocosm studies are crucial for gaining a more comprehensive understanding of how tagging influences fish behaviour.

Similar in number to field studies, 23 studies were conducted in laboratory settings using a variety of approaches. Although it has been suggested that predator avoidance is among the most relevant measures of behavioural impairments (Jepsen et al. 2008), we only identified one study since 2009 that has used predator avoidance as an endpoint (Walker et al. 2016). The lack of studies involving predation is likely attributable at least in part to difficulties securing permission to do so from animal care committees. Instead, several other endpoints related to predation vulnerability have been used, including exploratory and swimming behaviours (e.g., shoaling and schooling). For example, the behavioural effects of tag implantation in juvenile chinook salmon (*Oncorhynchus tshawytscha*) were compared between tagged and control fish in a new environment at 0, 1, and 4 days post-surgery (Singer et al. 2019). Only the emergence from shelter differed, with 46% of day-0 fish emerging compared to higher rates in subsequent days. Physiological endpoints have also been coupled with video monitoring to study exploratory and group swimming behaviours in European seabass (*Dicentrarchus labrax*; Georgopoulou et al. 2022). Despite physiological parameters being similar to controls 14 days after tagging, tagged fish had poorer swimming performance (Georgopoulou et al. 2022). These contrasting results between physiological and behavioural endpoints attest to the importance of understanding tagging effects using an array of techniques and endpoints.

2.8.8 Reproductive fitness

Eleven of 295 studies assessed the effects of tagging on reproductive fitness (*n* = 7 since 2009). Many of these studies only provided anecdotal or qualitative evidence. For example, genetic markers were used to show that captured lemon sharks (*Negaprion brevirostris*) were the offspring of a lemon shark that was tagged almost a decade prior (Smukall et al. 2019). In a mesocosm study, two minnow species (red shiner, *Cyprinella lutrensis* and the bluntnose minnow, *Pimephales notatus*) successfully spawned after PIT tagging (Pennock and Bruckerhoff 2020).

Although observations of tagged fish spawning are useful, there have been few studies designed to quantitatively evaluate how intracoelomic tagging influences reproductive fitness. Peressin et al. (2021) did so by hormonally inducing spawning in lab to assess how radio tagging influenced male and female reproductive capacity in curimba. Fecundity was not statistically different between tagged and untagged groups, however, sample sizes were low due to high tag expulsion and mortality. Tagging also took place three months before spawning when gonads were still in the resting stage, which is important as higher egg retention (i.e., reduced reproductive fitness) has been observed in intracoelomic tagged steelhead trout (*Oncorhynchus mykiss*) when tags were implanted in gravid females (Berejikian et al. 2007). Concerns about implanting tags in gravid females have been raised, as large gonads can reduce intracoelomic space and tags may be lost during reproduction or block the passage of eggs (Jepsen et al. 2015). While avoiding tagging gravid fish may help negate the negative effects of tagging on reproductive fitness, few (if any) studies have quantitatively examined this. Moreover, fish are often caught for tagging during their spawning period because it is typically the easiest time of the year to capture and sex fish in large numbers. Therefore, there remains a need to assess the impacts of tagging on both short- and long-term reproductive outputs.

2.8.9 Other endpoints

Tagging effects have been studied via a number of endpoints not described in Cooke et al. (2011). While migration was briefly discussed in the context of behaviour (e.g., residence time, departure directions), many papers studied migration beyond behavioural endpoints. Overall, we identified 22 studies examining migration dynamics, mainly migration speed (e.g., Brown et al. 2013c; Daniels et al. 2021; Verhelst et al. 2022) and success (Newton et al. 2016; Wargo Rub et al. 2020; Lennox et al. 2022). As migration combines swimming performance with complex environmental stimuli and social interactions, these studies provide valuable insights into how tagging effects manifest themselves in the applied realm. For example, lower nightly catches of migratory sea lamprey tagged with PIT and acoustic tags were observed compared to fish that were only PIT tagged (Nelson et al. 2021). Bass et al. (2020) also observed increased mortality in migratory juvenile sockeye salmon exposed to high tag burdens and gill clip biopsies (which are often used to study physiology and infectious agents; McCormick 1993; Jeffries et al. 2014; Stevenson et al. 2020). These studies raise important concerns about how tagging effects could lead to overestimation of both trapping efficiency and migration success.

2.9 Conclusions

Overall, both mortality and tag retention were significantly predicted by tag:fish mass ratios such that higher tag burdens led to lower tag retention and survival. With the ongoing miniaturization of acoustic transmitters, it is becoming increasingly feasible to tag fishes without imposing significant tag burdens. With that said, larger tags still offer greater power output (i.e., detection range) and battery life (Kessel et al. 2015), meaning that researchers need to balance study needs with acceptable limits for mortality and tag loss. Although tag burden should be chosen based on prior knowledge of the species of interest, tag burdens up to ~3–4% appear to offer a compromise between tag size and unwanted tagging effects. However, as only a modest portion of the variability in survival ($R^2 = 0.32$) and tag retention ($R^2 = 0.14$) was explained by the predictors used in our analysis, we caution against the use of a generalized tag burden limit.

Although statistical differences between families for survival or tag retention were only found in the family Sciaenidae, small sample sizes were common in most families, with many families not containing enough replicates to be grouped separately in analyses. The random forests used can provide some information on predicted effect sizes in each family (i.e., predicted differences in survival and tag retention), but greater sample sizes in poorly studied families are needed before accurate family-based predictions can be made.

Overall, tag burden expressed as tag:fish mass better predicted both mortality and tag retention compared to tag:fish length, and performed marginally better than tag:fish volume. It has been proposed that tag dimensions may be more important for predicting tagging effects in fishes with small body cavities relative to their mass (e.g., Moser et al. 2007; Robinson et al. 2021). While we did not see evidence of this, both the Petromyzontidae and Anguillidae (i.e., anguilliform fishes with small body cavities relative to their mass) had insufficient replicates to be grouped as individual families in analyses. Once again, additional research using a wider array of families would greatly help elucidate the drivers of survival, tag retention, and other important endpoints.

In addition to these small sample sizes, the modest predictive power of our meta-analyses could also be at least partially explained by variables we were unable to model. For example, we have described evidence of both surgeon experience and reproductive status altering tag retention and survival. However, given the small amounts of mainly qualitative data in the literature, we were unable to use these variables as predictors. We were also unable to include life stage as a predictor due to potential collinearity issues, lack of data reporting, and the subjective and inconsistent nature in which it was reported.

Although biases remain across the tagging effects literature towards freshwaters, developed regions, and laboratory environments, there has been important progress in understanding tagging effects using both saltwater species and field experiments since Cooke et al. (2011). There has also been progress made in addressing endpoints beyond mortality and tag retention, including growth, swimming performance, incision healing, and others. However, there are more than 30,000 species of fishes with diverse morphology, anatomy, physiology, and ecology. Much of the work on tagging effects to date has focused on fusiform shaped fishes in temperate regions, which means there are still substantial gaps in our understanding of these well-studied endpoints; it is unclear how much one can generalize from the findings we have summarized here. Several endpoints remain poorly studied, including reproductive fitness and immune responses. The roles of sex and reproductive status, tag coatings, sterility and antibiotics in governing tagging success also remain poorly understood.

If stakeholders and researchers are to be confident in the results of telemetry studies, continued tagging effects studies are important. We encourage where possible to incorporate some aspect of tagging validation in every electronic tagging study, and we emphasize the importance of working closely with fish health experts in developing project-specific tagging protocols. We also emphasize the importance of reaching out to individuals in our community working on similar species or questions to enable knowledge exchange. Ensuring that evidence guides decision-making is necessary to maintain the welfare status of tagged fishes and ensure that findings from fish tracking studies are defensible.

2.10 Figures and Tables

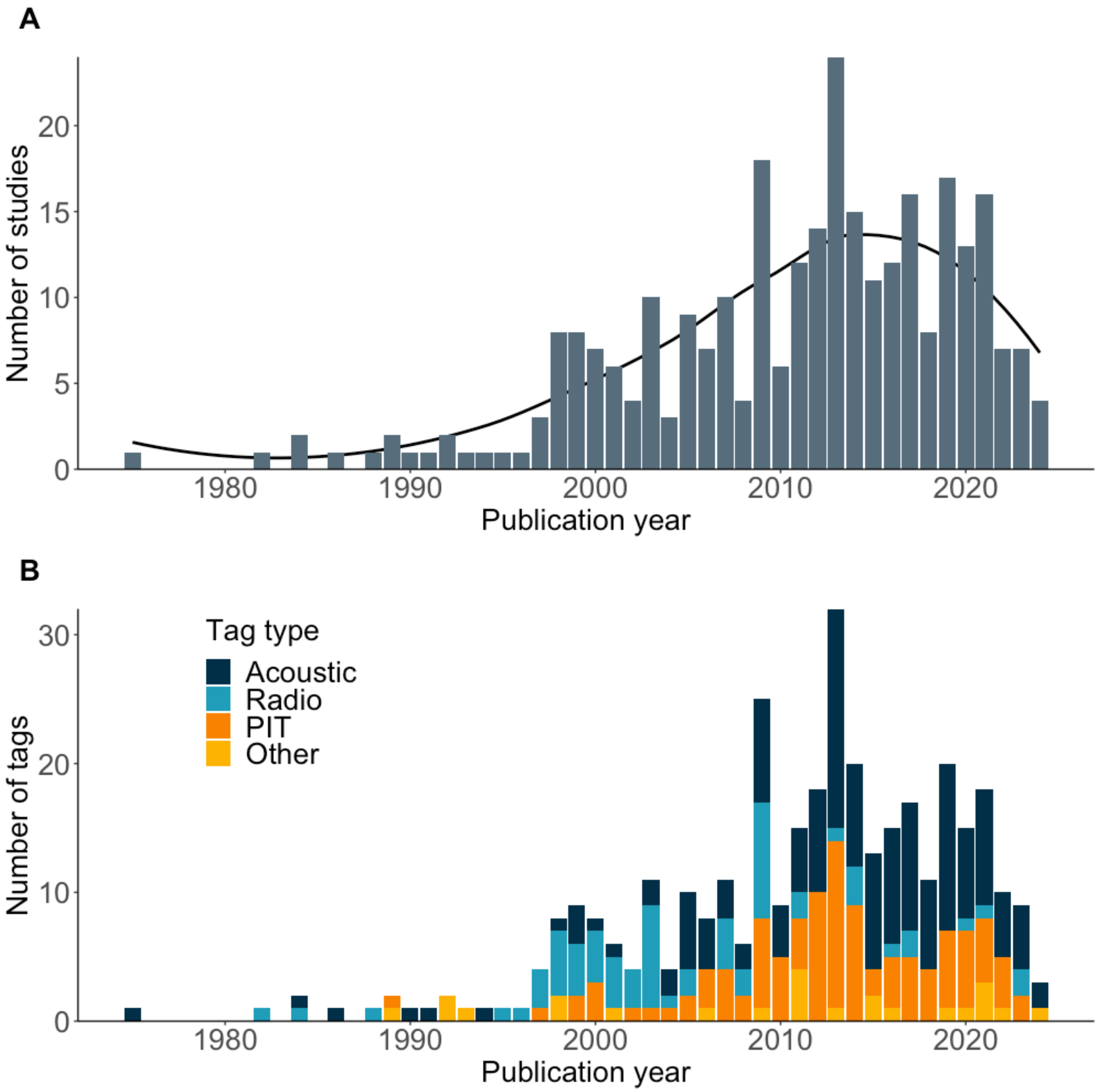

Figure 2.1. Temporal publication trends in studies examining intracoelomic tagging effects in fishes. (A) The number of studies published per year. (B) The distribution of tag types used per year. Data was extracted from *n* = 295 articles on April 16, 2024.

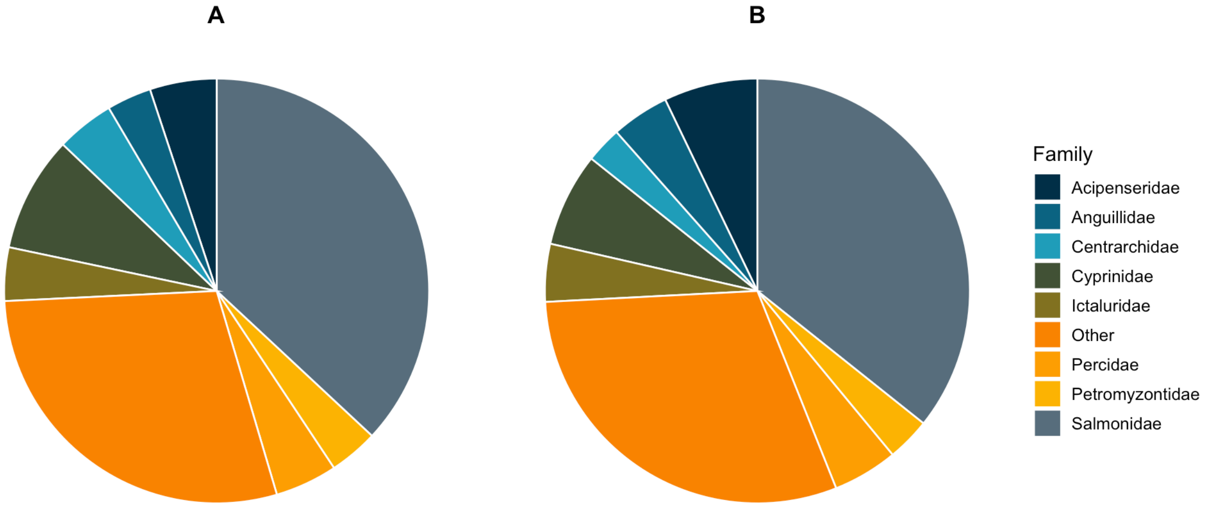

Figure 2.2: Frequency of tagging effects studies using various families of fishes. (A) Frequency of families across the entire tagging effects literature (*n* = 295 articles). (B) Frequency of families in tagging effects studies published since 2009 (*n* = 182 articles). Data was extracted on April 16, 2024.

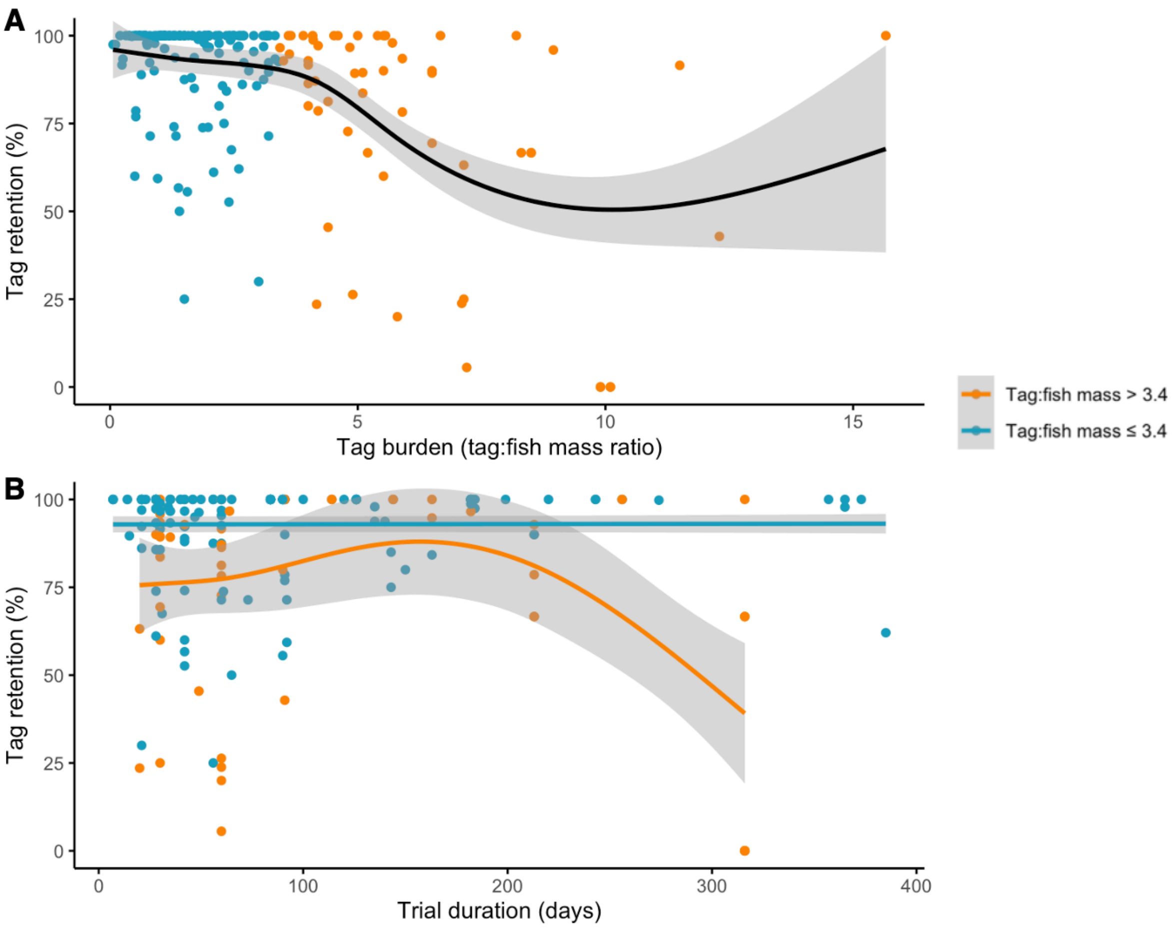

Figure 2.3. Scatterplots for retention of intracelomically implanted electronic tags from *n* = 74 studies, with generalized additive models (GAM) fit for visualization. A) Tag retention (%) as a function of tag burden (tag:fish mass ratio). B) Tag retention (%) as a function of trial duration in days. Across all trials (*n* = 215), mean tag retention was 87.05%. The GAM fit to the overall tag retention dataset indicated ~90% tag retention at a tag:fish mass ratio of 3.4. Fish implanted with tags ≤ 3.4% of their mass had mean tag retention of 92.9%, whereas those implanted with tags > 3.4% of their mass had mean tag retention of 73.8%.

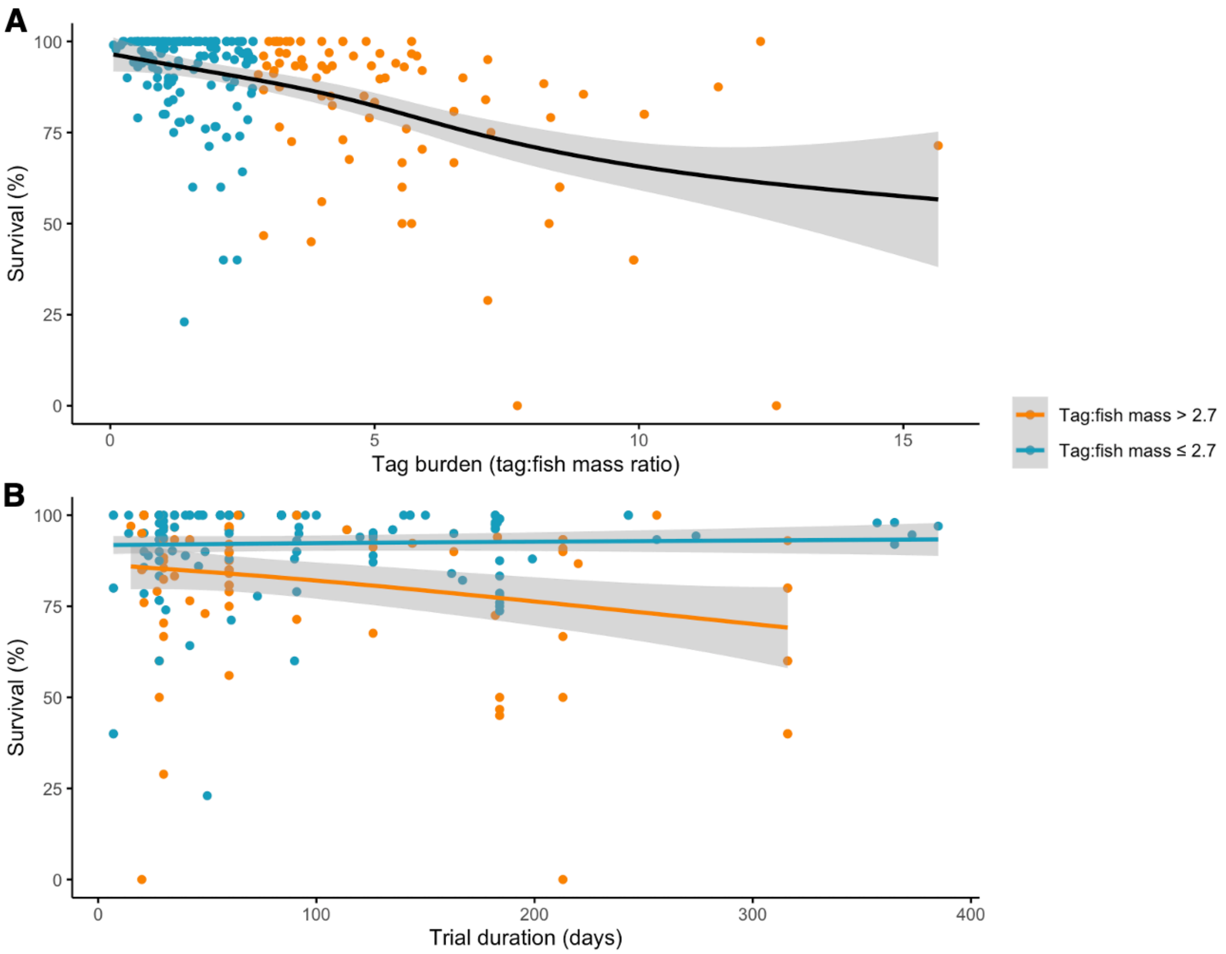

Figure 2.4. Scatterplots for survival of fish intracelomically implanted with electronic tags from *n* = 81 studies, with generalized additive models (GAM) fit for visualization. A) Survival (%) as a function of tag burden (tag:fish mass ratio). B) Survival (%) as a function of trial duration in days. Across all trials (*n* = 226), mean survival of tagged fish was 88.26%. The GAM fit to the overall dataset indicated ~90% survival at a tag burden of 2.7%; fish implanted with tags equal to or less than 2.7% of their mass had mean survival of 92.3%, whereas those implanted with tags greater than 2.7% of their mass had mean survival of 81.5%.

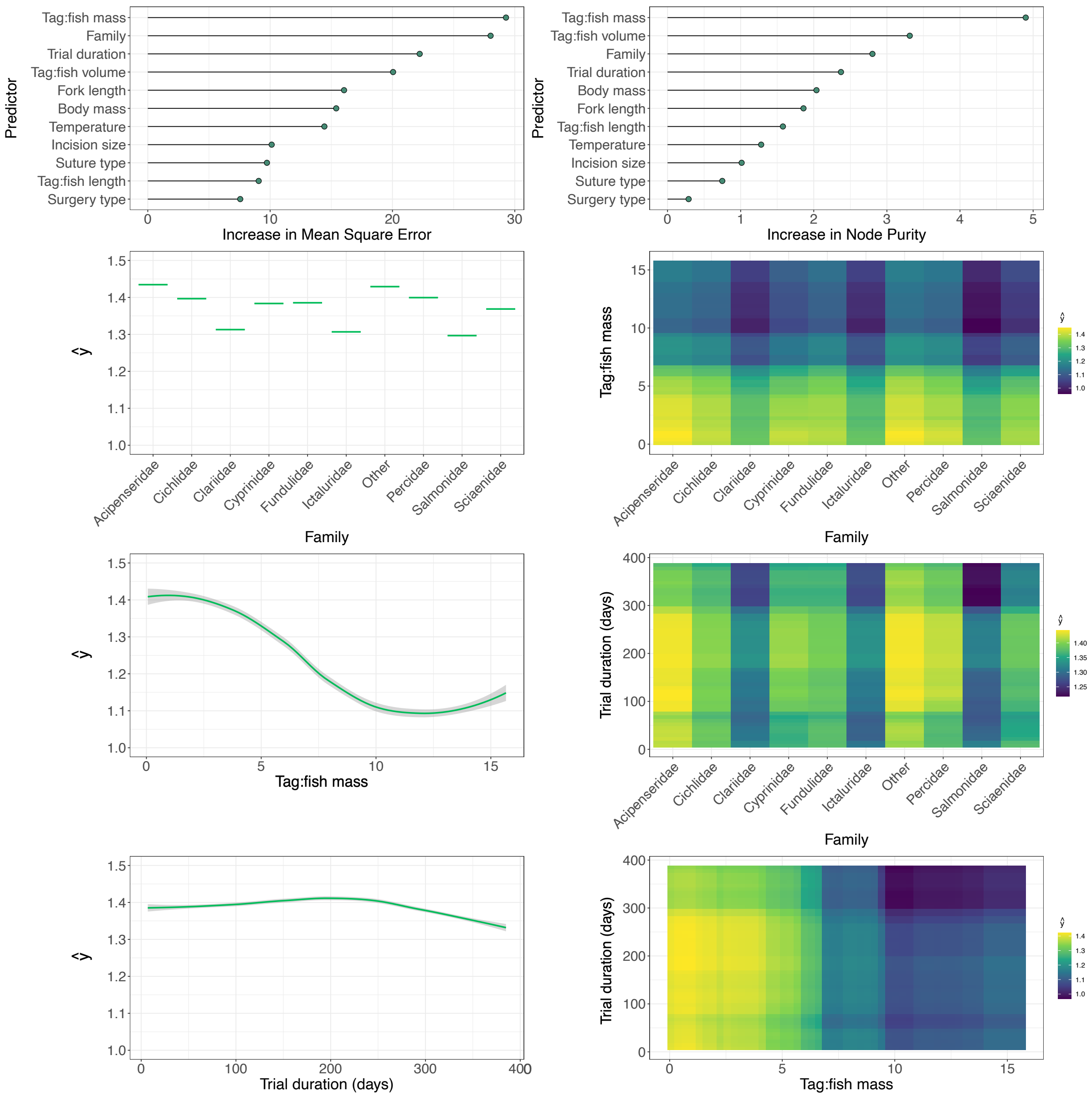

Figure 2.5. Random forest model outputs for retention of intracelomically implanted electronic tags from $n = 74$ studies. “% IncMSE” is the change in mean square error with randomly permuted variables and “IncNodePurity” is the change in the homogeneity of the groups created during random forest modelling; both are used to assess variable importance. Partial dependencies (ŷ) indicate the effect of the predictor levels on predicted effect sizes.

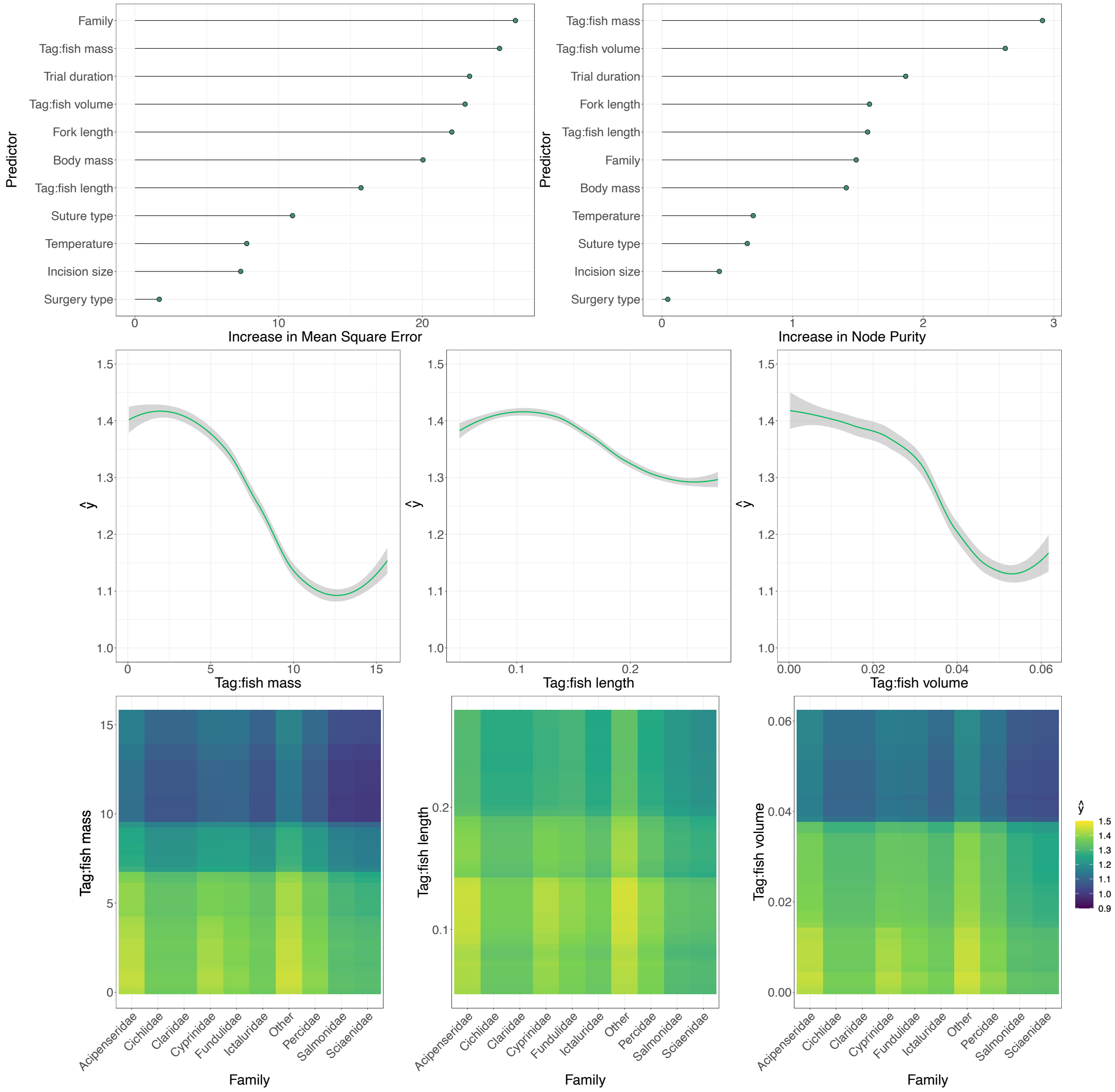

Figure 2.6. Random forest model outputs for tag retention data from studies where tag:fish mass, tag:fish length and tag:fish volume could all be determined (*n* = 130 trials). "% IncMSE" is the change in mean square error with randomly permuted variables and "IncNodePurity" is the change in the homogeneity of the groups created during random forest modelling; both are used to assess variable importance. Partial dependencies (ŷ) indicate the effect of the predictor levels on predicted effect sizes.

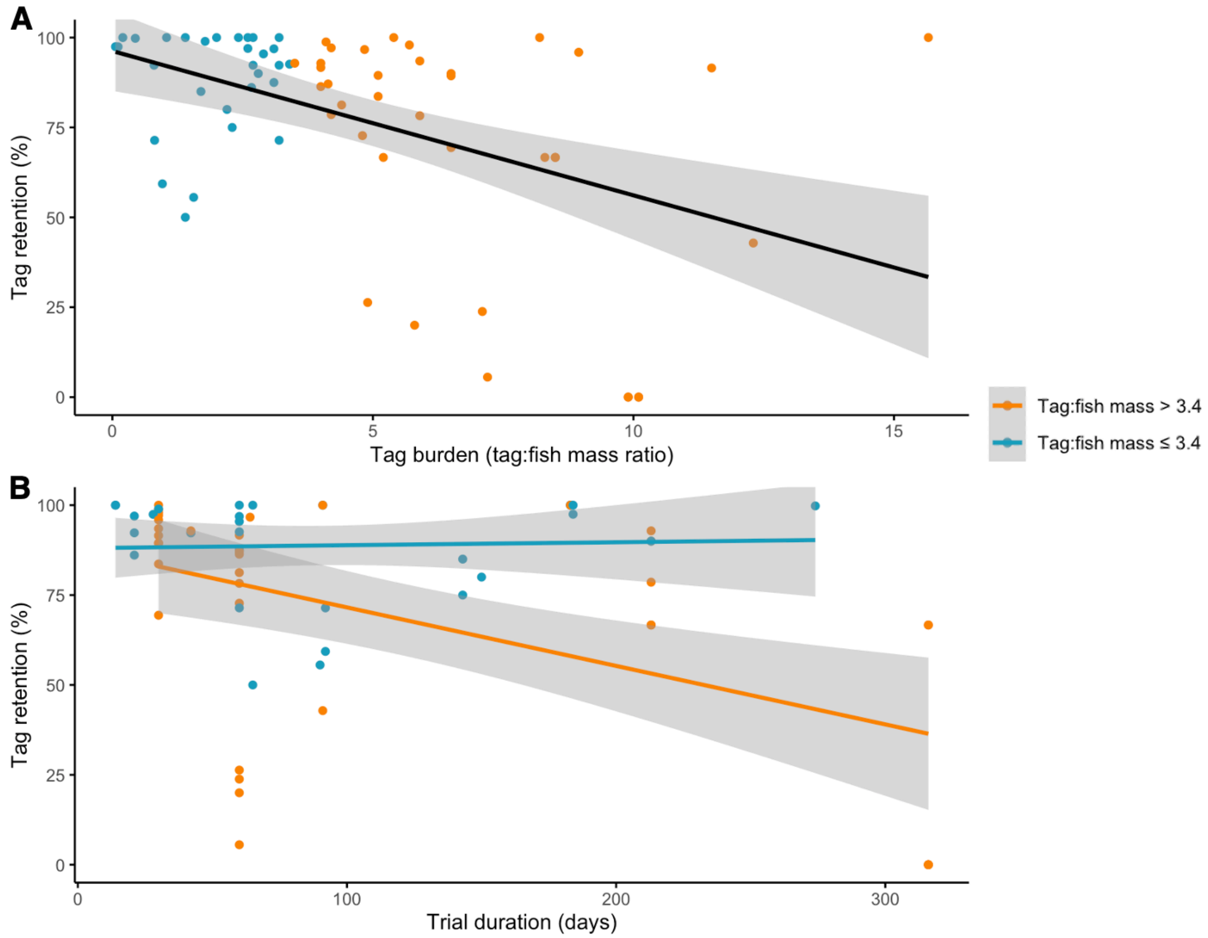

Figure 2.7. Scatterplots for retention of intracelomically implanted electronic tags in salmonids from *n* = 26 studies, with linear models fit for visualization. A) Tag retention (%) as a function of tag burden (tag:fish mass ratio). B) Tag retention (%) as a function of trial duration in days. Across all trials (*n* = 66), mean tag retention was 77.7%. Salmonids implanted with tags ≤ 3.4% of their mass had a mean tag retention of 88.8%, whereas those implanted with tags > 3.4% of their mass had mean tag retention of 68.7%.

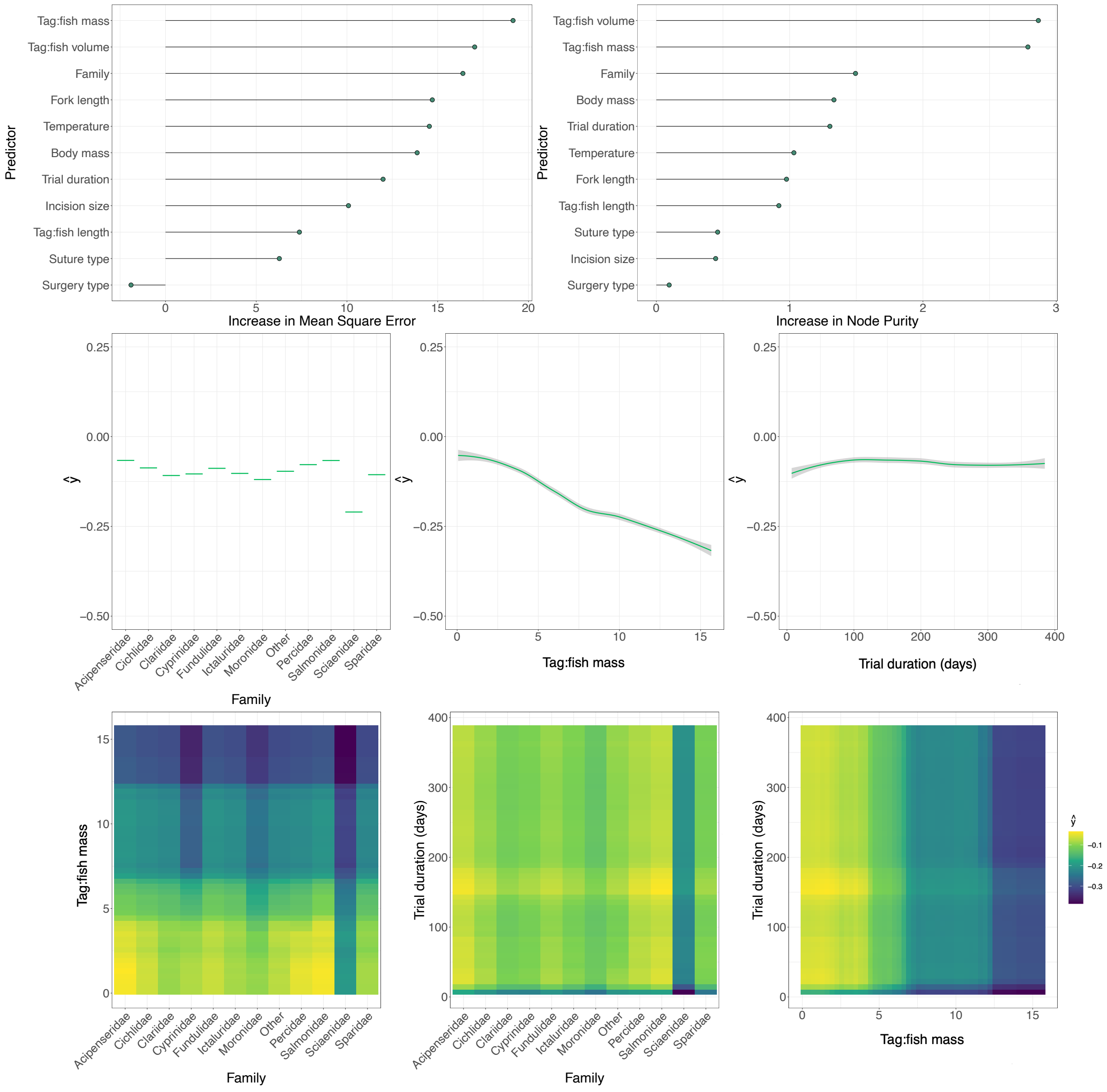

Figure 2.8. Random forest model outputs for survival of intracelomically tagged fishes from *n* = 81 studies. “% IncMSE” is the change in mean square error with randomly permuted variables and “IncNodePurity” is the change in the homogeneity of the groups created during random forest modelling; both are used to assess variable importance. Partial dependencies (ŷ) indicate the effect of the predictor levels on predicted effect sizes.

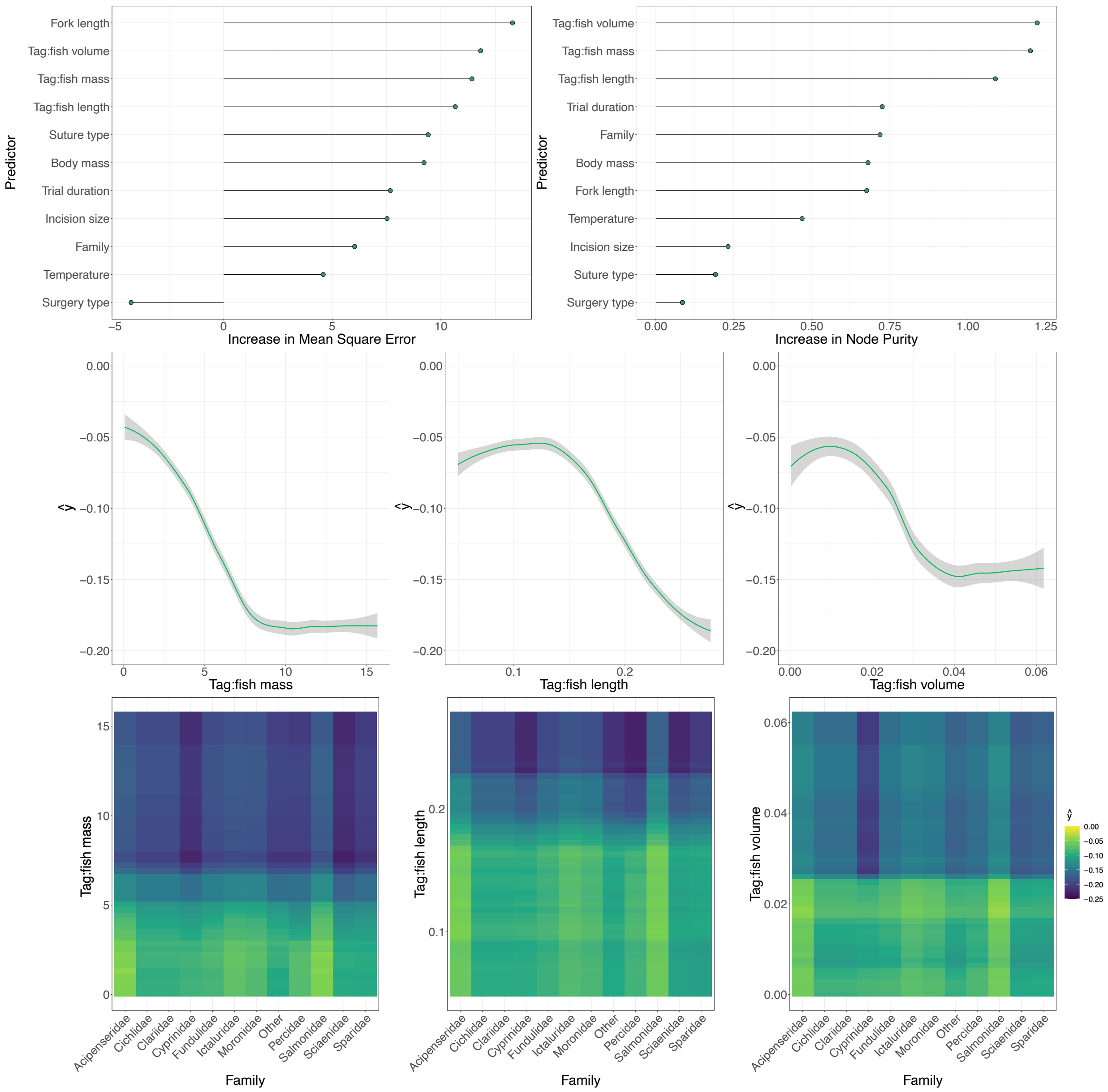

Figure 2.9. Random forest model outputs for survival of intracelomically tagged fishes from studies where tag:fish mass, tag:fish length and tag:fish volume could all be determined (*n* = 128 trials). "% IncMSE" is the change in mean square error with randomly permuted variables and "IncNodePurity" is the change in the homogeneity of the groups created during random forest modelling; both are used to assess variable importance. Partial dependencies (ŷ) indicate the effect of the predictor levels on predicted effect sizes.

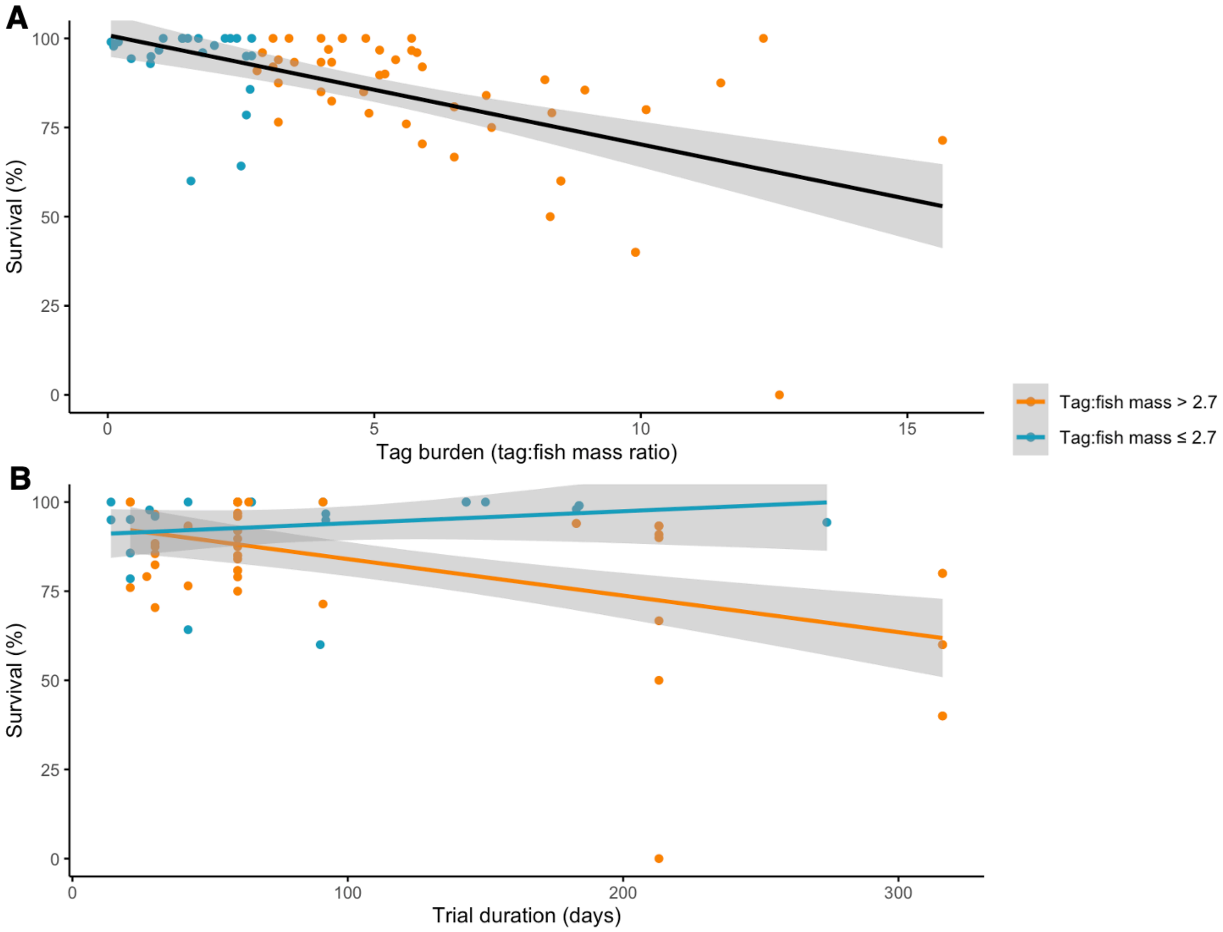

Figure 2.10. Scatterplots of survival data for salmonids intracelomically implanted with electronic tags from *n* = 28 studies, with linear models fit for visualization. A) Survival (%) as a function of tag burden (tag:fish mass ratio). B) Survival (%) as a function of trial duration in days. Across all trials (*n* = 73), mean survival was 86.3%. Salmonids implanted with tags ≤ 2.7% of their mass had a mean survival of 93.6%, whereas those implanted with tags > 2.7% of their mass had mean survival of 82.8%.

Table 2.1. Fixed effect terms of mixed effect models fit to tag retention data. Separate models were fit to the overall dataset and a salmonid-specific dataset. Bolded rows indicate statistical significance ($p < 0.05$).

Model	Parameter	E	SE	zval	pval	CI - Upper	CI-Lower
Overall (*k* = 205)	Family: Cichlidae	0.122	0.215	0.568	0.570	-0.299	0.525
	Family: Clariidae	-0.196	0.295	-0.663	0.507	-0.774	0.384
	Family: Cyprinidae	-0.041	0.120	-0.340	0.734	-0.277	0.195
	Family: Fundulidae	0.187	0.145	1.291	0.197	-0.097	0.470
	Family: Ictaluridae	-0.155	0.156	-0.992	0.321	-0.460	0.151
	Family: Other	0.039	0.093	0.417	0.677	-0.143	0.220
	Family: Percidae	0.009	0.130	0.072	0.943	-0.246	0.265
	Family: Salmonidae	-0.058	0.094	-0.621	0.535	-0.241	0.125
	Family: Sciaenidae	-0.136	0.146	-0.931	0.352	-0.422	0.150
	Trial duration	0.000	0.000	0.037	0.971	-0.001	0.001
	Tag:fish mass	**-0.051**	**0.010**	**-5.053**	**<0.001**	**-0.070**	**-0.031**
Salmonidae (*k* = 67)	**Trial duration**	**-0.002**	**0.001**	**-2.447**	**0.014**	**-0.003**	**-0.001**
	Tag:fish mass	**-0.047**	**0.014**	**-3.365**	**0.001**	**-0.075**	**-0.020**

Table 2.2. Fixed effect terms from mixed effect models fit to survival data. Separate models were fit to the overall dataset and a salmonid-specific dataset. Bolded rows indicate statistical significance ($p < 0.05$).

Model	Parameter	E	SE	zval	pval	CI-Upper	CI-Lower
Overall (k = 188)	Family: Cichlidae	-0.000	0.139	0.000	0.999	-0.272	0.272
	Family: Clariidae	-0.328	0.247	-1.327	0.184	-0.812	0.156
	Family: Cyprinidae	-0.124	0.091	-1.365	0.172	-0.301	0.054
	Family: Fundulidae	-0.047	0.121	-0.387	0.699	-0.283	0.190
	Family: Ictaluridae	-0.098	0.139	-0.704	0.481	-0.371	0.175
	Family: Moronidae	-0.146	0.104	-1.405	0.160	-0.350	0.058
	Family: Other	-0.073	0.066	-1.107	0.268	-0.203	0.056
	Family: Percidae	-0.024	0.098	-0.239	0.811	-0.216	0.169
	Family: Salmonidae	0.040	0.063	0.629	0.530	-0.084	0.164
	Family: Sciaenidae	**-0.298**	**0.114**	**-2.607**	**0.009**	**-0.523**	**-0.074**
	Family: Sparidae	-0.147	0.164	-0.896	0.370	-0.467	0.174
	Trial duration	0.000	0.000	0.976	0.329	-0.000	0.001
	Tag:fish mass	**-0.055**	**0.007**	**-8.285**	**<0.001**	**-0.068**	**-0.042**
Salmonidae (k = 58)	Trial duration	-0.001	0.000	-1.492	0.136	-0.001	0.000
	Tag:fish mass	**-0.041**	**0.007**	**-5.570**	**<0.001**	**-0.056**	**-0.027**

Chapter 3: Validation of a new acoustic telemetry transmitter for the study of predation events in small fishes

3.1 Abstract

Acoustic telemetry has emerged as an important tool for studying the movement and behaviour 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°C, 9.0–10.8°C, 16.0–20.0°C and 22.0–25.8°C. We also conducted false-positive tests where tagged rainbow trout were held at 10.0°C 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 also 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.

3.2 Introduction

Acoustic telemetry is widely used to study fish movement and behaviour 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 miniaturisation 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, behaviours 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 behaviours 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 and Philipp 2004). However, identifying predation events via shifts in behaviour 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 which 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 (0.65 g in air; 4.3 x 5.7 mm diameter x 12.7 mm length) and the smallest available tilt-based predation tag (Thelma Biotel LP6; 1.2g in air; 6.3mm diameter x 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 x 15.5 mm length; 307 kHz V3D) iteration of the acid-based predation tag. These new, smaller tags offer the potential to provide precise behavioural data from many smaller species and life-stages of prey fishes while also identifying 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 consumption of tagged prey by a predator and the tag's excretion from the predator after travelling 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 and 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*) as the model predator and juvenile rainbow trout (*Oncorhynchus mykiss*) 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.

3.3 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).

3.3.1 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 3.1). For use in the two cold-water predation trials, largemouth bass were collected from Rice Lake (Ontario, Canada) on October 26, 2022 via 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 20–23, 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 one month prior to the beginning of predation trials. 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, largemouth bass 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 river 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).

3.3.2 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 10-14s; estimated battery life 173 days; 4.0 mm diameter x 15.5 mm length; Figure 3.1). 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 anesthetized 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 anesthesia (total loss of equilibrium, slow opercular rate, no response to stimuli), body mass and total length were recorded (~15 s of air exposure). Once supine in the wetted surgical sling (Figure A2.1), 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 surgeon 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.

3.3.3 Predation trials

Largemouth bass were fed a total of 67 acoustically tagged rainbow trout across four water temperature treatments (Table 3.1). 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 a 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 three days. Bass used in cold trials were only force-fed acoustically tagged rainbow trout with a minimum of a 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.

3.3.4 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 3.1). Rainbow trout were fed *ad libitum* daily with 2 mm size pellets (EWOS, Surrey, B.C., Canada, https://www.ewos.com/ca).

3.3.5 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 modelled with a gamma distribution and log link function. The fully parameterized model is expressed as

$$\mathrm{Log}\ (S_t) = \beta_0 + \beta_1 \mathrm{T}_t + \beta_2 \mathrm{P}_t + r_t$$

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 3.2). Signal lag data was modelled 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 Akaike Information Criterion (AICc). Model assumptions were checked with visual inspections of a Q–Q plot and residuals against fitted values. Following model selection, pairwise 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’ 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 $\lambda(t)$, where

$$\lambda(t) = \lambda_0(t)\exp[\beta_1 \mathrm{T}_t + \beta_2 \mathrm{P}_t + r_t]$$

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 chi-squared test. Cox models were used to right-censor tags that were retained in predators beyond 30 days (since 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 analysis-of-variance (ANOVA) tables for model objects in the mixed effect Cox model were calculated using the ‘Anova’ function in the package ‘car’ (Fox and 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 were applied to calculate *p*-values adjusted for multiple comparisons where needed.

3.4 Results

3.4.1 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 3.2). Signal lag was best predicted by a combination of water temperature, prey mass and predator ID (Model ii; Table 3.2). 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 3.3). Post-hoc analyses revealed significant differences in signal lag ($p < 0.05$) in all pairwise comparisons of our water temperature groups (Table A2.1). 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 3.2). Force-feeding did not significantly influence signal lag ($F_1 = 0.006$; $p = 0.939$) (Figure A2.2).

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 signal lag, with less clear differentiation among temperatures (Figure 3.3). 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 A2.3). 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 A2.2). Force-feeding did not significantly influence tag retention periods ($F_1 = 0.71$; $p = 0.405$) (Figure A2.4).

3.4.2 False-positive trials

Of the 30 tagged fish used for false-positive trials, three 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}).

3.5 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 timescales (60 days, i.e., ~1/3 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.

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. While 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 12–22°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 warmwater predator we used here (e.g., salmonids that spend much of their lives at temperatures below 10°C) (Brannon et al. 2010; 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 and Tölg 1962). While 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 while the signal lags of V3D predation tags are suitable for most research applications above ~9°C, the large increase in both duration and variability of signal lag at colder temperatures, as well as the increased likelihood of failure described above, 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 suggest that prey mass only had a minor influence on signal lag compared to temperature. While 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 (Schultz et al. 2017; Halfyard et al. 2017). 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. Counterintuitively, 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 and 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 to 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 than the order in which the tags entered the predator, indicating that the tags did not create blockages. While tags were retained longer by certain individuals (as reflected by the significance of individual predator ID when modelling 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. While 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 represents about 1/3 of the expected lifespan of these transmitters. Since chemical reactions are accelerated by higher temperatures (Stockbridge et al. 2010), it therefore remains possible that false positives could occur at higher water temperatures and over longer timespans. 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 also not falsely triggering to indicate predation events.

In Chapter 2, our meta-analysis provided evidence that higher tag burdens led to lower survival and tag retention. Coupled with the evidence that increased tag burdens can negatively impact swimming performance, buoyancy, growth, or survival of tagged fish (e.g., Lacroix et al. 2004; Perry et al. 2001), the reduced dimensions and weight of the V3D predation offers the possibility to study predation events in fish species and earlier life-stages that may not have been possible before.

In summary, this chapter 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.

3.6 Figures and tables

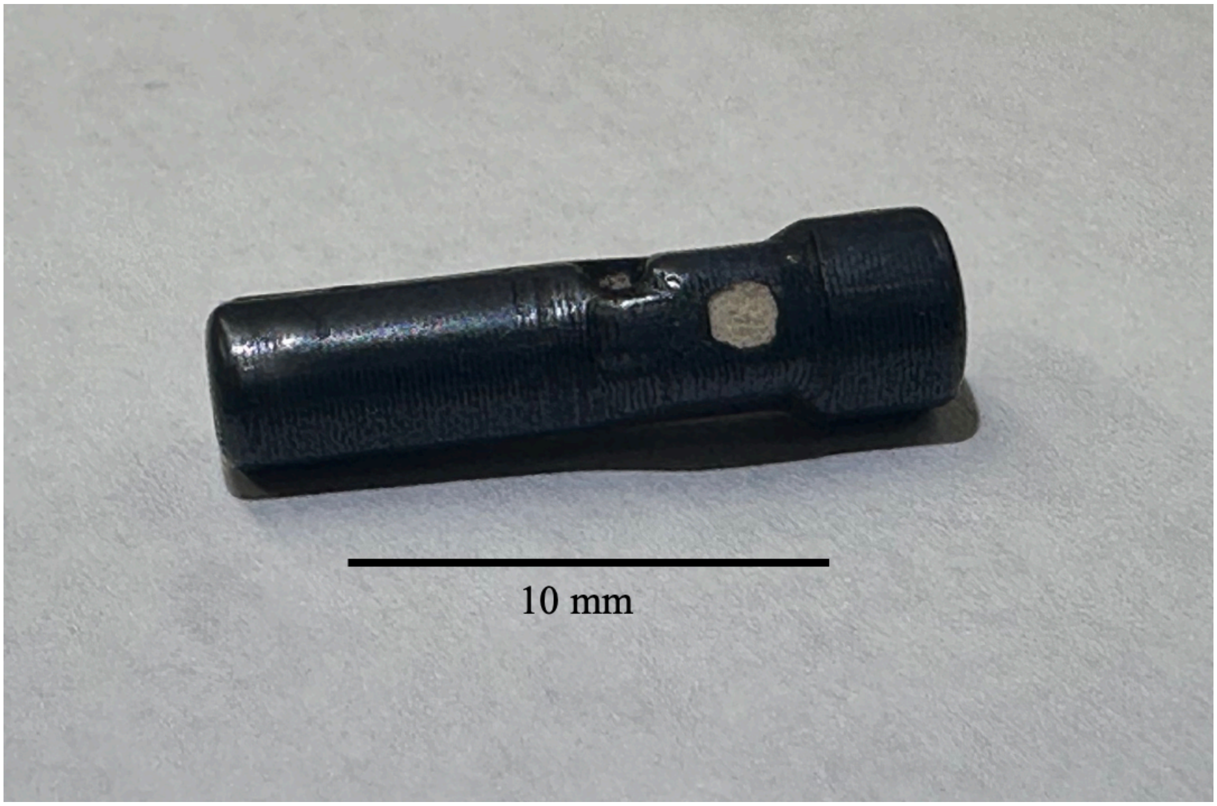

Figure 3.1. V3D predation tag with an intact biopolymer coating (white). This predation tag weighs 0.33 g in air, has a 141 dB acoustic power output at 307 kHz, and dimensions of 4.0 mm diameter x 15.5 mm length.

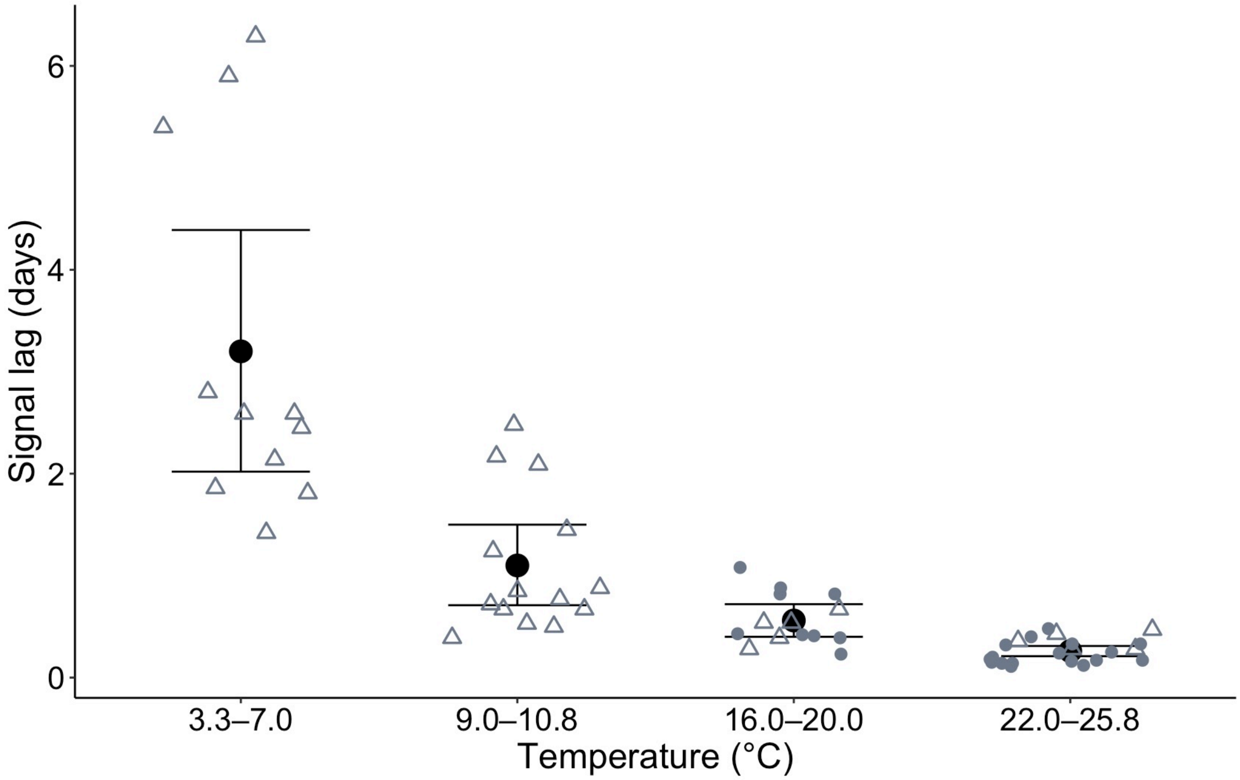

Figure 3.2. Signal lag time data of V3D predation tags at different water temperatures. Predation tags were surgically implanted in juvenile rainbow trout (*Oncorhynchus mykiss*) which were fed to largemouth bass (*Micropterus nigricans*). Small symbols represent individual signal lags. Large overlaid circles represent means of each treatment group, with 95% confidence interval 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 ($p < 0.05$).

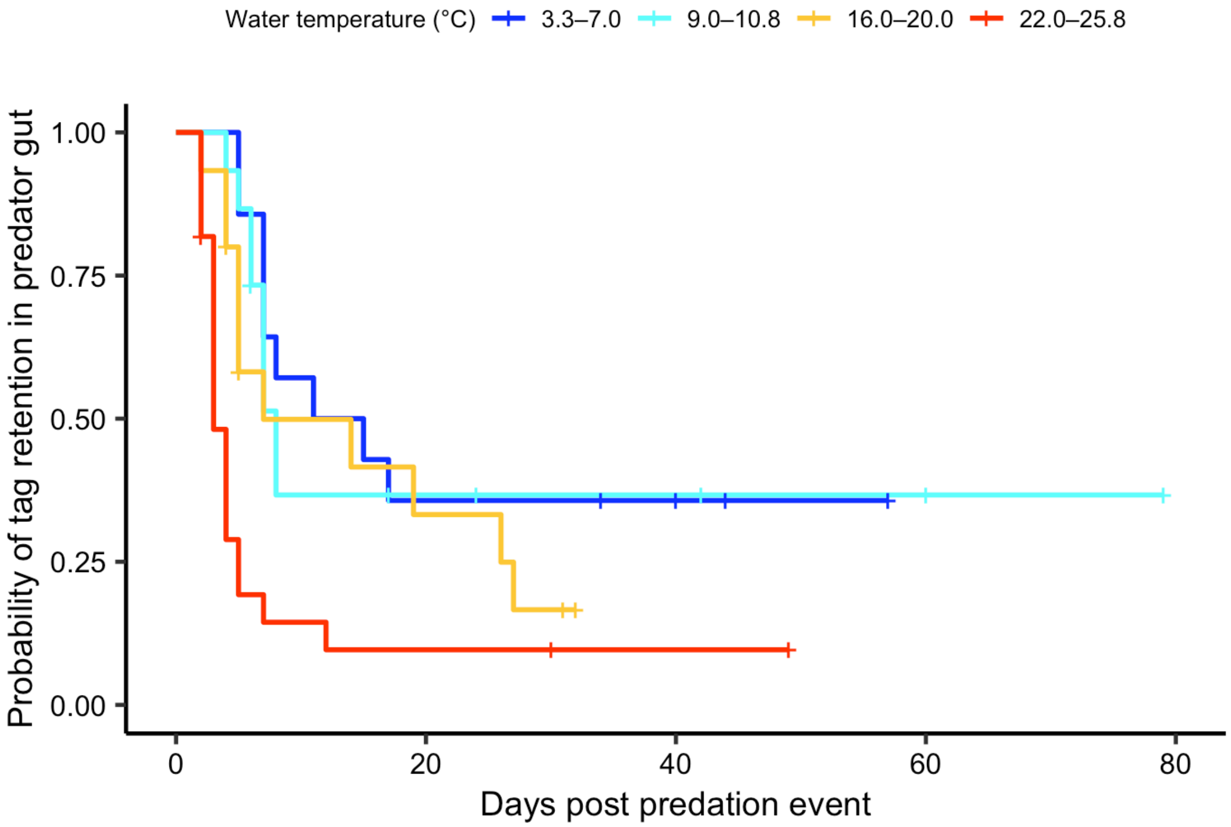

Figure 3.3. Kaplan Meier survival curves of tag retention data from V3D predation tags. Predation tags were surgically implanted in juvenile rainbow trout (*Oncorhynchus mykiss*) which were fed to largemouth bass (*Micropterus nigricans*). There were statistical differences in tag retention periods between 16.0–20.0 and 22.0–25.8°C ($p < 0.05$).

Table 3.1. Number of individuals, total length (mm) and body mass (g) of largemouth bass (LMB; *Micropterus nigricans*) and rainbow trout (RT; *Oncorhynchus mykiss*) used in different trial types and water temperatures. Superscript lettering indicates the use of the same individual fish.

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 positive	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

Table 3.2. Generalized linear mixed models evaluated based on Akaike's second order information criterion (AICc) for the signal lag of V3D predation tags. The bolded model was best fit overall and selected for further analysis. *K* = number of parameters. *ΔAICc* = mean difference between a model's AICc and that of the best fit model. *W* = AIC Weight. *LL* = log-likelihood. R^2 = trigamma conditional R^2. Factors included in analysis: Lag = signal lag (days); Temperature = water temperature (°C); Prey mass = prey body mass (g); Predator ID = individual predator ID.

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

Table 3.3. Fixed effect terms of the best-fit model for signal lag (Model ii; Table 2). *E* = estimated coefficients. *SE* = standard error. *df* = degrees of freedom. *t* = t value. *p* = p value. Temperature effects are relative to baseline temperature category.

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

Chapter 4: Behavioural impacts of MS-222 and electro-immobilization on wild fish assessed using a whole lake telemetry system

4.1 Abstract

Electronic tags have revolutionized our ability to study the behaviour and movement of fishes. To immobilize fish for surgical implantation of tags, tricaine methanesulfonate (‘MS-222’; a chemical sedative) and electrical currents (‘electro-immobilization’) are commonly administered. Despite the abundance of literature examining the physiological side effects of these immobilization methods, few studies have examined if using MS-222 or electro-immobilization during tagging alter the behaviours of fishes in the wild. To do so, we used a whole-lake telemetry system to compare recently tagged largemouth bass (*Micropterus nigricans*) and northern pike (*Esox lucius*) immobilized with either MS-222 or transcutaneous electrical nerve stimulation (TENS) to previously tagged (i.e., recovered) controls. We observed species-specific alterations in behaviour for the first 72 h after tagging: while northern pike only had reduced movement speed in fish immobilized with TENS compared to controls, largemouth bass tagged with either MS-222 or TENS exhibited substantial alterations in movement speed and movement types compared to controls (i.e., fish spent more time stationary and exhibited less burst and active swimming). Despite these short-term effects, the behaviours of both largemouth bass and northern pike were similar to controls within ~100-200 h of tagging, regardless of the immobilization technique used. Our results support the censoring of data from at least the first week post-tagging to avoid bias from the tagging process, as well as the use of TENS as a viable alternative for MS-222 given the similarity of recovery patterns among treatment groups.

4.2 Introduction

Over the past several decades, electronic tagging and tracking tools (e.g., biotelemetry and biologging) have revolutionized our ability to study the behaviour and movement of fishes in the wild (Cooke et al. 2013; Hussey et al. 2015). Although tags can be applied to fish in various ways (Bridger and Booth 2003; Cooke et al. 2013), the most common approach for long-term tracking studies involves the surgical implantation of tags (Matley et al. 2024a). Due to the relative invasiveness of this technique and need for fish to remain still during the procedure, fish are generally sedated or immobilized during surgical procedures (Jenkins et al. 2014).

Tricaine methanesulfonate ('MS-222') is one of the most widely-used sedatives for fishes worldwide and is capable of maintaining sedation for prolonged periods, allowing for complex surgical procedures (Ross and Ross 2009; Topic Popovic et al. 2012). Generally administered through immersion in a buffered solution, MS-222 blocks ion channels to prevent the generation and conduction of nerve impulses (Frazier and Narahashi 1975; Matthews and Varga 2012). Currently, MS-222 is among few chemical sedatives fully approved for use in food fish in Canada and the United-States (Food and Drug Administration 2024; Health Canada 2010). However, due to its slow metabolic clearance, fish sedated with MS-222 cannot be consumed for a period of 5 days in Canada (Health Canada 2010) or 21 days in the United States (Food and Drug Administration 2024). This makes the use of MS-222 undesirable for field studies where tagged fish may be harvested by people given that such prolonged holding periods are usually not logistically feasible.

As an alternative to chemical anesthetics, electrical currents have been used to immobilize fish by generating electrotetany (muscle contraction) or electronarcosis (unconsciousness and muscle relaxation), collectively referred to as 'electro-immobilization' hereafter (Barham et al. 1987; Summerfelt and Smith 1990). Electro-immobilization has been demonstrated as an effective alternative to MS-222 in immobilizing fishes (e.g., Prystay et al. 2017; Trushenski et al. 2012a; Trushenski et al. 2012b) and offers the advantages of its ease of use, lack of chemical hazards for researchers, rapid induction and recovery times, and for allowing fish to be released and consumed by humans immediately (e.g., Chiba et al. 2006; Jennings and Looney 1998; Trushenski and Bowker 2012).

Although the mechanisms by which electric currents immobilize fish are presumably the same as those of electrofishing, the ways in which different types and intensities of electrical currents affect fish are not well-understood (Reid et al. 2019). Furthermore, vertebral column fractures and relatively high rates of mortality have been reported with the use of some electro-immobilization techniques (e.g., Gaikowski et al. 2001; Redman et al. 1998; Walker et al. 1994), although these reported rates of injury are inconclusive and not fully understood (Reid et al. 2019). Moreover, it is unclear whether such methods depress the neurological system (thus providing anesthetic properties) (Reid et al. 2019). Finally, there is lack of knowledge on the potential latent behavioural consequences of electro-immobilization. As such, there has been some reluctancy from animal care committees in approving the use of electro-immobilization.

Both MS-222 and electro-immobilization can be effective in mediating physiological stress associated with handling and tagging (Bowzer et al. 2012; Durhack et al. 2020; Prystay et al. 2017; Trushenski and Bowker 2012; Trushenski et al. 2012a, 2012b). However, MS-222 and electro-immobilization both have physiological effects. MS-222 is known to alter plasma biochemistry, blood gases, hematological profiles, and stress biomarkers, with effects often persisting for days following exposure (reviewed in Priborsky and Velisek 2018). MS-222 forms an acidic solution with a pH as low as 2.8 in water (Ohr 1976), which may expose fish to a toxic acidic environment without adequate buffering (Carter et al. 2011). Although electro-immobilization is also associated with changes in hematological profiles and stress biomarkers, these physiological consequences appear quite variable in duration and severity across studies and species (reviewed in Reid et al. 2019).

Behaviour can be a useful indicator of stress and physiological injury in fishes (Beitinger 1990; Campbell et al. 2010). Despite an abundance of literature examining the physiological side effects of sedatives and immobilization techniques, relatively few studies have examined if MS-222 and electro-immobilization alter behaviours over extended periods (i.e., days-weeks). Rainbow trout (*Oncorhynchus mykiss*) reduced feeding behaviours during the first 24 h after sedation with MS-222, but the swimming performance of both rainbow trout and largemouth bass (*Micropterus nigricans*) (in addition to other behavioural metrics) was not impaired following sedation with MS-222 in lab or mesocosm environments (Anderson et al. 1997; Pirhonen and Schreck 2003; Prystay et al. 2017). Similar to MS-222, there is evidence that electro-immobilization has no short-term (< 24 h) impacts on largemouth bass swimming performance, although electro-immobilized fish may actually be more active post-immobilization than both control fish and those sedated using MS-222 (Abrams et al. 2018; Prystay et al. 2017). A few studies have also examined how tag implantation using electro-immobilization impacts migratory behaviours, with results appearing species specific. Electro-immobilization did not appear to influence migration timing in Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) (Balazik 2015) or time to exhibit positive rheotaxis in lake sturgeon (*A. fulvescens*) and shortnose sturgeon (*A. brevirostrum*) (Henyey et al. 2002). However, walleye (*Sander vitreus*) implanted with tags using electro-immobilization had longer downstream travel times than fish tagged in previous years (Wilson et al. 2017). Some recent work has also shown that post release condition and nest abandonment in smallmouth bass (*Micropterus dolomieu*) were similar between fish treated with MS-222, transcutaneous electrical nerve stimulation (TENS) and controls, but not those electrostunned using a portable electroanesthesia system (Reid et al. 2024).

Of the limited work examining the behavioural effects of these two immobilization techniques, much has done so by examining relatively simple metrics in laboratory environments, which likely does not represent the true complexity of the recovery process. For example, while some behavioural metrics (e.g., swimming speed) appear to return to normal in zebrafish (*Danio rerio*) just 30-minutes after sedation (Nordgreen et al. 2014), cognitive impairments have been reported for young-adult zebrafish for 48 hours following sedation with MS-222 (Fontana et al. 2021). Fish behaviour is driven by complex environmental stimuli and social interactions that cannot be fully recreated in laboratory studies (Fahlman et al. 2020; Magnhagen 2012). Therefore, there is a need to assess post-tagging recovery using immobilization techniques in natural environments.

Given the physiological impacts of these immobilization techniques and the scarcity of information regarding post-immobilization behaviours, many electronic tagging studies censor data from the first days to weeks post-tagging (e.g., Krause et al. 2020; Wright et al. 2019), assuming that behaviours were altered by tagging procedures. In addition to significant losses of data, this may not be an option for studies concerned with short-term behaviours such as the consequences of catch-and-release angling, stocking hatchery-raised fish, or migratory behaviours. To address this issue, we used a whole-lake telemetry system to compare recently tagged largemouth bass (*Micropterus nigricans*) and northern pike (*Esox lucius*) immobilized with either MS-222 or TENS to previously tagged (i.e., fully recovered) individuals of each species. We aimed to evaluate the time required for fish to re-establish normal behaviour following transmitter implantation, and if differences in recover patterns occurred between fish tagged with either MS-222 or TENS.

4.3 Methods

4.3.1 Study System

This study was conducted at Lindsay Lake (44.5373°N, 76.3897°W), a ~16 ha inland lake at the Queens University Biological Station in eastern Ontario (Figure 4.1). The shoreline surrounding Lindsay Lake is largely composed of rock, timber and thick macrophytes, with soft substrates and sparse amounts of macrophytes along the bottom of the majority of the lake. The lake has a maximum depth of ~10 m and supports a predatory fish community of largemouth bass and northern pike. Prey fish consist of more abundant pumpkinseed (*Lepomis gibbosus*) and bluegill (*Lepomis macrochirus*), as well as less abundant yellow perch (*Perca flavescens*), rock bass (*Ambloplites rupestris*), and various minnow species. The lake has a small, shallow (<1 m deep) channel that connects it with Poole Lake, another small private lake at the Queens University Biological Station. These lakes are on private land and fishing by the general public is not permitted.

In May 2023, Lindsay Lake was equipped with an array of 33 Innovasea HR3 high residence receivers, with an additional HR3 receiver placed at the mouth of Poole Lake to detect emigration from Lindsay Lake (Figure 4.1). Each receiver was placed approximately halfway in the water column, with a maximum distance of ~100 m between adjacent receivers. Receivers were retrieved and redeployed at approximately 6-month intervals. Stationary tags were also deployed at 5 locations in May 2023 to synchronize the internal clocks of the receivers and act as reference tags within the receiver array, with a V6-4x (nominal delay of 6-10 s) and V3-1x (nominal delay of 25-35 s) tag placed at each location (Figure 4.1).

4.3.2 Fish Tagging

All research detailed here was conducted in accordance with the Canadian Council on Animal Care (approved by Trent University) and under a scientific collection permit issued by the Ontario Ministry of Natural Resources and Forestry. Between May 2023 and May 2024, a total of 48 northern pike and 54 largemouth bass were collected via angling using a variety of lure types, with landing times limited to less than 60 s (Table 1). After capture, fish were placed in submerged holding bags (0.31 m diameter x 1.22 m length; Dynamic Aqua Supply Ltd., Surrey, BC, CA) and transported via boat to a tagging station on the shore. Prior to surgery, tags were tested to verify that the correct codes were being transmitted and were sterilized via immersion in an iodine solution (as were surgical instruments) before being rinsed with distilled water. Fish in trials using MS-222 were placed individually into an aerated holding tank (0.5 m width x 0.5 m depth x 1.5 m length) filled with lake water and 100 mg L^{-1} buffered MS-222 (Syndel, Nanaimo, B.C., Canada, https://syndel.com). The water bath was replaced for every four fish that were sedated. Once a fish reached stage 5 anesthesia (total loss of equilibrium, slowed opercular rate, and no response to stimuli), fish were placed in a wetted surgical sling. In electro-immobilization trials, TENS units (TENS 7000; Middleburg Heights, OH, U.S.A., https://tens7000.com) were used with a constant pulse rate (150 Hz) and pulse width (300 µs). The electrode leads were placed in the surgical sling such that the anode was placed toward the head and the cathode near the tail of the fish. Electrical intensity was increased incrementally until fish were immobilized and unresponsive to tactile stimulation, at which point surgery commenced.

Surgical methods in both trial types followed standard approaches in the field of fish telemetry (e.g., Wagner et al. 2011). Once supine in the wetted surgical sling (Figure A3.1), their gills were continuously irrigated with aerated lake water. Acoustic tags were then inserted intraperitoneally through a 5-10 mm incision in the abdominal wall anterior to the pelvic girdle and ~10 mm off the central midline. Fish tagged in the fall of 2023 were implanted with V6 tags (1.2 g in air; 19.3 mm length x 6.3 mm diameter; 151 dB output, 14-18 s nominal delay), whereas fish tagged in the spring of 2024 were implanted with V3 tags (0.3 g in air; 15 mm length x 4 mm diameter; 141 dB output, 10-14 s nominal delay). The incision was closed with a single 3–0 monofilament absorbable suture (Ethicon PDS II Plus polydioxanone, Ethicon US, www.ethicon.com) using a 3-2-2 surgeons knot. The sample sizes and fork lengths of the largemouth bass and northern pike in each treatment group are summarized in Table 1.

4.3.3 Analyses

The Vemco Positioning System (VPS) was used to produce fine-scale positioning estimates and horizontal position error (HPE) from telemetry data. HPE is an error estimate for each calculated position (Smith 2013) and was calculated for each tagged fish and for static V6 (n = 5) and V3 (n = 5) reference transmitters. All statistical analyses were conducted in version 4.3.2 (R CoreTeam 2024). Fish positions with HPE values > 3 were removed from the analysis, with remaining positions having a mean estimated positional error of ~1 m. Any fish with VPS positions consistently at the same location for at least two weeks were assumed to have died or lost their tags and were removed from the analysis.

Analyses were divided into two time bins for each species: 0–72 h and 0–14 days after surgery. This was done to more accurately describe both short- and intermediate-term behavioural responses to sedation and tagging. To compare previously tagged controls to newly tagged individuals, a centered timestamp was created for each tagging session, defined as the time between first and last releases of tagged fish. This timestamp was deemed the "time 0" for hours post release in control fish. Although these fish are not true "untagged" controls, tag burden (i.e., tag:body mass ratios) was estimated to be a maximum of 0.25%. Therefore, we assumed that the effects of the tag itself were negligeable and that the short-term behavioural effects of tagging subsided in the 6+ months since tagging. The use of controls allowed us to account for whole lake alterations (changes in water temperature, clarity, etc.) that may have induced behavioural changes.

First, we analyzed movement speeds by calculating the distance between consecutive VPS positions divided by the difference in time between positions. To reduce the possibility of underestimating movement speed due to missing detections, movement speeds were only calculated using steps where the elapsed time between positions was less than 10 minutes. For the first 72 hours after tagging, movement speeds were calculated from n = 309,256 positions for northern pike and from n = 212,264 positions for largemouth bass. For the two-week period after tagging, movement speeds were calculated from n = 1,551,865 positions for northern pike and from n = 955,099 positions for largemouth bass. We fit generalized additive mixed models (GAMM) with movement speed as the response variable using the *bam* function from the *mgcv* package (Wood 2011). Predictor variables included smoothing parameters for hours post release (grouped by treatment) and time of day (using cyclic cubic regression splines), as well as treatment, tagging season and total length as parametric terms. Individual fish ID was included as random effect to account for the repeated measures for each individual. Since fish were tagged with V6 tags in the fall and V3 tags in the spring, including season as a covariate allowed us to control for seasonal differences in behaviour and any differences in detection efficiencies between tag types. Models were fit with fast restricted maximum likelihood (fREML) methods with a gamma distribution and log link function. Tagging season and total length were removed in cases where they did not improve model fits ($p > 0.10$). Model fits were evaluated visually and using the function *gam.check* in the *mgcv* package.

Next, we analyzed movement types (MT). VPS positions were first separated into 5-minute segments; this timeframe was chosen to create a large number of segments while maintaining a high enough resolution to capture changes in MTs. We then used the function *as.itraj* from the package *adehabitatLT* (Calenge 2006) to define segments based on the following metrics: 1) sum of total distance travelled, 2) turning angle (relative angle), 3) movement speed and the 4) linearity ratio, defined as the distance between the first and last locations of a segment divided by the total distance (i.e., sum of each of the steps) (Heupel et al. 2012). Segments missing values for any of these four variables were removed from analysis, as well as segments with less than 3 detections. A correlation plot was produced using the *corrplot* function from *corrplot* package (Wei and Simko 2024) and was used to remove redundant variables with a correlation of > 60%. Due to high levels of collinearity between turning angle and linearity ratio, and between movement speed and distance traveled, we clustered movement types based solely on movement speed and linearity ratios. Over the 72 h post-tagging period, this created $n = 22{,}051$ segments for northern pike and $n = 17{,}284$ segments for largemouth bass. Over the two-week post-tagging period, $n = 111{,}032$ segments were created for northern pike and $n = 86{,}807$ segments were created for largemouth bass.

We then used the *kmeans* function (R CoreTeam 2024) to partition bursts into clusters using methods similar to those outlined by Bergen et al. (2022). To choose the number of clusters (i.e., k), the average silhouette widths (i.e., how close a datapoint is to datapoints of its own cluster relative to datapoints of the closest neighboring cluster) were bootstrapped with replacement from the original data set; we used $B = 100$ bootstrap samples each of size 1000 each and averaged the silhouette widths for each value of k. *K-means* clustering was then performed with 3 clusters with 10 randomly chosen initial cluster assignments.

We modeled the proportion of time fish spent exhibiting each MT using GAMMs. Predictor variables initially included smoothing parameters for hours post release (grouped by treatment) and time of day, treatment, tagging season and total length as parametric terms, as well as individual fish ID as random effect. Tagging season and total length were again removed in cases where they did not improve model fits ($p > 0.10$). Models were fit with fast restricted maximum likelihood (fREML) methods with a binomial distribution and logit link function.

4.4. Results

Overall, two northern pike ($n = 1$ MS-222; $n = 1$ TENS) were assumed to have died or lost their tags in the two-week period after tagging. These events were estimated to have occurred at ~54 h (MS-222) and ~120 h (TENS) after tagging and were identified by VPS positions being consistently detected in the same location for greater than 2 weeks.

4.4.1 Movement speed

In all groups, movement speeds changed significantly during the first 72 h after tagging (Figure 4.2; see supplement for GAMM outputs). During this 72 h period, northern pike tagged using TENS (0.053 ± 0.108 m s^{-1}) (mean ± standard deviation) were significantly slower ($t = -2.506$, $p = 0.012$) than previously tagged controls (0.064 ± 0.116 m s^{-1}), whereas pike tagged with MS-222 (0.061 ± 0.137 m s^{-1}) were not ($t = -0.847$, $p = 0.397$; Figure 2a). Model predictions indicated that the northern pike tagged using TENS return to similar movement speeds as control fish at ~30 h post-tagging (Figure 4.2a). Control largemouth bass were significantly faster (0.086 ± 0.142m s^{-1}) than those tagged with both TENS (0.081 ± 0.144 m s^{-1}) ($t = -2.564$, $p = 0.01$) and MS-222 (0.061 ± 0.105 m s^{-1}) ($t = -4.856$, $p < 0.001$) for the first 72 h after tagging (Figure 4.2b). While model predictions indicate that the largemouth bass tagged using TENS return to movement speeds similar to controls at ~40 h post-tagging, bass tagged using MS-222 remained slower throughout the entire 72 h post-tagging period (Figure 4.2b).

Movement speeds also changed significantly during the first two weeks after tagging across all treatment groups (Figure 4.3). During this period, movement speeds were similar between control northern pike (0.070 ± 0.129 m s^{-1}) and those tagged with MS-222 (0.070 ± 0.140 m s^{-1}) ($t = 0.430$, $p = 0.667$) or TENS (0.070 ± 0.159 m s^{-1}) ($t = 0.333$, $p = 0.739$; 4.3a). Movement speeds of control largemouth bass (0.087 ± 0.156 m s^{-1}) were not statistically different than those tagged with TENS (0.139 ± 0.194 m s^{-1}) ($t = 0.498$, $p = 0.619$) or MS-222 (0.105 ± 0.178 m s^{-1}) ($t = -1.440$, $p = 0.150$) during the first two weeks after tagging when accounting for the strong influence of season ($t = 3.806$; $p < 0.001$; Figure 4.3b).

4.4.2 Movement types

Although the exact values in each MT differed between species (see supplement for specific values for each species as well as GAMM model outputs), behaviours were consistently clustered into three MTs. First, MT1 was classified by high movement speeds and low–moderate linearity ratios, representing fish that were burst swimming. Second, MT2 was classified by very low movement speeds and linearity ratios, presumably representing stationary fish. Finally, MT3 was classified by low–moderate movement speeds and high linearity ratios, representing sustained swimming or cruising behaviours.

The proportion of time fish spent exhibiting each of the three MTs displayed changed significantly during the first 72 h after tagging (Figure 4.4). The MTs displayed by northern pike tagged with TENS or MS-222 were not significantly different from controls for 72 h after tagging (Table S2; Figure 4.4 a–c). In exception to MT1 (burst swimming) in TENS fish, all recently tagged largemouth bass exhibited significantly different ($p < 0.05$) MTs from controls for the first 72 h after tagging (Table S3; Figure 4.4 d–f). In general, recently tagged largemouth bass spent less time burst and sustained swimming compared to controls, spending more time stationary (Figure 4.4 d–f). Model predictions indicate that while the MTs of largemouth bass tagged using TENS began to return to control levels at ~48 h after tagging, the MTs of largemouth bass tagged using MS-222 remained different than controls for the entire 72 h period (Figure 4.4 d–f).

For the two-week post-tagging period, the proportion of segments classified as MT3 (sustained swimming) in northern pike sedated with TENS was marginally lower than that of controls ($t = -2.057$, $p = 0.040$; Figure 4.5 c). Based on model predictions, these differences only appeared to have occurred between ~100–150 h after tagging (Figure 4.5 c). The proportion of segments classified as MT2 was higher ($t = 2.917$, $p = 0.004$) in largemouth bass sedated with MS-222 compared to controls, and the proportion of segments classified as MT3 was lower in bass sedated with both MS-222 ($t = -2.146$, $p = 0.032$) and TENS ($t = -2.347$, $p = 0.019$) compared to controls for the first two weeks after tagging (Figure 4.5 e–f). Model predictions indicate that the MTs of recently tagged largemouth bass return to control levels around 150 h after tagging, regardless of treatment (Figure 4.5 e–f).

4.5 Discussion

Using acoustic telemetry and wild fish, we found that the procedure of intracoelomic tag implantation can have substantial impacts on fish movement during the first 72 h after tagging. The short-term effects (i.e., < 72 h after tagging) of tag implantation appeared to be species specific. Northern pike only had marginally lower movement speeds in fish sedated with TENS compared to controls, whereas largemouth bass sedated with either MS-222 or TENS exhibited substantial alterations in movement speed and MTs. Interspecific differences were expected given the taxonomic variation that exists in the physiological responses of fishes to sedatives, immobilization and tagging (reviewed by Cooke et al. 2011; Reid et al. 2019). However, it is notable that the movement speeds and behaviours of largemouth bass and northern pike immobilized with either method were broadly similar to one another for the first 72 h after tagging. It was instead the controls that differed between species, which was expected given that northern pike are a classic "sit and wait" ambush predator (Casselman and Lewis 1996; Craig 2008), whereas largemouth bass tend to be more active, opportunistic foragers (Hodgson and Kitchell 1987). Thus, recovering largemouth bass were more readily distinguished from more active controls, whereas recovering northern pike likely appeared similar to control fish that were likely ambushing prey (i.e., remaining stationary). Future experiments using acoustic tags with acceleration sensors could help further separate ambushing behaviours from those of recovering fish.

Despite the short-term impacts of tagging on movements, model predictions suggest that both largemouth bass and northern pike recovered within ~100-200 h (4-8 days) of tagging, regardless of the tagging method used. In largemouth bass, there was a greater proportion of segments classified as stationary rather than as sustained swimming during the initial ~100-150 h after tagging. As similar behavioural clusters as MT3 have been proposed as searching behaviours (Landry et al. 2019; McLean et al. 2014), these trends may represent a transition back to typical largemouth bass foraging behaviour (i.e., actively searching for food).

Overall, recovery patterns were similar between tagging methods. As the physiological effects of electro-immobilization in fishes are often similar to MS-222 (e.g., Durhack et al. 2020; Trushenski et al., 2012a, 2012b), the similarity in recovery patterns between treatments is not surprising. However, many of the physiological side effects of these treatments subside within 72 h of exposure (Gomulka et al. 2008; Phuong et al. 2017; Reid et al. 2022; Trushenski et al. 2012a; 2012b), which does not explain the prolonged recovery periods we observed. While some research has shown lingering physiological effects of exposure to MS–222 for up to 168 h (Matsche 2013), it is most likely the case that fish were rather recovering from the stress of being captured, handled, tagged, and released as opposed to the type of immobilization technique having an important effect. Although the role of electro-immobilization in inducing analgesia/sensory loss is debatable, the evidence of similar survival and recovery patterns of fish tagged while immobilized with TENS vs. MS-222 should be considered by animal care committees.

The physiological effects of intracoelomic tag implantation have been studied extensively (reviewed in Cooke et al. 2011; Matley et al. 2024b), with the effects of tagging being highly variable in both severity and duration. In comparison, very little work has been done to examine the time required to recover from tag implantation in the wild. In one study, common bream (*Abramis brama*) travelled further than previously tagged fish for the first 5 days after tagging, with no differences occurring 6–10 days after tagging (Gardner et al. 2015). While some studies have justified shorter recovery periods (i.e., less than 24 h) based on the recovery of equilibrium and typical behaviours in captivity (e.g., Pon et al. 2009), fish behaviour cannot be fully recreated in captivity (Fahlman et al. 2020; Magnhagen 2012). Although the consistency in recovery times between Gardner et al. (2015) and ours suggests that 100–200 h (~4–8 d) recovery periods may be sufficient, substantial taxonomic variation exists in the physiological and behavioural responses fishes to sedatives, immobilization techniques and tagging (Cooke et al. 2011; Reid et al. 2019; Topic Popovic et al. 2012). Therefore, we caution against the extrapolation of these behavioural responses to other species, even those in similar taxonomic groups. More work is needed assessing recovery from tag implantation in the wild using different tag sizes, species, and environments before such conclusions can be drawn.

In summary, our results indicate that intracoelomic tagging produces short-term (< 72 h after tagging) alterations in the movements of both northern pike and largemouth bass, regardless of being sedated or electro-immobilized. Despite these initial effects, both species appeared to recover to baseline movement patterns approximately 100–200 h after tagging. Electro-immobilization offers the advantages of its ease of use, lack of chemical disposal, rapid induction and recovery times, as well as allowing fish to be released and consumed by humans immediately (e.g., Chiba et al. 2006; Jennings and Looney 1998; Trushenski and Bowker 2012). Given the evidence that recovery patterns of electro-immobilized fish are similar to those sedated with MS-222 in the wild, our work supports electro-immobilization as a viable alternative for MS-222. We also support further investigation of electro-immobilization as a viable alternative for MS-222 from animal care committees.

4.6. Figures and tables

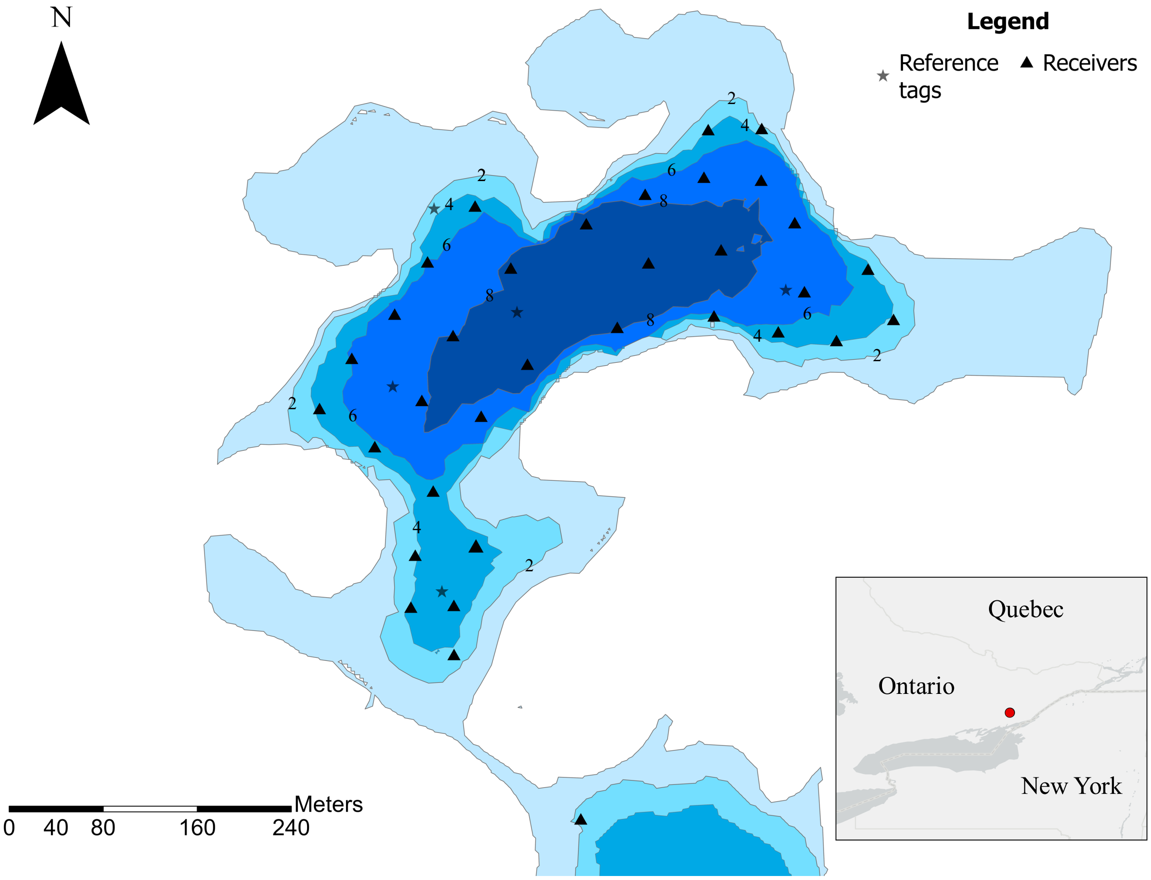

Figure 4.1. Bathymetry of Lindsay Lake (44.5373°N, 76.3897°W) and the positions of Innovasea HR3 receivers and reference tags used to study post-tagging behaviours of largemouth bass (*Micropterus nigricans; n* = 54) and northern pike (*Esox lucius; n* = 48) from May 2023 – May 2024. Numbers represent contour lines (in meters).

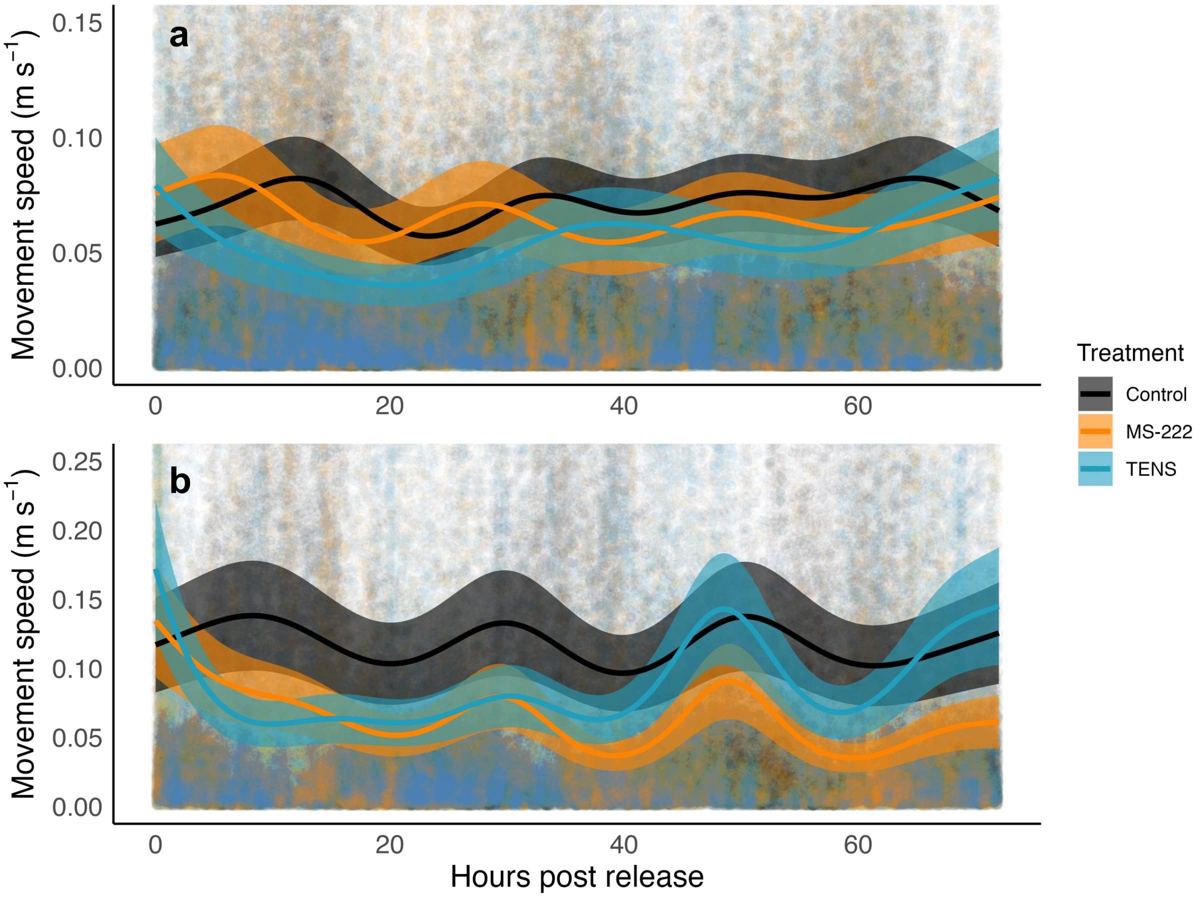

Figure 4.2. Movement speed of a) northern pike (*Esox lucius; n* = 48) and b) largemouth bass (*Micropterus nigricans; n* = 54) for 72 hours after intracoelomic tagging via sedation with MS-222 or electro-immobilization with TENS. Control fish were tagged ~6 months prior and were assumed to have fully recovered from tagging. Overlaid means ± 95% confidence intervals represent model predictions from generalized additive mixed models (Table A3.1). Movement speeds exceeding 0.15 m s^{-1} (a) and 0.25 m s^{-1} (b) were omitted from plotting to visualize model predictions.

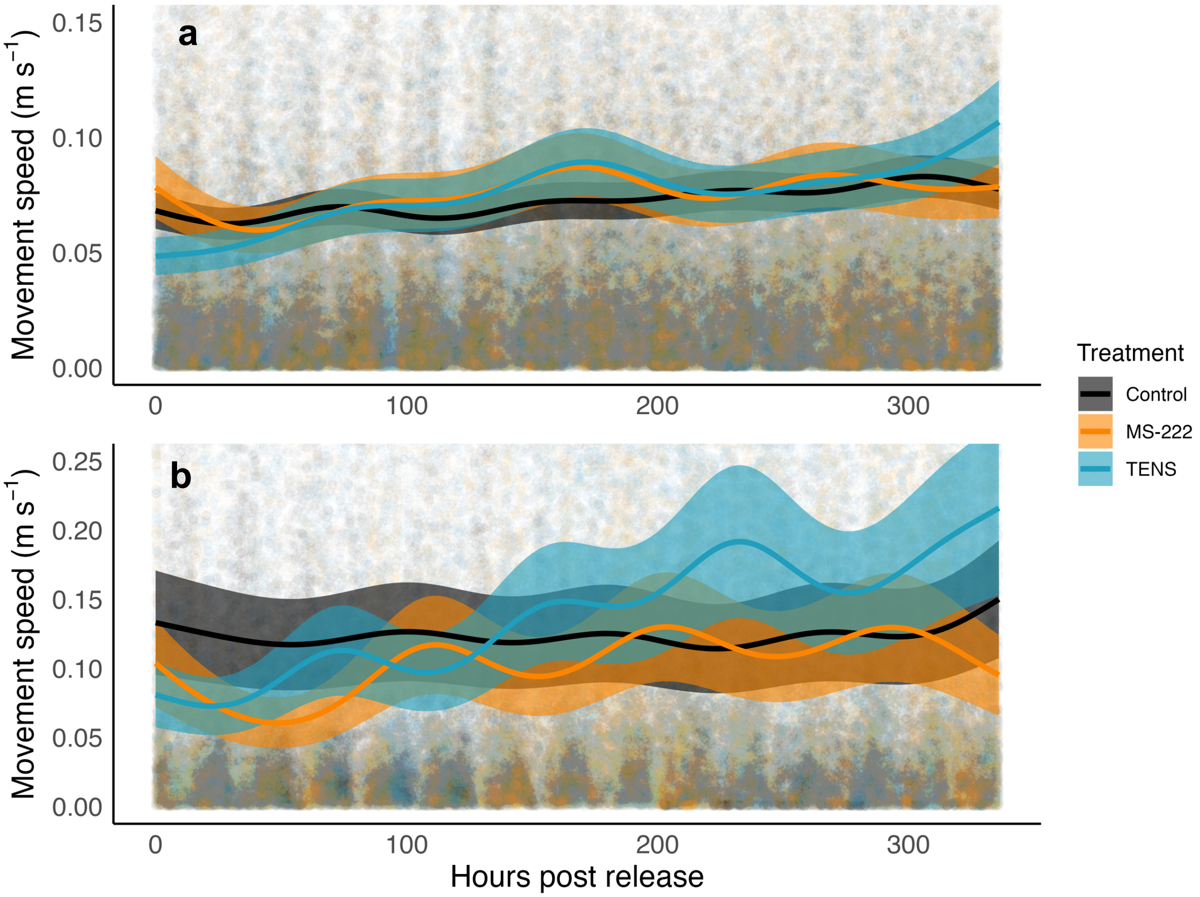

Figure 4.3. Movement speed of a) northern pike (*Esox lucius; n* = 48) and b) largemouth bass (*Micropterus nigricans; n* = 54) for 2 weeks after intracoelomic tagging via sedation with MS-222 or electro-immobilization with TENS. Control fish were tagged ~6 months prior and were assumed to have fully recovered from tagging. Overlaid means ± 95% confidence intervals represent model predictions from generalized additive mixed models (Table A3.1). Movement speeds exceeding 0.15 m s^{-1} (a) and 0.25 m s^{-1} (b) were omitted from plotting to visualize model predictions.

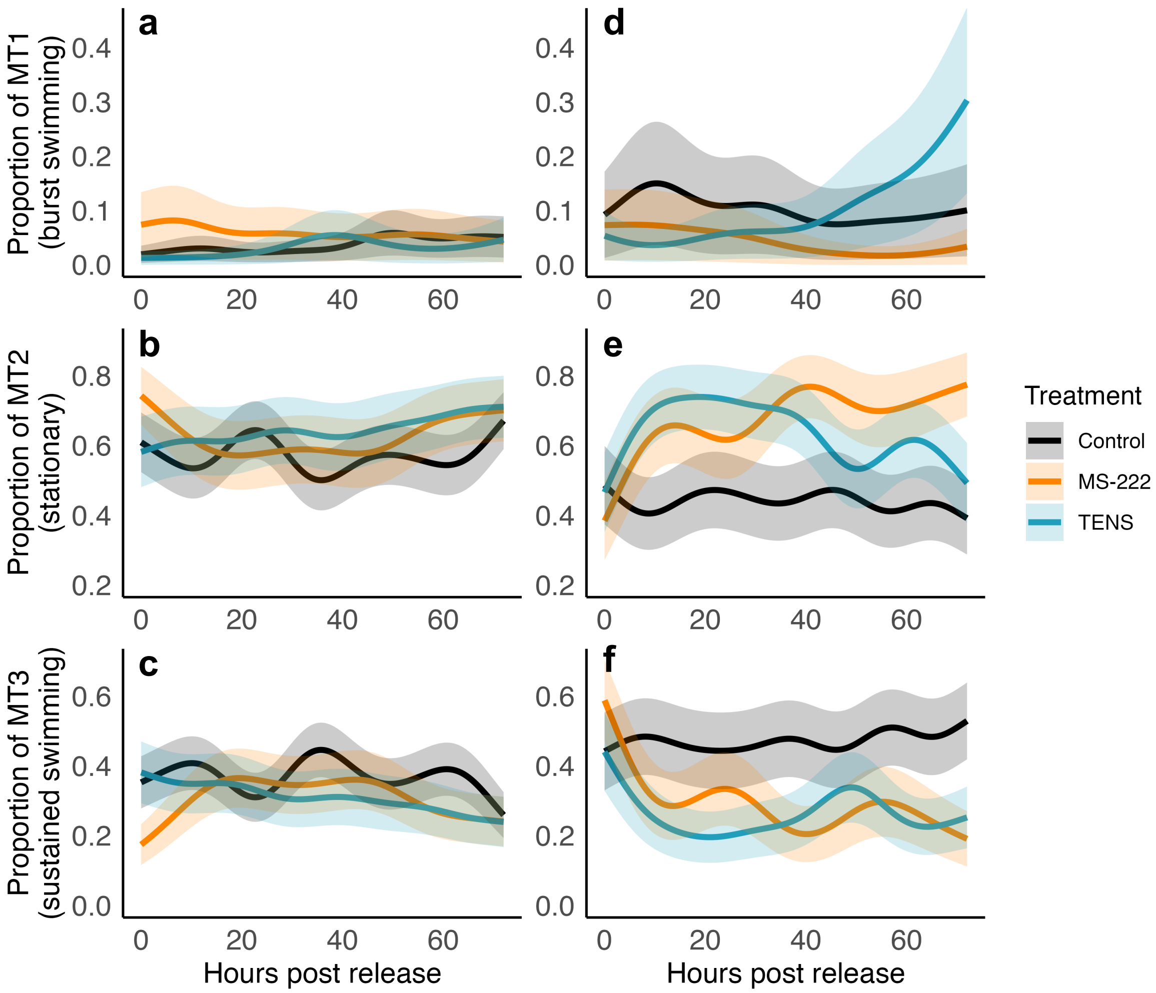

Figure 4.4. Predicted movement types of (a–c) northern pike (*Esox lucius; n* = 48), and (d–f) largemouth bass (*Micropterus nigricans; n* = 54) for 72 hours after intracoelomic tagging via sedation with MS-222 or electro-immobilization with TENS. MT1 was classified by high movement speeds and low–moderate linearity ratios, representing burst swimming. MT2 was classified by very low movement speeds and linearity ratios, representing stationary fish. Finally, MT3 was classified by low–moderate movement speeds and high linearity ratios, representing sustained swimming. Control fish were tagged ~6 months prior and were assumed to have fully recovered from tagging. Overlaid means ± 95% confidence intervals represent model predictions from generalized additive mixed models (Tables A3.2, A3.3)

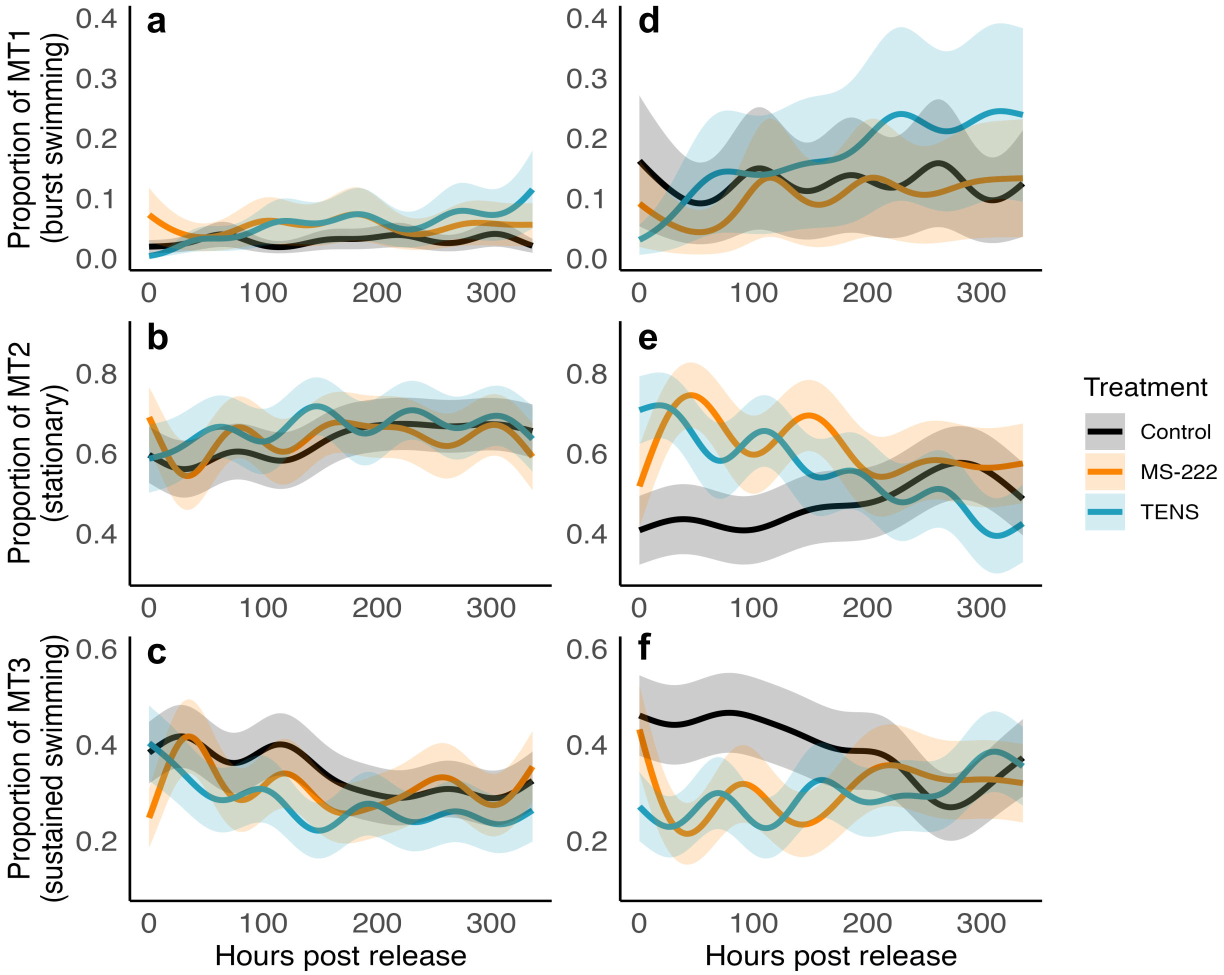

Figure 4.5. Predicted movement types of (a–c) northern pike (*Esox lucius; n* = 48), and (d–f) largemouth bass (*Micropterus nigricans; n* = 54) for 72 hours after intracoelomic tagging via sedation with MS-222 or electro-immobilization with TENS. MT1 was classified by high movement speeds and low–moderate linearity ratios, representing burst swimming. MT2 was classified by very low movement speeds and linearity ratios, representing stationary fish. Finally, MT3 was classified by low–moderate movement speeds and high linearity ratios, representing sustained swimming. Control fish were tagged ~6 months prior and were assumed to have fully recovered from tagging. Overlaid means ± 95% confidence intervals represent model predictions from generalized additive mixed models (Tables A3.4, A3.5).

Table 4.1. Tagging period, number of individuals and total length (mm) of largemouth bass (*Micropterus nigricans*) and northern pike (*Esox lucius*) tagged per experimental treatment. Control fish represent fish tagged months prior that were assumed to have fully recovered from tagging. Control fish for the Sep 28 – Oct 2, 2023 tagging period were tagged between May 04–06, 2023 (immobilized using TENS). Control fish for the May 01 – 07, 2024 tagging period were treatment fish tagged between Sep 28 – Oct 2, 2023. Fish in each tagging period were pooled for analysis.

Tagging period	**Species**	**Treatment**	**Total length (mm), mean ± SD (range)**	**Number of individuals**
Sep 28 – Oct 2, 2023	Northern pike	Control	644 ± 63 (545–735)	15
		TENS	624 ± 62 (515–665)	5
		MS-222	628 ± 49 (568–691)	5
	Largemouth bass	Control	430 ± 33 (376–481)	15
		TENS	421 ± 24 (387–445)	5
		MS-222	406 ± 58 (315–488)	6
May 01 – 07, 2024	Northern pike	Control	625 ± 55 (515–691)	9
		TENS	688 ± 32 (654–740)	7
		MS-222	660 ± 47 (595–705)	7
	Largemouth bass	Control	402 ± 39 (315–445)	9
		TENS	418 ± 11 (396–435)	11
		MS-222	425 ± 45 (346–477)	8
Total	Northern pike	Control	637 ± 60 (515–735)	24
		TENS	662 ± 55 (515–740)	12
		MS-222	647 ± 48 (595–705)	12
	Largemouth bass	Control	420 ± 37 (315–481)	24
		TENS	419 ± 15 (387–445)	16
		MS-222	417 ± 50 (315–488)	14

Chapter 5: General discussion

This thesis addressed potential sources of bias in electronic tagging studies to advance the methods used by future studies. I first provided the most comprehensive review and meta-analysis of intracoelomic tagging effects in fishes to date (Chapter 2), summarizing the existing literature and assessing the extent to which the research gaps identified by Cooke et al. (2011) have been filled in the *ca*. 15 years since. This chapter also included the first ever large-scale meta-analysis on tagging effects, examining the 2% rule using empirical evidence from a broad representation of all published studies. I then assessed the performance of a newly miniaturized predation-sensing acoustic transmitter (Chapter 3), demonstrating that these transmitters can largely mitigate predation biases by correctly identifying most predation events without false positives. Using a fine scale telemetry array, I finally examined if sedation via MS-222 and electro-immobilization via TENS alter the behaviours of fishes in the wild following tagging, and identified the time required for fish to re-establish normal behaviour following transmitter implantation (Chapter 4). Together, these chapters should help reduce bias in future tagging studies, and assist fishery managers and policy makers in understanding the reliability of data yielded from electronic tagging studies.

5.1 Findings and implications:

Prior to the research presented in Chapter 2, the 2% rule had not been empirically evaluated using a broad representation of fish species. It had been suggested that the 2% rule could be substantially extended (e.g., Smircich and Kelly 2014), with several papers demonstrating that tag burdens of 5-10% often did not have negative effects on fishes (e.g., Brown et al. 1999). My meta-analysis of tagging effects (Chapter 2) demonstrated that while survival and tag retention remain above 90% on average with tag burdens below ~3–4%, there is substantial heterogeneity between studies. While my results do suggest that the 2% rule is somewhat conservative, greatly extending the 2% rule without empirical evidence of species-specific tagging effects can be dangerous given the variability in tagging success between studies. This chapter encouraged the incorporation of some aspect of tagging validation in every study, especially when species-specific data relating to tagging effects is unavailable. With the ongoing miniaturization of acoustic transmitters, it is becoming increasingly feasible to tag fishes without imposing substantial tag burden. However, larger tags still offer greater performance (i.e., greater battery life and detection range). Therefore, while using the smallest tags possible is preferred to avoid unwanted tagging effects, tag burdens up to ~3–4% appear to offer a compromise between tag performance and unwanted tagging effects.

Beyond tag burden, Chapter 2 provides other important considerations to improve tagging protocols. For example, absorbable monofilament sutures either performed better or similarly to all other closure methods across the literature and should be used when sutures are required. I also identified that almost all studies found that surgeon experience had some effect on post-tagging outcomes. Therefore, training programs for surgical tagging (including feedback training) hold promise for reducing unwanted tagging effects in telemetry studies.

Chapter 3 then assessed the performance of a newly miniaturized acid-based predation-sensing acoustic transmitter (Innovasea V3D). Given the conclusions of Chapter 2 regarding the importance of minimizing tag burden, these miniaturized tags can help researchers study the predation of small fishes. For example, enormous amounts of resources are dedicated to rehabilitating salmon migrations (Jaeger and Scheuerell 2023) with smolt survival being an important driver of adult return rates and population productivity (Daniels et al. 2018). As predation can be one of the main drivers of smolt survival (Daniels et al. 2019), my results suggests that researchers studying smolt predation can be confident that the majority (i.e., ~90%) of predation events are identified and that false positives are unlikely to occur. The performance of V3D tags in cold (i.e., < 12 °C) water has important implications however: While tags are likely to still indicate most predation events at these cold temperatures, the increased duration and variability in signal lag could influence the conclusions derived from such studies. For example, researchers will likely have difficulties 'back-tracing' the time and location of predation events, meaning that predation hotspots will difficult to identify. Such limitations need to be considered in study designs.

Using a whole-lake telemetry system, I compared the post-tagging behaviours of largemouth bass and northern pike sedated with MS-222 or electro-immobilized with TENS. I demonstrated that recovery occurs within 100-200 h of tagging, regardless of the species or immobilization technique used. While substantial literature exists regarding induction periods and physiological side effects, this chapter provides new evidence of the validity of electro-immobilization as an alternative to chemical sedation using wild fish. I also provide evidence that the stress of capture, handling, and tagging likely has greater effects on recovery compared to the type of immobilization technique used. Therefore, utilizing the best practices discussed in Chapter 2 (e.g., minimizing tag burden, using experienced surgeons, absorbable monofilament sutures, etc.) should likely be of greater focus in tagging studies.

Chapter 4 also has important implications for the censoring of telemetry data. Several tagging studies have released fish and began using data collected within 2-48 h of tagging (e.g., Enders et al. 2007; Pon et al. 2009; Scruton et al. 2007), often without describing if and how recovery was quantified. While there is substantial interspecific variation in the responses of fishes to tagging, our results and those of Gardner et al. (2015) suggest that recovery periods longer than 48 h are likely required. However given the paucity of species-specific data regarding the recovery of fishes from tagging in the wild, I recommend censoring at least the first week of data to reduce the risk of behaviours being altered by tagging procedures.

5.2 Future research directions

Despite reviewing tagging effects in 295 studies, small sample sizes were common to most families. Before accurate family-based predictions of tagging effects can be made, additional research in poorly studied families is needed. For example, tag dimensions may be more important for predicting tagging effects in fishes with small body cavities relative to their mass (e.g., Moser et al. 2007; Robinson et al. 2021). However, there was insufficient data on the Petromyzontidae and Anguillidae (i.e., taxa with small body cavities relative to their mass) to be grouped as individual families in my analyses. Future studies using these specific taxa would be particularly useful for understanding the drivers of tagging effects, as well as in additional taxa with varying body morphology (e.g., compressiform fishes such as the genus Lepomis).

My review of the tagging effects literature identified other important areas for future study. First, the roles of sex, reproductive status, tag coatings, sterility and antibiotics in tagging success remain poorly understood. Given the evidence that foreign body responses play a role in tag expulsion, exploring immune responses in greater detail may help us better understand what scenarios lead to tag expulsion. This is particularly important since only a modest portion of the variability ($R^2 = 0.14$) in tag retention was explained by the predictors used in my analysis.

Studying the performance of V3D tags at low temperatures using species with different thermal performance curves for digestion than largemouth bass (a warmwater predator) would be useful. Since temperature is a strong driver of digestion speed in fishes (Bromley 1994), the performance of V3D tags may vary considerably when consumed by different taxa (e.g., salmonids that spend much of their lives at temperatures below 10°C). Indeed, consumption by cold-adapted predators is probably more likely in winter temperatures than is consumption by warmwater species like largemouth bass. The prolonged retention of V3D tags in the GI tract of predators may also relate to variation in gastrointestinal tract morphology. Therefore, future studies could explore the drivers of V3D tag retention times (potentially using inexpensive 'dummy' tags with individual IDs) using a variety of taxa.

Since there is substantial taxonomic variation in the physiological responses of fishes to sedation, electro-immobilization and tagging (reviewed by Cooke et al. 2011; Priborsky and Velisek 2018; Reid et al. 2019), it is logical that interspecific variation in behavioural recovery patterns from tagging would also occur. Before generalizations can be make about the time required for fishes to recover from tagging, assessing recovery in a variety of taxa in the wild is necessary. Furthermore, we only tagged predatory species in Chapter 4. While prolonged recovery patterns may not be particularly dangerous for large predatory species, behavioural alterations could potentially increase the susceptibility of smaller fishes to predation. Future studies using prey species and predation-sensing tags would therefore be useful. Since salmonids are the most commonly tagged taxa in acoustic telemetry studies (Matley et al. 2022) and are heavily predated as smolts (Daniels et al. 2019), this taxa may be a good start for future research.

Future studies should also explore additional chemical sedatives and electro-immobilization techniques beyond MS-222 and TENS. For example, a eugenol-based chemical sedative, AQUI-S (AQUI-S®, AQUI-S New Zealand, Ltd., Lower Hutt, NZ), is now available as an Investigational New Animal Drug with U.S. Fish and Wildlife Service approval. As the mechanisms of action of AQUI-S are not clearly understood (Calabrese et al. 2024), the behavioural responses of wild fishes to AQUI-S are unknown and represent an important avenue for future work. Furthermore, while TENS immobilizes fishes via continuous applications of pulsed low-voltage currents, electrostunning uses brief applications (e.g., 3–5 s) of high voltages currents to induce immobilization (Reid et al. 2019). Since electrostunning can yield different physiological effects and recovery times compared to TENS (reviewed by Reid et al. 2019), it would be useful to see if this translates to altered recovery patterns in the wild. The fishes used in tagging studies are sometimes captured via electrofishing (e.g., Petty et al. 2012). Although the mechanisms of electrostunning are presumably the same mechanisms underlying electrofishing (Reid et al. 2019), it would useful to understand how recovery periods are affected by the potentially compounding stressors of electrofishing and subsequent tagging (both using chemical sedatives and electro-immobilization).

5.3 Conclusions

Although electronic tagging studies hold great promise in informing EAFM, several barriers continue to hinder their use in addressing key management questions. If findings from electronic tagging studies are to be widely applied, fishery managers and policy makers need transparent evidence about if and how electronic tagging affects fishes. In an effort to advance the methods used by future studies and improve data reliability, this thesis addressed potential sources of bias in electronic tagging studies. I reviewed and analyzed the intracoelomic tagging effects literature in fishes, providing important recommendations for future studies. I also demonstrate how newly miniaturized predation-sensing transmitters can be used to mitigate predation biases in tagging studies. Finally, I examined how sedation via MS-222 and electro-immobilization via TENS alter the behaviours of fishes in the wild following tagging, as well as the time required for fish to re-establish normal behaviour following transmitter implantation. Together, this knowledge will be important for designing future electronic tagging studies, as well as for fishery managers and policy makers aiming to understand and apply the findings from acoustic telemetry studies.

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Appendix 1: Supplementary material for Chapter 2

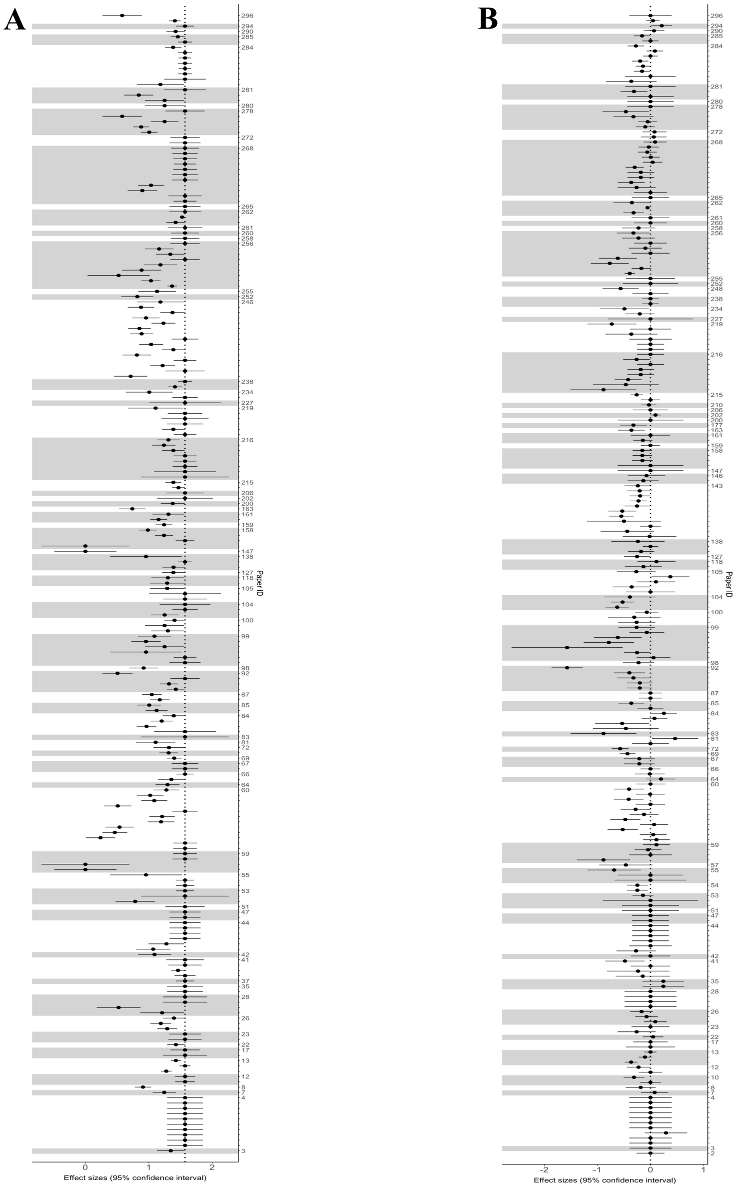

Figure A1.1. Forest plot of effect sizes and corresponding 95% confidence intervals for (A) tag retention and (B) survival. Unique studies are represented by a number ("Paper ID"; see Table A1.1 for paper details). For studies that had multiple experimental trials, individual effect sizes are represented by ticks following the paper ID. Effect sizes were calculated across 74 studies and 215 individual trials for tag retention and 81 studies and 226 individual trials for survival. Data was extracted on April 16, 2024.

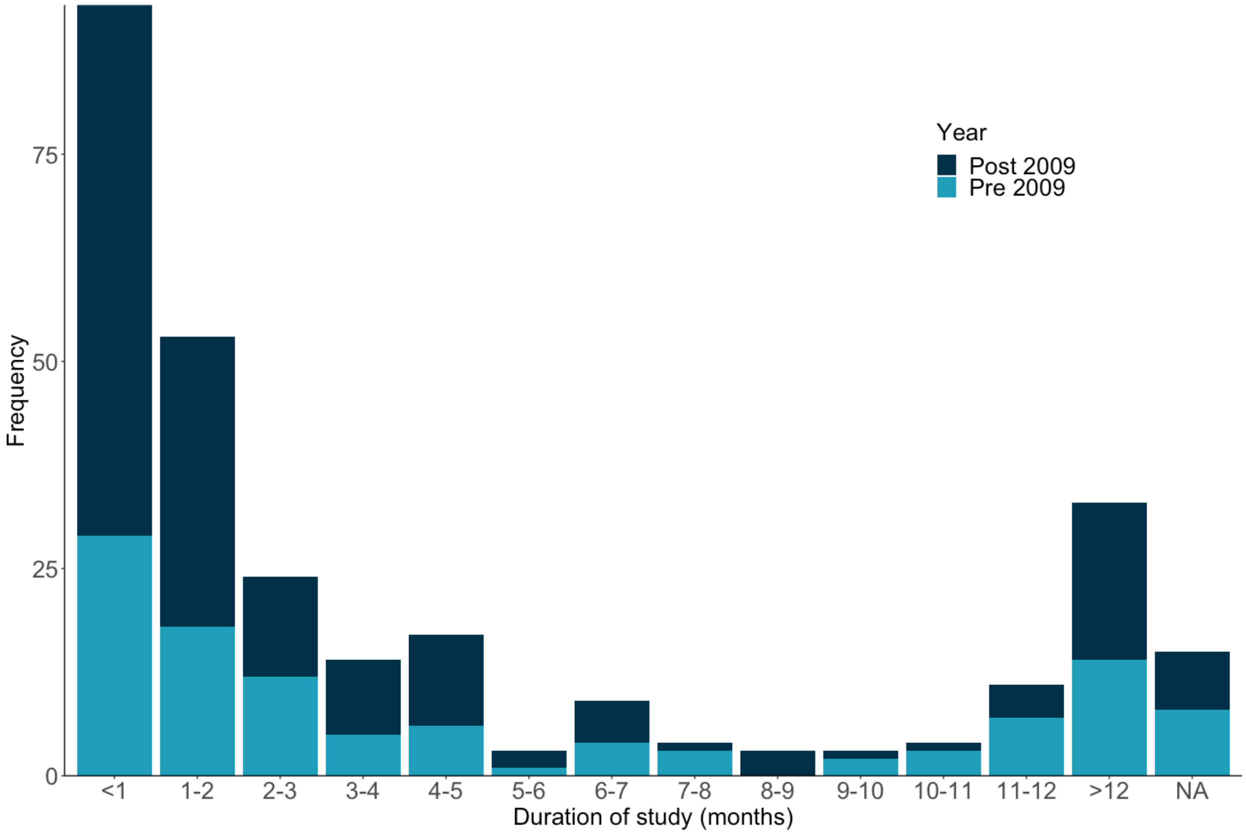

Figure A1.2. Patterns in the duration of studies examining intracoelomic tagging effects in fishes. For studies with experimental trials of varying durations, the study period was standardized to match the duration of the longest trial. Data was extracted from *n* = 295 articles on April 16, 2024; we excluded articles where study periods were not provided.

Table A1.1: The list of papers reviewed and relevant details can be found here:

https://doi.org/10.6084/m9.figshare.28810679.v1

Table A1.2. Unscaled *p* values for predictors fit to tag retention data from *n* = 74 studies using random forest algorithms. "% IncMSE" is the change in mean square error with randomly permuted variables and "IncNodePurity" is the change in the homogeneity of the groups created during random forest modelling. Bolded rows indicate statistical significance ($p < 0.05$).

Predictor	%IncMSE	IncNodePurity
Family	**0.040**	0.149
Trial duration	**0.010**	**0.020**
Temperature	0.376	0.931
Surgery type	0.505	1.000
Suture type	0.149	0.307
Tag:fish mass	**0.040**	**0.010**
Body mass	0.475	0.842
Fork length	0.257	0.644
Incision size	0.574	0.960
Tag:fish length	0.356	0.832
Tag:fish volume	0.089	**0.020**

Table A1.3. Unscaled *p* values for predictors fit to survival data from *n* = 81 studies using random forest algorithms. "% IncMSE" is the change in mean square error with randomly permuted variables and "IncNodePurity" is the change in the homogeneity of the groups created during random forest modelling. Bolded rows indicate statistical significance ($p < 0.05$).

Predictor	%IncMSE	IncNodePurity
Family	0.168	0.297
Trial duration	0.069	0.139
Temperature	0.099	0.188
Surgery type	0.861	0.842
Simplified suture type	0.297	0.683
Tag:fish mass	0.079	**0.010**
Fish mass	0.386	0.911
Fork length	0.248	0.634
Mean incision size	0.248	0.891
Tag:fish length	0.545	0.822
Tag:fish volume	0.248	**0.010**

Appendix 2: Supplementary material for Chapter 3

Figure A2.1. Surgery setup used for the acoustic tagging of rainbow trout (*Oncorhynchus mykiss*) with V3D predation tags.

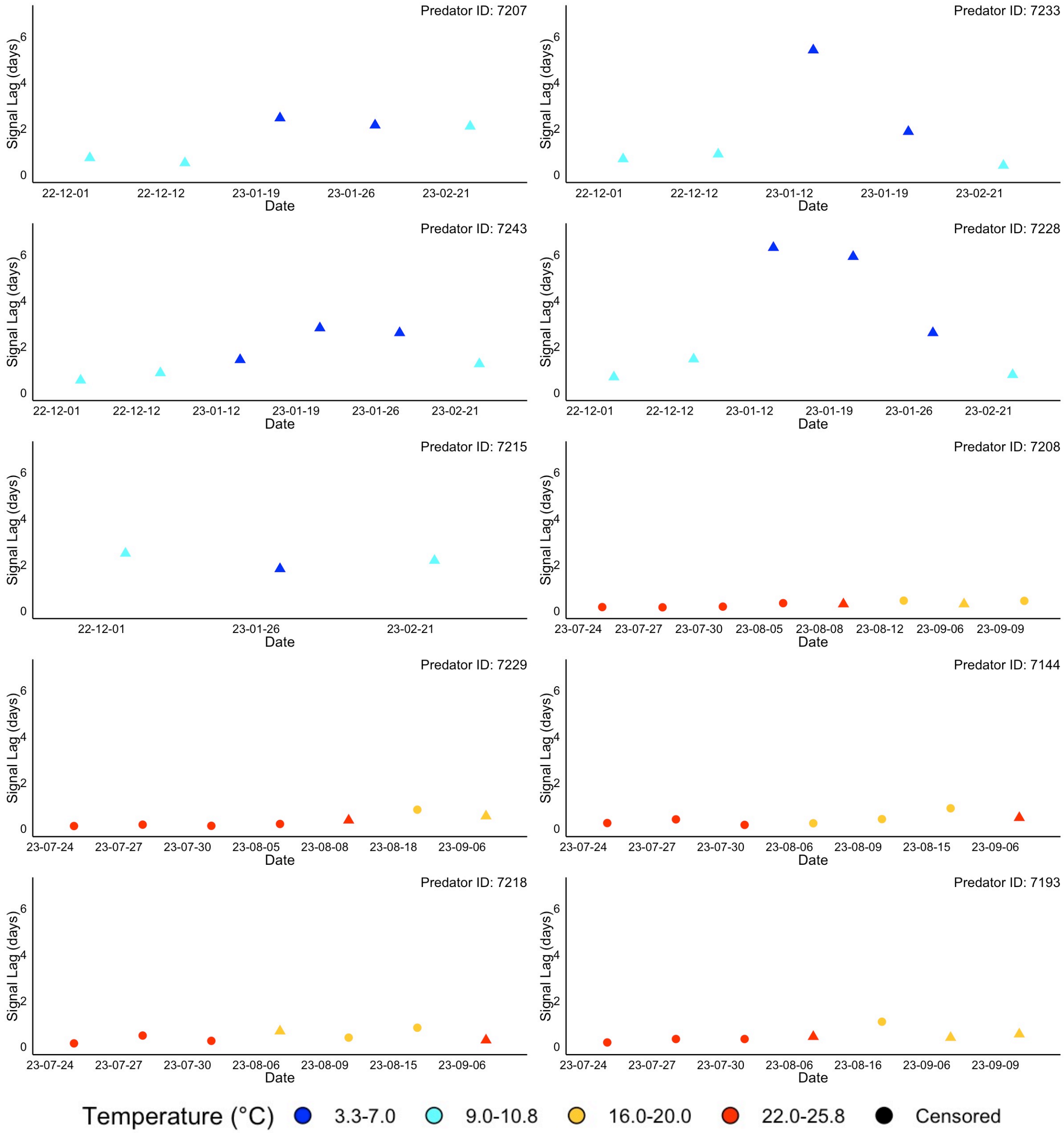

Figure A2.2. Signal lag data of V3D predation tags at different water temperatures per individual predator. Predation tags were surgically implanted in juvenile rainbow trout (*Oncorhynchus mykiss*) which were fed to largemouth bass (*Micropterus nigricans*). Triangular symbols represent trials where force-feeding was used.

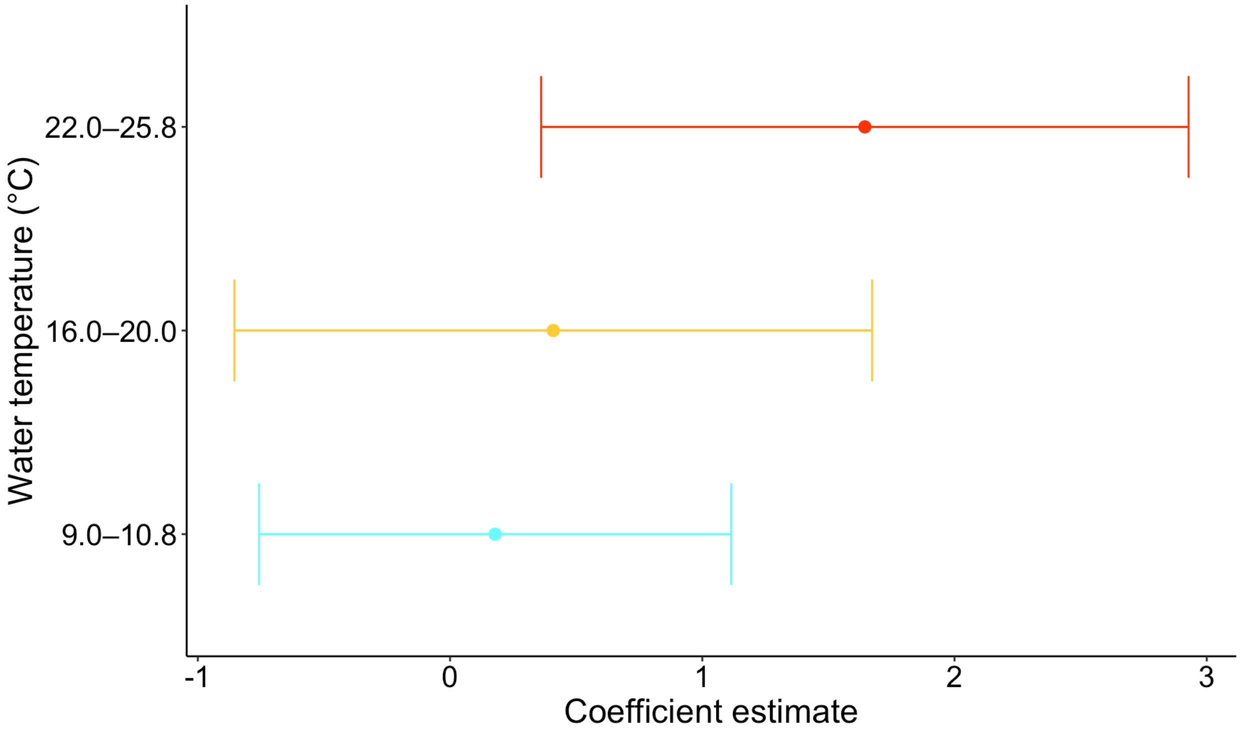

Figure A2.3. Coefficient estimates (i.e., log hazard ratios) of a mixed effects Cox model, which represents the effects of water temperature on tag retention periods relative to the baseline level of 3.3-7.0°C; larger coefficients represent a greater instantaneous probability of tag egestion relative to the baseline level. Error bars represent the 95% confidence interval of the coefficient.

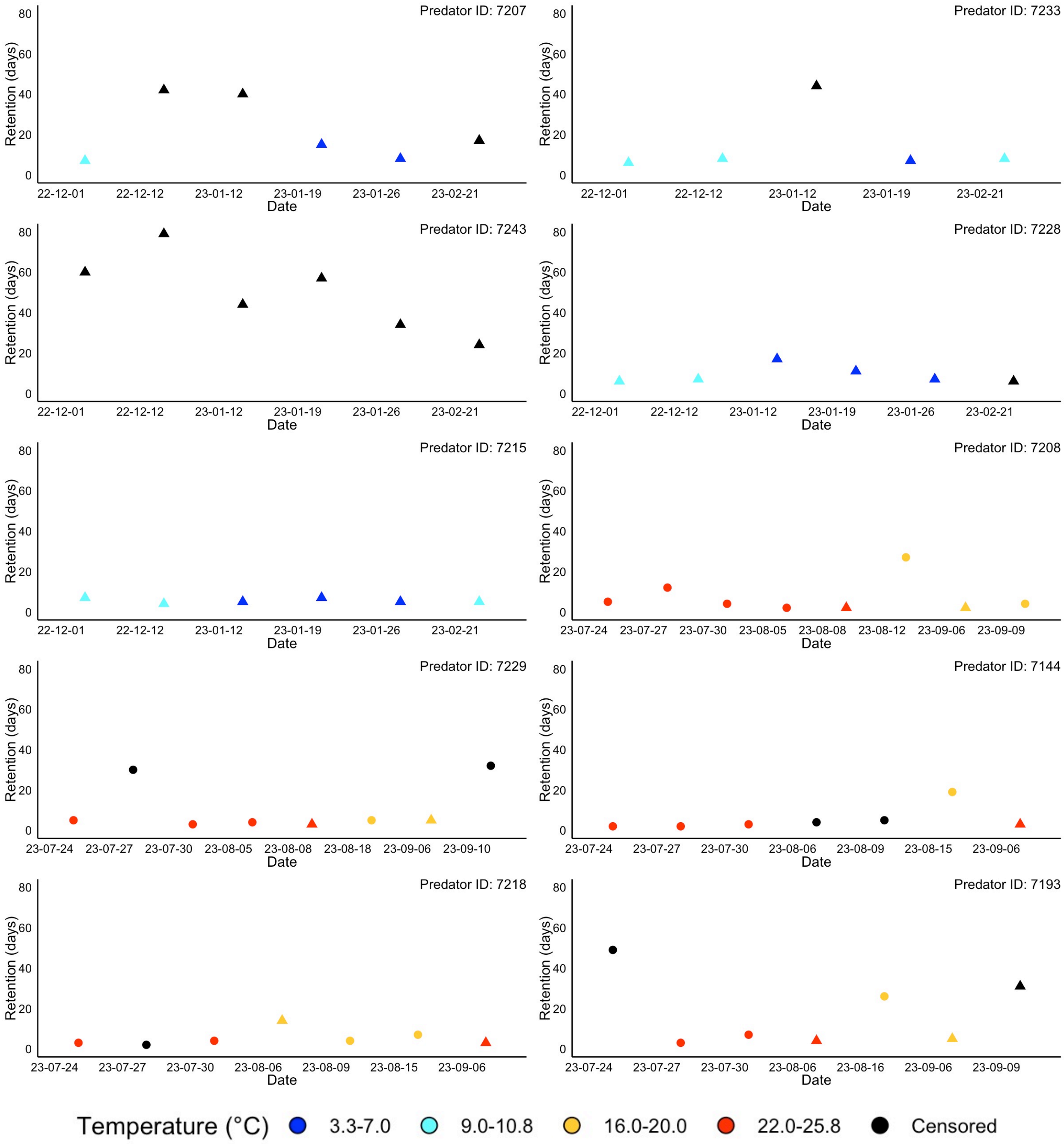

Figure A2.4. Tag retention data of V3D predation tags at different water temperatures per individual predator. Predation tags were surgically implanted in juvenile rainbow trout (*Oncorhynchus mykiss*) which were fed to largemouth bass (*Micropterus nigricans*). Triangular symbols represent trials where force-feeding was used; black symbols were censored in analysis.

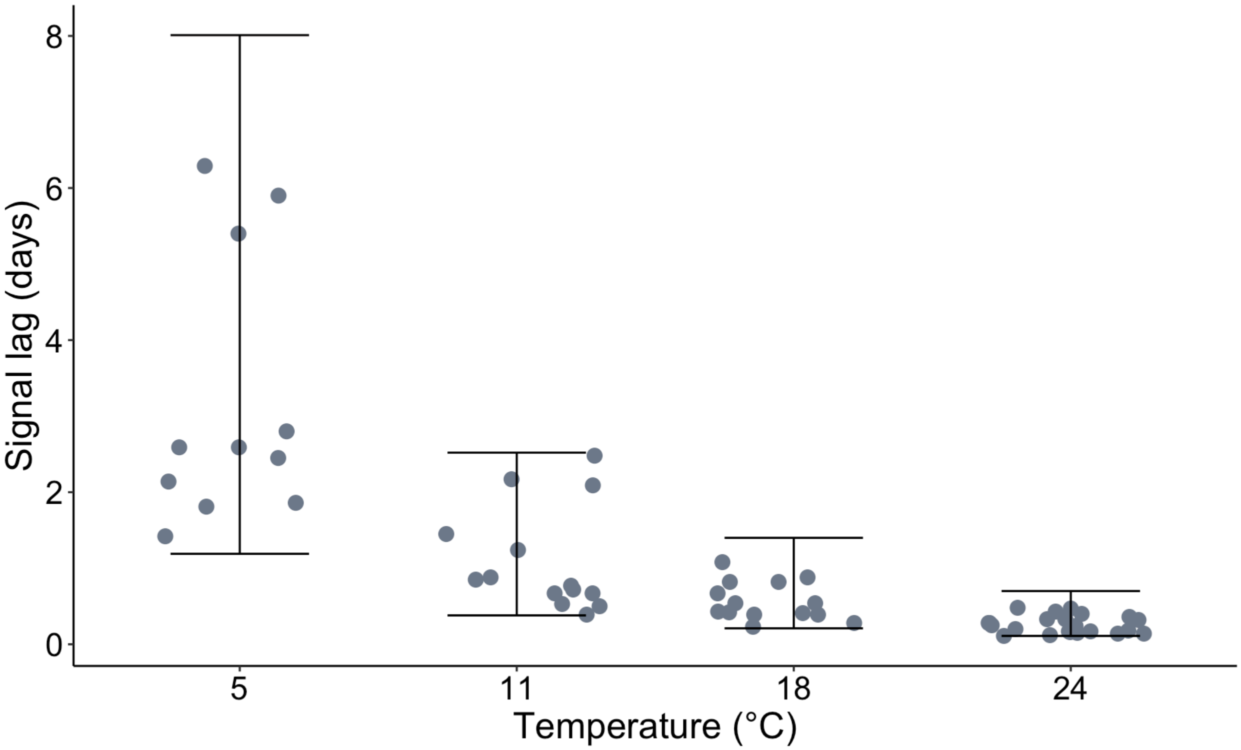

Figure A2.5. Prediction intervals generated by the best-fit model (model ii; Table 3.2) for signal lag data from V3D predation tags. Predation tags were surgically implanted in juvenile rainbow trout (*Oncorhynchus mykiss*) which were fed to largemouth bass (*Micropterus nigricans*). There were statistical differences signal lag between all water temperatures ($p < 0.05$; Table A2.2).

Table A2.1. Pairwise differences between model terms for signal lag times of V3D predation tags at various water temperatures based on estimated marginal means of the best-fit model (model ii; Table 2). *E* = estimated coefficients. *SE* = standard error. *df* = degrees of freedom. *z* = z ratio. *p* = *p* value.

Temperatures (°C)	*E*	*SE*	*df*	*z*	*p*
3.3–7.0 vs. 9.0–10.8	1.147	0.180	inf	6.354	<0.001
3.3–7.0 vs. 16.0–20.0	1.732	0.223	inf	7.765	<0.001
3.3–7.0 vs. 22.0–25.8	2.419	0.217	inf	11.161	<0.001
9.0–10.8 vs. 16.0–20.0	0.585	0.214	inf	2.737	0.032
9.0–10.8 vs. 22.0–25.8	1.272	0.211	inf	6.035	<0.001
16.0–20.0 vs. 22.0–25.8	0.687	0.152	inf	4.518	<0.001

Table A2.2. Pairwise differences between model terms for tag retention times of V3D predation tags at various water temperatures. Comparisons are based on estimated marginal means of the Cox mixed effects model. *E* = estimated coefficients. *SE* = standard error. *df* = degrees of freedom. *z* = z ratio. *p* = *p* value.

Temperatures (°C)	*E*	*SE*	*df*	*z*	*p*
3.3–7.0 vs. 9.0–10.8	-0.179	0.478	inf	-0.374	1.000
3.3–7.0 vs. 16.0–20.0	-0.409	0.645	inf	-0.634	1.000
3.3–7.0 vs. 22.0–25.8	-1.644	0.655	inf	-2.511	0.060
9.0–10.8 vs. 16.0–20.0	-0.231	0.650	inf	-0.355	1.000
9.0–10.8 vs. 22.0–25.8	-1.466	0.667	inf	-2.199	0.112
16.0–20.0 vs. 22.0–25.8	-1.235	0.445	inf	-2.778	0.033

Appendix 3: Supplementary material for Chapter 4

Figure A3.1. Surgery setup used for the intracoelomic implantation of acoustic transmitters in northern pike (*Esox lucius*) and largemouth bass (*Micropterus nigricans*). In this example, a largemouth bass is being immobilized using TENS. TENS pads were removed for trials using MS-222 as the sedative.

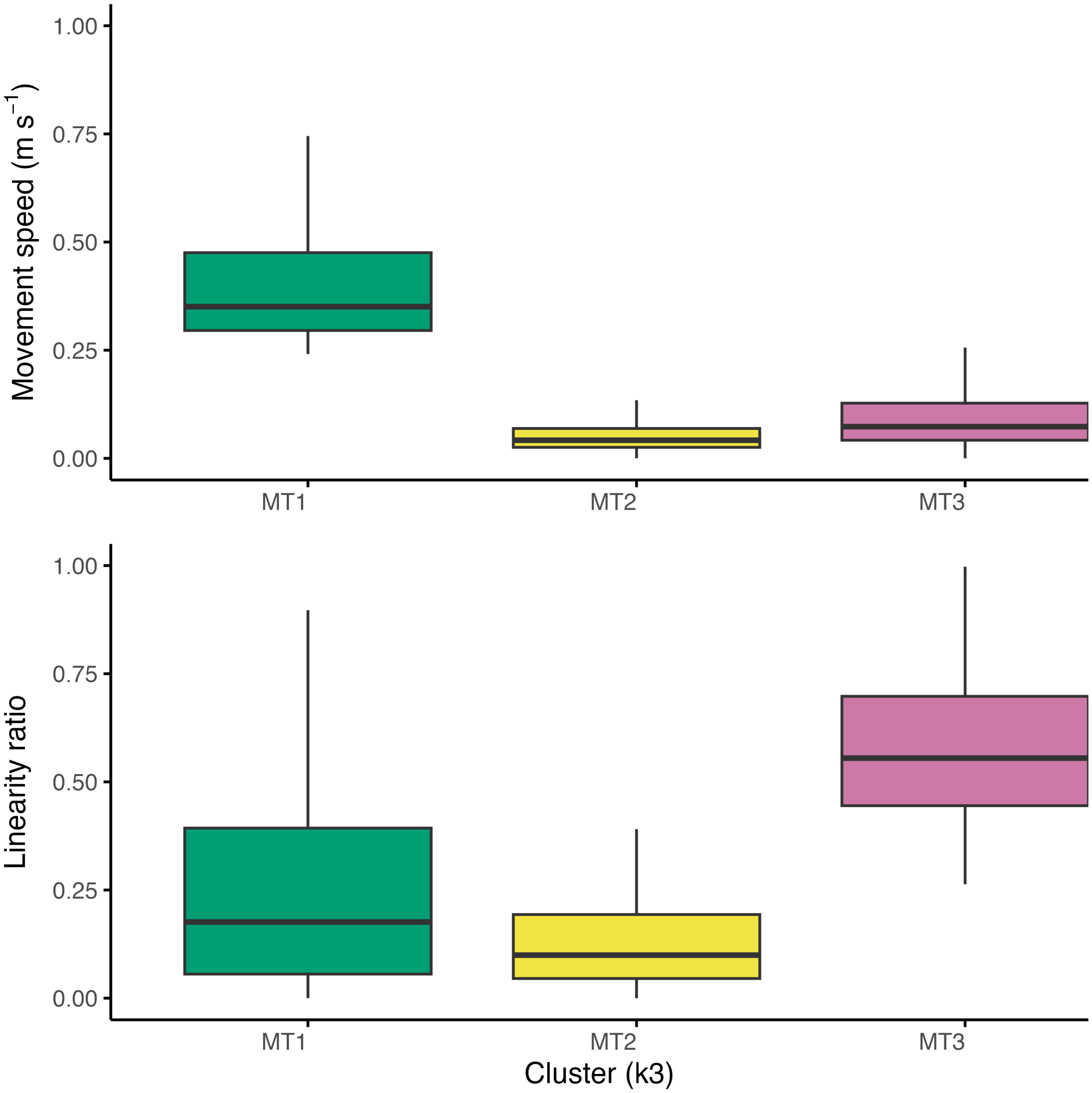

Figure A3.2. Boxplots of variables relevant to clustering VPS data from northern pike (*Esox lucius; n* = 48). Boxes visualize 25th, 50th, and 75th percentiles; whiskers extend to the 1.5 * interquartile range (i.e.., 75th–25th percentile). Variables used were the linearity ratio (the distance between the first and last locations of a burst divided by the total distance) and the mean movement speed (m s^{-1}).

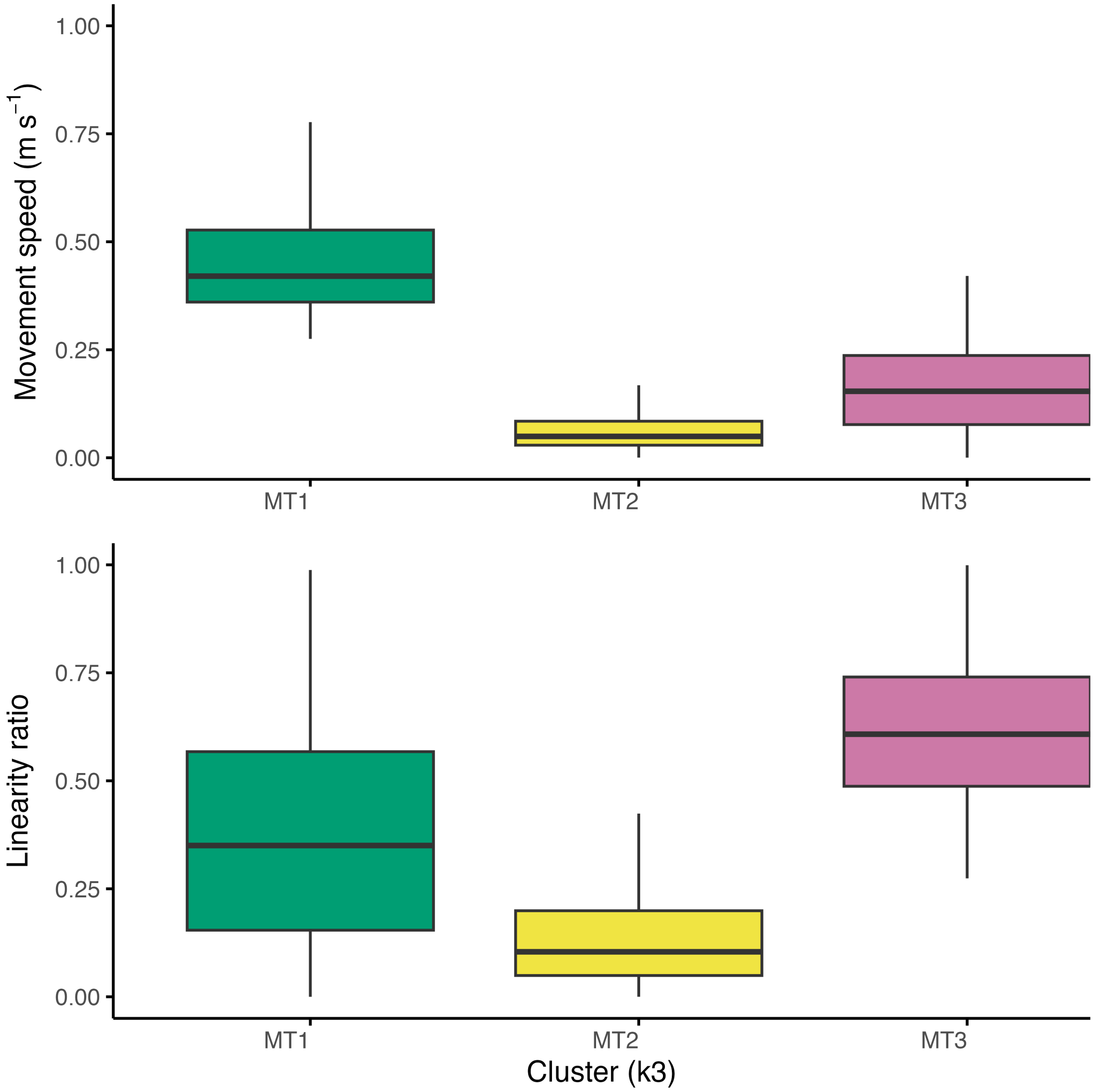

Figure A3.3. Boxplots of variables relevant to clustering VPS data from largemouth bass (*Micropterus nigricans, n* = 54). Boxes visualize 25th, 50th, and 75th percentiles; whiskers extend to the 1.5 * interquartile range (i.e.., 75th–25th percentile). Variables used were the linearity ratio (the distance between the first and last locations of a burst divided by the total distance) and the mean movement speed (m s^{-1}).

Table A3.1. Summary of GAMMs fit to movement speed (m s^{-1}) data from northern pike (*Esox lucius; n* = 48) and largemouth bass (*Micropterus nigricans, n* = 54) for 72 h or 2 weeks after intracoelomic tagging. Predictor variables included a smoothing parameter for hours post release (grouped by treatment), treatment, tagging season and total length (mm) as parametric terms, as well as individual fish ID as random effect. Bolded *p*-values indicate statistical significance ($p < 0.05$)

Model					
Northern pike 72 h	**Parametric coefficients**	***Est***	***SE***	***t***	***p***
	Intercept	-2.853	0.077	-36.997	**< 0.001**
	MS-222	-0.102	0.121	-0.847	0.397
	TENS	-0.295	0.118	-2.506	**0.012**
	Season	0.306	0.099	3.097	**0.002**
	Smooth terms	***edf***	***Ref.df***	***F***	***p***
	s(Control)	8.839	8.991	42.64	**< 0.001**
	s(MS-222)	8.629	8.962	21.75	**< 0.001**
	s(TENS)	8.302	8.872	102.92	**< 0.001**
	s(Time of day)	7.841	8.000	252.23	0.981
	s(ID)	40.089	41.000	651.64	**< 0.001**
Largemouth bass 72 h	**Parametric coefficients**	***Est***	***SE***	***t***	***p***
	Intercept	0.249	0.676	0.368	0.713
	MS-222	-0.654	0.135	-4.856	**< 0.001**
	TENS	-0.341	0.133	-2.564	**0.010**
	Total length	-0.006	0.002	-4.136	**< 0.001**
	Season	0.523	0.113	4.619	**< 0.001**
	Smooth terms	***edf***	***Ref.df***	***F***	***p***
	s(Control)	8.868	8.995	37.48	**< 0.001**
	s(MS-222)	8.951	8.999	151.12	**< 0.001**
	s(TENS)	8.938	8.999	180.90	**< 0.001**
	s(Time of day)	7.403	8.000	1056.42	0.357
	s(ID)	42.306	44.000	174.44	**< 0.001**
Northern pike 2 weeks	**Parametric coefficients**	***Est***	***SE***	***t***	***p***
	Intercept	-2.671	0.057	-46.959	**< 0.001**
	MS-222	0.043	0.100	0.430	0.667
	TENS	0.033	0.100	0.333	0.739
	Smooth terms	***edf***	***Ref.df***	***F***	***p***
	s(Control)	8.879	8.996	203.00	**< 0.001**
	s(MS-222)	8.807	8.989	94.17	**< 0.001**
	s(TENS)	8.682	8.970	312.87	**< 0.001**
	s(Time of day)	7.864	8.000	356.83	0.999
	s(ID)	41.873	42.000	17798.28	**< 0.001**
Largemouth bass 2 weeks	**Parametric coefficients**	***Est***	***SE***	***t***	***p***
	Intercept	-0.567	0.683	-0.830	0.407
	MS-222	-0.197	0.137	-1.440	0.150
	TENS	0.068	0.136	0.498	0.619
	Total length	-0.004	0.002	-2.726	**0.006**
	Season	0.438	0.115	3.806	**< 0.001**
	Smooth terms	***edf***	***Ref.df***	***F***	***p***
	s(Control)	8.860	8.994	52.45	**< 0.001**
	s(MS-222)	8.952	8.999	341.42	**< 0.001**
	s(TENS)	8.961	9.000	1019.94	**< 0.001**
	s(Time of day)	7.935	8.000	9003.73	1.000
	s(ID)	45.600	47.000	57501.68	**< 0.001**

Table A3.2. Summary of GAMMs fit to movement types (MT) from northern pike (*Esox lucius;* $n = 48$) for 72 h after intracoelomic tagging. MT1 was classified by high movement speeds and low–moderate linearity ratios, representing burst swimming. MT2 was classified by very low movement speeds and linearity ratios, representing stationary fish. Finally, MT3 was classified by low–moderate movement speeds and high linearity ratios, representing cruising or sustained swimming. Predictor variables included a smoothing parameter for hours post release (grouped by treatment), treatment, tagging season and total length (mm) as parametric terms, as well as individual fish ID as random effect. Bolded *p*-values indicate statistical significance ($p < 0.05$).

Model					
Northern pike 72 h MT1	**Parametric coefficients**	***Est***	***SE***	*z*	*p*
	Intercept	-4.736	0.314	-15.072	**< 0.001**
	MS-222	0.621	0.485	1.283	0.199
	TENS	-0.196	0.492	-0.398	0.691
	Season	1.108	0.404	2.745	**0.006**
	Smooth terms	***edf***	***Ref.df***	***Chi .sq***	*p*
	s(Control)	8.931	8.998	1078.2	**< 0.001**
	s(MS-222)	8.766	8.984	232.9	**< 0.001**
	s(TENS)	7.725	8.589	366.0	**< 0.001**
	s(Time of day)	7.695	8.000	1646.3	**< 0.001**
	s(ID)	39.325	42.000	6282.9	**< 0.001**
Northern pike 72 h MT2	**Parametric coefficients**	***Est***	***SE***	*z*	*p*
	Intercept	3.551	1.313	2.705	**0.007**
	MS-222	0.221	0.240	0.922	0.357
	TENS	0.380	0.250	1.516	0.129
	Total length	-0.003	0.002	-1.690	0.091
	Season	-1.896	0.203	-9.361	**< 0.001**
	Smooth terms	***edf***	***Ref.df***	***Chi .sq***	*p*
	s(Control)	8.989	9.000	3722.1	**< 0.001**
	s(MS-222)	8.710	8.977	853.7	**< 0.001**
	s(TENS)	8.941	8.999	894.6	**< 0.001**
	s(Time of day)	7.775	8.000	5017.6	0.311
	s(ID)	38.397	41.000	24524.7	**< 0.001**
Northern pike 72 h MT3	**Parametric coefficients**	***Est***	***SE***	*z*	*p*
	Intercept	-4.035	1.125	-3.588	**< 0.001**
	MS-222	-0.255	0.206	-1.240	0.215
	TENS	-0.305	0.214	-1.421	0.155
	Total length	0.004	0.002	2.271	**0.023**
	Season	1.754	0.173	10.117	**< 0.001**
	Smooth terms	***edf***	***Ref.df***	***Chi .sq***	*p*
	s(Control)	8.988	9.000	3615.0	**< 0.001**
	s(MS-222)	8.780	8.987	941.4	**< 0.001**
	s(TENS)	8.942	8.999	996.6	**< 0.001**
	s(Time of day)	7.781	8.000	4560.2	**0.036**
	s(ID)	38.393	40.000	16095.8	**< 0.001**

Table A3.3. Summary of GAMMs fit to movement types (MT) from largemouth bass (*Micropterus nigricans, n* = 54) for 72 h after intracoelomic tagging. MT1 was classified by high movement speeds and low–moderate linearity ratios, representing burst swimming. MT2 was classified by very low movement speeds and linearity ratios, representing stationary fish. Finally, MT3 was classified by low–moderate movement speeds and high linearity ratios, representing cruising or sustained swimming. Predictor variables included a smoothing parameter for hours post release (grouped by treatment), treatment, tagging season and total length (mm) as parametric terms, as well as individual fish ID as random effect. Bolded *p*-values indicate statistical significance ($p < 0.05$).

Model					
Largemouth bass 72 h MT1	**Parametric coefficients**	***Est***	***SE***	***z***	***p***
	Intercept	3.155	3.017	1.046	0.296
	MS-222	-1.550	0.610	-2.541	**0.011**
	TENS	-0.262	0.583	-0.449	0.653
	Total length	-0.018	0.007	-2.621	**0.009**
	Season	2.172	0.500	4.344	**< 0.001**
	Smooth terms	***edf***	***Ref.df***	***Chi .sq***	***p***
	s(Control)	8.909	8.997	703.0	**< 0.001**
	s(MS-222)	8.835	8.989	346.2	**< 0.001**
	s(TENS)	8.801	8.987	1514.8	**< 0.001**
	s(Time of day)	7.440	8.000	2363.7	**< 0.001**
	s(ID)	41.362	47.000	4535.3	**< 0.001**
Largemouth bass 72 h MT2	**Parametric coefficients**	***Est***	***SE***	***z***	***p***
	Intercept	0.630	0.208	3.033	**0.002**
	MS-222	1.359	0.326	4.171	**< 0.001**
	TENS	1.180	0.326	3.619	**< 0.001**
	Season	-1.925	0.278	-6.915	**< 0.001**
	Smooth terms	***edf***	***Ref.df***	***Chi .sq***	***p***
	s(Control)	8.914	8.998	468.2	**< 0.001**
	s(MS-222)	8.872	8.995	1632.2	**< 0.001**
	s(TENS)	8.929	8.998	1776.0	**< 0.001**
	s(Time of day)	7.887	8.000	30138.7	**< 0.001**
	s(ID)	43.467	46.000	8569.1	**< 0.001**
Largemouth bass 72 h MT3	**Parametric coefficients**	***Est***	***SE***	***z***	***p***
	Intercept	-0.875	0.193	-4.542	**< 0.001**
	MS-222	-1.012	0.302	-3.364	**< 0.001**
	TENS	-1.223	0.302	-4.047	**< 0.001**
	Season	1.442	0.258	5.589	**< 0.001**
	Smooth terms	***edf***	***Ref.df***	***Chi .sq***	***p***
	s(Control)	8.863	8.994	380.6	**< 0.001**
	s(MS-222)	8.825	8.991	1386.5	**< 0.001**
	s(TENS)	8.860	8.994	1095.2	**< 0.001**
	s(Time of day)	7.875	8.000	24413.4	**< 0.001**
	s(ID)	43.600	47.000	8255.0	**< 0.001**

Table A3.4. Summary of GAMMs fit to movement types (MT) from northern pike (*Esox lucius; n* = 48) for 2 weeks after intracoelomic tagging. MT1 was classified by high movement speeds and low–moderate linearity ratios, representing burst swimming. MT2 was classified by very low movement speeds and linearity ratios, representing stationary fish. Finally, MT3 was classified by low–moderate movement speeds and high linearity ratios, representing cruising or sustained swimming. Bolded *p*-values indicate statistical significance ($p < 0.05$).

Model					
Northern pike 2 week MT1	**Parametric coefficients**	***Est***	***SE***	***z***	***p***
	Intercept	-4.116	0.219	-18.794	**< 0.001**
	MS-222	0.640	0.347	1.844	0.065
	TENS	0.567	0.352	1.610	0.107
	Season	0.462	0.288	1.601	0.109
	Smooth terms	***edf***	***Ref.df***	***Chi .sq***	***p***
	S(Control)	8.954	8.999	1094	**< 0.001**
	s(MS-222)	8.797	8.988	361	**< 0.001**
	s(TENS)	8.908	8.997	1831	**< 0.001**
	s(Time of day)	7.802	8.000	2360	0.73
	s(ID)	40.882	43.000	88304	**< 0.001**
Northern pike 2 week MT2	**Parametric coefficients**	***Est***	***SE***	***z***	***p***
	Intercept	3.365	1.037	3.245	**0.001**
	MS-222	0.031	0.189	0.163	0.871
	TENS	0.182	0.197	0.924	0.356
	Total length	-0.003	0.002	-1.888	0.059
	Season	-1.539	0.159	-9.695	**< 0.001**
	Smooth terms	***edf***	***Ref.df***	***Chi .sq***	***p***
	s(Control)	8.921	8.998	7289	**< 0.001**
	s(MS-222)	8.971	9.000	1603	**< 0.001**
	s(TENS)	8.962	9.000	1575	**< 0.001**
	s(Time of day)	7.979	8.000	338124	0.641
	s(ID)	39.939	40.000	300708	**< 0.001**
Northern pike 2 week MT3	**Parametric coefficients**	***Est***	***SE***	***z***	***p***
	Intercept	-3.752	0.957	-3.921	**< 0.001**
	MS-222	-0.162	0.174	-0.926	0.354
	TENS	-0.375	0.182	-2.057	**0.040**
	Total length	0.003	0.001	2.289	**0.022**
	Season	1.544	0.146	10.544	**< 0.001**
	Smooth terms	***edf***	***Ref.df***	***Chi .sq***	***p***
	s(Control)	8.958	8.999	8891	**< 0.001**
	s(MS-222)	8.974	9.000	2181	**< 0.001**
	s(TENS)	8.944	8.999	2962	**< 0.001**
	s(Time of day)	7.975	8.000	267720	0.666
	s(ID)	39.927	40.000	309968	**< 0.001**

Table A3.5. Summary of GAMMs fit to movement types (MT) from largemouth bass (*Micropterus nigricans, n* = 54) for 2 weeks after intracoelomic tagging. MT1 was classified by high movement speeds and low–moderate linearity ratios, representing burst swimming. MT2 was classified by very low movement speeds and linearity ratios, representing stationary fish. Finally, MT3 was classified by low–moderate movement speeds and high linearity ratios, representing cruising or sustained swimming. Bolded rows indicate statistical significance ($p < 0.05$).

Model					
Largemouth bass 2 week MT1	**Parametric coefficients**	***Est***	***SE***	***z***	***p***
	Intercept	3.267	2.784	1.174	0.241
	MS-222	-0.379	0.574	-0.661	0.509
	TENS	0.437	0.569	0.767	0.443
	Total length	-0.017	0.0067	-2.549	**0.011**
	Season	1.926	0.483	3.986	< **0.001**
	Smooth terms	***edf***	***Ref.df***	***Chi .sq***	***p***
	s(Control)	8.948	8.999	822.6	< **0.001**
	s(MS-222)	8.920	8.998	1169.9	< **0.001**
	s(TENS)	8.858	8.993	5592.1	< **0.001**
	s(Time of day)	7.884	8.000	9913.3	< **0.001**
	s(ID)	46.080	52.000	31000.1	< **0.001**
Largemouth bass 2 week MT2	**Parametric coefficients**	***Est***	***SE***	***z***	***p***
	Intercept	0.834	0.175	4.769	< **0.001**
	MS-222	0.774	0.266	2.917	**0.004**
	TENS	0.433	0.265	1.634	0.102
	Season	-1.937	0.224	-8.641	< **0.001**
	Smooth terms	***edf***	***Ref.df***	***Chi .sq***	***p***
	S(Control)	8.836	8.992	7402	< **0.001**
	s(MS-222)	8.958	8.999	2673	< **0.001**
	s(TENS)	8.974	9.000	9415	< **0.001**
	s(Time of day)	7.979	8.000	147980	0.992
	s(ID)	46.446	49.000	434342	< **0.001**
Largemouth bass 2 week MT3	**Parametric coefficients**	***Est***	***SE***	***z***	***p***
	Intercept	-1.189	0.140	-8.472	< **0.001**
	MS-222	-0.458	0.213	-2.146	**0.032**
	TENS	-0.500	0.213	-2.347	**0.019**
	Season	1.306	0.180	7.244	< **0.001**
	Smooth terms	***edf***	***Ref.df***	***Chi .sq***	***p***
	s(Control)	8.885	8.996	8156	< **0.001**
	s(MS-222)	8.939	8.999	1540	< **0.001**
	s(TENS)	8.959	8.999	2302	< **0.001**
	s(Time of day)	7.972	8.000	71186	0.963
	s(ID)	46.212	49.00	157758	< **0.001**