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Acoustic telemetry in freshwater habitats: the influence of macrophytes on acoustic transmitter detection efficiency and identifying predation using novel transmitters

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By

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DECLARATION OF CO-AUTHORSHIP/PREVIOUS PUBLICATION

I. Co-Authorship

I hereby declare that this thesis incorporates material that is result of joint research, as follows:

Chapter 3 of this thesis was co-authored with Dr. Jordan Matley and Natalie Klinard under the supervision of Dr. Aaron Fisk and Dr. Scott Colborne. The key ideas, primary contributions, experimental designs, data analysis, interpretation, and writing were performed by the author. Co-authors contributed to experimental design, data analysis, writing, and manuscript edits.

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This thesis includes one original paper that has been previously published/submitted for publication in peer reviewed journals, as follows:

Chapter 2: Identification of predation events in wild fish using novel acoustic transmitters (*Manuscript submitted for publication in Animal Biotelemetry in October 2019*)

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ABSTRACT

Acoustic telemetry is a popular tool to study the movements of animals and has resulted in substantial ecological knowledge gain. To effectively carry out acoustic telemetry studies, many technical and biological considerations must be made. This thesis aimed to fill gaps in knowledge pertaining to two common considerations in passive acoustic telemetry studies, particularly in nearshore freshwater habitats: understanding the influence of macrophytes on the detection efficiency and range of acoustic telemetry equipment and identifying whether or not tagged animals have been consumed by an aquatic predator. Through the application of detection range testing and hydroacoustic surveys, it was revealed that distance and macrophyte biovolume interact to significantly influence the detection efficiency of acoustic transmitters, and this influence varied significantly based on the seasonal growth and senescence of macrophytes. The distance at which 50% of transmissions were successfully detected ranged from 5.5 m (± 139.6 S.D.) to 186.8 m (± 114.4 S.D.) and was significantly correlated to seasonal fluctuations in macrophyte biovolume. One of the first field applications of novel transmitters that identify predation events of tagged individuals indicated that 31.7% of tagged fish (n = 60) were apparently predated, and variable detection patterns were demonstrated using spatial metrices to examine the transmitter movements before and after the apparent predation event. The novel information presented in this thesis regarding the significant seasonal influence of macrophytes on detection efficiency and range and the application of acoustic transmitters that identify predation events in the wild will inform and improve future acoustic telemetry studies.

DEDICATION

This thesis is dedicated to my parents, Patricia and Adam.

Thank you for your endless support.

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CHAPTER 1

General Introduction

1.1 Thesis Overview

The study of aquatic animal movements is of great interest to researchers working to protect and manage aquatic resources (Cooke et al. 2016). Animal movement data allows for knowledge to be gained regarding survival, habitat use, migrations, or species interactions. Acoustic telemetry is a popular tool to gain knowledge about aquatic animal ecology through the study of their movements (Hussey et al. 2015), and the use of this tool is growing in freshwater systems. However, there are common considerations to make in acoustic telemetry studies, two of which are the focus of this thesis. First, it is essential to consider the performance of telemetry equipment when planning and analyzing data in acoustic telemetry studies. Macrophytes are a key aspect of preferred nearshore habitat for many temperate freshwater fish species at some point in their life cycle (Jude and Pappas 1992; Wei et al. 2004). As a result, vegetated habitats often have high abundances of fish, and it is thus important to study fish movements in these habitats. Macrophytes are known to influence the efficiency of acoustic telemetry equipment (Stasko and Pincock, 1977), so it is important to quantify the effects of seasonal macrophyte growth on performance in order to effectively interpret telemetry data, but no studies have specifically addressed this. Second, in acoustic telemetry studies where the potential exists for a tagged fish to be consumed by a predator, it is important to consider whether the detection data represents the movements of the targeted fish or the larger animal that ate it. It can be difficult to decipher whether a tagged animal had been consumed by a predator when analyzing acoustic telemetry data, which is a likely occurrence in acoustic telemetry studies of small fishes (e.g. Daniels et al. 2019), and a likely occurrence in nearshore vegetated areas where both predators

and prey are known to forage (Jude and Pappas 1992). Novel acoustic transmitters have been recently developed to identify when a tagged animal has been consumed by a predator (Halfyard 2017), but the reliability of these tags in the wild has not been demonstrated in detail (Daniels et al. 2019; Klinard et al. 2019a). The focus of this thesis is to address these knowledge gaps in acoustic telemetry studies to improve the application of this tool in temperate freshwater systems.

1.2 Spatial Ecology

Movement is one of the key aspects of an organism's ecology and is often necessary for survival, especially in aquatic environments. Aquatic animal movements range from fine-scale movements that can be measured on the scale of meters to large migrations over hundreds of kilometers to facilitate activities necessary for their full life history including foraging, evading predation, and reproduction. For example, some tiger sharks (*Galeocerdo cuvier*) show cyclical patterns of fine-scale residency to feed on fledgling albatrosses near a single Hawaiian atoll in the summer, then swim thousands of kilometers away to different foraging grounds when this prey resource runs out (Meyer et al. 2010). Whale sharks (*Rhincodon typus*) are believed to thermoregulate by spending long periods of time at the surface after deep dives into colder water (Thums et al. 2013). In a large temperate freshwater lake, ciscoes (*coregonus spp.*) and their primary predator, siscowet (*Salvelinus namaycush siscowet*), both exhibited diel vertical migrations that were consistent with ciscoes evading predation and siscowet responding to changes in prey dispersal (Hrabik et al. 2006). Pacific salmon (*Oncorhynchus spp.*) migrate from marine environments to freshwater rivers to spawn, where they provide a seasonal food source for various predators and their carcasses provide nutrients to various biota as well as riparian vegetation (Helfield and Naiman 2006). Aquatic animal movements play a significant role not

only in individual fitness and population dynamics, but also the structure and function of ecosystems.

Knowledge of aquatic animal movement can be useful for fisheries management and aid in the prediction of how aquatic animals will respond to environmental changes at the population-level, ultimately improving conservation efforts which are increasingly important due to anthropogenic stressors such as climate change (Lucas and Baras 2000; Bowler and Benton 2005; Brooks et al. 2017). Movement data can be used to improve the restoration of species spawning habitats, for example, movement data for an lake sturgeon (*Acipenser fulvescens*) population allowed for the identification of sites for constructed spawning reefs that lake sturgeon are likely to encounter and use (reviewed by Brooks et al. 2017). Aquatic animal movements have also been used to assess the efficacy of marine reserves, for example, a marine reserve was deemed too small based on the movements of exploited fish species outside of the protected area (Chateau and Wantiez 2009). Movement data can also be used to evaluate the success of stocking efforts by providing information on the dispersal and survival of fish species post-stocking, for example, stocked razorback suckers (*Xyrauchen texanus*) exhibited low survival based on movement data due to suspected predation by a non-native fish species (Karam et al. 2008). Thus, understanding the causes and consequences of aquatic animal movements is of great interest to those working to protect and manage aquatic ecosystems, and tools to accomplish this are in high demand.

1.3 Acoustic Telemetry

Methods to study fish movements include observational techniques such as hydroacoustic surveys or visual observation via video or diving, and capture-dependent techniques such as recreational and commercial catch analysis or mark-recapture techniques (Lucas and Baras

2000). Electronic tagging technology is one of the most effective means to study animal movements in their natural environment by allowing researchers to overcome obstacles that have hindered the study of aquatic animal movements in the past: the inability to directly observe or relocate them due to the vastness, low visibility, and complexity of their habitat (Hussey et al. 2015). Acoustic telemetry is an increasingly popular tool used to study the movements of aquatic animals that has allowed for meaningful contributions to our understanding of the ecology of aquatic animals in both marine and freshwater ecosystems (Hussey et al. 2015). Acoustic telemetry involves transmitters that are attached to aquatic animals via methods such as intracoelomic implantation or external attachment and emit uniquely coded ultrasonic signals. Transmissions from tagged animals swimming within proximity of acoustic receivers listening at the same frequency will be recorded as time-stamped detections. Tags come in a variety of sizes that can vary in their battery lifespan and power output based on how they are programmed. The continued miniaturization of transmitters allows for smaller species and life stages to be studied, while larger tags can transmit further for longer periods of time due to larger battery sizes (up to ten years in some cases; Hussey et al. 2015). Different frequencies of sound can be used depending on the study objectives; lower frequencies tend to travel further distances but require bigger transducers and therefore higher frequency transmitters are frequently used to study smaller aquatic animals because the tags can be made smaller (Melnychuk 2012). In studies with many tagged individuals, transmitters can be programmed to emit acoustic signals at randomized intervals of time to avoid overlap or collisions of transmissions from multiple tags, which would otherwise result in the inability of receivers to record those detections (Voegeli et al. 1998; Heupel et al. 2006). In addition to presence and location data, some transmitters can be equipped to provide additional data such as temperature or depth (Hussey et al. 2015), and more recently,

transmitters have been developed to identify predation of tagged animals (Halfyard et al. 2017; Daniels et al. 2019; Klinard et al. 2019a).

Acoustic telemetry in aquatic environments can involve active and/or passive tracking of individuals depending on study design and objectives. Active tracking typically involves an acoustic receiver with an omnidirectional hydrophone that is deployed off the side of a vessel to follow individual fish movements. Passive monitoring allows for continuous monitoring of multiple tagged individuals in the surrounding environment via the deployment of multiple acoustic receivers that are moored within the water body at fixed locations and log detection data that can be uploaded upon receiver retrieval (Heupel et al. 2006). In passive acoustic telemetry studies, receivers are configured to suit the study objectives, but two approaches are primarily used: (1) receivers are used to create gates along potential migration routes to learn about broad-scale movements or animals moving in or out of an area (Thorstad et al. 2011; Halfyard et al. 2012; Logan and Lowe 2019), and (2) receivers are placed closely together in a grid formation frequently referred to as an array to learn about fine-scale movements (Hedger et al. 2008; Hammerschlag et al. 2017; Nakayama et al. 2018). While both active and passive telemetry methods are useful, the popularity of passive acoustic telemetry has increased recently due to advances in receiver technology and increasing affordability of the equipment (Kessel et al. 2014).

The application of passive acoustic telemetry has many benefits as opposed to active tracking: limited labour aside from the deployment, maintenance, and retrieval of receivers; continuous daily monitoring for the duration of array deployment and the tag's battery life; the ability to track multiple tagged fishes at the same time; limited disturbance to the animals' behaviour (aside from tagging and associated effects, see Cooke et al. 2011); and the ability to

collaborate with other researchers to form telemetry networks (Kessel et al. 2014). As with all technologies, there are considerations to make when designing and interpreting passive acoustic telemetry studies, such as the need to either test or predict receiver placements that will be relevant to the study animal's ecology, the fact that the animal will only be detected if it is within a certain proximity (i.e. the detection range) of a receiver, and investigating the assumption that the detection data represents the movements of the tagged animal (and not the predator that consumed the tagged animal). The latter two considerations will be the focus of this thesis.

1.4 Range Testing in Acoustic Telemetry Studies

One of the primary considerations in passive acoustic telemetry studies is that the tagged animals must be within a certain proximity of the receivers in order for their movements to be monitored (reviewed by Kessel et al. 2014). This requires the consideration of the detection efficiency (*DE*) of transmitters, which is the probability of a transmission from a tag being successfully detected by a receiver, and detection range (*DR*), which describes the receiver-tag distance at which transmissions will be successfully detected given a specific *DE* (Melnychuk, 2012). Many variables are known to influence *DR* and *DE* in acoustic telemetry studies, some of which can be controlled by the user, and some of which rely on environmental conditions or animal behaviour. Receiver spacing is a key aspect of ensuring efficient *DR* and *DE* because when carefully considered, it can result in providing a minimum threshold of detections, however, this can be difficult to accomplish because the *DE* of transmitters are influenced by variable characteristics of aquatic systems such as temperature, noise, depth, and physical obstructions such as macrophytes (Simpfendorfer et al. 2008; Cooke et al. 2013). Despite being an important factor in the analysis of acoustic telemetry data, the effects of these variables on *DE* and *DR* are often not well understood or reported by individual studies (Kessel et al. 2014).

1.5 Identifying Predation in Acoustic Telemetry Studies

Another consideration in the interpretation of passive acoustic telemetry studies is determining if the detections represent the movements of the targeted individuals. Determining the fate of tagged individuals is a necessary step in data analysis for all telemetry studies, as mortality may occur while the tag is still active, and care should be taken so that detections are not misinterpreted as the healthy animal's behaviour. Additionally, advancements in telemetry technology have resulted in the miniaturization of tags, allowing smaller animals that are more vulnerable to predation to be tagged, it is increasingly more important to consider mortality in telemetry studies. Previous studies have inferred predation through sudden temperature or depth changes (e.g. Béguer-Pon et al. 2012), but those studies relied on ancillary sensor data which are not available with smaller tags. Others have been able to infer predation through pre-existing knowledge of predator behaviour (Gibson et al. 2015), but clear changes in detection data do not always occur after a predation event. Many methods to infer predation rely on assumptions of 'normal' behaviour, which can result in subjective predation estimates. A recent advancement in acoustic telemetry technology has resulted in the development of predation tags that are able to identify when a predation event has occurred (Halfyard et al. 2017), but so far literature regarding their use is limited (Daniels et al. 2019; Klinard et al. 2019a), and the use of 180 kHz predation transmitters has yet to be demonstrated in the wild. Predation tags will not only aid in the interpretation of acoustic telemetry data, overcoming a major obstacle in many telemetry studies, they have the potential to provide novel information regarding predation and species interactions, particularly when used in fine-scale receiver arrays that allow for frequent detections.

1.6 The Laurentian Great Lakes

The Laurentian Great Lakes (hereafter Great Lakes) are comprised of five of the world's largest interconnected freshwater lakes (Erie, Huron, Ontario, Michigan, Superior) that are home to a diverse community of fish species. The Great Lakes are bordered by both Canada and the United States of America where 10% of Americans and 30% of Canadians reside within their basin (Danz et al. 2007). Throughout the Great Lakes, human activities have led to habitat alterations such as shoreline modification, coastal wetland draining and filling, and channelization of tributaries (Jones et al. 2006). The Great Lakes face numerous anthropogenic stressors such as pollution and species invasions that threaten ecosystems and the species that exist within them, with nearshore habitats facing the highest cumulative ecosystem stress (Allan et al. 2013). Nearshore habitats within the Great Lakes are important to most fish species at some point in their life cycle (Jude and Pappas 1992), so it is important that efforts are made to rehabilitate and monitor fish species in these critical habitats. The use of telemetry is widespread within the Great Lakes, primarily in efforts to better manage the fisheries and conserve fish communities that are of great economic and cultural value (Brooks et al. 2017). In fact, a network of collaborative telemetry researchers called the Great Lakes Acoustic Telemetry Observation System (GLATOS, https://glatos.glos.us/) exists for data-sharing that improves ecological knowledge that can be gained from telemetry research within the Great Lakes (Krueger et al. 2018). Despite the growing number of telemetry studies in the Great Lakes, very few studies have reported detailed detection range testing (e.g. Hayden et al. 2016; Klinard et al. 2019b), leaving gaps in our understanding of acoustic telemetry equipment performance in this temperate freshwater system. For example, despite the importance of nearshore habitats to fishes of the Great Lakes and the complex interactions between species that occur there, there have

been no studies to test the influence of seasonal macrophyte growth that occurs in temperate freshwater systems on the performance of acoustic telemetry equipment.

1.7 Study Species

Yellow perch (*Perca flavescens*) is a common fish species in the Great Lakes that is fished both commercially and for sport. Yellow perch are abundant in coastal wetlands which they utilize for spawning and nursing (Jude and Pappas 1992) and they traverse between these habitats and open water throughout their life cycle. Due to their abundance in nearshore habitats in most of the Great Lakes, yellow perch likely play an important role in trophic connectivity. Thus, the abundance and potential importance of yellow perch as a prey species make for an ideal species to study the application of predation transmitters in the wild.

1.8 Study System

This study is based in the Detroit River of the Laurentian Great Lakes. The Detroit River is a 45 km channel that comprises the lower portion of the Huron-Erie Corridor, connecting Lake St. Clair to Lake Erie (Manny et al. 1988). The main navigation channel is maintained as part of the Great Lakes-St. Lawrence Seaway with depths of at least 8.2 m (but as deep as 14 m) to facilitate commercial navigation. A diverse variety of fish species, including piscivorous species ranging from largemouth bass (*Micropterus salmoides*) to muskellunge (*Esox masquinongy*), rely on the river's nearshore habitats for activities such as spawning and nursing (Bennion and Manny 2011; Lapointe 2014), therefore many species likely face predation pressures. The interactions of the fishes within these habitats are complex, and involve a mixture of life history stages, where juveniles and small fishes are not only likely to be abundant members of a community, they represent a critical component of the food web that supports the complex fish

community, including fishes important to economic activity throughout the region (Shillinger et al. 2012).

1.9 Thesis Objectives

This thesis will provide novel information regarding the application of acoustic telemetry in shallow vegetated freshwater habitats as well as the application of predation tags in the wild in a fine-scale receiver array that will aid future acoustic telemetry research in the Great Lakes and beyond by providing data that will inform the design, implementation, and interpretation of acoustic telemetry studies.

Chapter 2 of this thesis aims to examine the detection range of acoustic receivers in a freshwater riverine environment and determine the effects of tag depth and spatiotemporal variation in submerged macrophyte biovolume on detection efficiency and range of acoustic transmitters. In many freshwater ecosystems, one of the factors confounding detection range and efficiency is the presence of submerged macrophytes. Submerged macrophytes can greatly reduce signal intensity and affect receiver performance, limiting the efficiency of passive acoustic telemetry studies in vegetated areas which tend to be important fish habitats (Cooke et al. 2013). In the Detroit River, macrophyte growth varies seasonally and, at its peak, can result in a detection range of less than 10 m (unpublished data). I conducted range testing involving the use of sentinel tags placed at known distances from a receiver to quantify detection range throughout the study period. I hypothesized that tag depth will influence *DE* with tags lower in the water column exhibiting lower *DE* due to higher density of macrophytes I hypothesized that macrophyte biovolume will significantly reduce detection range and efficiency due to the attenuation of sound signals and predicted that at peak biovolumes, *DE* and *DR* will be extremely low (<50% detection probability at 10 m).

Chapter 3 of this thesis aims to demonstrate the functionality of novel predation tags in a freshwater riverine environment with a high diversity of predator and prey species using a fine-scale acoustic telemetry array. Predation transmitters are a relatively novel technology and their application in natural settings to date so far is limited (Daniels et al. 2019; Klinard et al. 2019), particularly the use of smaller (V5 tags) in fine-scale arrays. The use of predation tags in fine-scale arrays may provide more detailed detection data pre- and post-predation that can help in the identification of falsely triggered tags and allow for inferences to be made regarding what species consumed the tagged animal. I surgically implanted 60 yellow perch with predation transmitters and analyzed their pre- and post-predation detection data to make inferences regarding the functionality of the transmitters in natural settings.

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CHAPTER 2

Reduction of acoustic transmitter detections in relation to freshwater submerged macrophyte biovolume

2.1 Introduction

Acoustic telemetry is a widely used tool for monitoring the movements of aquatic animals (Hussey et al. 2015). By outfitting animals with acoustic transmitters (i.e. tags) that emit coded ultrasonic frequency sounds, researchers can track individuals either actively or passively creating a timestamped detection history of tagged animals that are within a certain proximity of receivers. Active tracking involves tracking tagged animals manually and can be useful to learn about survival or animals whose movements are not well understood, particularly in large bodies of water (e.g. Zeller 1997; Flavelle et al. 2002; Havn et al. 2017). However, active tracking requires labour, both in terms of personnel and time spent tracking, and has increased risk for unintended disturbances to animal behaviour due to the actions of the observers actively tracking them (e.g. boat noise; Mueller 1980). In comparison, passive acoustic telemetry permits long-term monitoring of tagged animals that are within the detection range of at least one of (usually) multiple receivers fixed in the water column. There are, however, a number of logistical considerations associated with passive acoustic telemetry studies, among which are: the need for multiple receivers, knowledge or predictions of target species spatial use to inform receiver configuration, and the fact that researchers are only able to account for animals that are within the detection range of one or more receivers (Kessel et al. 2014).

As sound travels through water it attenuates due to spreading of the soundwave and the absorption of sound by water and environmental factors (Voegeli and Pincock 1996), thereby influencing the successful detection of acoustic signals. The successful implementation of

acoustic telemetry requires an understanding of detection efficiency (*DE*), the probability of a transmission being successfully detected by a receiver, detection range (*DR*), the distance between tags and receivers at which successful detection occurs given a specific *DE*, and the environmental variables that influence these metrics (Melnychuk 2012). Experimental design can and should accommodate variation in *DE* and *DR* (Kessel et al. 2014). Receiver (or sentinel tag) depth, orientation, or mooring system must be carefully considered in each unique study system to maximize the *DE* of acoustic transmissions (Clements et al. 2005; Huveneers et al. 2016) and receiver spacing can be optimized to ensure the *DR* of receivers overlaps (e.g. Espinoza et al. 2011). Additionally, tag specifications can be customized to maximize *DE* and *DR*: acoustic frequency can influence the distance transmissions can travel (lower frequencies tend to travel further; Melnychuk 2012), power output can influence both *DE* and *DR* (Kessel et al. 2015; Klinard et al. 2019), and transmission rate can reduce signal collisions among multiple tags in the same area (Voegeli et al. 1998).

Factors external to the equipment can influence the propagation of sound in water between transmitters and receivers resulting in variable *DE* and *DR*. Physical obstructions such as submerged aquatic macrophytes (Stasko and Pincock 1977; Hightower et al. 2001) or topography (Cagua et al. 2013) can block, reflect, or distort signals (Simpfendorfer et al. 2008). Stratified layers in the water column, for example thermoclines (temperature) or haloclines (salinity), can cause sound to refract and change speed as it travels through the water column (Medwin and Clay 1998; Heupel et al. 2006; Huveneers et al. 2016). Background noise occurring at the same frequency of the transmissions is caused by factors such as wind generated waves (Voegeli and Pincock 1996), biological noise, and anthropogenic sounds (Heupel et al. 2006) can reduce *DE*. Animal behaviour can also influence *DE*, for example by occupying

depths outside of the horizontal plane of greatest receiver sensitivity, occupying habitats outside of the detection range, or occupying structures that cause signal interference (for more detailed reviews see Heupel et al. 2006; Simpfendorfer et al. 2008; Melnychuk 2012). The factors that influence *DE* and *DR* can vary through both space and time, necessitating the quantification of *DE* and *DR* across periods that capture both the short-term and seasonal variation in the study to accurately infer animal movement from detection data. The importance of controlling for variable *DE* in data interpretation was demonstrated in a study by Payne et al. (2010), which showed how fluctuations in *DE* (as exhibited by sentinel tags) could be mistaken for movement patterns of fish in the absence of controls. In general, the effects of environmental variables on detection efficiency and range are rarely quantified in acoustic telemetry studies, particularly in temperate freshwater systems (Klinard et al. 2019) and nearshore habitats where fish biodiversity is frequently higher than open water areas (Vadeboncoeur et al. 2011).

In the Laurentian Great Lakes, nearshore habitats are used by most fish species at some point in their life history (Jude and Pappas 1992; Wei et al. 2004; Vadeboncoeur et al. 2011; Trebitz and Hoffman 2015). Nearshore habitats in the Great Lakes typically contain macrophytes that provide structural complexity for fishes seeking refuge from predation, abundant invertebrate food resources, habitats for spawning and nursing, and protection from wave energy (Francis et al. 2014). Therefore, vegetated aquatic environments are key habitats in which to study fish movements and behaviour in order to inform management and increase recruitment. However, seasonal growth of macrophytes can attenuate acoustic transmission intensity and reduce receiver detection range by blocking the direct path between tags and receivers, introducing the need for rigorous testing of acoustic telemetry equipment in macrophytes. In some freshwater systems, fish activity in areas with dense macrophytes has resulted in low

detection efficiencies. For example, European catfish (*Silurus glanis*) were detected and accurately positioned within a freshwater reservoir until they moved into nearshore macrophyte beds where they could no longer be passively monitored and active tracking was required to locate the fish (Carol et al. 2007). Furthermore, whole-lake active tracking to estimate natural and fishing mortality of striped bass (*Morone saxatilis*) in a freshwater lake was impaired by macrophyte density to such an extent that two out of six fish whose deaths were attributed to natural mortality could not be located until seasonal senescence reduced vegetation density (Hightower et al. 2001). In temperate ecosystems, seasonal growth and senescence of submerged macrophytes would result in both spatial and temporal variation in *DE* and *DR*. Despite the animal diversity likely to be found in the vegetated habitats of temperate freshwater ecosystems, to our knowledge, no study has attempted to quantify the effects of seasonal variation in submerged macrophyte biovolume on *DE* and *DR* in these environments in order to inform experimental design and interpretation of detection data.

In this study, we investigated the effect of variable submerged macrophyte biovolume on the *DE* and *DR* of acoustic transmitters in a nearshore freshwater ecosystem. The study was carried out in the Detroit River, which contains nearshore vegetated habitats that are critical to the survival of many of the fish species that live in or pass through the river (Lapointe et al. 2010). In particular, nearshore environments are known as nursery and juvenile habitat for a variety of fishes from the Great Lakes region (Jude and Pappas 1992; Trebitz and Hoffman 2015) and, therefore, we were interested in the *DE* and *DR* of smaller fish tags (i.e. 5 mm in diameter) operating at higher frequencies (i.e. 180 kHz) than those typically used for larger fish and open water environments. The primary objectives of this study were to (1) determine the overall *DR* in nearshore shallow areas of the Detroit River and examine the temporal variation in

DE at distances of up to 75 m, (2) quantify the effects of variable submerged macrophyte biovolume on the *DE* of acoustic transmitters, and (3) compare the effects of tag location in the water column on both *DE* and *DR* in relation to vegetation. To address these objectives, *DE* and *DR* was monitored using 180 kHz sentinel tags suitable for small-sized fish likely to inhabit nearshore environments (V9 high power output; Vemco Ltd., Bedford, NS, Canada). As macrophytes cause the sound waves produced by acoustic tags to attenuate, we expected there to be a negative relationship between both *DE* and *DR* and macrophyte density, with the greatest reductions occurring during the summer months (July and August) when macrophyte growth and biovolume is at its maximum extent. If the transmissions of tags near the benthos and those suspended in the water column differ in *DE* and *DR*, then characteristics of the organisms tagged may need to be incorporated into receiver deployment planning. The results of this study will provide insights and necessary quantitative data for the application of acoustic telemetry in freshwater ecosystems that contain macrophytes, especially nearshore habitats that are often biological hotspots of activity.

2.2 Methods

Study site

This study was carried out in the Detroit River, a 45 km connecting channel that forms the lower-third of the corridor connecting Lake Huron and Lake Erie in the Laurentian Great Lakes (Edwards et al. 1989). This study was carried out in an area near the midpoint of the river along the shoreline of LaSalle, ON (42.242, -83.108; Fig. 2.1). The habitat in this area consists of shallow flats (1 – 2.5 m deep) that extend from the shoreline to the edge of a navigation channel where depth increases to a maximum of 10 m. The shallow nearshore area grows dense patches of submerged aquatic macrophytes during the spring and summer that begin to senesce in late

summer into autumn significantly altering the physical structure of these shallow habitats throughout the seasons. While macrophytes were not surveyed or identified in this study, common species in this area include *Potamogeton spp.*, *Najas flexilis*, *Valissneria americana*, and *Elodea canadensis*, among others.

Range testing

Range testing was completed between June and November 2018. The first tests involved two short-term deployments of coarse-scale tests (from June 2 – 6, 2018 and June 29 - July 5, 2018), followed by a long-term deployment involving simultaneous fine- and coarse-scale testing in the same location as the short-term deployments (July 30 – November 1 2018). The short-term tests were comprised of a 180 kHz VR2W acoustic receiver (Vemco Ltd., Bedford, NS, Canada) deployed with five sets of two V9-2x 180 kHz high power output sentinel tags (10 tags total; 143 dB; Vemco Ltd., Bedford, NS, Canada) at distances of 5, 10, 25, 50, and 75 m from the receiver. In the long-term deployment, the fine-scale test was placed immediately before the coarse-scale test along the same line. Long-term deployments included fine-scale tests involving the same five sets of tags mentioned above at distances of 0.5, 1.0, 1.5, 2.0 and 3.0 m from a receiver (Fig. 2.2a), while coarse-scale tests involved five receivers deployed at distances of 5, 10, 25, 50, and 75 m from the first set of tags in the fine-scale test (at 0.5 m; Fig. 2.2b). All receivers were moored in place in cinder blocks with PVC tubes cemented within them to hold the receivers. Receiver moorings were attached to a rope with a buoy at the surface of the water.

Tag deployments included two tags attached to a rope with 3-5 ring weights to anchor one end and a buoy at the water's surface to assess differences in *DE* at two different depths in the water column. For each tag deployment, the two tags were placed at different depths from the surface to assess the influence of potential fish position in the water column on detection

efficiency. Tags closer to the surface at ~ 30 cm in depth are hereafter referred to as tags at high depth, while tags closer to the bottom at ~ 90 cm are hereafter referred to as tags at low depth. Tags were placed in the same order and depth in the water column throughout all tests; the six tags at the first three positions in the test were programmed to transmit every 600 s on average (randomized between 550 – 650 s) and the four tags at the last two positions in the test were programmed to transmit every 300 s on average (randomized between 270 – 330 s), these average delays between transmissions are hereafter referred to as the nominal delay of the transmitters.

Macrophyte mapping

Submerged aquatic macrophyte biovolume (% volume of macrophytes in the water column) was measured throughout the study period using hydroacoustics and automated data processing with BioBase (https://www.biobasemaps.com/), an online cloud-based processing service for aquatic spatial data (Navico, Minneapolis, MN, USA). Sonar imagery was collected using a Lowrance Elite-4 Chirp sonar unit paired with a single-beam Lowrance 83/200 kHz transducer set to 200 kHz, mounted to the aft side of a 6.7 m research boat. The vessel completed two 80 m passes surrounding the range test area at speeds of $\leq$ 5 km/h to ensure minimal signal interference. Sonar logs were uploaded to BioBase, where spatial data layers were produced for depth, macrophyte height, and vegetation biovolume. In general, one GPS point was recorded per second and 5 to 30 acoustic signals were produced per GPS point. BioBase's algorithm used the acoustic signals that provided data about the tallest plant that intercepted the acoustic cone, which in turn was used to calculate the average proportion of plant height to water depth (i.e. percent biovolume) for each GPS point. Macrophyte growth to the surface causes high acoustic interference which was automatically assumed to be 100% macrophyte biovolume. If

macrophyte biovolume was less than 5% on average at any one point it was set to zero as it was within the margin of error. A uniform heat map of predicted macrophyte biovolume was produced from the point data collected in the surveys using the depth and macrophyte height data (Radomski and Holbrook 2015; Valley 2016; Helminen et al. 2019).

Data analysis

All range test detection data was compiled using VUE version 2.5.0 (Vemco Ltd., AMIRIX Systems Inc., Bedford, Nova Scotia, Canada) and exported to R (R Core Team 2018) via RStudio for further analysis.

Overall spatial and temporal variability in detection efficiency

To address the first objective of estimating the overall *DR* and temporal variation in *DE*, the long-term fine- and coarse-scale detection data were used. Deployment and retrieval days were removed from the dataset to provide detection measures for uninterrupted 24 h periods only from 31 July – 31 October 2018. Daily *DE* values were calculated as a proportion of possible detections for each tag-receiver pair by dividing the number of logged detections per day by the number of expected detections per day as determined based on the nominal delay of the tags (144 for a nominal delay of 600 s, 288 for a nominal delay of 300 s).

A generalized linear model (GLM) was used to assess the relationship between daily *DE* (response variable) with receiver-tag distance and tag depth (categorical predictor variables) using a binomial family structure and a logit link function. To evaluate the performance of the system, a metric that represented the distance at which *DE* was 0.50 was used to identify the maximum effective distance after which detection data would be too sparse for meaningful inferences to be made (also used by Welsh et al. 2012 and Selby et al. 2016). The distance ± S.E. (in meters) at which a *DE* value of 0.50 occurred is hereafter referred to as D_{50}. The *DE*-distance

relationships for low and high tag depths were independently examined using GLM models (response = daily *DE*; predictor = distance) and the *dose.p* function in the package 'MASS' (Venables and Ripley 2002) was used to estimate D_{50}. Finally, to examine temporal variation in *DE*, the relationship between *DE* and time was modelled for each distance and tag depth using a GLM (response = daily *DE*; predictor = day).

Influence of variable macrophyte biovolume on DE and DR

Macrophyte biovolume grids were exported from BioBase as point-feature files in WGS84 coordinate system where X = longitude, Y = latitude, and Z = macrophyte biovolume value. Macrophyte biovolume values represented the proportion of the water column occupied by macrophytes from 0 – 1, where 0 indicated no macrophytes in the water column and 1 indicated the entire water column was filled with macrophytes. Exported grids were imported into R and converted to raster format using the *raster* function from the package 'raster' (Hijmans 2019). To address the second objective, coarse-scale tag-receiver pairs (5 – 75 m) apart were used from both short-term and long-term deployments as detection efficiency was relatively stable at fine-scale distances (≤ 5 m) from the primary receiver (see results for objective 1 below). The coordinates for each tag-receiver pair in the coarse-scale test were used to generate straight lines connecting each pair using the *SpatialLines* function in the package 'sp' (Pebesma and Bivand 2005; Bivand, Pebesma, and Gomez-Rubio 2013). The vegetation biovolume values were extracted along each line for each map using the *extract* function from the package 'raster' (Hijmans 2019; Fig. 2.3). The extracted biovolume values were averaged for each line to produce a mean biovolume representing vegetation cover between each tag-receiver pair on each day vegetation mapping occurred.

In addition to macrophyte biovolume, water temperature was considered as a candidate environmental variable to include in analysis because it has been shown to influence the way sound attenuates in water (Medwin and Clay 1998) and plays a role in the seasonal growth of macrophytes (Barko et al. 1982). Hourly water temperature data were collected using HOBO Pendant temperature loggers (Onset, Cape Cod, MA, USA) deployed in nearby shallow areas of the Detroit River. Average daily water temperatures were calculated for each day vegetation mapping occurred and ranged from 8.7 – 25.8°C. To evaluate collinearity between the predictor covariates of water temperature and macrophyte biovolume, we used the *rcorr* function in the package 'Hmisc' (Harrell Jr. 2018) to produce a matrix of the Pearson pairwise correlations among *DE*, macrophyte biovolume, and water temperature. Mean macrophyte biovolume values and water temperature were found to be collinear (pairwise cc = 0.89; $p < 0.001$) thus daily average temperature was excluded from the analysis.

For the nine days with vegetation maps (two during the short-term deployments and seven during the long-term deployments), *DE* was calculated by binning detection data into 2-hour groups to balance maximizing the variation in *DE* captured for each day with a higher number of possible *DE* values. Two of the macrophyte maps represented days with partial detection data (i.e. equipment retrieval days; July 5 and November 1), to account for this, these maps were instead paired with the previous full day of detections for analysis (July 4 and October 31, respectively), under the assumption that macrophyte biovolume was unlikely to significantly vary over a single 24-hour period.

To assess the influence of macrophyte biovolume on *DE*, we used GLMs with a binomial family and a logit link function. Only coarse-scale distances were included in this analysis due to minimal variation in DE < 5 m (see results for objective 1 below). The response variable was 2-

hour *DE* values calculated for each of the five distances on each day macrophyte mapping occurred, and predictor variables included mean macrophyte biovolume for each distance (continuous), distance between receiver and tags (categorical), tag depth (categorical), and an interaction between macrophyte biovolume and distance. McFadden's pseudo R^2 was determined using the function *pR2* from the package 'pscl' (Jackman 2017) to assess the variance explained by the model. To determine D_{50}, the function *dose.p* from the package 'Hmisc' (Harrell Jr. 2018) was used on each of 9 GLMs that represented the relationship between *DE* and distance on each of the 9 days included in the analysis. To estimate how macrophytes influenced *DE* independently of distance, five separate GLMs for each tag-receiver distance (5, 10, 25, 50, and 75 m) were used and included 2-hour *DE* values (response variable), variable average biovolume for each distance on each day of testing, and the categorical variable of tag depth. Analysis of variance (ANOVA) was used to analyze the amount of variance that each variable contributed to *DE* for each GLM (using the *Anova* function in the 'car' package).

2.3 Results

Overall spatial and temporal patterns in detection efficiency

The long-term range test was deployed in the Detroit River for 93 full days from 31 July 2018 until 31 October 2018, producing a total of 231,676 detections. Tags low in the water column were detected a total of 117,540 times while higher tags were detected a total of 114,136 times (3% difference). Overall, the *DE* of sentinel tags exhibited a negative relationship with the distance between tags and receivers across the entire study period. Daily *DE* varied from 0 – 0.99 overall and mean daily *DE* ranged from 0.94 (± 0.02 S.D.) at distances ≤ 2 m to 0.10 (± 0.24 S.D.) at 75 m (Table 2.1). Fine-scale distances (0.5, 1, 1.5, 2, and 3 m) had an average daily *DE* of 0.94 (± 0.31 S.D.) while coarse-scale distances (5, 10, 25, 50, and 75 m) had an average daily

DE of 0.43 (± 0.44 S.D.). Distances ≤ 2 m experienced minimum daily *DE* of 0.85 – 0.90 for both tag depths, however, high tags at distances of 3 and 5 m exhibited minimum daily *DE* values of 0.30 and 0.03 while their lower counterparts exhibited minimum daily *DE* values of 0.90 and 0.76, respectively, indicating that while tag depth does not significantly influence *DE* overall, it may play a role in influencing *DE* for brief periods of time at some shorter distances. Distances of 10 and 25 m exhibited greater mean daily *DE* at low tag depths than higher depths, with differences of 0.07 and 0.13 respectively, while 50 and 75 m had similar mean daily *DE* values for both tag depths (Table 2.1).

The GLM looking at the influence of distance and tag depth on DE indicated that distances > 5 m were significantly correlated with *DE* (all $p < 0.001$), but tag depth did not have significant effects ($p = 0.132$; Table 2.2). Overall, D_{50} (± S.E.) for high tags was 27.6 ± 1.5 m and low tags had a D_{50} of 30.2 ± 1.6 m (Fig. 2.4).

Distances of ≤ 5 m had relatively consistent high *DE* throughout the duration of the study (0.88 ± 0.17 to 0.94 ± 0.02), while distances of 10 m and greater experienced high variation in *DE* (0 – 0.91 ± 0.11) and a general increase in *DE* over time (Fig. 2.5; Table 2.3). In comparison, there was temporal variation in *DE* at distances ≥ 10 m indicating that there were likely environmental variables significantly influencing *DE* in addition to distance.

Influence of variable macrophyte biovolume on DE and DR

Mean daily macrophyte biovolume (proportion of water column containing macrophytes), as measured along the line from the farthest tag, ranged from 0.01 – 0.9. In general, as macrophyte biovolume decreased, *DE* increased at distances ≥ 10 m throughout the study period (Fig. 2.6). The GLM exploring the relationship between *DE* (2 hour bins) and mean macrophyte biovolume, distance, and tag depth (with an interaction between distance and mean

macrophyte biovolume) indicated that both macrophyte biovolume (ANOVA, $X^2 = 348.33$, df = 1, $p < 0.001$) and distance (ANOVA, $X^2 = 487.59$, df = 4, $p < 0.001$) had significant effects, tag depth did not (ANOVA, $X^2 = 3.20$, df = 1, $p = 0.73$), and the interaction between distance and macrophyte biovolume was significant (ANOVA, $X^2 = 79.56$, df = 4, $p < 0.001$; Fig. 2.7). The model had a McFadden's pseudo R^2 value of 0.55. The interaction between distance and macrophyte biovolume had greater effects on *DE* at higher biovolumes and greater distances (Fig. 2.8). For the most part, higher macrophyte biovolumes were associated with lower *DE*; the highest daily average biovolume (0.977) resulted in a D_{50} (± S.E.) of 11.8 ± 1.3 m and the lowest daily average biovolume (0.014) resulted in a D_{50} of 167.7 ± 85.0 m (Fig. 2.7; Table 2.4).

The results of the five GLMs modeling the influence of macrophytes and tag depth on *DE* at each distance indicated that macrophytes significantly influenced *DE* at all distances (ANOVA, all $p < 0.001$), except 5 m (ANOVA, $p = 0.61$), and that tag depth significantly influenced *DE* at 50 m only (ANOVA, $p = 0.038$; see Table 2.5 for full summary of ANOVA results). This is supported by results from the first objective, where distances ≤ 5 m did not exhibit consistent variability in *DE* across time (Fig. 2.5).

2.4 Discussion

This is the first study to directly study and quantify the effects of macrophyte biovolume on the performance of acoustic telemetry tags and receivers. The results indicated that the *DE* of sentinel transmitters in a shallow littoral area of the Detroit River was highly variable at distances > 5 m. Interacting effects between tag-receiver distances and submerged aquatic macrophyte biovolume significantly influenced *DE* through both space and time, indicating that greater distances were more sensitive to seasonal changes in macrophyte biovolume. In general,

DE and *DR* were significantly reduced by the presence of macrophytes until they senesced completely in the fall.

The effective detection range of the acoustic receivers varied significantly throughout the study period. The overall relationship between *DE* and distance indicated that this system exhibited D_{50} at 27.6 ± 1.5 m for high tags and 30.2 ± 1.6 m for low tags (Fig. 2.4); when accounting for variation in macrophyte biovolume, D_{50} was 11.8 ± 1.3 m at the highest daily mean macrophyte biovolume in July and increased to 167.7 ± 85.0 m at the lowest daily mean macrophyte biovolume in October (Table 2.4). A previous study in a nearby area in the Detroit River found similar results: the detection range for two V9 180 kHz sentinel tags was < 40 m (the minimum distance tested) from 6 July until 25 August 2015, and upon relocating the tags to the same range test site used in this study on 25 August 2015, detection range was < 50 m until the first week of October and < 75 m until mid-October (the two tags were placed 50 and 75 m from a focal receiver; Klinard et al. 2018), though the specific effects of macrophyte were not examined in this study. Despite differences in power output and acoustic frequency that could result in greater detection range relative to this study, a marine range test study using both V13 and V16 69 kHz tags (147 and 152 dB power output, respectively) in various reef habitats found that high densities of physical structures in the environment caused acoustic signals to be impeded or disrupted (Selby et al. 2016). Specifically, in a reef environment with high structural complexity, range testing resulted in a D_{50} of 30.7 m (95% CI: 8.1 – 56.7 m), similar to the overall D_{50} in this study. The effective detection range in the freshwater nearshore environment tested here is thus comparable to the effective detection range observed in structurally complex reef environments which are also critically important to many marine animal species, however

studies in temperate freshwater environments require the consideration of the effects of seasonal changes in the environment that can drastically influence *DE*.

In general, as macrophyte biovolume decreased the *DE* of acoustic transmitters increased, demonstrating the seasonal dampening effect of macrophytes on the *DE* of acoustic transmitters. The effect of macrophytes on *DE* was greater at large distances between tag and receiver. In systems where macrophyte growth is seasonal, i.e. temperate freshwater ecosystems, the effect of macrophytes on *DE* will vary over time. For example, we saw *DE* at 75 m increase from 0 when macrophytes were present to > 0.75 when macrophytes had senesced by the end of October (Fig. 2.5), exemplifying the significant seasonal influence of macrophytes on the *DE* of acoustic transmitters in this system. The correlation between macrophyte biovolume and *DE* indicates that macrophytes are the primary driver of *DE* and *DR* in this shallow nearshore temperate freshwater system throughout spring, summer, and fall. In other systems that are more stable, e.g. tropical rivers and lakes, the effects of macrophytes may be more constant over time. Regardless of the ecosystem, when macrophytes are present, their effects on acoustic detections is significant and should be quantified and incorporated into study design and analysis.

This study tested the influence of macrophytes on *DE* and *DR* in a shallow nearshore area in the spring, summer, and fall, and results showed increased *DE* and *DR* in the fall when macrophytes senesced. However, we only range tested until late October, and *DE* and *DR* in the winter months may be influenced by other seasonal variables (e.g. ice cover and/or associated noise). Indeed, in a previous study, range tested until 25 November 2015 in the same nearshore area of the Detroit River found that mean weekly *DE* at 50 m peaked at 0.84 (± 0.05 S.D.) in early November and decreased to 0.50 (± 0.20 S.D.) by the last week of the study in late November, and similarly *DE* at 75 m peaked at 0.48 (± 0.31 S.D.) in early November and

decreased to 0.24 (± 0.26 S.D.) by the last week of their study (Klinard et al. 2018), indicating other seasonal effects may dampen *DE* into the winter months. While the primary purpose of this study was to assess the influence of macrophytes on *DE* and *DR*, future studies should include overwinter range tests to explore the variables that drive *DE* and *DR* in shallow nearshore areas in the winter months.

While there was a generally negative relationship between *DE* and macrophyte biovolume, the lowest DE values were not associated with the days of peak macrophyte density (Table 2.4). The highest average macrophyte biovolume of 0.98 occurred on July 31st, but the associated D_{50} was the third lowest reported (11.8 ± 1.3 m). The second lowest D_{50} (6.9 ± 0.6 m) occurred on August 9th with an average macrophyte biovolume of 0.88, and the lowest D_{50} (5.5 ± 139.6 m) occurred on August 14th with an average macrophyte biovolume of 0.62 (Table 2.4). The decrease in *DE* despite decreasing macrophyte biovolume could have been related to the type of growth present. Between July 31st and August 9th, a thick floating algal mat, likely *Cladophora glomerata* (Higgins et al. 2008), formed on the surface of the water in the observation area that persisted into September. In temperate areas, *Cladophora* has been reported to have mid-summer sloughing events where the filaments detach and produce large floating mats (Higgins et al. 2006). These algal mats can reduce the density of macrophytes by blocking sunlight. Although currently speculative, it is possible that the observed algal mat reduced total macrophyte biovolume by reducing density near the substrate while still having a significant effect on *DE*, perhaps through the attenuation of transmissions that would have otherwise reflected off the water surface. Additionally, it is likely that algal filaments suspended in the water column caused increased scattering and absorption of acoustic signals during this time. Algal blooms are the focus of many research efforts due to their widespread nature and impacts

on ecosystems (Auer et al. 2010; Ho and Michalak 2015; Carmichael and Boyer 2016), but further investigation is needed into the effects of algal blooms and composition of macrophyte community on acoustic transmissions.

Macrophyte biovolume and water temperature were correlated as expected because temperature is a primary factor in the seasonal growth cycles of macrophytes in temperate ecosystems (Barko et al. 1982; Steel et al. 2014). Water temperature can directly influence *DE* because temperature affects the density of water and therefore the speed at which sound can propagate (higher temperatures result in higher sound speeds and vice versa; Medwin and Clay 1998). Daily average water temperatures in this system ranged from 8.6 – 25.8°C. Based on the speed of sound in pure water at different temperatures reported by Del Grosso and Mader (1972), the speed of sound would only change 3.8% within the temperature range observed in this study, and therefore water temperature alone is unlikely to account for significant variation in *DE* (Heupel et al. 2008 also found the differences in the speed of sound across the observed temperature range in their study to be negligible). The influence of water temperature on *DE* is most notable in deeper water bodies with a thermocline, which causes the signal to distort as it traverses through a sudden change in density (Medwin and Clay 1998). However, in the well-mixed shallow waters of the Detroit River (< 2 m) there was no thermocline. In this system, temperature likely acts as an accurate proxy variable that encompasses a variety of seasonal effects, including macrophyte biovolume.

Depth can influence the *DE* of acoustic transmitters because the vertical position occupied by study animals or sentinel tags in relation to receivers affects the direct distance that transmissions must travel in addition to the possibility of vertical heterogeneity within the water column (e.g. due macrophytes or density gradients due to temperature). In shallow ecosystems,

such as the one investigated here, we predicted that macrophytes near the benthos would result in decreased *DE* for tags low in the water column relative to those higher in the water column, as low tags would be within submerged vegetation more frequently than high tags (i.e. when vegetation was not dense to the surface at peak macrophyte biovolume). Although tags lower in the water column (i.e. 0.9 m depth) exhibited higher *DE* than those closer to the surface (i.e. 0.3 m depth; Fig 2.3), tag depth did not significantly influence *DE*. Presumably, the observed differences occurred because transmissions near the surface were more likely to be influenced by changes in weather such as wind-induced noise and introduction of sound scattering air bubbles (Gjelland and Hedger 2013). Additionally, low tags were within the same plane as the receivers' hydrophones which may have resulted in slightly greater detection efficiency due to their acoustic transmissions occurring in a plane of higher receiver sensitivity (Clements et al. 2005; Melnychuk 2012). In this study, both tag depths experienced consistently high *DE* at distances ≤ 2 m, but the first signs of variation in *DE* occurred for high tags at 3 and 5 m which displayed low minimum daily *DE* values (Table 2.1), indicating that environmental variables (i.e. wind, rain) may have short-term influences on *DE* for high tags at tag-receiver distances as short as 3 m despite their close proximity. Overall, our results show that tag depth does not have significant effects on *DE* in the nearshore shallow (< 2 m depth) area tested.

Tag and receiver depth may have significant effects in deeper areas of rivers or lakes where there is increased potential for environmental variation throughout the water column. For example, a range study in a large deep (50 – 60 m) freshwater lake tested the effects of tag depth on *DE* and found that shallow tags (11 m) had lower *DE* than deep tags (50 m) across a variety of different sized 69 kHz tags (Klinard et al. 2019). In a reef environment, Cagua et al. (2014) found differing results in two study sites: one site with clear water and otherwise similar

environmental conditions across tags aside from depth found no differences in *DE* among different tag depths, while deeper tags in the another site had lower *DE,* likely due to blocking by the benthos (but also possibly due to biological noise or increased turbidity). Future studies in nearshore habitats should assess the influence of macrophytes on *DE* across a greater range of depths; since macrophytes are not likely to occupy the entire water column in deeper waters (and eventually do not occur at all), the resultant heterogeneity in the water column would likely cause variation in the influence of depth on *DE* across distance. For example, in this study, had we chosen to orient our range test towards the navigation channel where depth increases, tag depth may have played a more significant role in the deeper areas where macrophytes do not grow to the surface. The inconsistencies among studies highlight the importance of considering and testing the effects of different equipment depths in acoustic telemetry studies as it can influence the *DE* based on different environments and conditions.

In this study we demonstrated how seasonal changes in macrophyte biovolume can result in significant variation in the performance of passive acoustic telemetry technology and quantified this relationship for the first time using a novel approach. The results indicated that the seasonal interactive effects of distance and macrophyte biovolume on the detection efficiency of acoustic transmitters is the primary driver of detection range in shallow nearshore habitat of the Detroit River through late spring until fall. Periods of low detection range can result in fewer detections of fish, but the detections that do occur result in more accurate locations of fish because the detection range is limited. Additionally, periods of low detection range can be improved with additional receiver deployments in macrophyte rich areas or supplementary manual tracking to locate fish that are not within detection range of passive receivers (e.g. Carol et al. 2007). The results of this study will help to inform researchers and improve passive

acoustic telemetry studies in vegetated freshwater habitats that are key at some point in the life cycles of many freshwater fish species. Future studies investigating the influence of macrophytes on *DE* and *DR* should also assess the composition of the macrophyte community and potential differences in the influence different species of macrophytes have on the attenuation of acoustic transmissions. Future studies in nearshore freshwater habitats should perform both passive and mobile range testing within the study site prior to initiating the study to aid in study design. They should also include a greater range of depths present in littoral habitats to study how the influence of tag or receiver depth on *DE* can vary in deeper habitats with greater vertical heterogeneity or across increasing depth. Additionally, future studies should continue comprehensive range testing while tagged animals are in the system to account for the effects of environmental variation during data analysis. While learning about aquatic animal movements in nearshore habitats in temperate freshwater systems is associated with constraints due to macrophyte cover, range testing and supplemental monitoring can help to account for the effects and these studies will contribute to our knowledge of their ecology and aid in conservation and management efforts.

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Table 2.1 Summary of daily detection efficiency of acoustic transmitters (mean ± S.D.), minimum, and maximum from 31 July 2018 – 31 October 2018, averaged for each distance. Values for high and low tag depths, respectively, are separated by /.

Distance (m)	Mean daily DE ± S.D.	Min. daily DE	Max. daily DE
0.5	0.94 ± 0.02 / 0.94 ± 0.02	0.90 / 0.88	0.99 / 0.99
1	0.94 ± 0.02 / 0.94 ± 0.02	0.85 / 0.87	0.99 / 0.98
1.5	0.94 ± 0.02 / 0.94 ± 0.02	0.89 / 0.88	0.99 / 0.98
2	0.94 ± 0.02 / 0.94 ± 0.02	0.90 / 0.90	0.97 / 0.97
3	0.92 ± 0.08 / 0.94 ± 0.01	0.30 / 0.91	0.97 / 0.98
5	0.90 ± 0.14 / 0.93 ± 0.03	0.03 / 0.76	0.99 / 0.99
10	0.52 ± 0.43 / 0.59 ± 0.42	0 / 0	0.98 / 0.98
25	0.31 ± 0.42 / 0.44 ± 0.42	0 / 0	0.98 / 0.97
50	0.21 ± 0.37 / 0.20 ± 0.33	0 / 0	0.97 / 0.97
75	0.10 ± 0.24 / 0.10 ± 0.27	0 / 0	0.94 / 0.89

Table 2.2 Summary of the generalized linear model results of daily detection efficiency of acoustic transmitters against distance and tag depth for 93 days of detections in the Detroit River between 31 July 2018 – 31 October 2018.

Predictor variable	Estimate	Standard error	Statistic	P value
Intercept	2.654	0.316	8.407	< 0.001
Distance 1	< 0.001	0.437	0.002	0.999
Distance 1.5	-0.008	0.437	-0.018	0.985
Distance 2	-0.050	0.433	-0.115	0.909
Distance 3	-0.187	0.421	-0.446	0.656
Distance 5	-0.378	0.406	-0.930	0.352
Distance 10	-2.534	0.343	-7.391	< 0.001
Distance 25	-3.255	0.344	-9.450	< 0.001
Distance 50	-4.129	0.359	-11.500	< 0.001
Distance 75	-4.967	0.395	-12.580	< 0.001
Tag depth low	0.211	0.140	1.505	0.132

Residual deviance: 595.736 on 1849 degrees of freedom
Null deviance: 1564.2 on 1859 degrees of freedom

Table 2.3 Summary of daily detection efficiency of acoustic transmitters (mean ± S.D.) for each tag-receiver distance averaged for August, September, and October 2018.

Distance (m)	Mean daily DE ± S.D.		
	August	**September**	**October**
0.5	0.94 ± 0.02	0.94 ± 0.02	0.94 ± 0.02
1	0.94 ± 0.02	0.94 ± 0.02	0.94 ± 0.02
1.5	0.94 ± 0.02	0.94 ± 0.02	0.94 ± 0.02
2	0.94 ± 0.01	0.94 ± 0.01	0.94 ± 0.02
3	0.94 ± 0.01	0.91 ± 0.09	0.93 ± 0.02
5	0.93 ± 0.02	0.88 ± 0.17	0.93 ± 0.02
10	0.11 ± 0.25	0.65 ± 0.37	0.91 ± 0.11
25	0	0.3 ± 0.34	0.84 ± 0.22
50	0	0.03 ± 0.12	0.58 ± 0.39
75	0	0	0.3 ± 0.36

Table 2.4 Summary of the daily mean temperature (°C), overall daily biovolume (proportion of macrophyte height in water column), and the distance (m) at which detection efficiency (2 hour) of acoustic transmitters is 0.50 (D_{50} ± S.E.) for each of the days included in the macrophyte analysis.

Date	**Daily mean temperature (°C)**	**Daily mean biovolume**	**D_{50} (m)**
2018-06-05	18.2	0.76	39.8 ± 3.1
2018-07-04	23.9	0.95	15.7 ± 2.2
2018-07-31	23.0	0.98	11.8 ± 1.3
2018-08-09*	25.1	0.88	6.9 ± 0.6
2018-08-14*	25.8	0.62	5.5 ± 139.6
2018-10-05	16.9	0.07	40.4 ± 3.3
2018-10-12	15.5	0.03	49.0 ± 3.5
2018-10-25	8.7	0.01	167.7 ± 85.0
2018-10-31	9.1	0.04	186.8 ± 114.4

*denotes days with an algal mat on the surface of the water that may have further impeded detection efficiency

Table 2.5 Analysis of variance results for the generalized linear models looking at the influence of mean macrophyte biovolume and tag depth on DE (2 hour) at each distance.

Distance (m)	Predictor	χ^2	df	p-value
5	Mean macrophyte biovolume	0.256	1	0.613
	Tag depth low	0.168	1	0.682
10	Mean macrophyte biovolume	39.942	1	< 0.001
	Tag depth low	1.149	1	0.284
25	Mean macrophyte biovolume	167.686	1	< 0.001
	Tag depth low	0.063	1	0.802
50	Mean macrophyte biovolume	120.124	1	< 0.001
	Tag depth low	4.306	1	0.038
75	Mean macrophyte biovolume	100.89	1	< 0.001
	Tag depth low	0.02	1	0.889

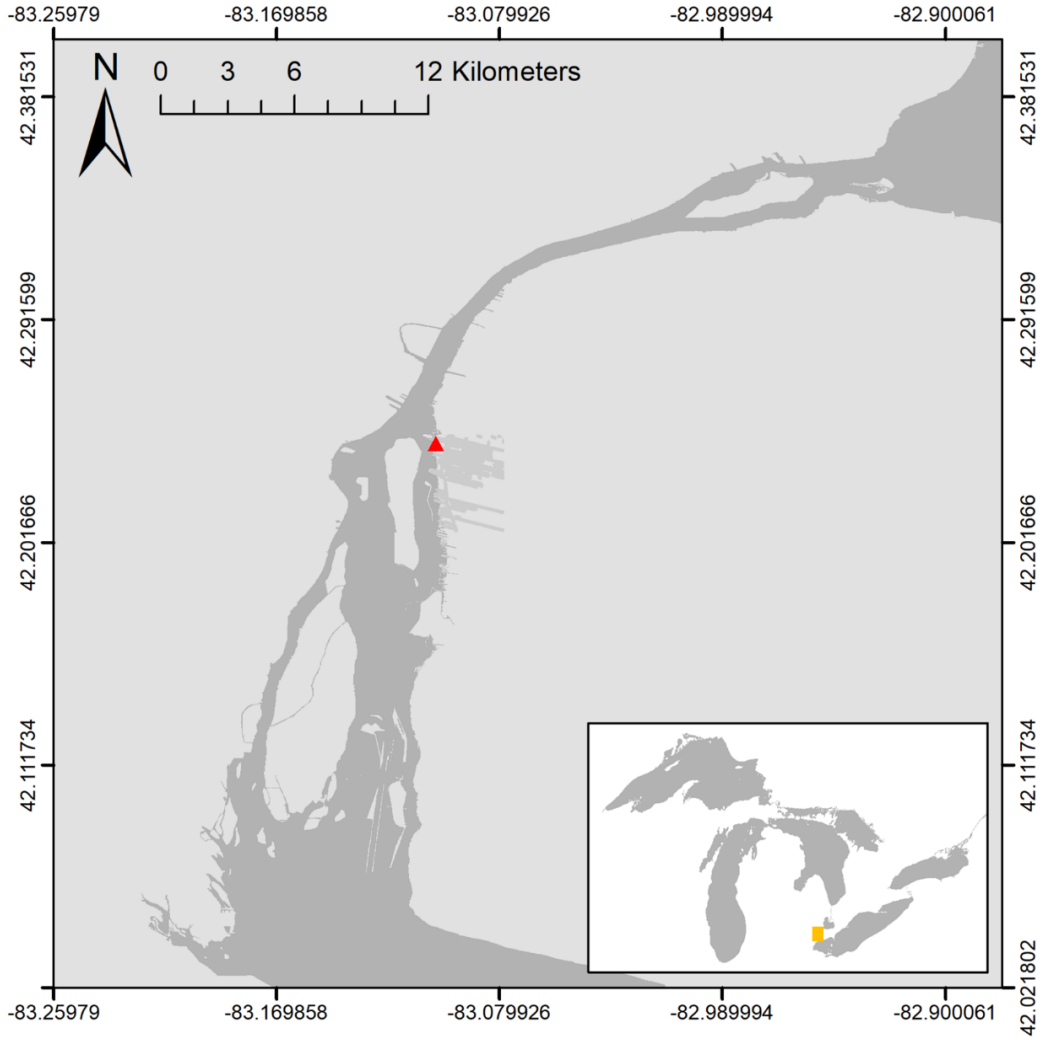

Figure 2.1 Range test location within the Detroit River (42.242, -83.108) marked with a red triangle. The inset map marks the location of the Detroit River within the Laurentian Great Lakes with an orange square. See Fig. 2.2 for range test configuration.

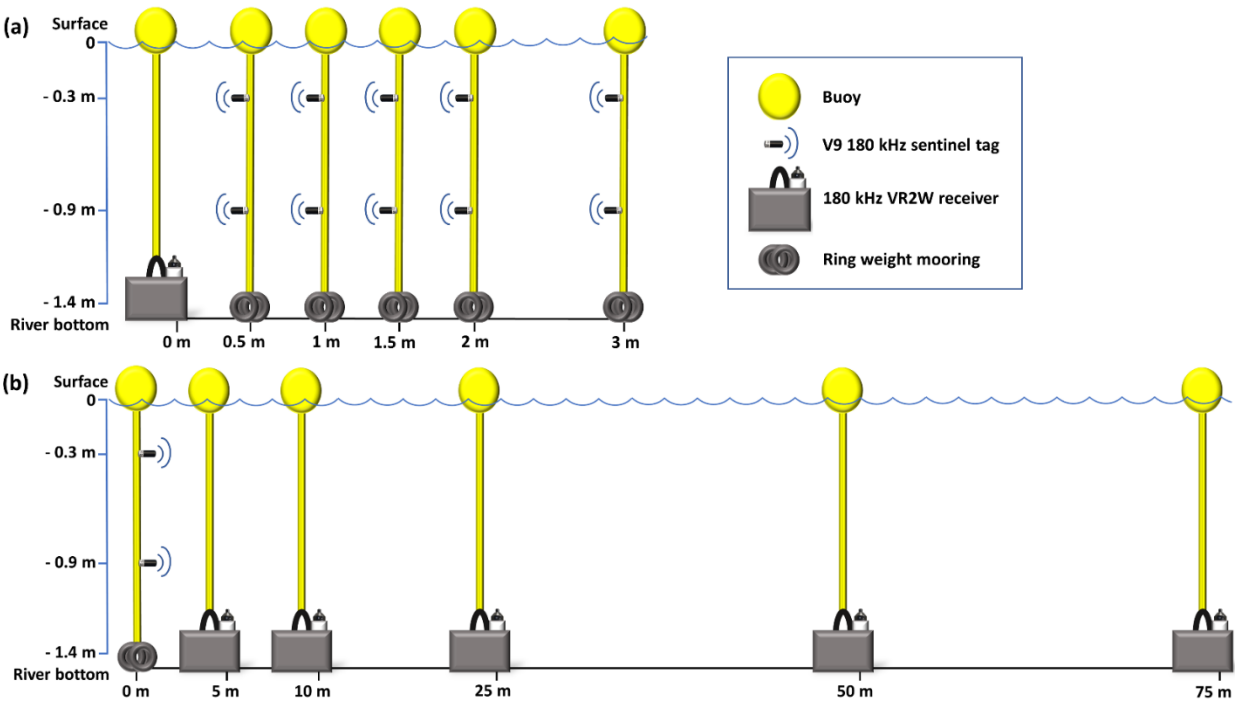

Figure 2.2 Configuration of receiver and sentinel tag deployments in the Detroit River from 30 July – 1 November 2018. a) fine-scale tests were deployed with one 180 kHz VR2W receiver and five sets of V9 180 kHz sentinel tags (high power output) at two depths at distances of 0.5, 1.0, 1.5, 2.0, and 3.0 m. The first three sets of tags have a nominal delay of 600 s (randomized from 550 – 650 s) and the last two sets have a nominal delay of 300 s (randomized between 270 – 330 s); b) coarse-scale tests were deployed with one set of V9 180 kHz sentinel tags (the same tags deployed at 0.5 m in the fine-scale test; 10 minute nominal delay) and five 180 kHz VR2W receivers moored at distances of 5, 10, 25, 50, and 75 m from the tags. In both configurations, receivers were moored in PVC pipes set in concrete blocks with a buoy attached to a rope for ease of retrieval. Tags were attached at two depths (0.3 and 0.9 m from the surface) along a rope that had ring weights on one end and a buoy at the surface. For location of testing see figure 2.1.

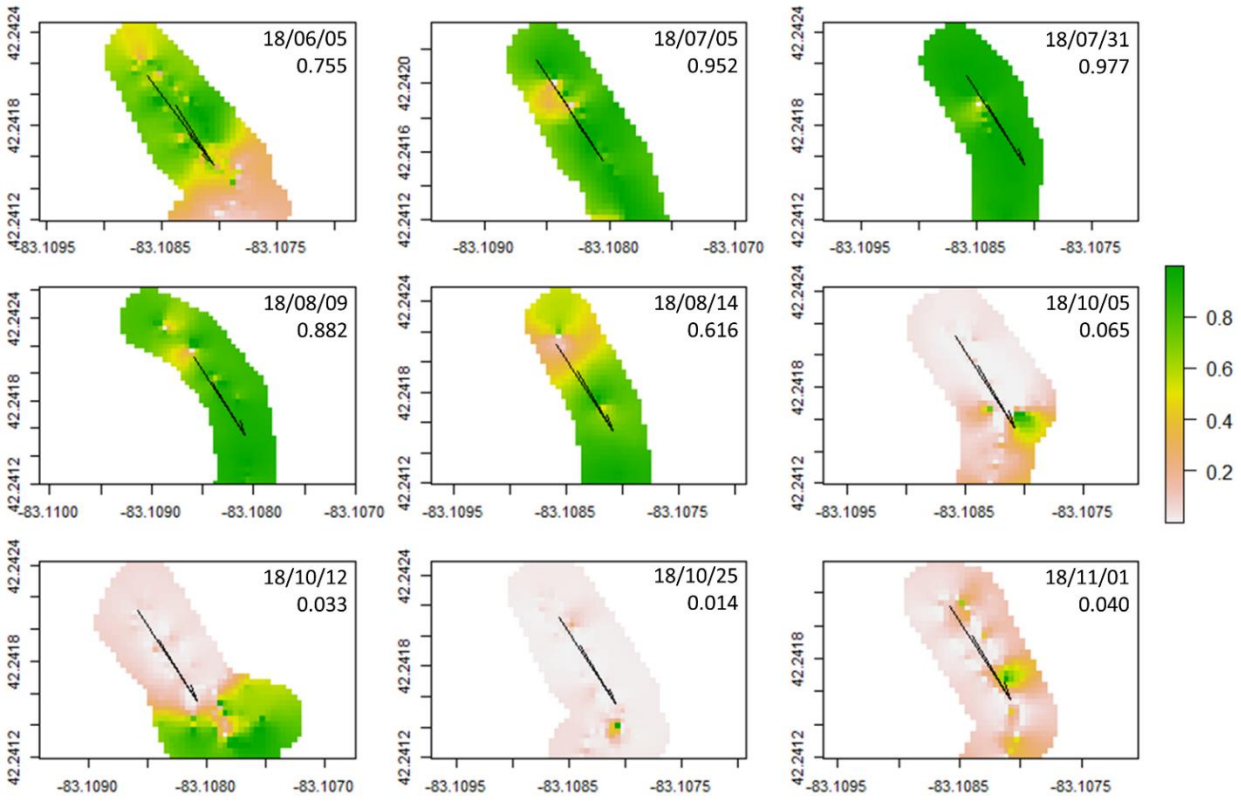

Figure 2.3 Raster images of the macrophyte biovolume heatmaps covering the range test site in the Detroit River. Lines on each plot connect each unique tag-receiver pair (not all lines are visible due to overlap). For each of 5 lines on each map, macrophyte biovolume values were extracted and averaged to produce a value representative of the overall biovolume between each tag-receiver pair. Daily average macrophyte biovolume values were calculated using the data for each of those lines and reported in the top right corner of each raster image with the date mapping occurred in the format yy/mm/dd.

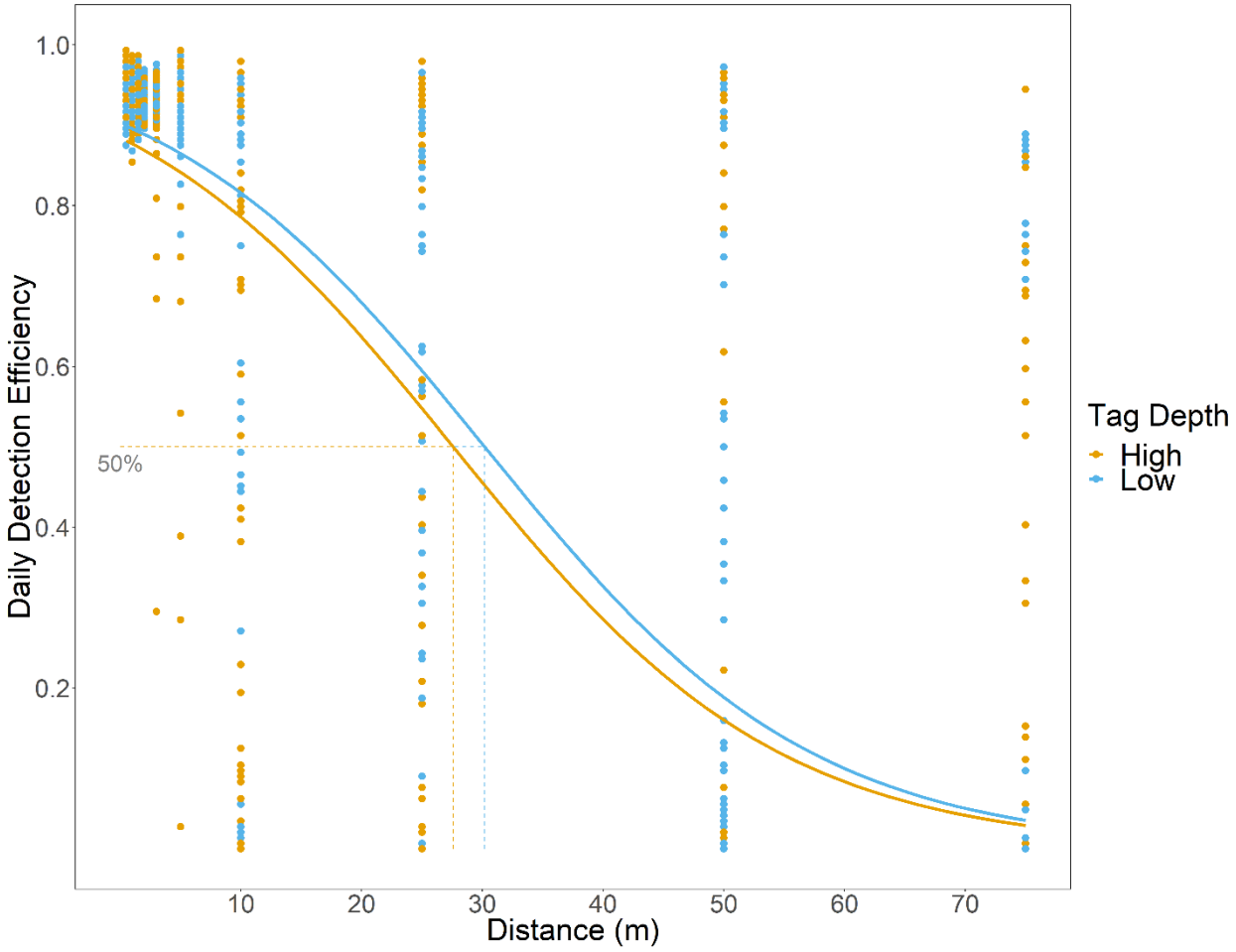

Figure 2.4 Overall trend in daily detection range for each tag depth throughout long-term range testing in the Detroit River from 31 July – 31 October 2018. Tags were V9 180 kHz with high power output. Orange line represents the logistic relationship between detection efficiency and distance for tags higher (1.1 m from bottom) in the water column and the blue line represents the same relationship for tags lower (0.5 m from bottom) in the water column. Points on the graph represent daily detection efficiencies for high and low tags. Dotted lines represent the distances at which detection efficiency is 0.50 (i.e. D_{50}) for high and low tags.

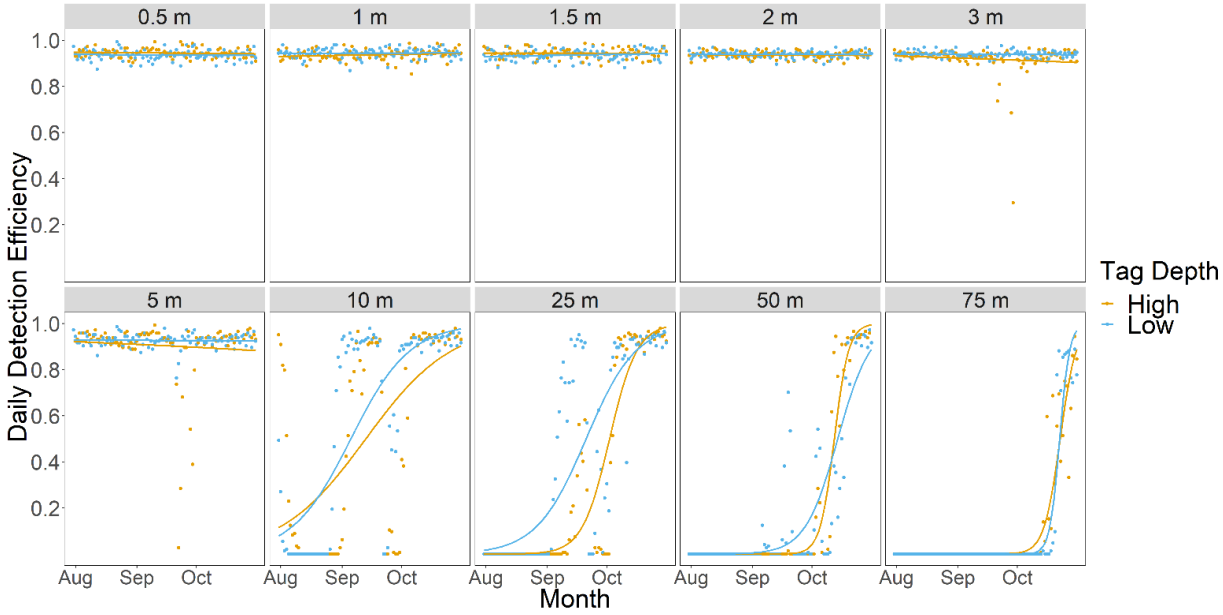

Figure 2.5 Trends in daily detection efficiency across time for each tag-receiver distance in the Detroit River from 31 July – 31 October 2018. Tags were V9 180 kHz with high power output. Orange and blue lines represent the relationship between daily detection efficiency and time for tags high in the water column and tags low in the water column, respectively. Orange and blue dots represent the individual daily detection efficiency estimates for high and low tags, respectively.

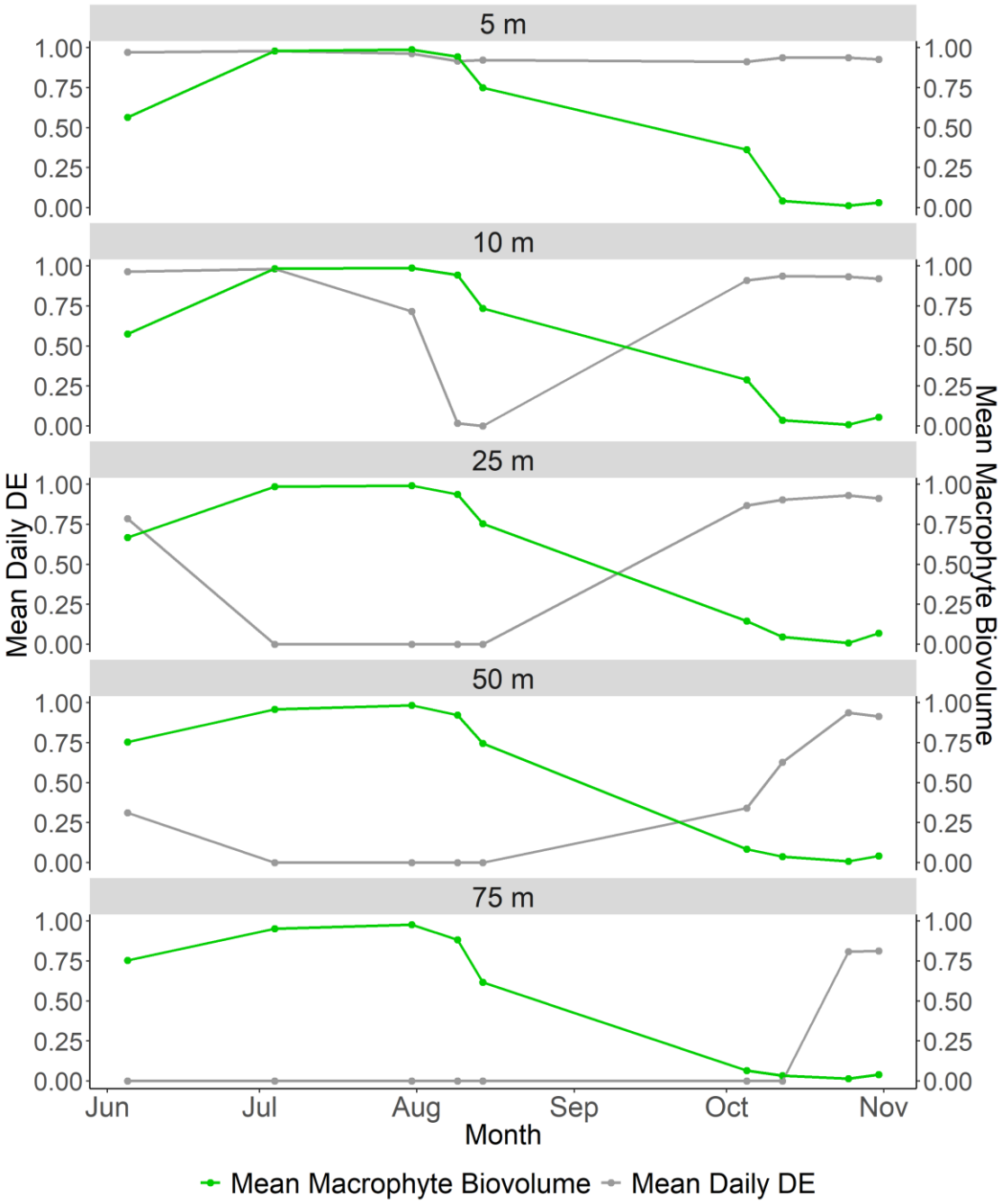

Figure 2.6 Mean daily detection efficiency of acoustic transmitters and mean macrophyte biovolume at each distance for the nine days in the vegetation analysis from 5 June – 31 October 2018 in the Detroit River (using V9 180 kHz high power output tags).

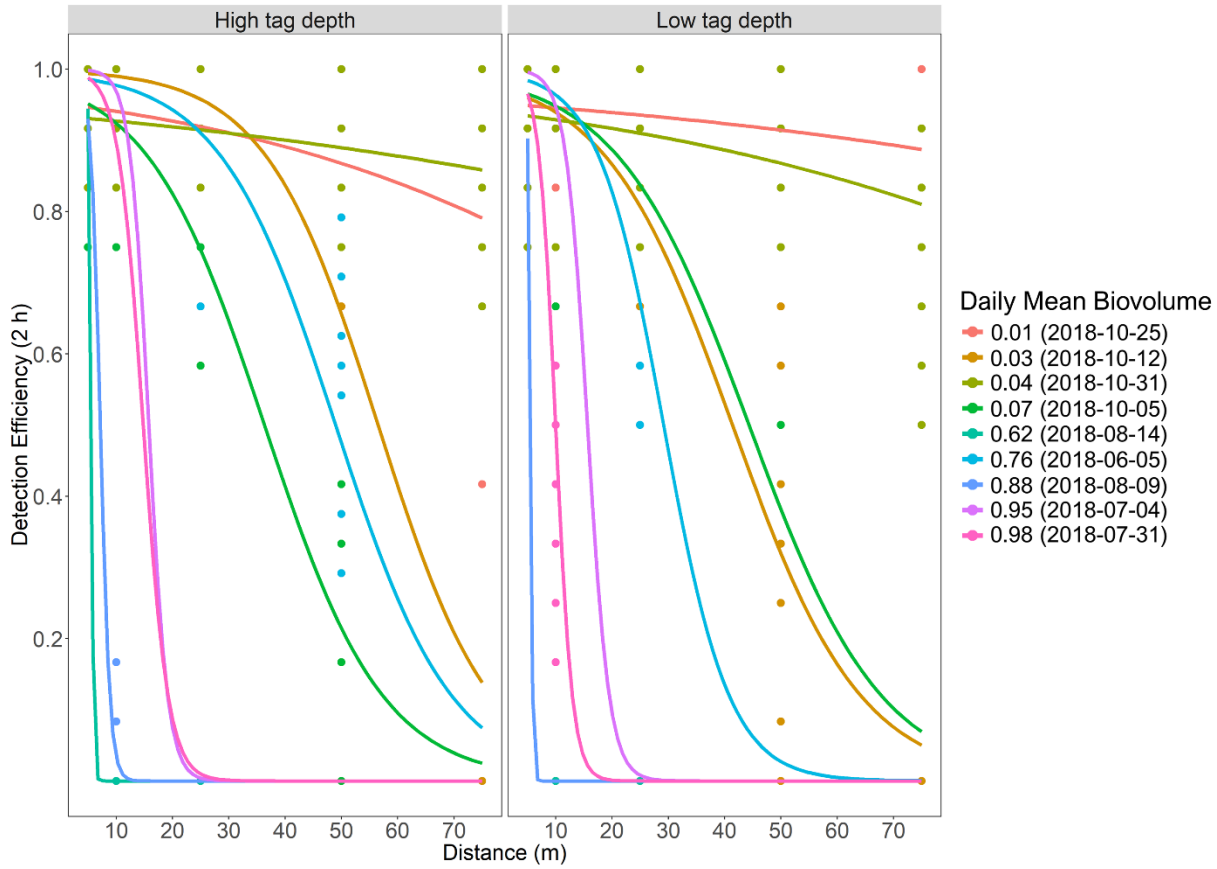

Figure 2.7 The influence of variable daily average macrophyte biovolume on the relationship between detection efficiency of acoustic transmitters (2-hour bins) and distance (m), i.e. detection range, at high and low tag depths (V9 180 kHz high power output tags) in the Detroit River. Each coloured line represents a different daily average biovolume. See table 2.4 for a summary of D_{50} at each daily average macrophyte biovolume and daily average temperature.

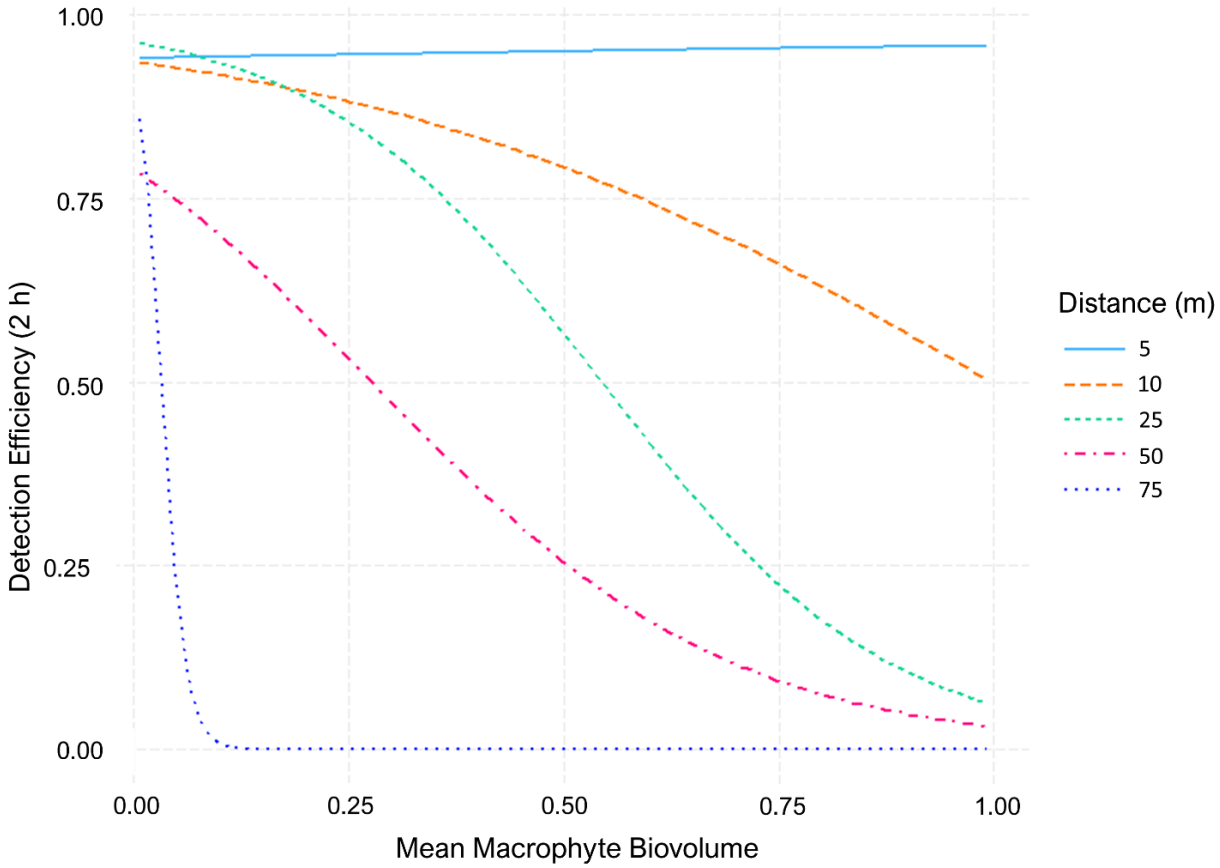

Figure 2.8 The interaction between the detection efficiency of acoustic transmitters (2-hour bins; V9 180 kHz high power output) and mean macrophyte biovolume at each of five distances tested in the Detroit River

CHAPTER 3

Identification of predation events in wild fish using novel acoustic transmitters

3.1 Introduction

Mortality can result from factors such as disease, physiological stressors, senescence, and predation. Identifying mortality of individuals in their natural environment is important for understanding ecological and biological processes; however, disentangling the possible sources of mortality can be difficult because direct observations of death are rare, especially in aquatic ecosystems. Predation is a significant driver of mortality in aquatic environments (Christensen 1996), influencing behavioural interactions, trophic dynamics, and community structure across ecosystems (Creel and Christianson 2008). Many studies have explored predation by observing fishes in laboratory, mesocosm, or manipulated natural settings (Werner et al. 1983; Power et al. 1985; Hambright 1991), but these studies are often not representative of the complex interactions that occur in nature. Alternatively, field observations often require intense labour, pose the risk of observer effects influencing behaviour through disturbance, and are spatiotemporally fragmented (Karam et al. 2008; Halfyard et al. 2012). As a result, much about predation in natural aquatic settings remains unknown.

Acoustic telemetry is a frequently used method of studying aquatic animal movement to infer behaviour and survival in natural settings (Hussey et al. 2015) and past studies have used changes in movement patterns or ancillary sensor data, e.g., depth profiles, to identify possible predation events (Friedl et al. 2013; Gibson et al. 2015). The miniaturization of transmitters has allowed researchers to study the movement and mortality of smaller animals (Clark et al. 2016; Lennox et al. 2017), which are more vulnerable to predation, creating a greater potential for

predation bias in telemetry studies (Gibson et al. 2015; Klinard et al. 2019). A recent technological advancement allows for the passive detection of predation in the wild; newly developed acoustic transmitters (hereafter predation tags) change their transmitted identification code following predation events (Halfyard et al. 2017). The switch from a non-predated ID code to a post-predation ID code is triggered when a biopolymer on the tag's surface is digested after predation.

The potential application of predation tags is wide-ranging and will improve telemetry studies (e.g. tagging effects, quality control, etc.), in addition to informing ecological processes such as natural mortality, predator-prey interactions, and predation risk. However, preliminary tools or methods still need to be developed to appropriately interpret and communicate the application of predation tags in natural settings. The goal of this study was to demonstrate the detection data obtained from predation tags in a freshwater river. We did this by implanting 60 predation tags into yellow perch (*Perca flavescens*) in the Detroit River and tracked the fate of those tags using a fine-scale receiver array. We examined the movement patterns of apparently predated tags before and after the tag ID switched to assess the possible detection outcomes from these tags and discuss their use as evidence of predation.

3.2 Materials and Methods

Study site and acoustic array

This study was conducted from May 2018 – January 2019 in a 34 ha segment of the Detroit River (Fig. 1), a predator-rich connecting channel in the Laurentian Great Lakes where prey species have been shown to exhibit localized movements (Klinard et al. 2018a). To track tagged prey fish, an array of 21 VR2W-180 kHz acoustic receivers (Vemco Ltd., Nova Scotia, Canada) was maintained within the study area. Receivers were moored on the river bottom

within cinder blocks that were spaced 65-270 m apart and varied in depth from 1 m near shore to 6 m along the channel. Receivers were moored along the bottom to avoid anthropogenic interference (e.g. damage by boat motors) and to capture detections throughout the entire water column. Water temperatures ranged from 0 - 27°C throughout the study period from May 2018 - January 2019.

Fish capture and acoustic tag implantation

Sixty yellow perch (103-190 mm total length, 13-81 g wet weight) were implanted with Vemco V5D-180 kHz predation tags (0.68 g in air; nominal delay of 300 s; 173 day tag life) in May (n = 40) and July (n = 20) 2018. Maximum tag burden (tag weight relative to fish weight) was 5.23%, within acceptable ranges based on recent studies of other small fish species (Brown et al. 2010; Smircich and Kelly 2014; Klinard et al. 2018b). Prior to implantation, tags were tested to verify that the proper pre-predation ID code was being transmitted. The first six fish tagged were anesthetized in a buffered solution of tricaine methanesulfonate (MS-222; 100 mg/L) and the rest were electrosedated using a PES unit to avoid the withdrawal period associated with chemical anesthetics that may increase tagging effects (Trushenski et al. 2012; 4 sec pulsed DC, 100 V, 30 Hz, and 25% duty cycle; Smith-Root Inc, Washington). Surgical tagging procedures followed methods as described by Klinard et al. (2018a).

Data analysis

Data analysis and presentation focused only on tags that indicated a predation event. To evaluate patterns in pre- and post- predation behaviour, space use was quantified with a roaming index, calculated as the number of unique receivers a fish was detected on within 2 h intervals divided by the total number of receivers in the array (Matley et al. 2015). To visually assess changes in behaviour, movement paths were plotted using centres of activity (COA;

Simpfendorfer et al. 2002) which were calculated as averaged positions of each individual's location within 30-minute time intervals. A 30-minute timestep was chosen after visual analysis of COAs calculated with different timesteps (5, 15, 30, and 120 minutes). COAs with less than two detections per timestep were removed from analysis to account for the potential presence and effects of false positive detections.

Detection data was divided into four stages: 1) *Non-predated*, which represented the behaviour of the tagged perch prior to predation; 2) *Lag period*, which included the 24 hour period prior to the first post-predation detection and potentially combined prey and predator behaviour during the time it takes for the tag ID to switch (i.e. signal lag); 3) *Predated < 24 h*, which indicated the 24 hour period after the first post-predation detection during which time the predators movements were detected; and 4) *Predated > 24 h*, which accounted for the remainder of the detection data, during which time the likelihood of the tag being expelled by the predator increases depending on variable retention times (Gibson et al. 2015; Jepsen et al. 2015; Halfyard et al. 2017). A period of 24 hours was chosen for the lag period to span the maximum time for digestion of the prey and biopolymer to occur (< 24 h), which varies based on temperature and prey size (Halfyard et al. 2017). This was a conservative time period, as manufacturer testing of the production version of the predation tag (that differs from those tested in Halfyard et al. 2017) had a mean (± S.D.) signal lag of 5.8 (± 2.6) h at 13°C (D. Webber, personal communication). Furthermore, these same manufacturer tests (n = 20 tags) reported a single false positive, i.e., the predation tag switched to the predation ID without predation occurring, on day 111 of a 299-day trial with fish held at 20°C.

3.3 Results and Discussion

In this study, we demonstrated the application of predation tags in a natural setting using a fine-scale array. All 60 tagged yellow perch were detected after release, producing 501,277 detections from 5 May 2018 – 15 January 2019, at which point all tags reached their maximum lifespan. The 60 tags had an average of 8,354 detections each (± 9084.0 S.D.), ranging from 119-51,474 detections, and were detected for an average of 96.9 days (± 72 S.D.), ranging from 0.8-224.8 days. A total of 19 apparent predation events, i.e., the transmission signal of the tag switched, were detected (31.7% of tagged fish; Table 3.1; Fig. 3.2) between May and September. Mean water temperature at time of the first post-predation detection (which does not always represent the temperature during the signal lag period if gaps in detections occurred) was 22.6°C ± 3.2°C (mean ± S.D.; range 15°C – 26°C). Non-predated tags were detected for 0.7 – 98.9 days prior to the apparent predation events (mean ± S.D. = 36 ± 35.4 days; Table 3.1). Out of 69,445 post-predation detections, there were four instances in which tags (YP12 and YP26) reverted back to their pre-predation transmission codes for 1 – 2 detections, either representing momentary tag reversions, as seen in laboratory studies (A. Fisk, unpublished observations), or the product of transmission collisions from multiple tags or environmental noise interference.

We observed a number of possible predation tag detection scenarios in the Detroit River (see table 3.2 for a summary of the general categories) but to demonstrate the possible interpretations of the movement data we focused on a subset of six of the apparently predated individuals (interpretations for all 19 fish that code switched are presented in the appendix). Changes in space use were observed for Tag YP10 which exhibited a distinct increase in total space use following the predation code switch (Fig. 3.3ab), including movements across the navigation channel that were not typical of this tagged perch or similarly sized sunfish tagged in

the same array (Klinard et al. 2018a). Instead of increased spatial use, Tag YP22 displayed altered habitat use within the array after the code switch and moved further south in the array (Fig. 3.3cd). In comparison to the tags that showed changes in space use after triggering, Tag YP23 was predated almost immediately after release as indicated by the absence of non-predated detections, but was subsequently detected on a single receiver for 178 days, consistent with a transmitter passing through the digestive system of a predator and being expelled within range of a receiver station (Fig. 3.3ef). Similarly, Tag YP39 did not exhibit a clear change but was detected on a single receiver over 87 days after predation, which again, is a detection pattern consistent with a predator-expelled tag (Fig. 3.3gh). Tag YP38 was triggered 95 days after tagging (over half of its battery lifespan) but did not show space use changes (Fig. 3.3ij) before post-predation detections ceased 2 days after the tag was triggered, indicating that despite a lack of evident change in space use, the predator may have migrated out of the receiver array. Finally, Tag YP42 indicated a predation event two days post-release but detections ceased on the fourth day, with no clear changes and too few detections to consider behaviour when inferring fate (Fig. 3.3kl), however, it is not likely to be a false positive because tags were tested immediately prior to implantation and false positives were rare in laboratory tests (see above). Overall these detection scenarios demonstrated the variety of predation tag patterns that can be observed with a single study array over a relatively short period of time, but which need to be considered individually to make inference about the fates of individual fish.

There are multiple possible interpretations for the movement patterns observed from predation tags that distinguish them from presence/absence tags most frequently used in acoustic telemetry studies. Transmitters that exhibited both a code switch and clear changes in space use before and after predation, e.g., location of activity or size of activity range, would have the

highest confidence of a predation event occurring due to the coupling of behaviour changes with the tag trigger mechanism. Apparent predation events based on a code switch with few detections following the switch add a degree of uncertainty because it is possible for non-resident predators to have carried their prey out of the receiver range or for the tag to have malfunctioned and registered a false positive. It is not possible to conclusively identify false positives, however, since laboratory tests of these predation tags reported a 95% success rate for identifying predation events (D. Webber, personal communication), chances of false positives occuring are low. Finally, environmental conditions affecting the performance of acoustic receivers cannot be discounted. For example, tags that have code switched may not be detected for weeks or months after a predation event but changes in receiver detection efficiency could bring these tags into detection range, adding uncertainty to the location and timing of predation events. Predation tags do not replace the need for researchers to consider each of the apparent predation events detected (see Table 2 for summary) and use their knowledge of the study system and species involved to infer and present arguments for the likely fates of individual fish.

Altogether, these changes in behaviour before and after the ID code switch present evidence that predation tags can identify predation events in natural settings. It is important to consider that in addition to the potential for false positives resulting in overestimates of apparent predation, natural predation levels may also be overestimated due to increased vulnerability to predation due to tagging effects, or underestimated if predators that consume tagged fish leave the receiver array before the tag ID switches. The variation in behaviour post tag-switch also suggests that there may have been different predators, providing opportunities to learn about the predators consuming tagged fishes. In the past, telemetry studies have inferred predation or mortality via behavioural changes that were deemed atypical of the study species, mirrored

known behaviour of another species, or resulted in ceased movement (Friedl et al. 2013; Gibson et al. 2015). Other studies used changes in ancillary sensor data (e.g. depth or temperature) to deduce predation of tagged individuals (Lacroix 2014; Wahlberg et al. 2014), however these sensors are not always available with small tags and significantly reduce battery lifespan, limiting this method to larger species. Pairing predation tags with methods used in the many telemetry studies that have been able to show support of predation has the potential to produce strong arguments for predation.

Predation tags can also serve as a valuable tool for investigating the effects of human interactions on predation risk and predator evasion. For example, the process of capturing and surgically implanting tags in fish has been shown to influence post-release behaviour, thus researchers must consider these effects when analysing post-release detection data and attempt to assess the effects of tagging whenever possible (Adams et al. 1998; Wilson et al. 2017). In our study, Tag YP23 was apparently consumed within hours of tagging, which may have been caused by reduced predator evasion due to tagging effects, despite efforts made to reduce the stress of handling, surgery, and optimize recovery time. Additonally, numerous species are hatchery-reared and released in large numbers therefore resulting in research regarding the survival of stocked fish and questions about their vulnerability to predation following release (Bettinger and Bettoli 2002; Daniels et al. 2019; Flowers et al. 2019). The use of predation tags may provide estimates of mortality that can be used to refine stocking methods to increase the number of fish surviving following introduction. Consequently, this technology can be used as an explorative tool associated with the multiple facets of spatial ecology research and conservation efforts.

Gaining insight into natural mortality of animals in aquatic ecosystems has proven to be difficult in the past and methods are often indirect or labour-intensive. Acoustic telemetry is a valuable tool used to learn about the behaviour and survival of aquatic animals (Hussey et al. 2015), but until recently had limited ability to provide evidence of mortality, particularly predation-induced mortality. We have demonstrated one of the first successful applications of predation tags designed to specifically identify predation events in natural settings and provide evidence that the tags function effectively based on behavioural changes before and after predation. While these predation tags do not remove all uncertainty about the fate of tagged individuals, they provide a level of inferential power not previously available to telemetry studies and open new avenues for insights into spatial ecology of wild populations.

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Table 3.1 Summary of detections for apparently predated tagged yellow perch in the Detroit River.

Tagging group	ID	Total length (mm)	Total detections	Total receivers	Days with detections	Timespan detected (days)	Total timespan detected (days)
May 2018	*YP02*	126	17389 / 136	16 / 4	74 / 14	98.9 / 80.6	179.9
	YP10	108	2703 / 151	17 / 13	11 / 3	10 / 6.4	16.5
	YP12	182	3276 / 1295	13 / 6	55 / 50	53.9 / 58.4	113.1
	YP17	115	2963 / 3	15 / 2	33 / 3	62.1 / 82.1	153.5
	YP19	115	11778 / 1696	14 / 2	85 / 22	87.3 / 92.1	180.0
	YP22	118	2870 / 275	12 / 9	19 / 4	18.3 / 3.2	21.5
	YP23	176	703 / 50771	15 / 8	2 / 180	1 / 179	180.0
	YP26	175	5671 / 107	7 / 1	31 / 9	30.5 / 21.4	53.0
	YP33	181	116 / 28	6 / 6	2 / 2	0.7 / 0.9	25.0
	YP34	118	575 / 443	6 / 8	3 / 4	2.4 / 2.4	4.8
	YP38	133	12750 / 22	10 / 6	90 / 2	95.4 / 1.1	96.6
	YP39	140	13025 / 561	11 / 1	84 / 13	93.5 / 85.9	179.9
July 2018	*YP42*	106	377 / 36	2 / 4	4 / 2	2.8 / 0.5	3.8
	YP43	160	1548 / 2364	8 / 3	35 / 58	37.2 / 131.4	168.6
	YP44	180	2283 / 1206	10 / 9	27 / 53	26.1 / 153.8	179.9
	YP47	160	4038 / 11	11 / 1	29 / 1	28.3 / 0.2	29.4
	YP51	103	597 / 8266	4 / 2	4 / 44	2.6 / 132	134.6
	YP52	109	239 / 2037	2 / 1	3 / 47	1.7 / 146.9	148.6
	YP54	154	640 / 33	7 / 2	32 / 5	31.4 / 138.1	169.7
	Mean	139.9	4396.9 / 3654.8	9.8 / 4.6	32.8 / 27.2	36 / 69.3	107.3
	S.D.	29.4	5264.8 / 11567.7	4.6 / 3.5	30.6 / 42.3	35.4 / 63.6	71.2
	Range (pre)	103 – 182	116 – 17389	2 – 17	2 – 90	0.7 – 98.9	3.8 - 180
	Range (post)		3 - 50771	1 – 13	1 – 180	0.2 – 179	

Data for pre-predation and post-predation are separated by / for applicable metrics. Days with detections indicates the number of unique days the ID code was detected in the array. Timespan detected indicates the timespan the ID code could have been detected in the array based on the difference between the release date and time and the timestamp of the last detection of the pre-predated ID and the difference between the first and last detection timestamp of the post-predated ID. Total timespan detected is the difference between the date and time of the last detection of the post-predation ID and the release date and time.

Table 3.2 Proposed ranking of fate assignments to acoustic predation transmitters.

Fate	Transmitter state	Movement patterns	Notes
Non-predated	Non-predated code	No changes	Assumes that fish are regularly detected during transmitter lifespan.
Predated	Code switched	Changes in total area and/or locations of activity	Sudden changes in movement patterns and continued detections could be inferred as a resident predator that remains in the area.
Predated	Code switched	Few detections	No movement pattern information for potential behavioural inference of fate, more likely outcome when there are fewer receivers or migratory predators that move away from focal areas shortly after predation.
Predated	Code switched	Similar location and home range	Increasing possibility of a false positive over time.
False positive (Not predated but tag switches)	Code switched	Similar location and home range	Hard to distinguish from previous entry. Based on laboratory trials this is less likely to occur in the first weeks following tagging, but probability increases over time since release. May be a more important factor as longer lasting transmitters are developed.
False negative (Predated without tag switch)	Non-predated code	Distinct changes	Unlikely based on laboratory trials, e.g. Halfyard et al. (2017).

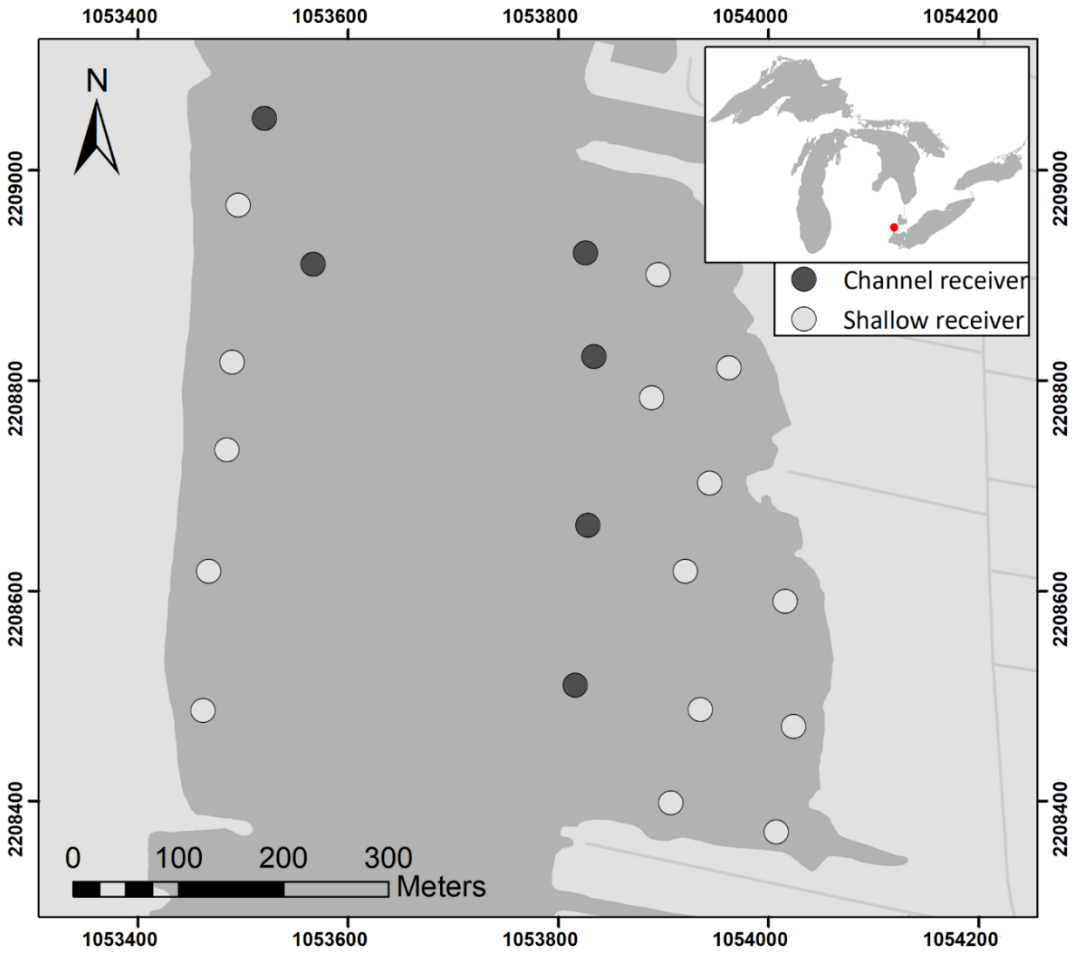

Figure 3.1 Map of the acoustic telemetry VR2W-180kHz receivers (Vemco Ltd.) deployed in the shallow river margins and along the edge of a shipping channel in the Detroit River between the shorelines of LaSalle (eastern boundary) and Fighting Island (western boundary). Red dot in map inset identifies location of study site within the Laurentian Great Lakes.

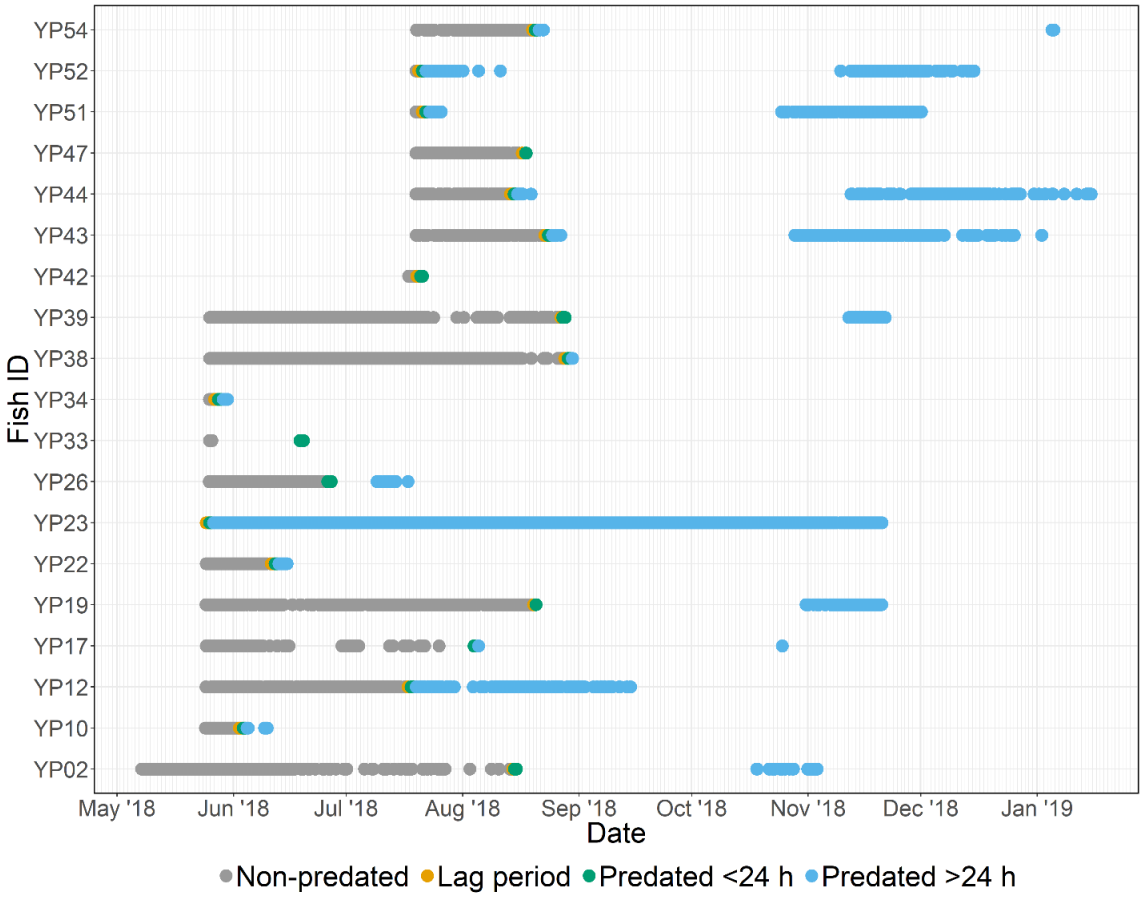

Figure 3.2 Detections of predated yellow perch (*Perca flavescens*) in the Detroit River. Colours differentiate the stages of the predation event: grey indicates perch detections, orange indicates detections within 24 hours before the first post-predation detection, green indicates detections within 24 hours after the first post-predation detection, and blue indicates the remainder of the detections (including those of expelled tags).

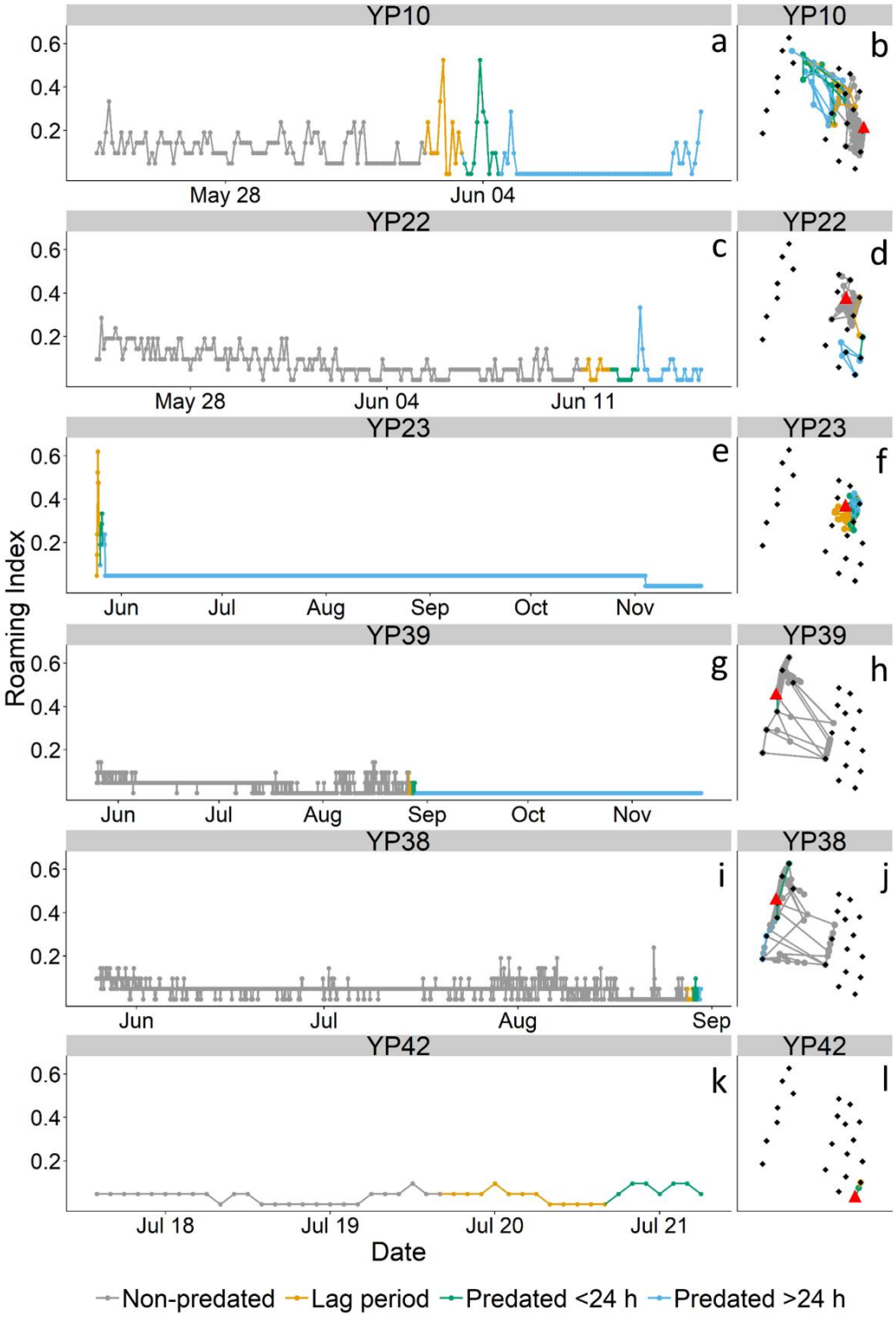
YP10
a
YP10
b
YP22
c
YP22
d
YP23
e
YP23
f
YP39
g
YP39
h
YP38
i
YP38
j
YP42
k
YP42
l
Roaming Index
0.6
0.4
0.2
May 28
Jun 04
Jun 11
Jun
Jul
Aug
Sep
Oct
Nov
Jul 18
Jul 19
Jul 20
Jul 21
Date
Non-predated
Lag period
Predated <24 h
Predated >24 h

Figure 3.3 Roaming index plots (left) and movement paths (right) of six predated yellow perch (*Perca flavescens*) in the Detroit River. Roaming indexes were calculated as the number of receivers that each tag was detected on per two-hour period as a proportion of the total number of receivers in the array. Centres of activity (COA) used to plot the movement paths were calculated using a 30-minute timestep. Black dots in movement path plots represent the 21 stations deployed in the Detroit River (see Fig. 3.1). Red triangles indicate the release point of the tagged fish.

CHAPTER 4

General Discussion

4.1 Summary

The study of aquatic animal movement is important in understanding the habitat use, foraging, and spawning activities that allow animals to survive and reproduce successfully. Knowledge gained through studies of aquatic animal movement aids in the management and conservation of fish while contributing to our basic ecological knowledge for the species we study. Acoustic telemetry is a popular tool to study animal movements in both marine and freshwater environments. Advancements in telemetry technology have resulted in the development of smaller, more powerful, longer lasting tags, that allow for small or juvenile fishes to be studied using telemetry (Hussey et al. 2015).

The use of acoustic telemetry in the Laurentian Great Lakes is growing in attempts to maintain or restore healthy fish populations and habitat. Small and juvenile fishes in the Great Lakes tend to rely on nearshore areas with structurally complex habitats for foraging and protection from predators (Jude and Pappas 1992; Francis et al. 2014), but in order to study their use of these critical habitats, the performance of the acoustic tags and receivers in these habitats must be considered. It is important to assess the detection efficiency of acoustic transmitters and detection range of receivers to understand how these factors influence the detection data during analysis. Typically, the primary constraint in acoustic telemetry studies in nearshore vegetated habitats is how seasonal changes in submerged aquatic macrophyte growth affects the performance of the equipment (Cooke et al. 2013); however, these effects have yet to be quantified in

temperate freshwater habitats in acoustic telemetry literature. Additionally, since smaller fish are likely to have a greater number of potential predators and therefore higher rates of predation, the study of small fish using acoustic telemetry requires researchers to consider whether the detection data represents the movements of the tagged fish or predator(s) that ate them, which often not possible to decipher. This challenge has resulted in the development of predation transmitters that allow for the detection of predation of tagged individuals (Halfyard et al. 2017), but the detection data that results from this novel technology has not been demonstrated in depth for the smaller sized tags in a fine-scale array (Daniels et al. 2019; Klinard et al. 2019). Understanding the influence of macrophytes and predation on acoustic telemetry detection data in shallow nearshore areas will help researchers to plan and execute studies in areas that are important to the fitness of freshwater fishes which will ultimately lead to the improved conservation and management of aquatic animals and habitats that are key to their survival.

In chapter 2, I used detection data collected from a range test performed in a seasonally vegetated shallow nearshore area in the Detroit River to demonstrate how detection efficiency and detection range varied spatially and temporally. I paired the range test detection data with macrophyte biovolume data collected through hydroacoustic surveys to demonstrate how the interaction between distance and seasonal changes in macrophyte biovolume significantly influenced the detection efficiency of acoustic transmitters and the detection range of receivers across time. Detection efficiency was assessed at tag depths of ~ 0.30 m and ~0.90 m below the surface and did not significantly influence the detection efficiency of the transmitters. Overall, the

distance ± SE (m) at which 50% of the detections were successfully detected (D_{50}) for high and low tags were 27.6 ± 1.5 m and 30.2 ± 1.6 m, respectively. The highest measured mean daily biovolume of 0.98 resulted in a D_{50} of 11.8 ± 1.3 m, while the lowest mean daily biovolume of 0.04 resulted in a D_{50} of 167.7 ± 85.0 m. These results indicate that the seasonal growth and senescence of macrophytes in the nearshore areas of the Detroit River is the primary determinant of detection efficiency and detection range during the spring through fall, and that detection efficiency and range are likely less constrained in winter months. This chapter demonstrated the relationship between seasonal macrophyte biovolume and changes in the performance of acoustic telemetry equipment in a shallow nearshore temperate environment and can be used by future researchers to inform their study design and range testing.

In chapter 3, I used the detection data from 19 apparently predated yellow perch (*Perca flavescens*) out of 60 that had been surgically implanted with predation transmitters to demonstrate the variable detection patterns that occurred pre and post-predation in a species-diverse habitat in the Detroit River within a fine-scale receiver array. Over a period of 5 months 31.7% of tagged fish were apparently predated after 0.7 – 98.9 days post-release. Using spatial metrices to compare space use before and after predation, several detection patterns were observed: some tags exhibited clear behavioural changes and eventually went stagnant indicating tag expulsion resulting in high confidence of predation; some tags exhibited no behavioural changes but eventually appeared to be expelled from a predator; some tags switched soon after release and displayed too few detections before and after predation to make any meaningful inferences; other tags indicated predation and had too few post-predation detections to

infer behavioural changes, indicating the predator likely left the receiver array. Of all the observed scenarios, there were no clear instances of false positives, which occurred in only 5% of tags tested in laboratory settings. Different patterns in movements post-predation indicated it is likely that different species were consuming the tagged fish. Overall this chapter demonstrated that the use of predation tags seems promising, not only by aiding the interpretation of telemetry data, but also by providing insights into species interactions and predation. The data presented can be used by others who are planning and interpreting studies using this novel technology.

4.2 Conclusion

The data presented in this thesis fills gaps in the current literature regarding the application of acoustic telemetry in natural settings, particularly in nearshore temperate freshwater habitats. We demonstrated the significant seasonal influence of macrophytes on the detection efficiency and range of acoustic telemetry equipment for the first time. While it is important that acoustic telemetry studies in different study sites evaluate variation in detection range and efficiency in their study since the drivers of range can vary even within a system, the observed effective detection ranges throughout seasonal changes in macrophyte biovolume in this study can be used to inform future studies and provides a technique to measure and quantify the effects of macrophytes on detection efficiency and detection range. Future studies can work to incorporate the spatiotemporal variation in detection efficiency and range into detection analysis, which few studies have demonstrated (e.g. Winship et al. 2012; Pedersen and Weng 2013; Winton et al. 2018). The relatively low detection ranges observed in this study would result in accurate locations of the tagged fish, and gaps in the detection ranges between receivers can be

monitored with manual tracking to account for fish occupying space outside the detection ranges of receivers.

We demonstrated one of the first field applications of V5 predation transmitters and the detection patterns one can expect to encounter using these novel transmitters in a fine-scale array. The use of these tags in telemetry studies will improve researchers abilities to reduce predation bias in their telemetry studies, which has been a common goal of many studies, but until recently, was not easy to determine when studying small animals due to their inability to house additional sensors that allow for the identification of behavioural changes post-predation (e.g. depth sensors; Thorstad et al. 2011). Daniels et al. (2019) demonstrated how predation transmitters can improve estimates of predation bias in smolt survival studies relative to survival estimates produced via modeling. Due to the coarse-scale nature of their receiver positioning and relatively short time span of post-predation detections (mean of 0.75 days), they were unable to make inferences regarding predator behaviour. The predation tag detection data presented in this thesis provides insights into the inferences that can be made when predation tags are used in a fine-scale array. Future studies can combine the use of predation tags and behavioural measures inferred from fine-scale detection data to reduce uncertainty associated with either method (i.e. false positives in predation tags or inaccurate behavioural inferences). Furthermore, they can use predation tags in fine-scale arrays to learn more about species interactions, perhaps reveal information that can help to determine what species are predating tagged fish, compare behaviours that may be more likely to lead to predation, investigate predation risk across size, and aid in the assessment of survival (e.g. Daniels et al. 2019; Klinard et al. 2019). Combined, the knowledge gained from this thesis can be

used to improve acoustic telemetry study design and interpretation in studies that intend to utilize predation transmitters in nearshore environments of the Great Lakes or similar temperate freshwater habitats.

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APPENDIX

Table A 1 Summary of assumed fate for each tagged individual detected as predated (chapter 3).

Tag ID	Day of first predation detection	Fate	Justification
YP2	99	Predated	Increase in spatial use following code switch then a detection pattern consistent with a predator-expelled tag after a gap in detections.
YP10	10	Predated	Sudden increase in spatial use surrounding predation event and change in habitat use post-predation.
YP12	55	Unclear (predated or false positive)	Similar spatial use before and after code switch.
YP17	71	Unclear (predated or false positive)	Too few post-predation detections to be certain, but 2 of 3 post-predation detections occurred on the same receiver months apart consistent with tag expelled from a predator. Since activity levels were low prior to predation, it is possible that this tag falsely triggered inside of a dead tagged fish. Post-predation detections would be removed by most false detection filters.
YP19	88	Predated	Reduced spatial use and detection pattern post-predation consistent with dropped tag. Perhaps predated > 24 h before first post-predation detection.
YP22	18	Predated	Clear change in habitat use.
YP23	1	Predated	Predated soon after release. Tag is clearly dropped. False positive unlikely because tag was tested directly prior to implantation and false positives in all laboratory testing of tag prototypes occurred later in the study (Halfyard et al. 2017; D. Webber, personal communication).
YP26	32	Predated	Decrease in spatial use change surrounding code switch. Few post-predation detections all on one receiver consistent with tag expelled from predator.

Tag ID	Day of first predation detection	Fate	Justification
YP33	24	Unclear (predated or false positive)	Code switched after a gap in detections. Too few detections over a short period of time (4 days with detections across 24 days).
YP34	2	Predated	Increase in spatial use following code switch. False positive unlikely so soon after release.
YP38	95	Predated	No clear changes. Detections cease soon after tag triggers. Likely that predator left array but also a possible false positive, but this does not explain why detections would stop post-predation.
YP39	94	Predated	No clear spatial use changes but eventually detected as dropped.
YP42	3	Predated	Detected for four days total. Unlikely a false positive because tags were tested immediately prior to release and false positives were unlikely to occur soon after release.
YP43	37	Predated	No clear change in spatial use but tag appears dropped across 5 month period.
YP44	26	Predated	Clear changes in spatial use and clear dropped tag across 5 months.
YP47	29	Predated	Sudden decrease in spatial use. Only 11 post-predation detections on 1 day.
YP51	3	Predated	Code switch soon after release. Clear dropped tag after 3-month gap in detections.
YP52	2	Unclear (predated or false positive)	Code switched soon after release. Only ever detected on two receivers. Clear dropped tag after 3-month gap in detections.
YP54	32	Predated	No clear changes but movements sustained surrounding predation event, few post-predation detections but tag appears to have been expelled by predator.

Included are the Tag ID, the number of days post-release upon which the first post-predation signal occurred, the assigned fate based on tag and movement data, and the justification used for the classification.

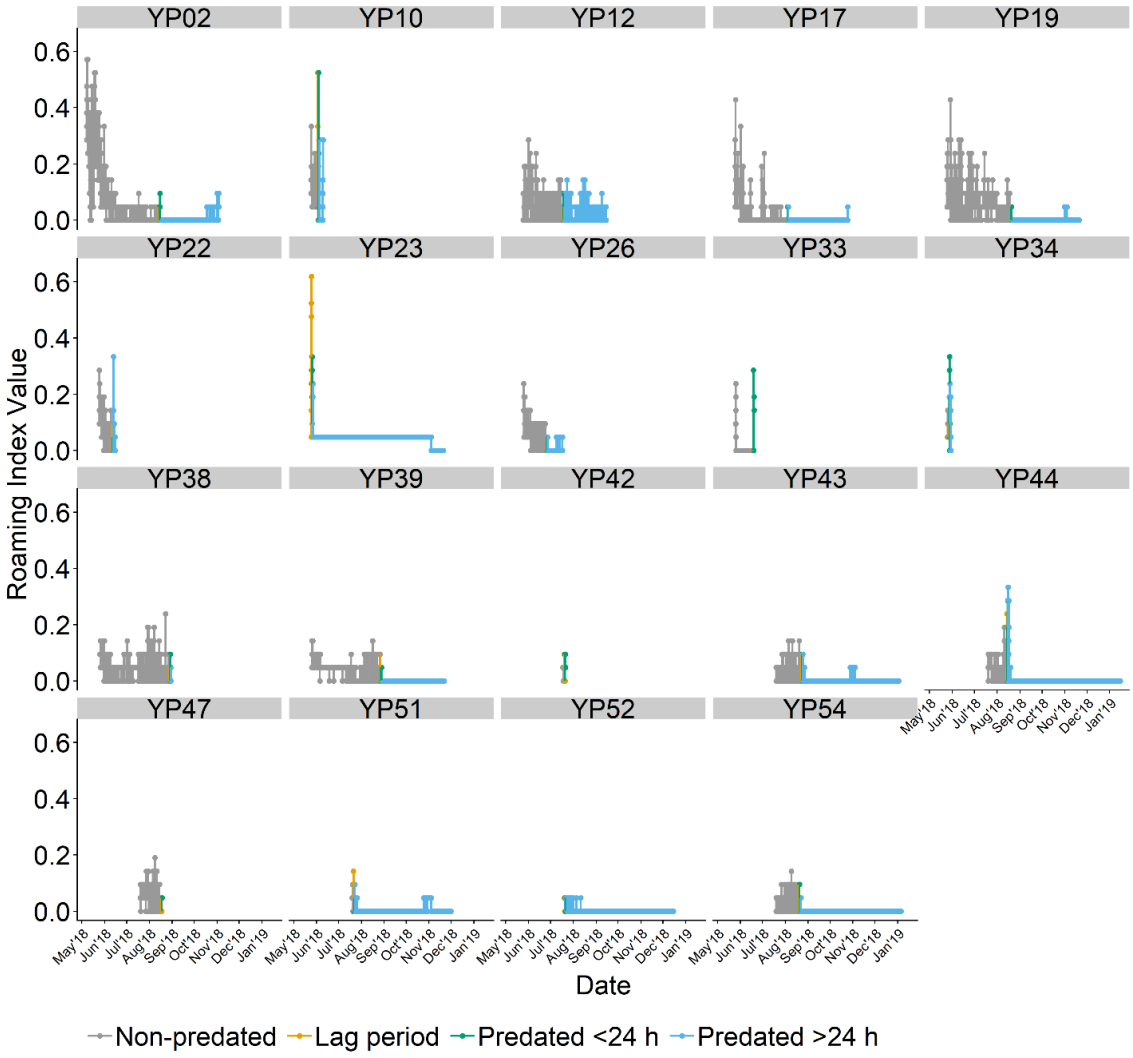

Figure A 1 Roaming index plots for all 19 apparently predated tags across the entire study period. Roaming indexes were calculated as the number of receivers each tag was detected on per two-hour period divided by the total number of receivers in the array (chapter 3).

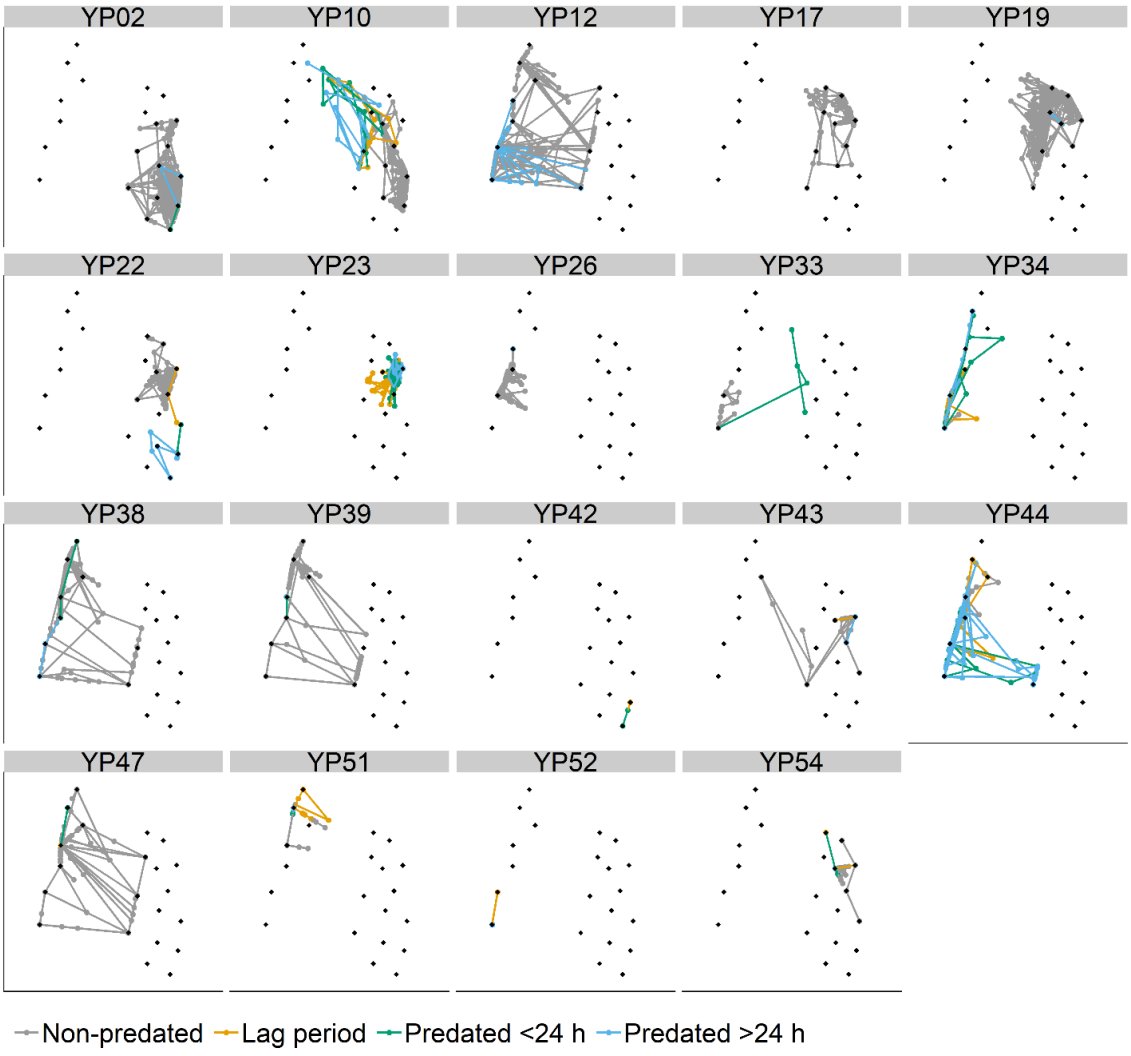

Figure A 2 Centres of activity (COA) for all 19 apparently predated tags. COAs were calculated as the average position of the tag within a 30-minute timestep. Black dots represent station locations in the Detroit River (see Fig. 3.1; chapter 3).

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