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Application of acoustic telemetry to understand post-stocking behaviour of bloater (Coregonus hoyi), a reintroduced fish in Lake Ontario

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Application of Acoustic Telemetry to Understand Post-Stocking Behaviour of Bloater (*Coregonus hoyi*), a Reintroduced Fish in Lake Ontario

by

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Application of Acoustic Telemetry to Understand Post-Stocking Behaviour of Bloater (*Coregonus hoyi*), a Reintroduced Fish in Lake Ontario

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DECLARATION OF CO-AUTHORSHIP/PREVIOUS PUBLICATION

I. Co-Authorship

I hereby declare that this thesis incorporates material that is a result of joint research, which was undertaken under supervision of Drs. Aaron Fisk and Timothy Johnson. The collaboration is covered in Chapters 2 and 3 of the thesis. The Chapter 2 manuscript was coauthored by N.V. Klinard, E.A. Halfyard, J.K. Matley, A.T. Fisk, and T.B. Johnson. The Chapter 3 manuscript was coauthored by N.V. Klinard, J.K. Matley, E.A. Halfyard, M. Connerton, A.T. Fisk, and T.B. Johnson. Throughout this thesis, main ideas, data analysis, and interpretation were performed by the author, and the contribution of co-authors was through theoretical knowledge input, help with statistical analysis of the data, and guidance through the writing process, including revisions of the drafts.

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II. Previous Publication

This thesis includes 1 original paper that has been previously submitted for publication in a peer reviewed journal, as follows:

Chapter 2: The influence of dynamic environmental interactions on detection efficiency of acoustic transmitters in a large, deep, freshwater lake (*Manuscript submitted to Animal Biotelemetry: submitted March 2019*)

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ABSTRACT

Fish stocking is a common practice in freshwater and marine systems worldwide aimed to supplement naturally occurring wild populations, re-establish extirpated species, or introduce non-native species for recreation or management. Bloater (*Coregonus hoyi*), a deepwater cisco extirpated from Lake Ontario in the 1980s, are stocked annually with the aim of re-establishing a self-sustaining population. However, challenges exist in determining the fate of bloater post-release due to difficulty monitoring them, an issue for stocked fish worldwide. This thesis used acoustic telemetry to determine the post-stocking movement, behaviour, and survival of hatchery-reared bloater in Lake Ontario and evaluated the performance of acoustic telemetry in a large, freshwater lake. Detection range testing revealed the probability of a receiver detecting a transmission from an acoustic transmitter in Lake Ontario varied both spatially and temporally and was influenced by dynamic interactions of environmental conditions, particularly ice thickness and thermal stratification. Following release, tagged bloater dispersed rapidly, underwent extensive diel vertical migrations, and exhibited survival (34%) beyond two weeks post-stocking. Collectively, this thesis presented novel information on bloater ecology to help inform reintroduction practices, demonstrated the value of acoustic telemetry in restoration studies, and addressed one of the major assumptions associated with the performance of telemetry in various environments.

DEDICATION

I would like to dedicate this thesis to my parents, Amarjit and Edward Klinard, for fostering my love of science and sense of wonder from a young age and always providing me with unwavering love and support.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Fish Stocking

Global fish stocks are in constant fluctuation as a result of numerous stressors they are subject to including overharvesting, climate change, urbanization, and the impacts of invasive species in combination with the effects of natural recruitment variability (Cowx 1994; Worm et al. 2009; Halpern et al. 2012). As a result, stocks of fish are often depleted, which can affect the food web at multiple trophic levels and alter the stability of the ecosystem making it more vulnerable to further stressors (Pace et al. 1999; Daskalov et al. 2007). To compensate for this loss, fishes are stocked in freshwater and marine systems worldwide with the aim of increasing the abundance of species that have experienced population declines to restore aquatic environments to a more natural state and create recreational and commercial fishing opportunities (Holčík 1991; Halverson 2008). However, the issue with stocking remains that we are largely unaware of the fate of these fishes post-stocking primarily due to difficulty monitoring them. Several methods exist to quantify stocking success including mark-recapture, hydroacoustic surveys, and fisheries data that provide us with basic information about survival and location estimates, however, there is a lack of finer resolution data about post-stocking survival, movement, and behaviour. This is a problem not only in oceans, but also in smaller water bodies such as the Laurentian Great Lakes that are stocked with more than 20 million fishes annually (Zimmerman and Krueger 2009; Mandrak and Cudmore 2010; Bunnell et al. 2014).

The Laurentian Great Lakes consist of five large post-glacial lakes (Lakes Superior, Michigan, Huron, Erie, Ontario) in North America that are connected by a series of major channels to form the world's largest freshwater ecosystem (Manny et al. 1988; Magnuson et al. 1997). With approximately 34 million people in Canada and the United States of America living within the Great Lakes basin, this freshwater system plays an important ecological, economic, and cultural role in North America (Magnuson et al. 1997). For humans, the Great Lakes provide an essential inland shipping route, support recreational and commercial fisheries, and supply water for domestic, agricultural, and industrial uses. The various lakes and connecting channels make this a unique aquatic ecosystem consisting of a variety of habitat types that support a diverse range of freshwater fish species. However, major modifications beginning in the early 20th century such as overharvesting, inadvertent non-native species introductions, and pollution have altered the quality and quantity of aquatic habitats and created stressors that negatively impact the native fish community (Christie 1973; Crossman 1991; Mills et al. 2003). As a result, fish stocking has been ongoing in the Great Lakes since the late 20th century and now supports world-class recreational fisheries, maintains ecological stability and integrity, and aids in the restoration of native species (Zimmerman and Krueger 2009; Mandrak and Cudmore 2010; Bunnell et al. 2014).

1.2 Deepwater Ciscoes in the Great Lakes

Deepwater ciscoes (*Coregonus* spp.) are a diverse assemblage of species that once comprised an integral part of the native fish community of the Laurentian Great Lakes (Eshenroder et al. 2016). Prior to European settlement, each of the Great Lakes supported a complex of nearshore and deepwater ciscoes (Baldwin 1999; Eshenroder et al. 2016). A total of seven deepwater cisco species (*C. hoyi, C. reighardi, C. alpenae, C. zenithicus, C. johannae, C. kiyi, C. nigrippinis*) were once present across all five of the lakes with each lake possessing several taxa (Bunnell et al. 2012; Bunnell et al. 2014; Eshenroder et al. 2016). Early fisheries in the Great Lakes used beach seines to target the spring feeding migrations and autumn spawning migrations of nearshore ciscoes (*C. artedi*) (Eshenroder et al. 2016). As fisheries expanded and demand for ciscoes grew, the exploitation of nearshore ciscoes resulted in fisheries moving further offshore to harvest deepwater forms. The late 1800s marked the start of deepwater cisco fisheries throughout the Great Lakes. By the late 1900s, the extreme pressure of high commercial production had caused the depletion and extirpation of many of the deepwater cisco populations throughout the Great Lakes (Anneville et al. 2015; Eshenroder et al. 2016). Presently, two forms are considered to be extinct (*C. johannae, C. reighardi*) and several others are extirpated from lakes they were historically present in (Table 1.1) (Eshenroder et al. 2016).

1.3 Bloater in Lake Ontario

Lake Ontario was the first of the Great Lakes to be settled by Europeans and fished intensively (Eshenroder et al. 2016). Fishing for deepwater ciscoes in Lake Ontario began after 1875 and initially focused on the largest form, *C. reighardi* (Eshenroder et al. 2016). Overharvesting of *C. reighardi* resulted in a reduced population by the late 1920s that in turn led to bloater being targeted by fisheries. Until the mid-1950s, bloater were an abundant forage fish in Lake Ontario but became scarce as a result of a dramatic population decline associated with overharvesting and invasive rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*) (Wells 1969; Christie 1974; Mills et al. 2003). Although *C. hoyi* persisted in Lake Ontario longer than the other three deepwater ciscoes (*C. reighardi, C. kiyi, C. nigripinnis*), the last documented catch was in 1983 (Owens et al. 2003).

1.4 Bloater Restoration

The population decline of deepwater ciscoes in Lake Ontario during the mid to late 20th century coincided with alewife becoming the dominant species in the offshore prey fish community and constituting a greater proportion of piscivore diets (Brandt 1986; Hoyle 2015; Mumby et al. 2018). Consumption of alewife can lead to thiamine deficiency resulting in negative impacts at multiple life stages and early mortality syndrome in piscivores (Fitzsimons et al. 1999; Brown et al. 2005; Honeyfield et al. 2005). Predatory fish species in Lake Ontario, such as trout and salmon, contribute significantly to the local and regional economies through recreational fisheries in addition to playing an important ecological role in controlling non-native prey fish abundances (Honeyfield et al. 2012). Although alewives are an offshore forage fish that serves as prey for top predators, restoring fauna to resemble the historic offshore prey fish community may improve recruitment of ecologically and economically important species.

Loss of bloater in Lake Ontario has resulted in a vacant deepwater niche in the lake (Christie 1973). Although alewives partially inhabit the deep water that bloater would typically occupy, during the period of thermal stratification they are restricted to the meta- and epilimnion and thus, cannot fully replace bloater (Adkinson & Morrison 2014). The energy demands of alewife during winter are much lower than bloater, further contributing to decreased consumption of deepwater prey during this season (Bergstedt & O'Gorman 1989; Baldwin 1999). Limited fish predation on large populations of prey in deeper waters during periods of thermal stratification creates a disconnect in the lower trophic levels of the food web that can lead to large potential energy losses. Seasonal migrations of alewife and smelt into deeper areas of the lake do not transfer enough energy from the benthic to the pelagic food web to compensate for the empty niche that bloater once occupied (Baldwin 1999). Restoration of deepwater ciscoes may increase stability of lower trophic levels in the food web, resulting in greater energy transfer to higher trophic level organisms and improved overall food web structure (USFWS 1995).

To address the issues caused by the loss of deepwater ciscoes in Lake Ontario, Canadian and American agencies have partnered to implement a restoration plan including captive rearing and stocking with the goal of re-establishing a self-sustaining population of bloater in the lake (OMNRF 2015). Establishing a self-sustaining population of bloater will help restore fish native to Lake Ontario, thus increasing biodiversity, improving ecological integrity and resilience, and serving as a basis for the reintroduction and management of other native species throughout the Great Lakes. As a prey species that has been extirpated from Lake Ontario for several decades and is now reared in a hatchery and stocked into a foreign environment, it is difficult to predict and assess the survival and proliferation of bloater after introduction.

1.5 Bloater Ecology

Research on bloater in Lake Ontario is limited to gill net surveys and harvest data prior to their extirpation in the 1980s (Koelz 1929; Stone 1947). Existing knowledge of bloater ecology in the Great Lakes is primarily a result of research conducted in Lakes Huron, Michigan, and Superior and is limited seasonally (Clemens and Crawford 2009). A large proportion of studies on bloater have focused on their depth distribution and the physiological ability of deepwater ciscoes to exploit deep sections of large lakes (e.g., Hrabik et al. 2006; Jensen et al. 2006; Clemens and Crawford 2009). Much of what is known about the vertical space use of bloater has been revealed through hydroacoustic and trawl surveys used to identify and verify the presence of bloater at specific depths (Clemens and Crawford 2009). It has been suggested in recent decades that bloater and other deepwater ciscoes undergo diel vertical migration (DVM) in which they ascend through the water column at night to facilitate planktivory on epibenthic mysids (*Mysis relicta*) (Eshenroder et al. 1998; TeWinkel and Fleischer 1999). The inability to track individually identifiable bloater across depths has resulted in limited knowledge regarding the extent, frequency, and amplitude of DVM. Survey data suggests that adult bloater frequently occupy depths ranging from 36 to 110 m although they have been captured with less frequency beyond this range with one reported capture as shallow as 9 m in Lake Michigan (Koelz 1929; Jobes 1949; Wells 1968; Brown et al. 1985). Hrabik et al. (2006) typically captured bloater in Lake Superior in midwater trawls at depths of 30 m with few captured >50 m, suggesting they undergo less extensive DVM than other ciscoes that migrate to 150 m. It has also been suggested that juvenile bloater (80-145 mm fork length) migrate vertically through a wider range of depths than adult bloater (>145 mm fork length) (Eshenroder et al. 1998).

While a variety of studies suggest the movement and habitat use of bloater is strongly linked to depth preference, the horizontal space use of bloater is relatively less studied. Similar to vertical space use, knowledge of horizontal bloater distributions is based primarily on hydroacoustic surveys and catch data from trawls. As bloater exhibit preference for a cool, narrow temperature range corresponding to hypolimnetic temperatures (Wells 1968; Crowder and Crawford 1984; Eshenroder et al. 1998), their horizontal space use appears to be partially thermally driven. Adult bloater have been shown to inhabit deep offshore waters in the fall where they overwinter and then move into shallow inshore waters during the summer (Koelz 1929; Wells and Beeton 1963; Wells 1968; Argyle 1992). Although inshore movement has been observed in several lakes, the timing and degree of inshore movements varies across lakes (Jobes 1949; Dryer 1966; Wells 1968). Not only is our knowledge of bloater ecology mainly limited to data from extant populations, but the resolution and quality of data is restricted by gear avoidance as well (Clemens and Crawford 2009).

1.6 Acoustic Telemetry

Fish movements and distributions influence the structure and function of aquatic ecosystems (Hussey et al. 2015). The development and technological advancement of various types of telemetry has provided new insight into aquatic animal movements, interactions, and how environmental conditions influence the spatial and temporal distribution of organisms (Kilfoyle and Baggeroer 2000). Passive acoustic telemetry is a method of tracking that involves the transmission of sound signals through water from an electronic transmitter that is surgically implanted, inserted into the stomach, or externally attached to an organism (Hussey et al. 2015). Detections of acoustically tagged animals are recorded and logged by receivers moored at fixed locations that are later retrieved for processing (Kessel et al. 2014). Electronic tags can now be equipped with sensors that measure physical parameters such as temperature and depth or detect important biological events, such as the predation of a tagged prey fish (Halfyard et al. 2017). The fine-scale data provided by telemetry has revolutionized the observation of aquatic animal movements, allowing us to address more complex questions about the ecology, physiology, and behaviour of aquatic organisms (Espinoza et al. 2011).

Advantages of using acoustic telemetry in aquatic animal studies include performing long term studies across vast spatial scales, continuous 24 hr data collection, monitoring in diverse environments, and tracking multiple individuals simultaneously on a single receiver array (Kessel et al. 2014). The use of acoustic telemetry has aided in identifying previously unknown animal behaviours such as spawning and foraging activities (e.g., Flavelle et al. 2002) and revealed patterns of seasonal movements and migrations of several species (e.g., Welch et al. 2009). However, using acoustic telemetry brings forth a new suite of possible issues that include tagged animals moving beyond the range of receivers, predation, tag collisions, and the effect of environmental conditions on detection range (*DR*) (Simpfendorfer et al. 2008; Kessel et al. 2014). These issues can be mitigated through experimental design that considers appropriate receiver array positioning, the use of sentinel tags to quantify detection rate and range, and including sufficient sample sizes. Acoustic telemetry presents a unique opportunity to observe fish following stocking at a resolution that was previously unattainable to inform on post-release movements, behaviour, and survival of stocked fishes.

Analysis and interpretation of acoustic telemetry data is dependent not only on the movements of tagged individuals, but also the distribution and performance of receivers to detect acoustic signals. In particular, the *DR* of acoustic receivers is a primary consideration when designing telemetry studies. There are several factors that can impact the performance of receivers in various environments. First, the deployment method and mooring of the receiver could impact performance (Lacroix and Voegeli 2000). For example, the depth of the receiver and the orientation and type of equipment used to moor receivers could interfere with signal reception (Clements et al. 2005). Second, environmental noise caused by a range of factors including biological components of the ecosystem, human influences, and physical factors could reduce signal reception if they are within the range of frequencies that the receiver detects (Simpfendorfer et al. 2008). Third, increased heterogeneity of the environment such as stratification, density gradients, bottom topography, and high suspended matter could interfere with signal transmission (Voegeli and Pincock 1996; Thorstad et al. 2000). Fourth, high densities of tagged individuals within range of a receiver can result in signal collisions (Voegeli et al. 1998). Finally, the movement and behaviour of animals into less favourable environments could lead to reduced or partial signal transmissions. Thus, researchers must be aware of the possible factors affecting their acoustic receiver transmission range and performance in certain environments and understand how to evaluate these measures for more accurate data interpretation.

1.7 Thesis Overview

This thesis provides novel information on bloater ecology that helps to inform reintroduction efforts for bloater in Lake Ontario and serves as a basis for the reintroduction and management of other stocked fishes in the Great Lakes using acoustic telemetry. It also demonstrates the value of using acoustic telemetry to improve restoration studies and evaluates the performance of telemetry in a large freshwater lake to facilitate more accurate interpretation of telemetry data. The study site is located in the St. Lawrence Channel, which is a deep underwater valley near the Canada-USA border in eastern Lake Ontario. The channel is approximately 4 km wide, reaching depths of 50-60 m in the center of the valley and bordered by shallow water reefs less than 20 m deep on either side. The St. Lawrence Channel was chosen as the study site because it offers suitable deep water (>50 m) to be consistent with historical bloater habitat and shallow areas (<20 m) that may be exploited by fish. Shallow bathymetry may also occasionally constrain movement of tagged bloater to the valley and increase the probability of detection. Connection of the channel to the open lake allows for placement of acoustic receivers designed to detect movement of bloater emigrating from the study site into the deeper lake habitat. Thus, in combination with suitable acoustic receiver array design, the location of this study site permits determination of directional movement of bloater towards multiple habitat types.

Chapter 2 of this thesis aims to address knowledge gaps in acoustic telemetry literature by utilizing an extensive telemetry dataset from a large, deep, freshwater lake to answer questions about the relationship between detection efficiency (*DE*) and the environment through time and space. Based on preliminary range testing results from fall 2015 and the open water structure of the study site, I predicted that average *DE* during the entire study period will be high (>80% at 600 m for a V9 tag). I hypothesized that power output of the tags will influence *DR* and predicted that tags of higher power output will have larger *DR* and that close proximity detection interference (CPDI) will occur due to the large detection distances. As thermoclines can cause the reflection and refraction of transmitter signals (Voegeli and Pincock 1996; Singh et al. 2009), I predicted that *DE* and receiver performance will be higher in the winter when the thermocline is absent compared to the fall and spring periods. However, I also predicted that the presence of ice during the winter may have a similar effect on transmitter signals as a thermocline, resulting in a decrease in *DE* and performance. Finally, I hypothesized that that density will impact *DE* and predicted that *DE* will be low initially due to the influx of transmitters released into the system during stocking and will increase following the dispersal of tagged bloater in the acoustic receiver array.

Chapter 3 of this thesis aims to examine the initial post-release survival, 3D movement, and behaviour of hatchery-reared bloater stocked in Lake Ontario using acoustic transmitters with pressure (depth) sensors. Due to the high initial mortality (>50%) that is sometimes associated with stocked fish (e.g., Hanson and Margenau 1992; Aprahamian et al. 2004) in combination with the challenges of acclimating to a new environment, I predicted high initial mortality (>50%) and that survival of remaining live fish will increase through time. Given the preference of bloater for deeper colder water, I hypothesized that movement of bloater would be thermally driven and predicted that if dispersal was rapid, movement would follow the deeper bathymetry surrounding the study site. As several instances of DVM have been observed in bloater, I hypothesized that bloater would exhibit DVM and predicted that it would occur shortly after release. Finally, the formation of shoals by other coregonid species (Röusch 1987; Ptak et al. 1998) led me to predict that bloater will exhibit schooling behaviour shortly after release.

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Table 1.1 Status of the major forms of deepwater ciscoes (*Coregonus* spp.) in the Great Lakes. Forms in Lake Huron that have introgressed into a hybrid swarm are considered to be extirpated/extinct, although elements of their morphology may persist. Extant forms are in bold. Adapted from Eshenroder et al. (2016).

Major Form	**Lake**				
	Superior	**Michigan**	**Huron**	**Erie**	**Ontario**
C. alpenae	–	Extinct	Introgressed	Extinct	–
C. hoyi	**Extant**	**Extant**	Introgressed	–	Reintroduced
C. johannae	–	Extinct	Extinct	–	–
C. kiyi	**Extant**	Extirpated	Introgressed	–	Extirpated
C. nigripinnis	Uncertain	Extinct	Extinct	–	–
C. reighardi	Uncertain	Extinct	Introgressed	–	Extinct
C. zenithicus	**Extan**t	Extirpated	Introgressed	–	–

CHAPTER 2

THE INFLUENCE OF DYNAMIC ENVIRONMENTAL INTERACTIONS ON DETECTION EFFICIENCY OF ACOUSTIC TRANSMITTERS IN A LARGE, DEEP, FRESHWATER LAKE

2.1 Introduction

Acoustic telemetry is a valuable tool that is used to investigate the movement and behaviour of aquatic organisms. The ability to passively track the movement of tagged individuals on fine spatial and temporal scales has played an important role in the research of aquatic ecosystems and informing fisheries management and conservation strategies (Hussey et al. 2015; Brooks et al. 2017; Crossin et al. 2017). Recent advances in acoustic telemetry, such as the miniaturization of transmitters and increased battery power, have enabled scientists to address questions about the fundamental ecology of aquatic organisms that were previously unattainable including their distributions, survival, spawning, habitat use, and trophic interactions (Cooke et al. 2013; Donaldson et al. 2014; Hussey et al. 2015).

Passive acoustic telemetry requires an acoustic transmitter (hereafter tag) that emits ultrasonic sounds at specific intervals (pings) to be detected, decoded, and recorded by a submerged acoustic hydrophone and receiver (hereafter receiver) at a fixed location (Heupel et al. 2006). When the receiver successfully detects and decodes a transmitted sequence of pings (hereafter detection), the time, tag ID, and any additional sensor measurements, such as pressure (depth) or temperature, associated with the detection are recorded.

Detection efficiency (*DE*) is defined as the probability of successfully detecting a single transmission of a tag, whereas detection range (*DR*) refers to the distance from a receiver that a transmission is estimated to be detected, given a specific *DE* (Melnychuk 2012). Detection efficiency depends primarily on the distance between the tag and receiver at the time of signal transmission due to the geometric spreading of the wavefront through water, but there is a suite of biotic and abiotic factors that also influence the rate of energy attenuation and absorption of sound as the signal travels through water (Melnychuk 2012; Hayden et al. 2016). It is important to comprehend the relationship between *DE* and different factors in a telemetry study to understand the quality of information obtained, enable more accurate interpretation of telemetry data, and ultimately, to make stronger inferences about the ecology of the study organisms. For example, Payne et al. (2010) demonstrated that variation in *DE* of tagged cuttlefish (*Sepia apama*) created the appearance of diel activity patterns that were not necessarily present.

Some variables that influence the strength of a signal as it approaches a receiver may be controlled through study design (Lacroix and Voegeli 2000; Clements et al. 2005), such as acoustic tag power output, transmission interval, receiver orientation, and receiver depth. However, there are many other factors associated with environmental conditions or animal behaviour that are difficult to control for (Simpfendorfer et al. 2008). Factors affecting *DE* may remain relatively constant throughout the duration of a study, such as the refraction and reflection of signals caused by bathymetry and submerged structures, or the dissolved particle concentration of marine versus freshwater environments. Factors that may be more likely to change temporally include turbidity, air entrainment, algal blooms, ice cover, wind, water flow, waves, precipitation, water temperature, and water column stratification (Voegeli and Pincock 1996; Thorstad et al. 2000). In addition, environmental noise can be caused by external human influence (e.g., boat motors; Heupel et al. 2006) or biological components of the environment (e.g., snapping shrimp; Heupel et al. 2006) and may interfere with receipt of the transmission pings that make up a detection (Voegeli et al. 1998). Furthermore, a high density of tags within the *DR* of a receiver can result in transmissions from multiple acoustic tags arriving at the receiver at approximately the same time and causing a collision of signals, preventing one or more tags from being decoded or creating a false detection sequence (Pincock 2012).

Detection efficiency and *DR* within a receiver array are unique for each study and should be evaluated prior to the start of an acoustic telemetry project to help inform study design. The most common technique employed to quantify *DE* is static range testing, which uses acoustic tags deployed at fixed distances (i.e., sentinel tags) from a receiver (Hayden et al. 2016). Static range testing is often performed for long durations (e.g., weeks, months) to capture temporal scales relevant to the study objectives and evaluate the impacts of varying environmental conditions (Kessel et al. 2014). Mobile range testing is used less frequently and is performed by towing an acoustic tag near receivers to evaluate *DE* and *DR* at a specific time and environmental condition (Jossart et al. 2017). Mobile range testing is less comprehensive and may be misleading depending on the environmental conditions, boat motor noise, time of day, and depth of tag (Kessel et al. 2014). Nevertheless, the most effective method of range testing varies by study and ultimately depends on the objectives, environment, and characteristics of the study animals.

As acoustic telemetry has become an increasingly popular method to track aquatic animals in the past three decades, studies evaluating *DE* and *DR* have similarly become more prevalent to accompany this growth (Kessel et al. 2014). Detection range has been examined across vast spatial scales in a variety of environments (Kessel et al. 2014) revealing that the effect an environmental variable has on *DE* can often be unique to that location (Huveneers et al. 2016, Jossart et al. 2017). For example, How and de Lestang (2012) and Cagua et al. (2013) found that water temperature had a significant negative relationship with *DE* on reefs in south-western Australia and Saudi Arabia, respectively, while Simpfendorfer et al. (2008) and Heupel et al. (2008) found no significant effect of water temperature on *DE* in a Florida river and lagoon. Similarly, different studies reported a significant positive relationship (Cagua et al. 2013), significant negative relationship (Gjelland and Hedger 2013, Huveneers et al. 2016), and no significant relationship (Singh et al. 2009; Stocks et al. 2014) between *DE* and wind speed. While several studies have evaluated the impact of individual environmental variables on *DE* (e.g., Selby et al. 2016; Jossart et al. 2017), few studies have considered the interactions between them and how these relationships may change spatially (e.g., Cagua et al. 2013). Since *DE* is ultimately a function of distance and a combination of environmental variables, it is valuable to understand not only the temporal variability in *DE* caused by environmental conditions, but how spatial variation impacts this relationship as well.

The majority of range test studies occur in marine environments with a focus on reef ecosystems despite the increasing prevalence of acoustic telemetry in freshwater systems. The Laurentian Great Lakes is the world’s largest freshwater system and hosts numerous acoustic telemetry projects under the Great Lakes Acoustic Telemetry

Observation System (GLATOS, https://glatos.glos.us) with over 76 projects, 44 species and 11,500 tagged fishes and more than 285 million detections as of February 2019. However, there are few *DE* and *DR* studies in the Great Lakes to support the vast assortment of telemetry projects (e.g., Binder et al. 2016; Hayden et al. 2016). Further, acoustic telemetry studies in temperate or northern freshwater lakes also encounter seasonal thermal stratification and winter ice cover. The effect of these abiotic conditions on acoustic gear performance is poorly understood.

In this study, we aimed to address knowledge gaps in acoustic telemetry literature by utilizing an extensive telemetry dataset from a large, deep, freshwater lake to answer questions about the relationship between *DE* and the environment through time and space. We examined spatial and temporal variability in the *DE* and *DR* of three acoustic tag types over a 7-month period (Oct. 2015 – May 2016) in Lake Ontario, the 10th largest lake by volume in the world. We chose to analyze *DE* and *DR* in Lake Ontario because of its wide range of depths, variable habitats, seasonal fluctuations (e.g., thermal stratification, ice cover), and the availability of an extensive telemetry receiver array. Our specific objectives were: (1) to determine *DR* in Lake Ontario for three types of acoustic tags, (2) to examine spatial and temporal variability in *DE* across tags of different power output, and (3) to assess the relationship between *DE* and environmental variables and evaluate the relative impact of interactions between distance and environmental variables on *DE*.

2.2 Methods

Study site

The telemetry study was performed in the St. Lawrence Channel of eastern Lake Ontario (43° 55.517' N, 76° 31.354' W) from August 2015 to May 2016 (Fig. 2.1). The St.

Lawrence Channel is a deep underwater valley located near the Canada-USA border that extends 24 km to form a major connection between Lake Ontario and the St. Lawrence River. This bathymetric feature is approximately 4 km wide, reaching depths of 50-60 m in the center of the valley and bordered by shallow water reefs less than 20 m deep on either side. In August 2015, five acoustic receivers (69-kHz VR2W; Vemco Ltd., Bedford, NS, Canada) were deployed at a depth of approximately 55 m (instrument depth ~ 52 m) and spaced 100-150 m apart to achieve a set of distances at which to measure *DE* (Fig. 2.1; Fig. 2.2). A total of 8 acoustic tags (Vemco Ltd., Bedford, NS, Canada) were also deployed in four groups at different distances and depths in the center of the study site (Fig. 2.2). These included three V9-2x 69-kHz range tags (power output 145 dB, nominal delay 1800 s), one V13-1X 69-kHz range tag (power output 153 dB, nominal delay 1800 s), and four V16-6X 69-kHz range tags (power output 158 dB, nominal delay 1800s) to test *DE* and *DR* for tags of varying power and battery life. All tags had an estimated battery life of > 400 days. The first group of tags (one V9, one V16) and the second group of tags (one V16) were deployed on tag moorings that consisted of a cinder block (~16 kg) anchor connected to a 28cm (11") trawl float by a 3 m length of 1.1 mm (7/16") polypropylene rope (Fig. 2.2). The tags were attached approx. 2 m from bottom. The third and fourth groups of tags were deployed attached to a receiver mooring that featured a length of rope with a buoy extending to 10 m below the surface that was outfitted with HOBO Pendant loggers to track changes in water temperature at various depths in the water column. One group of tags (one V9, one V13, oneV16) was situated below the thermocline at a depth of 50 m while the other group (one V9, one V16) was above the thermocline at a depth of 11 m to evaluate the impact of tag depth and thermal stratification on *DE* (Fig. 2.2).

An array of 85 acoustic receivers (69-kHz VR2W) was deployed in October 2015 as part of a project to track the movements of tagged bloater (*Coregonus hoyi*) in Lake Ontario (Fig. 2.1). The acoustic receivers in this receiver array were utilized in addition to the initial five receivers in the range test study to record detections of sentinel range tags throughout the study period. The receiver moorings were composed of concrete cylinders (~62 kg) as the anchors connected to two 28 cm (11") trawl floats by a 3 m length of 1.1 mm (7/16") polypropylene rope with inline nylon swivels. Receivers were attached midway along the rope with the hydrophone pointing upwards to be suspended ~2 m above the lake bottom. An approx. 30 m weighted rope was attached to the concrete anchor at one end and a cinder block at the other end to serve as a drag line for grappling when retrieving the receivers for download. All range tags were removed from the system in May 2016.

Data analysis

The complete receiver array, including the 85 receivers from the bloater telemetry project and the five receivers for range testing, was deployed from 22 October, 2015 to 23 May, 2016 (215 days). To ensure consistency across detection distances and probabilities, only detections for these dates were used in analyses.

Receiver performance

To verify that *DE* was not unduly biased by external factors affecting the performance of acoustic receivers, we evaluated receiver performance in relation to noise levels and sources for the entire study period following methods described by

Simpfendorfer et al. (2008). The amount and source of noise in the system was estimated for two receivers by calculating the noise quotient (NQ), which compares the expected number of pings based on the number of synchronization intervals from detections to the actual number of pings recorded by the receiver. The NQ was calculated for two scenarios; all tags produce detections consisting of 8 pings, and all tags produce detections consisting of 10 pings. Since we are unable to determine where a ping originated from (pings in this study are from a combination of 8- and 10-ping tags) the true NQ lies somewhere between these two calculated NQ values. Five of our range tags had a 10-ping sequence and the other three had an 8-ping sequence. A total of 70 bloater (*Coregonus hoyi*) were tagged with transmitters that had an 8-ping sequence (nominal delay 120 s) and stocked in the center of the inner circle of the array on 9 November, 2015. With the vast majority of pings originating from 8-ping tags, it is likely that the true NQ is more accurately represented by the conservative 8-ping NQ than the overestimate of the 10-ping NQ.

Spatial variability in detection efficiency

To examine spatial variability in *DE* across tag types and depths, detection data were separated into five categories: deep V9, shallow V9, deep V13, deep V16, and shallow V16, where deep refers to tags at ~50 m depth and shallow refers to tags at ~11 m depth. Analyses were performed separately for each tag category. For each tag and receiver combination, *DE* was calculated for each day of deployment by dividing the number of detections by the expected number of transmissions per day (48 for a nominal transmission interval of 1800 s). Daily *DE* was used to estimate *DE* for the entire study period using generalized additive mixed models (GAMMs) to explain the *DE* as a function of the distance between tags and receivers. GAMMs use non-parametric smoothing functions to describe nonlinear trends between predictor and response variables (Wood 2006; Zuur et al. 2009). The *gamm* function in the R package 'mgcv' fits a smoothing curve through the data using regression splines and was used to fit all GAMMs as it allows for autocorrelation and variance structures and random effects. We controlled for heterogeneity in the data by including tag-receiver combinations as a random effect with one intercept for each tag-receiver combination. A first-order auto-regressive moving average (ARMA) correlation structure was included in the model to account for temporal autocorrelation between detections on adjacent days nested within each tag-receiver combination. The distance covariate was fit with a penalized regression spline smoother to reduce the potential of overfitting the data when estimating the *DE* between sampled distances. A common occurrence in acoustically reflective environments is close proximity detection interference (CPDI), which is defined as a low *DE* for tags in close proximity to the receiver with peak *DE* occurring at an intermediate distance from the receiver (Kessel et al. 2015, Scherrer et al. 2018). To minimize the underfitting bias of smaller distances closer to the receiver where CPDI may occur, the largest appropriate basis dimension (*k*) was selected for the distance smoother in each model. The *gam.check* function in the R package 'mgcv' was used to assess model fit by visually evaluating residual plots and running diagnostic tests to ensure adequate basis dimensions for each smooth. The GAMM results were used to predict an overall *DE* for distances from 100 – 7000 m in 1 m increments. Model predicted *DE* was used to create an overall range curve across distance for the duration of the study.

Temporal variability in detection efficiency

To examine temporal variability in *DE* across the five tag categories, the distance GAMMs that were previously fit for the entire study period were used to predict three distances (D_1, D_2, D_3) at which *DE* corresponded to rates of 0.25, 0.50, and 0.75 for each tag category. These three distances were calculated for each tag category to determine relevant distances that would be equivalent to the same mean *DE* across tag categories. The following analyses were conducted individually for each tag category. Detection data were grouped by day and modelled using GAMMs to create a single *DR* curve across distance for each day (215 days) of the study. All GAMMs were fit following the same methods described above. Model coefficients for each daily GAMM were used to estimate sentinel tag *DE* for the corresponding day at each of the three previously calculated distances (DE_{D1}, DE_{D2}, DE_{D3}). The DE_{D1}, DE_{D2}, and DE_{D3} were grouped by week to calculate the mean and standard error of *DE* and examine overall trends in *DE* through time.

Effect of environmental variables on detection efficiency

The following methods were conducted individually for each tag type (V9, V13, V16) to analyze and facilitate comparison of the impact of environmental variables on *DE* among tag types. For each tag and receiver combination, *DE* was calculated for each day of deployment.

Environmental data were obtained from online databases and multiple instruments deployed in the study site to examine the effects of each environmental variable on *DE*. Daily mean temperatures at 10 and 50 m were calculated from measurements taken every hour by HOBO Pendant loggers (Onset, Cape Cod, Massachusetts) deployed at various depths in the study site near the sentinel tags. Daily surface water velocity and ice thickness data were calculated from hourly readings taken at the center of the receiver array archived in the Great Lakes Observing System (GLOS) online database (http://data.glos.us/glcfs/). The daily difference in temperature between 10 and 50 m – the depth range between the shallow and deep tags – was used to calculate a variable that represented the strength of the thermocline.

To evaluate possible drivers of temporal patterns in *DE*, a suite of environmental variables (henceforth covariates) were considered: surface water velocity, ice thickness, water temperature at 10 m, water temperature at 50 m, thermocline strength, receiver depth, tag depth, depth difference between tag and receiver, distance between tag and receiver, week, and month. Since tagged fish were present in the system during range testing, we also included the number of fish detections as a covariate to account for any possible variability in *DE* caused by an influx of fish transmissions interfering with receipt of range tag transmissions. We assessed collinearity of these covariates using Pearson's pairwise correlation coefficient to verify independence prior to inclusion in additional analyses. Highly collinear pairs included water temperature at 10 and 50 m (pairwise cc = 1.0), water temperature at 10 m and month (pairwise cc = 0.8), water temperature at 50 m and month (pairwise cc = 0.8), week and month (pairwise cc = 0.9), week and water temperature at 50 m (pairwise cc = 0.7), and receiver depth and distance between tag and receiver (pairwise cc = -0.7). As such, water temperature at 10 m, water temperature at 50 m, month, and week were considered as a single covariate represented by water temperature at 50 m in further analyses. Receiver depth and distance between tag and receiver were also considered a single covariate represented by distance from receiver. Daily averages of the remaining covariates were linked to the respective daily *DE*.

GAMMs were used to examine non-linear trends in time series of *DE* as a function of surface water velocity, ice thickness, water temperature at 50 m, thermocline strength, tag depth, depth difference between tag and receiver, number of fish detections, and distance between tag and receiver, all of which were continuous variables except for tag depth. All GAMMs were fit following the methods described in the above-listed analyses. The optimal ARMA correlation structure was determined using the *auto.arima* function in the R package 'forecast' and the highest order correlation structure that produced the smallest Akaike Information Criterion (AIC) while allowing for model convergence was used.

To account for the influence of distance on the trajectory of the smooth for each of the environmental covariates, we included interaction terms for distance and each applicable covariate in addition to the main effect smooth terms for each variable (Sóskuthy 2017). We used 'tensor product interactions' in the GAMM, which are conceptually very similar to interactions in linear models (Sóskuthy 2017). A pool of candidate models was created with selected model parameters matching hypothesized explanatory variables. AIC model selection was used to identify the best fitting GAMM. Adjusted R^2 is defined as the variation explained by only the independent variables that affect the dependent variable. Statistical analyses were performed using R version 3.5.2 (R Core Team 2018), and statistical significance was assumed at $\alpha = 0.05$.

2.3 Results

Detection summary

A total of 769,423 acoustic transmissions were detected from eight stationary acoustic tags on 75 acoustic receivers in northeastern Lake Ontario from 22 October, 2015 to 23 May, 2016 (Fig. 2.1; Table 2.1). A nominal transmission delay of 1800 s resulted in an expected 48 transmissions for each acoustic tag per day. The average number of detections per day for each receiver was similar within tag types with V9 tags exhibiting the lowest number of daily detections (3.1 ± 9.4 detections day^{-1}) and V16 tags exhibiting the highest number of daily detections (7.9 ± 13.2 detections day^{-1}) (Table 2.1). The shallow V9 and V16 tags were detected at a greater maximum distance (6.4 km and 9.3 km, respectively) than their deeper counterparts and had a lower number of daily detections (3.1 ± 9.4 and 6.9 ± 12.5 detections day^{-1}, respectively) than the deep tags. The maximum distance detected ranged from 5.9 km to 9.3 km although detections at these distances occurred infrequently, resulting in a *DE* of nearly zero (Table 2.1).

Receiver performance

The highest level of noise as indicated by the conservative 8-ping NQ was observed on the receiver closer to the sentinel range tags (~600 m distance) and ranged from -23852 to 706 with a mean value of -669.7 (± 2196.3 SD) (Fig. 2.3a). The largest peak in noise occurred on the day after tagged bloater were stocked in the array (10 November, 2015). The receiver farther from the sentinel range tags (~4.3 km distance) experienced smaller magnitudes of noise ranging from -2669 to 902 with a mean of -192.0 (± 476.5 SD) (Fig. 2.3b).

Spatial variability in detection efficiency

Detection efficiency of the sentinel range tags in Lake Ontario displayed an overall negative relationship with distance between the tag and receiver for the duration of the study (Fig. 2.4; Table 2.2). The effects of CPDI were visible in the *DR* curves of the deep V9, deep V13, deep V16, and shallow V16 tags as indicated by low or fluctuating *DE* at distances closer to the receiver (Fig. 2.4). The shallow V9 tag did not experience CPDI and had the highest *DE* (0.97) at the distance closest to the receiver (100 m) (Fig. 2.4; Table 2.2). *DE* and *DR* increased with higher power output of the tags, however, the size of the region impacted by CPDI also increased with higher power output (Fig. 2.4). Beyond the distance impacted by CPDI, shallow tags consistently had lower *DE* than deep tags of the same power output (Table 2.2). All model smoothing splines were significant. Model fit estimated by adjusted R^2 ranged from 0.824 to 0.895.

Temporal variability in detection efficiency

Estimated DE_{D1}, DE_{D2}, and DE_{D3} fluctuated through time displaying a similar overall trend across all tag categories (Fig. 2.5). Weekly *DE* was relatively variable during the first month of the study and then decreased in early December through February, increased rapidly through March, remained relatively constant in April and then fluctuated more in May (Fig. 2.5). Weekly *DE* was less variable in shallow tags (maximum range 0.53) than in deeper tags (maximum range 0.75), which is especially notable during the last 5 weeks of 2015 and first four weeks of 2016 (Fig. 2.5). Tags with higher power output often exhibited less variable *DE*, suggesting a more consistent *DE* through time. Daily *DE* was less variable at short and long distances for a given tag-receiver with increased variation of *DE* at intermediate distances (Fig. 2.5). The stocking of 70 tagged bloater showed no evident impact on weekly *DE* trends (Fig. 2.5). Model fit for all daily GAMMs estimated by adjusted R^2 ranged from 0.732 to 0.997 and was higher than 0.800 for 98% of models.

Effect of environmental variables on detection efficiency

The best fitting GAMMs as identified by the lowest AIC scores were the full model excluding tag depth for the V9 and V16 tags and the full model excluding tag depth, depth difference between tag and receiver, and the interaction between distance and depth difference for the V13 tag (Table 2.3). All smooth and interaction terms in the best fitting models were significant. Partial effects of individual environmental variables included in the best fitting models indicate that distance has the largest effect on *DE* for V9, V13, and V16 tags and the effect of individual environmental variables is similar among tag types (Fig. 2.6). Estimates of summed effects of the interactions from the best fitting GAMMs for V9 and V16 tags revealed that the extent to which *DE* declines with distance is influenced by environmental variables (Fig. 2.7). As the distance between tag and receiver increased, thermocline, water velocity, and ice thickness had a diminishing effect on *DE* (Fig. 2.7a-f) and water temperature had an increasing effect on *DE* (Fig. 2.7g; Fig. 2.7h). Collinear variables that were not included as covariates in the models but were also significant were water temperature at 10 m, week, month, and receiver depth. Model fit for the best fitting GAMMs for each tag type estimated by adjusted R^2 ranged from 0.908 to 0.916.

Maximum recorded *DR* occurred once (26 October, 2015) for the shallow tags at 9.3 km when surface water velocity and temperature difference between 10 and 50 m were 0.04 m s^{-1} and 0.09 ºC, respectively, relative to the period averages of 0.10 ± 0.08 m

s^{-1} and 0.22 ± 0.69 ºC. Similarly, the maximum recorded *DR* occurred twice (26 October, 2015 and 7 December, 2015) for the deep tags at 8.2 km when surface water velocity and temperature difference between 10 and 50 m averaged 0.04 ± 0.00 m s^{-1} and 0.13 ± 0.05 ºC, respectively. Most detections at maximum range occurred when ice was not present, the thermal gradient was relatively small, and surface water velocity was low.

2.4 Discussion

The present study demonstrated that the probability of a receiver detecting a transmission from an acoustic tag in Lake Ontario varies both spatially and temporally and is influenced by environmental conditions. While many range studies examine the effects of individual environmental variables, we illustrated the complex and dynamic relationship that exists between detection efficiency and the environment. The primary factor that influences *DE* and *DR* in acoustic telemetry studies is the distance between tag and receiver due to the physics of sound propagation in water (Hayden et al. 2016). The power output of the tag also has a strong impact on *DE* and *DR* as tags with high power are inherently able to transmit stronger sound signals that can travel greater distances (Heupel et al. 2006). Finally, an assortment of biotic and abiotic factors in the environment can influence the rate of energy attenuation and sound absorption as the signal travels through water (Melnychuk 2012). Interestingly, we found that the effect of environmental variables on *DE* and *DR* varies across distance and tag types, demonstrating the complex interaction of multiple factors that influence *DE* and *DR*.

This study reports higher *DE* at greater tag-receiver distances than many previously published studies as well as a greater maximum *DR*. For example, we detected transmissions from our tags at a maximum distance of 9.3 km whereas many studies report maximum *DR* below 1 km (e.g., Cagua et al. 2013; Hazel et al. 2013; Jossart et al. 2017). The main reason for these differences is the relatively less dense and less dynamic freshwater environment of Lake Ontario relative to many marine or coral reef settings. Similar to our findings, Hayden et al. (2016) observed a maximum *DR* of 11.8 km in Lake Huron, a large temperate freshwater lake in the Great Lakes. All of the tags in this study exhibited similar relationships between *DE* and distance, and *DR* increased as power output increased.

Ambient noise resulting from the environment and tag collisions from the presence of tagged fish was unlikely to have significantly impacted receiver performance or influenced *DE* measures for the duration of the study. Prior to the date that tagged bloater were stocked in the array, the NQ was always positive and thus, noise was primarily from environmental sources. Following the release of tagged bloater, the NQ fluctuated between positive and negative values and never decreased below -5000, signifying input from both the environment and tags, although tags often produced higher levels of noise. The NQ for the further receiver was less variable than for the receiver closer to the range tags, which is likely a result of tagged bloater remaining in the center of the array during the range study (see Chapter 3). Aside from the stocking event, the range of NQ values experienced in this study was smaller than other studies (e.g., -16050 to 161574; Simpfendorfer et al. 2008), indicating that ambient noise was unlikely to have impacted receiver performance.

This study examined detection patterns across a depth range of 50 m. Relatively few range studies have incorporated tag depth as a variable in their analyses; those that have are often at shallower depths of < 20 m (e.g., Cagua et al. 2013; Scherrer et al.

2018). Detection efficiency in our study was lower for shallow tags compared to the deep tags of the same power output. Similarly, Scherrer et al. (2018) observed greater *DE* and *DR* for tags at depth (15 m) than for tags closer to the surface (1 m). In contrast, Cagua et al. (2013) found that increasing proximity of the tag to the bottom in a coral reef habitat significantly reduced the probability of detecting the tag. Inconsistencies in the effects of tag depth across studies may indicate that the effects of tag depth are dependent on the characteristics of the environment (e.g., local bathymetry, environmental noise, bottom composition, etc.). In reef environments, there is more environmental noise closer to the benthos that interferes with *DE* as a result of noisy marine animals (e.g., snapping shrimp, parrotfishes), as well as irregular bottom topography. In a freshwater environment, as demonstrated in this study, levels of biological noise at depth are expected to be limited, and deeper waters may provide a barrier to the effects of some environmental conditions (e.g., wind, precipitation) that could impact *DE*. Many telemetry studies focus on surface-oriented species (e.g., salmon) and most receiver deployments are bottom-oriented, thus it is important to consider the influence of tag depth on gear performance.

A notable difference in *DE* across tag categories was the variability at distances close to the receiver as a result of CPDI. Although CPDI is a phenomenon that has been defined in aquatic acoustic telemetry literature (Kessel et al. 2015), some studies have shown that the size of the radial region impacted by CPDI increases with power output and tag depth (Kessel et al. 2015; Scherrer et al. 2018). The effect of CPDI may have been underestimated in this study as the minimum tag-receiver distance was 100 m and residual signal power, and thus the potential for CPDI, would increase at shorter distances. If unaccounted for, CPDI could lead to decreased performance of an acoustic telemetry array and the production of less reliable detection data that could be misinterpreted during analysis. This may be particularly problematic for sedentary species or home-range studies, but less problematic for migratory species expected to move past a receiver as the tags would be detected prior to entry into the CPDI and post-exit. A primary challenge in range analysis is selecting a model that can accurately represent the *DR* profiles that are characteristic of range studies (Hayden et al. 2016). While many range studies have used a variety of linear and nonlinear models to describe *DE* and *DR* (e.g., Hayden et al. 2016; Huveneers et al. 2016; Selby et al. 2016), we chose to implement GAMMs in part because of their ability to accommodate decreased *DE* at distances typically affected by CPDI while allowing for autocorrelation structures, variance structures, and random effects. Researchers generally aim for the maximum possible *DR* and thus employ the most powerful tags the study species can physically accommodate (Kessel et al. 2014), but the effects of CPDI on higher power output tags is worth further consideration in study design depending on the scale of the study, the resolution of data sought, and the study objectives.

The temporal variation observed in our study suggests that short-term range studies may not be representative of *DE* over longer time intervals, particularly in systems that have a lot of seasonal variation in environmental conditions, such as thermoclines and seasonal ice that vary within and between years. Over the 7-month study period, we observed a high degree of variability in *DE* that was inconsistent through time. Temporal trends were similar across tag types, indicating that variability in *DE* was caused by temporal changes in the study system rather than tag characteristics. Decreased *DE* during winter months may be a result of the noise created during periods of ice formation and break up interfering with acoustic signal reception. Most range assessment studies have focused more on spatial variation (e.g., Roy et al. 2014; Steel et al. 2014) or have occurred over a shorter term that may not reveal the same magnitude of temporal variability (e.g., Espinoza et al. 2011; Baktoft et al. 2015). As such, to identify periods of high and low *DE* in temperate systems like Lake Ontario, it is recommended to deploy sentinel range tags for the entire duration of the telemetry study.

Models with the best fit for each tag type included the majority of covariates with all terms in the model being significant, suggesting that *DE* may be related to a complex interaction of multiple biotic and abiotic parameters that can vary across spatial and temporal scales. Temporal variation in *DE* is largely influenced by changes in environmental conditions (Huveneers et al. 2016). For instance, the low *DE* that was experienced during winter months is likely associated with a combination of lower water temperatures, an isothermal water column, increased ice cover, or other environmental changes that are characteristic of the winter season. Huveneers et al. (2016) compiled a summary of the influences of environmental variables on *DE* from numerous range studies, illustrating the variability observed across studies. For instance, while some studies reported tag depth and wind speed as not being significant (e.g., Shroyer and Logsdon 2009; Cotton 2010), other studies reported a significant negative relationship (e.g., Cagua et al. 2013) or a significant positive relationship (e.g., Gjelland and Hedger 2013) with *DE*.

Depth can be an important factor in telemetry studies because it can increase Euclidean distances between a tag and receiver and transmission signals may cross vertically heterogeneous or stratified layers. Our results suggest that the difference in depth between our tags and receivers had a significant effect on *DE* as this term was included in the most parsimonious models for V9 and V16 tags, but not for the V13 tag, which experienced less inherent depth variability due to study design logistics. Tag depth was also not included in the final model for each tag type, suggesting that the depth of the equipment does not affect *DE* as much as the range of depth between the tag and receiver. Shroyer and Logsdon (2009) conducted a range study in freshwater lakes and rivers with tag depths of up to ~30 m and also found no significant impact of tag depth on *DE.* The influence of equipment depth – both tags and receivers – appears to strongly depend on other characteristics of the system such as bathymetry and environmental noise. Receiver depth was not directly examined due to collinearity with distance, but also had a significant impact on *DE*. Receiver depth presented a possible confounding factor as deeper receivers tended to be closer to the sentinel tags than shallower receivers due to bathymetry. However, it is arguable that while both tag depth and receiver depth should be considered in a telemetry study, including the depth difference between the tag and receiver as a variable partially accounts for variable receiver depth. To reduce the potential effects of equipment depth on *DE*, telemetry studies should be designed based on the expected depth used by the study species and associated environmental structure or conditions that will impact *DE*.

Water temperature and thermal gradients have been found to impact *DE* due to environmental changes associated with water temperature (e.g., increased activity in ectothermic organisms) and the reflection and distortion of sound signals by thermal gradients (Radford et al. 2008; How and de Lestang 2012; Kaplan et al. 2015). Water temperature may be correlated with the presence of benthic organisms such as snapping shrimp in marine environments, the density of small biological organisms in the water column, or vegetation growth, some of which have been attributed to decreases in *DE* (Cotton 2010). Our study is consistent with others in finding that increased temperature and thermal stratification negatively impact *DE*. Huveneers et al. (2016) reported four other range studies that assessed the effects of thermal stratification and all studies found a negative relationship with *DE* (Singh et al. 2009; Shroyer and Logsdon 2009; Cagua et al. 2013; Mathies et al. 2014). The majority of our study period occurred when the lake was isothermal or a relatively weak thermal gradient was present. Unfortunately, these data do not encompass the summer season when thermal stratification is more pronounced, hence we cannot directly comment on its effect, although we predict the thermocline would result in a much stronger impact on *DE*. For example, Singh et al. (2009) reported a 75% reduction in *DE* in water with a 5 ºC temperature difference. The maximum temperature difference we observed in the water column during our study was ~3 ºC, which is relatively small compared to the ~15 ºC temperature difference observed within our array in the summer. Since thermally stratified water columns can reflect and distort acoustic transmissions, it is especially important to consider the depth of receivers and the study animal where seasonal thermoclines may be present, such as the Great Lakes. Water temperature at 10 m, week, and month were not directly examined due to collinearity with water temperature at 50 m. Water temperature at 10 m would have the same effect as water temperature at 50 m, with increased temperatures closer to the surface resulting in decreased *DE*. Temporal parameters such as week and month are often correlated with environmental variables in a system like Lake Ontario, where seasonal environmental changes are prevalent. While we believe that our environmental variables captured the temporal trends in *DE* in Lake Ontario, week or month might be beneficial in identifying reduced receiver performance over time or the effects of other variables that might have a more linear trend such as a biofouling.

Surface water velocity is typically related to wind speed, wave height, and current, all of which are variables that have been previously examined in *DE* and range studies (e.g., Simpfendorfer et al. 2008; Gjelland and Hedger 2013; Stocks et al. 2014). Wind speed, wave height, and current typically have either no effect or a negative relationship with *DE* (e.g., Mathies et al. 2014; Stocks et al. 2014). In our study, there was an immediate decrease in *DE* as soon as water velocity approached 0.1 m s^{-1}. Environmental conditions that disturb the water's surface can alter sound signals. Under some circumstances, variables such as surface water velocity or ice thickness can decrease *DE* by distorting sound transmissions (e.g., tag pings). Alternatively, they can also cause reflection of transmissions downward through the water column to the receivers, which may increase *DE*. In our study, ice thickness had a relationship with *DE* where *DE* was high when there is no ice, fluctuates at ice thicknesses of 0.02 – 0.12 m, and then increases again when ice thickness exceeds 0.12 m. Since most range assessment studies are conducted in tropical marine environments, few studies have examined the impact of ice on detection of acoustic transmissions (e.g., Kessel et al. 2016). Our results suggest that during periods of ice formation and ice break up, there may be additional acoustic noise in the environment that impacts *DE* (e.g., ice cracking and abrasion) whereas thicker ice may be more stable, thus creating high *DE* similar to when ice is not present in the lake. It is possible that this could be a result of the thick ice reflecting acoustic signals downward through the water column. Alternatively, thick and stable ice may form a barrier between wind-generated noise and the telemetry gear and reducing wind-generated waves.

A variable that is often overlooked in retrospective range analyses is the number of fish detections occurring on the receivers throughout the study period. The duration of a complete acoustic transmission varies by manufacturer but is ~3.5 s for Vemco tags (Selby et al. 2016). During the time that one transmission is being detected and recorded by a receiver, a transmission from another tag could arrive at the receiver and interfere with the receiver's ability to properly decode either signal (Voegeli et al. 1998; Pincock 2012). Large numbers of fish present in an array at the same time increase the probability of these signal code collisions occurring (Pincock 2012). The number of tagged fishes concurrently present in a system can depend on the animal's behaviour (e.g., schooling, highly resident species, animals with small space use, migratory species, etc.) and thus, it is important to consider these variables in study design when selecting the nominal delay of tags and the sample size. Retrospective analysis of receiver performance in relation to noise levels and sources in our study suggested that noise produced by environmental sources and tagged fish present in the system were not at levels that would have a significant impact on *DE*. Inclusion of the number of fish detections in the best fitting model was likely a result of increased detection of tagged fish associated with increased *DE*.

A possible confounding factor in our study stems from calculating *DE* as a daily metric. We calculated *DE* at a daily level because the tags used were programmed with nominal delays (e.g., 1750 – 1850 s) to avoid potential conflicts with other tags in the area and it is not possible to predict when the tag was expected to transmit. Due to the nominal delay of the tags, alternative analyses were not possible, such as treating each transmission as a binomial distribution at the 30-minute scale. Calculating *DE* at a daily level allowed for more possible values of *DE* (i.e., a maximum of 48 transmissions per day results in 49 possible values of *DE* as a daily metric) than using a shorter time period. For predictor variables that vary throughout the day (e.g., wind is often highly variable) we are likely to miss the effect of extreme values on *DE* via this averaging. The "instantaneous effect" of these environmental conditions is likely to be more extreme than the averages we present, potentially resulting in periods throughout a day when *DE* and *DR* are compromised. As such, the influence of environmental conditions on *DE* presented in this study may be an underestimate.

Here, we conducted range testing using an extensive telemetry dataset in a system that is underrepresented in acoustic telemetry range studies and contributed to our understanding of acoustic telemetry performance in freshwater. As more researchers incorporate telemetry technologies in their studies, it becomes increasingly important to address associated issues to improve the quality of data and interpretation. The unique performance of acoustic telemetry arrays that has been demonstrated in a variety of environments highlights the value of incorporating methods for *in situ* range testing and retrospective analysis of *DE* in study design. While many range studies have been executed to determine *DE* and *DR* and how they fluctuate spatially and temporally in a system, we propose that trying to quantify individual effects of environmental variables may vastly oversimplify the dynamic interactions that occur amongst a suite of environmental conditions. Our study revealed that the effect of individual environmental conditions may increase or decrease with changes in distance or depth and is inconsistent across tag types as illustrated by interactions we presented between different variables. Range studies are valuable in determining *DE* and *DR* prior to a telemetry study to inform study design and retrospective analysis of range is important to determine changes in *DE* and the potential impacts of the environment throughout a telemetry study. However, unless one environmental variable or interaction has an overwhelming effect on *DE* and *DR* at a specific location or during a certain period and the exact location and depth of the study animal is known, it may be difficult to assess range in a manner that can be applied directly to detection data of tagged animals. We recommend conducting range studies concurrent with animal telemetry to estimate variation in *DE* and *DR* that most closely matches the environment experienced by study animals. Future range studies in freshwater lakes should compare static and mobile range testing to evaluate how accurately *DE* of a sentinel tag represents that of a mobile tag to inform on whether static range testing can be used to accurately interpret detections of mobile tagged individuals.

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Table 2.1 Summary of detections for sentinel range tags deployed in northeastern Lake Ontario from 22 October, 2015 to 23 May, 2016 (215 days). Detections day^{-1} represents the average number of detections per day across all 75 unique receivers that tags were detected on (mean ± standard deviation), whereas detections day^{-1} receiver^{-1} represents the average number of detections per day of a tag at each of the 75 receivers (mean ± standard deviation). Total receivers is the total number of unique receivers that the tag was detected on for the duration of the study.

Tag	Type	Station	Depth (m)	Total detections	Detections day^{-1}	Detections day^{-1} receiver^{-1}	Total receivers	Max distance detected (km)
1	V9	1	50	78562	365.4 ± 123.0	4.9 ± 11.1	48	5.9
2	V9	3	50	75942	353.2 ± 118.1	4.7 ± 11.3	49	5.9
3	V9	3	10	49207	228.9 ± 65.4	3.1 ± 9.4	41	6.4
4	V13	3	50	92054	428.2 ± 140.1	5.7 ± 11.8	67	8.2
5	V16	1	50	127242	591.8 ± 203.2	7.9 ± 13.2	71	7.8
6	V16	2	50	121028	562.9 ± 194.1	7.5 ± 13.2	71	8.0
7	V16	3	50	113388	527.4 ± 178.6	7.0 ± 12.9	67	7.1
8	V16	3	10	112000	520.9 ± 162.5	6.9 ± 12.5	74	9.3

Table 2.2 Detection efficiencies (0-1) ± standard error for various tag power outputs and depths at set distances ranging from 100 – 2400 m in Lake Ontario. Detection efficiencies were estimated from GAMMs calculated for each tag category using detection data from 22 October, 2015 to 23 May, 2016.

	Tag Category				
Distance (m)	**V9 50 m**	**V9 11 m**	**V13 50 m**	**V16 50 m**	**V16 11 m**
100	0.87 ± 0.03	0.97 ± 0.06	0.84 ± 0.04	0.78 ± 0.04	0.85 ± 0.03
200	0.85 ± 0.02	0.91 ± 0.04	0.83 ± 0.03	0.80 ± 0.02	0.84 ± 0.03
300	0.84 ± 0.02	0.85 ± 0.03	0.82 ± 0.02	0.82 ± 0.02	0.84 ± 0.02
400	0.83 ± 0.02	0.77 ± 0.03	0.82 ± 0.02	0.84 ± 0.02	0.83 ± 0.02
500	0.83 ± 0.02	0.68 ± 0.03	0.82 ± 0.02	0.85 ± 0.02	0.82 ± 0.02
600	0.81 ± 0.02	0.59 ± 0.03	0.81 ± 0.02	0.86 ± 0.02	0.80 ± 0.02
700	0.78 ± 0.02	0.50 ± 0.02	0.80 ± 0.02	0.86 ± 0.01	0.78 ± 0.02
800	0.73 ± 0.02	0.40 ± 0.02	0.77 ± 0.02	0.85 ± 0.02	0.75 ± 0.02
900	0.67 ± 0.02	0.32 ± 0.03	0.74 ± 0.03	0.83 ± 0.02	0.72 ± 0.02
1000	0.59 ± 0.02		0.70 ± 0.03	0.81 ± 0.02	0.68 ± 0.03
1100	0.51 ± 0.02		0.65 ± 0.03	0.78 ± 0.02	0.64 ± 0.03
1200	0.44 ± 0.02		0.59 ± 0.03	0.76 ± 0.02	0.60 ± 0.03
1300	0.38 ± 0.02		0.53 ± 0.03	0.73 ± 0.02	0.56 ± 0.03
1400	0.34 ± 0.02		0.47 ± 0.03	0.70 ± 0.02	0.52 ± 0.03
1500	0.30 ± 0.02		0.42 ± 0.03	0.65 ± 0.02	0.48 ± 0.02
1600	0.25 ± 0.02		0.36 ± 0.03	0.58 ± 0.02	0.45 ± 0.02
1700			0.31 ± 0.02	0.50 ± 0.02	0.41 ± 0.02
1800			0.27 ± 0.02	0.42 ± 0.02	0.37 ± 0.02
1900				0.35 ± 0.02	0.33 ± 0.02
2000				0.32 ± 0.02	0.29 ± 0.02
2100				0.30 ± 0.02	0.25 ± 0.02
2200				0.30 ± 0.02	
2300				0.28 ± 0.02	
2400				0.26 ± 0.02	

Table 2.3 Summary information for the global model and candidate models summarizing the detection efficiency (*DE*) of V9, V13, and V16 tags deployed in northeastern Lake Ontario from 22 October, 2015 to 23 May, 2016 (215 days) as a function of environmental variables.

	V9			V13			V16		
Model	**AIC**	**ΔAIC**	**Adj. R^2**	**AIC**	**ΔAIC**	**Adj. R^2**	**AIC**	**ΔAIC**	**Adj. R^2**
DE~ti(*D*,*th*)+ti(*D*,*v*)+ti(*D*,*i*)+ti(*D*,*t*)+ti(*D*,*d*)+ti(*D*,*f*)+s(*D*)+s(*th*)+s(*v*)+s(*i*)+s(*t*)+s(*d*)+s(*f*)+*tag*	-33302.38	13.31	0.908	-10256.59*	15.31	0.916	-38410.15	13.44	0.907
DE~ti(*D*,*th*)+ti(*D*,*v*)+ti(*D*,*i*)+ti(*D*,*t*)+ti(*D*,*d*)+ti(*D*,*f*)+s(*D*)+s(*th*)+s(*v*)+s(*i*)+s(*t*)+s(*f*)+*tag*	-33290.74	24.95	0.903	-10262.80*	9.10	0.916	-38417.44	6.15	0.907
DE~ti(*D*,*th*)+ti(*D*,*v*)+ti(*D*,*i*)+ti(*D*,*t*)+ti(*D*,*d*)+ti(*D*,*f*)+s(*D*)+s(*th*)+s(*v*)+s(*i*)+s(*t*)+s(*d*)+s(*f*)	**-33315.69**	0	0.908	-10256.59	15.32	0.916	**-38423.59**	0	0.908
DE~ti(*D*,*th*)+ti(*D*,*v*)+ti(*D*,*i*)+ti(*D*,*t*)+ti(*D*,*f*)+s(*D*)+s(*th*)+s(*v*)+s(*i*)+s(*t*)+s(*f*)+*tag*	-33183.61	132.08	0.876	**-10271.90***	0	0.916	-38386.14	37.45	0.902
DE~ti(*D*,*th*)+ti(*D*,*v*)+ti(*D*,*i*)+ti(*D*,*f*)+s(*D*)+s(*th*)+s(*v*)+s(*i*)+s(*t*)+s(*f*)+*tag*	-33302.38	13.31	0.908	-10256.59*	15.32	0.916	-38410.15	13.44	0.907
DE~ti(*D*,*th*)+ti(*D*,*v*)+ti(*D*,*i*)+ti(*D*,*t*)+ti(*D*,*d*)+ti(*D*,*f*)+*tag*	-31771.10	1544.59	0.506	-9848.60*	423.30	0.532	-36451.32	1972.27	0.301
DE~ti(*D*,*th*)+ti(*D*,*i*)+ti(*D*,*t*)+s(*D*)+s(*th*)+s(*i*)+s(*t*)+*tag*	-31137.84	2177.85	0.866	-9797.52*	474.38	0.907	-36344.31	2079.28	0.894
DE~ti(*D*,*th*)+s(*D*)+s(*th*)+s(*v*)+s(*i*)+s(*t*)+s(*d*)+s(*f*)+*tag*	-31888.07	1427.62	0.883	NA	NA	NA	-36931.68	1491.91	0.898
DE~ti(*D*,*th*)+ti(*D*,*v*)+ti(*D*,*f*)+s(*D*)+s(*th*)+s(*v*)+*tag*	-32725.26	590.43	0.868	-10191.39*	80.51	0.909	-37737.01	686.58	0.894
DE~s(*D*)+s(*th*)+s(*v*)+s(*i*)+s(*t*)+s(*d*)+s(*f*)+*tag*	-31358.25	1957.44	0.851	-9523.10*	748.80	0.886	-36686.94	1736.65	0.890
DE~s(*D*)+s(*th*)+s(*t*)	-30345.57	2907.12	0.836	-9315.11	956.79	0.880	-35697.19	2726.40	0.881

DE is the daily probability of detecting an acoustic transmission. s() indicates a smoother and ti() indicates a tensor product interaction. Environmental variables included were distance between tag and receiver (*D*), thermocline strength (*th*), surface water velocity (*v*), ice thickness (*i*), temperature at 50 m (*t*), depth difference between receiver and tag (*d*), number of fish detections (*f*), and tag depth (*tag*). All models included an ARMA autocorrelation structure to account for temporal autocorrelation in data and tag-receiver combinations as a random effect. Akaike information criteria (AIC), delta AIC, and estimated adjusted coefficient of determination (Adj. R^2) are summarized for each model. The lowest AIC scores are bolded for each tag type to identify the best fitting model. An asterisk (*) denotes models that did not include *tag* as a covariate due to the lack of tags present at more than one depth. NA signifies that the model would not converge.

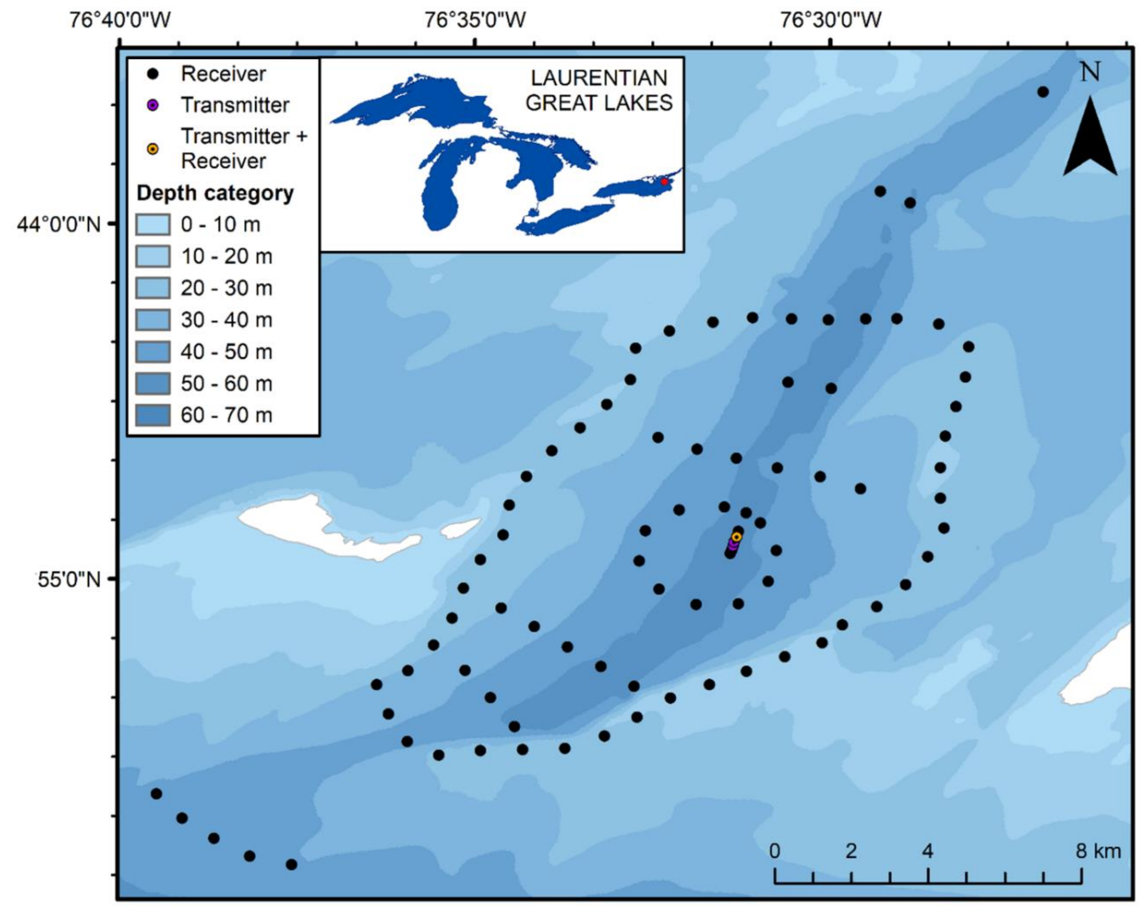

Figure 2.1 Bathymetry and location of the tag and receiver moorings in northeastern Lake Ontario. Red circle in map inset signifies location of study site within the Laurentian Great Lakes. See Fig. 2.2 for fine-scale tag positions.

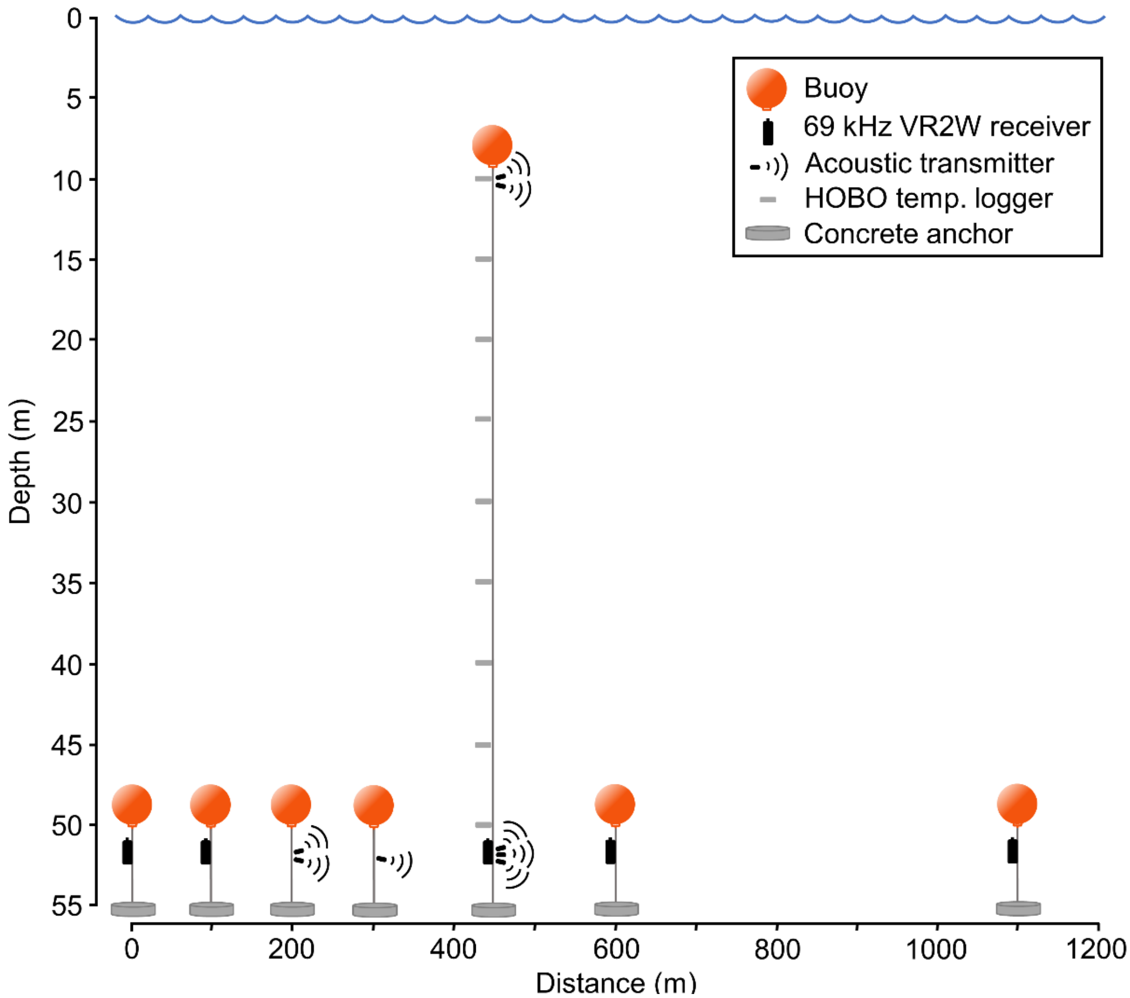

Figure 2.2 Design of tag and receiver moorings deployed in the center of the Lake Ontario receiver array. See Fig. 2.1 for locations.

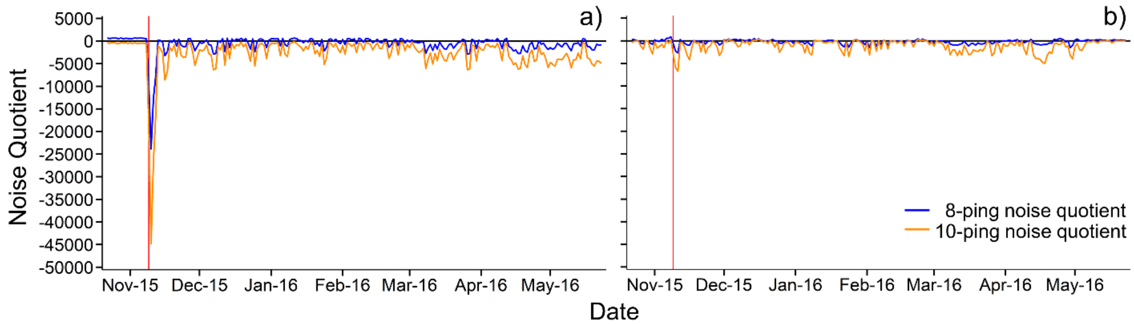

Figure 2.3 Estimates of the daily noise quotient (NQ) for (a) a receiver ~600 m from the sentinel range tags, and (b) a receiver ~4.3 km from the sentinel range tags. Blue and orange lines indicate a NQ calculated on the pretense of all tags having an 8-ping and 10-ping sequence, respectively. The vertical red line signifies the date that 70 tagged bloater (*Coregonus hoyi*) were stocked into the center of the receiver array (9 November, 2015).

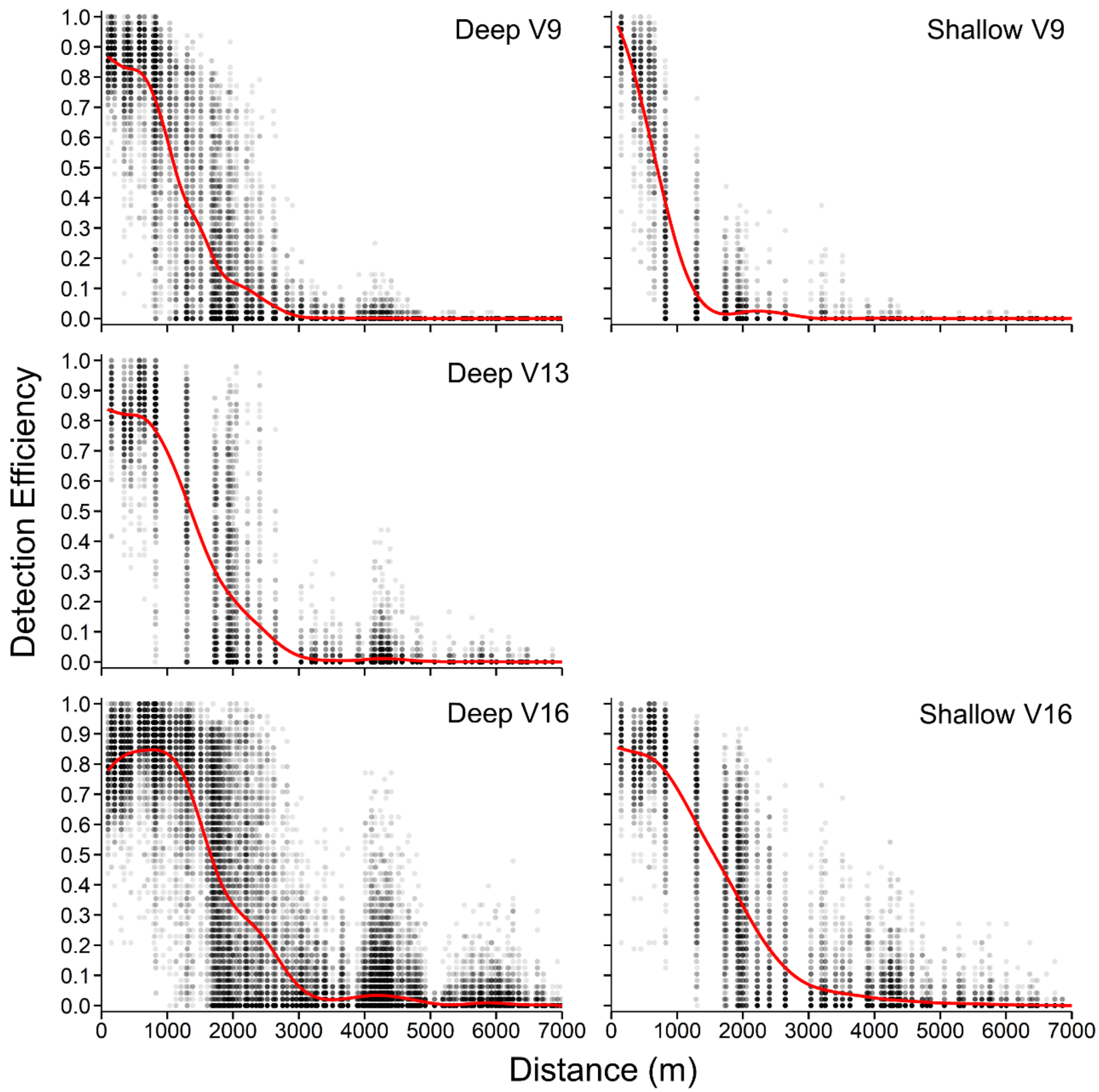

Figure 2.4 Detection efficiency (*DE*) profiles estimated for the entire study period (22 October, 2015 to 23 May, 2016) by tag power output and depth from deployments in northeastern Lake Ontario. Grey circles represent daily *DE* (0-1) and red lines represent the overall spatial profile of *DE* for each tag category.

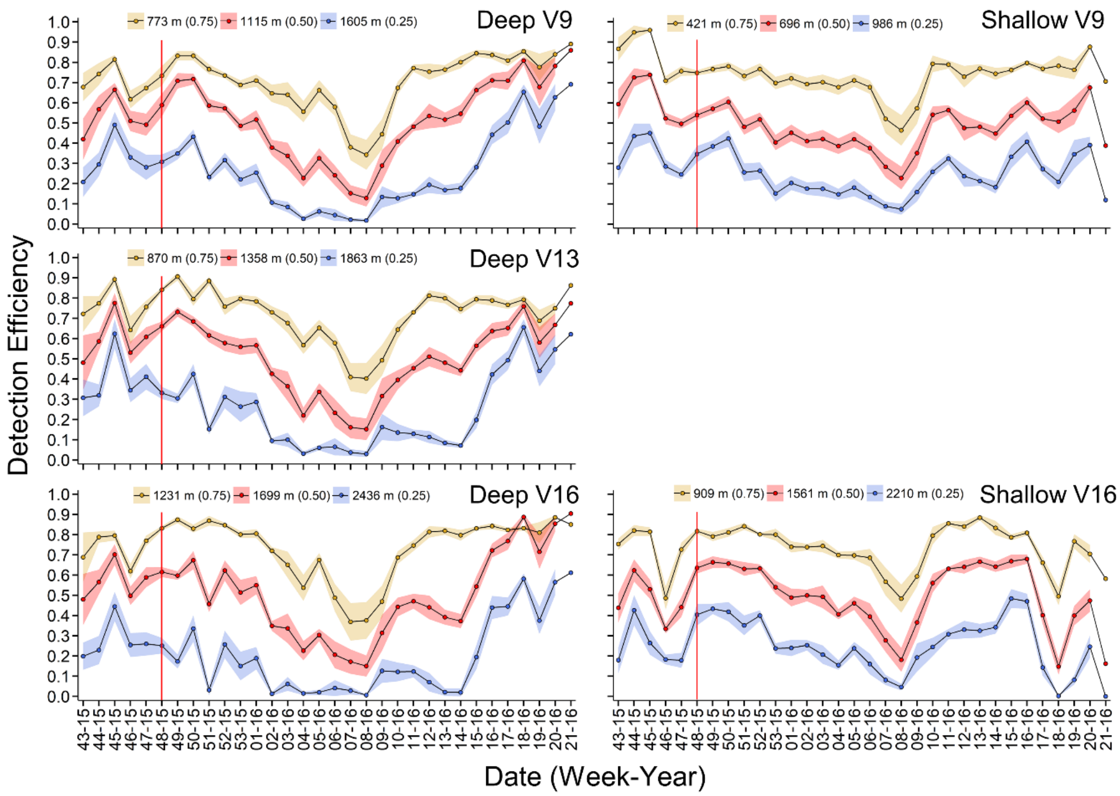

Figure 2.5 Detection efficiency (*DE*) time series estimated for three distances (DE_{D1}, DE_{D2}, DE_{D3}) by tag type and depth from deployments in northeastern Lake Ontario. Circles represent weekly *DE* (0-1) and ribbons signify standard error for each tag category. Vertical red line indicates date of release of tagged bloater. Date is shown in the format of week-year.

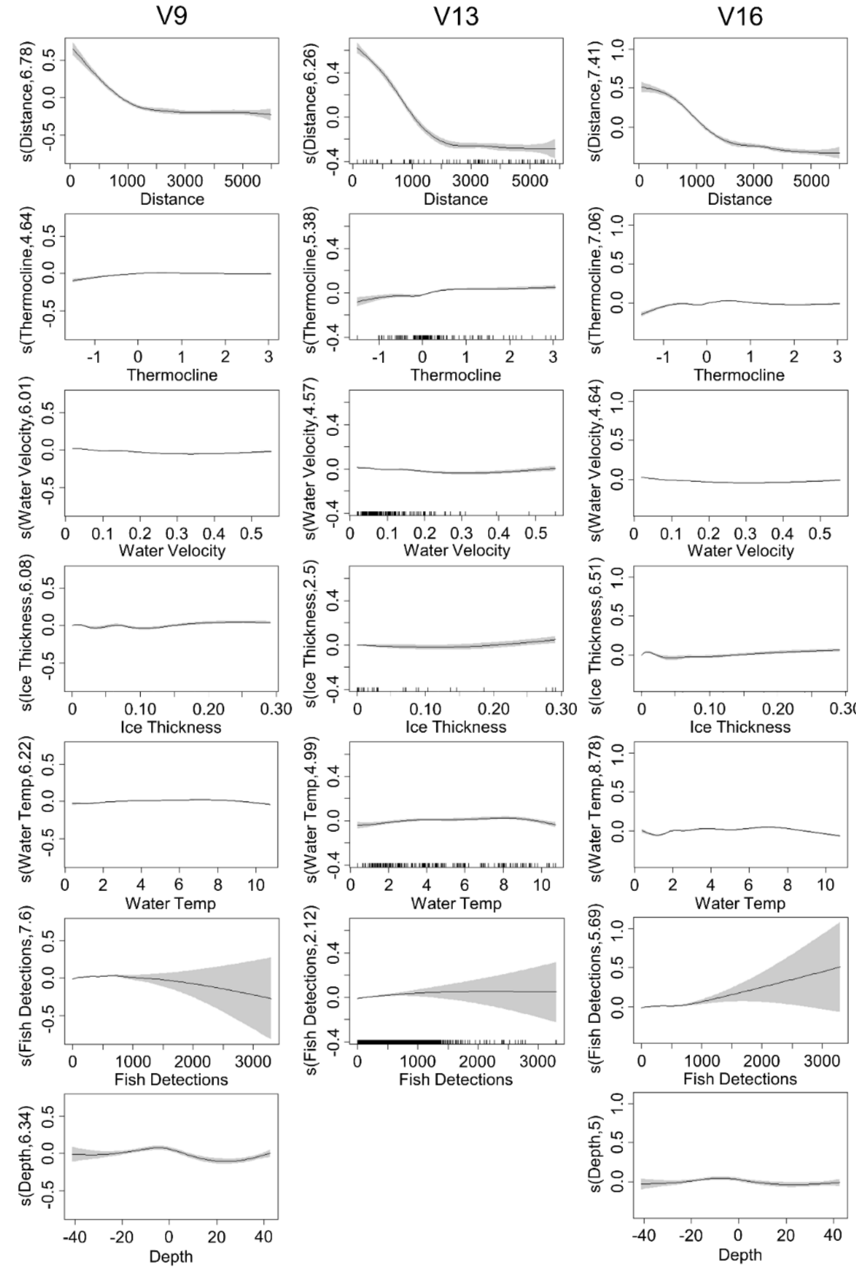

Figure 2.6 Partial effects of nonlinear environmental variables on detection efficiency (*DE*) for each of the three best fitting generalized additive mixed models (GAMMs) for the V9, V13, and V16 tags, respectively. Environmental variables included are distance between tag and receiver (m), thermocline index, surface water velocity (m s^{-1}), ice thickness (m), temperature at 50 m (ºC), number of fish detections, and depth difference between tag and receiver (m). Thermocline index represents the strength of the thermocline where zero signifies thermal homogeneity and values increasing in either direction from zero indicate an increasing thermal gradient. Positive values of depth difference indicate that the tag is shallower than the receiver whereas negative values indicate that the tag is deeper than the receiver. Shaded areas represent the 95% confidence interval around each smooth term.

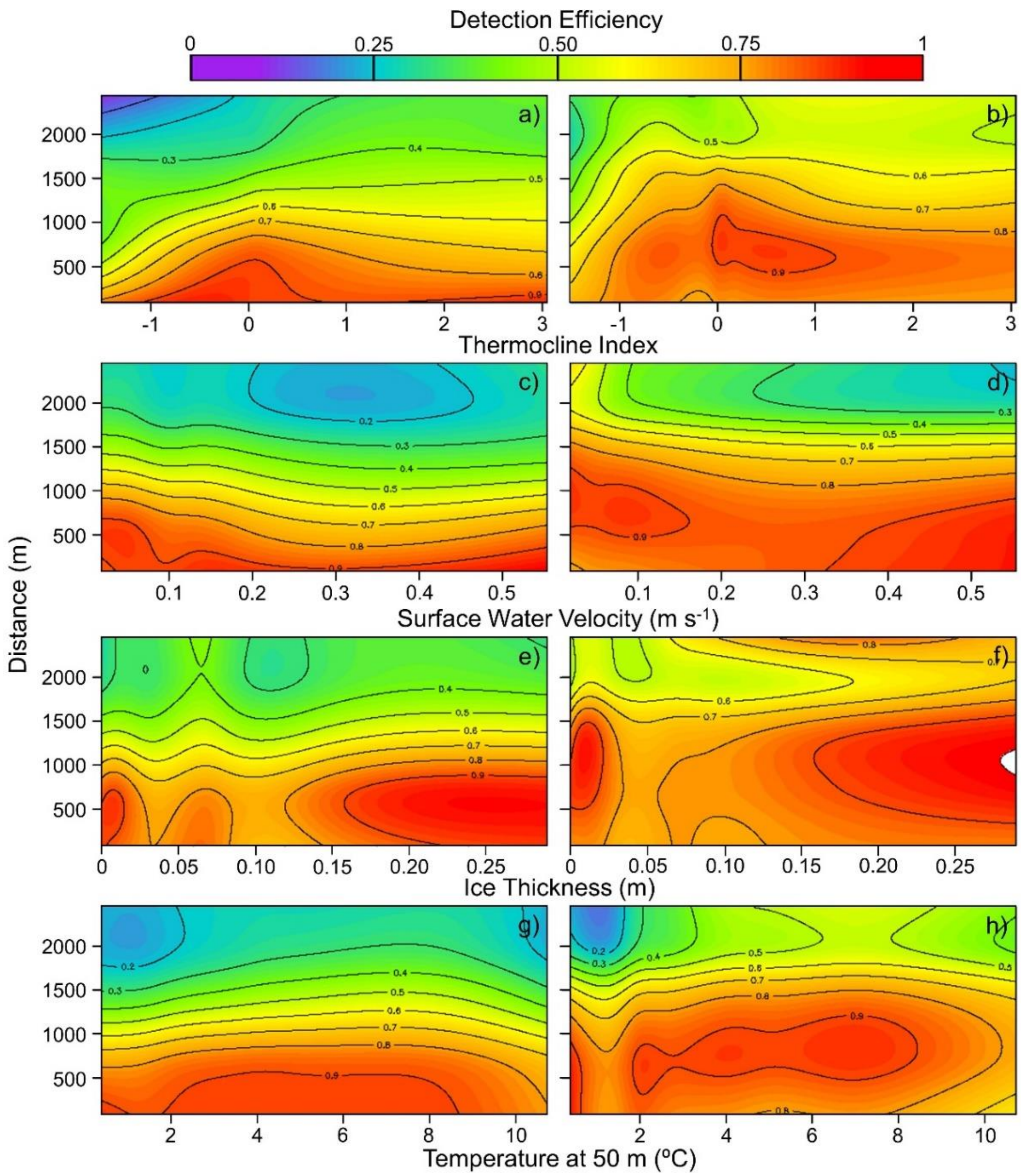

Figure 2.7 Summed effects of nonlinear interaction between distance (m) and environmental variables on detection efficiency (*DE*) for V9 tags and V16 tags from deployments in northeastern Lake Ontario: (a) thermocline index for V9; (b) thermocline index for V16; (c) surface water velocity (m s^{-1}) for V9; (d) surface water velocity (m s^{-1}) for V16; (e) ice thickness (m) for V9; (f) ice thickness (m) for V16; (g) temperature at 50 m (ºC) for V9; (h) temperature at 50 m (ºC) for V16. Thermocline index represents the strength of the thermocline where zero signifies thermal homogeneity and values increasing in either direction from zero indicate an increasing thermal gradient. Contour lines and colour represent *DE* (0-1).

CHAPTER 3

POST-STOCKING MOVEMENT AND BEHAVIOUR OF A REINTRODUCED FISH: BLOATER (*COREGONUS HOYI*) IN LAKE ONTARIO

3.1 Introduction

Fish stocking is a common practice in freshwater and marine systems worldwide aimed to supplement naturally occurring wild populations, re-establish extirpated species, or introduce a non-native species for recreation or management (Cowx 1994; Worm et al. 2009; Halpern et al. 2012). Despite the long history of fish stocking and its prevalence today, determining the fate and ecological role of fish post-release is largely unknown primarily due to difficulty monitoring them. Several methods exist to quantify stocking success including mark-recapture, hydroacoustic surveys, and fisheries data that provide us with basic information about survival and location estimates, however, there is a lack of finer resolution data about post-stocking survival, movement, and behaviour.

The Laurentian Great Lakes consist of five large post-glacial lakes (Lakes Superior, Michigan, Huron, Erie, Ontario) in North America that are connected by a series of natural channels to form the world's largest freshwater ecosystem. More than 20 million fishes have been stocked into the Great Lakes annually since the late 20th century to mitigate the effects of overharvesting and non-native species introductions that have negatively impacted the native fish community and to supplement valuable non-native fisheries (e.g., Pacific salmon) (Zimmerman and Krueger 2009; Mandrak and Cudmore 2010; Dettmers et al. 2012; Bunnell et al. 2014). Various native and non-native fish species are stocked yet relatively little is known about the post-stocking ecology of many species, especially those at lower trophic levels.

Deepwater ciscoes (*Coregonus* spp.) are a diverse group of species that once comprised an integral part of the native fish community of the Laurentian Great Lakes (Eshenroder et al. 2016). As forage fishes that inhabit deep water and migrate vertically in the water column, deepwater ciscoes link deep benthic production and higher trophic level piscivores, serving as an important connection and source of energy within Great Lakes food webs (Favé and Turgeon 2008; Honeyfield et al. 2012; Ives et al. 2018). Presently, most deepwater ciscoes are extinct or have suffered local extirpations that restrict them to Lakes Superior and Huron, while the shallow-water form of cisco (*C. artedi*) persists in all Great Lakes but Lake Erie (Phillips and Ehlinger 1995; Baldwin 1999; Eshenroder et al. 2016). An exception to this is bloater (*C. hoyi*), a deepwater cisco that is extant in Lakes Huron, Michigan, and Superior (Favé and Turgeon 2008; Eshenroder et al. 2016). Until the mid-1950s, bloater were an abundant forage fish in Lake Ontario but underwent a dramatic population decline in the 1950s as a result of overharvesting and the introduction of the non-native species rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*) (Wells 1969; Christie 1974; Mills et al. 2003). Despite bloater persisting longer in Lake Ontario than the other three deepwater ciscoes (*C. reighardi*, *C. kiyi*, *C. nigripinnis*), the last documented catch was in 1983 (Owens et al. 2003).

Research on bloater in Lake Ontario was limited to gill net surveys and harvest data prior to their extirpation in the 1980s (Koelz 1929; Stone 1947). Current knowledge of bloater ecology in the Great Lakes is based on observations from Lakes Huron, Michigan, and Superior and is limited seasonally (Clemens and Crawford 2009). A large proportion of studies on bloater have focused on their depth distribution and the physiological ability of deepwater ciscoes to exploit deep sections of large lakes (e.g., Hrabik et al. 2006; Jensen et al. 2006; Clemens and Crawford 2009). Much of what is known about the vertical space use of bloater has been revealed through hydroacoustic and trawl surveys used to identify and verify the presence of bloater at specific depths (Clemens and Crawford 2009). It has been suggested in recent decades that bloater and other deepwater ciscoes undergo diel vertical migration (DVM) in which they ascend through the water column at night to facilitate planktivory on epibenthic mysids (*Mysis relicta*) (Eshenroder et al. 1998; TeWinkel and Fleischer 1999). The inability to track individually identifiable bloater across depths has resulted in limited knowledge regarding the extent, frequency, and amplitude of DVM. Survey data suggests that adult bloater frequently occupy depths ranging from 36 to 110 m although they have been captured less frequently beyond this range, with one reported capture as shallow as 9 m in Lake Michigan (Koelz 1929; Jobes 1949; Wells 1968; Brown et al. 1985). Nighttime midwater trawls in Lake Superior showed peak abundance around 30 m with few captured >50 m (Hrabik et al. 2006). It has also been suggested that juvenile bloater (80-145 mm fork length) migrate vertically through a wider range of depths than adult bloater (>145 mm fork length) (Eshenroder et al. 1998).

While a variety of studies suggest the movement and habitat use of bloater is strongly linked to depth preference, the horizontal space use of bloater is less well studied. Similar to vertical space use, knowledge of horizontal bloater distributions is based primarily on hydroacoustic surveys and trawl catch. As bloater exhibit preference for a narrow range of cool temperatures corresponding to hypolimnetic temperatures (Wells 1968; Crowder and Crawford 1984; Eshenroder et al. 1998), their horizontal space use appears to be partially thermally driven. Based on historic catch data, adult bloater are believed to inhabit deep offshore waters in the fall where they overwinter and then move into shallow inshore waters during the summer (Koelz 1929; Wells and Beeton 1963; Wells 1968; Argyle 1992). Although inshore movement has been observed in several lakes, the timing and degree of inshore movements varies across lakes (Jobes 1949; Dryer 1966; Wells 1968). Not only is our knowledge of bloater ecology mainly limited to data from extant populations, but the resolution and quality of data is restricted by gear avoidance as well (Clemens and Crawford 2009).

The extirpation of bloater in Lake Ontario has contributed to alewife becoming the dominant species in the offshore prey fish community and constituting a greater proportion of piscivore diets (Brandt 1986; Hoyle 2015; Mumby et al. 2018). Although alewives often inhabit the offshore water that bloater would typically occupy, they are restricted to the meta- and epilimnion during periods of thermal stratification and have lower energy demands thank bloater during the winter, resulting in decreased consumption of deepwater prey (Bergstedt & O’Gorman 1989; Adkinson & Morrison 2014). Seasonal migrations of alewife and smelt into deeper areas of the lake restrict the transfer of energy from the benthic to the pelagic food web, and do not fully compensate for the empty deepwater niche that bloater once occupied (Baldwin 1999; Favé and Turgeon 2008). Furthermore, consumption of alewife by predatory fish species, such as trout and salmon, has led to a thiamine deficiency that causes early mortality syndrome affecting recruitment of piscivores throughout the Great Lakes (Fitzsimons et al. 1999;

Brown et al. 2005; Honeyfield et al. 2005). Many of the higher trophic level piscivores in Lake Ontario contribute significantly to the local and regional economies through recreational fisheries in addition to playing an important ecological role in controlling non-native prey fish abundances (Honeyfield et al. 2012).

To address the issues caused by the loss of deepwater ciscoes in Lake Ontario, Canadian and American agencies have developed a binational restoration plan including captive rearing and stocking with the goal of re-establishing a self-sustaining population of bloater in the lake (OMNRF 2015). Establishing a self-sustaining population of bloater will help restore fish native to Lake Ontario, thus increasing prey fish diversity, improving ecological integrity and resilience, and serving as a basis for the reintroduction and management of other native species throughout the Great Lakes. Lake Ontario has changed substantially in the four decades since bloater last occurred in the lake (Mills et al. 2003) and there is limited experience culturing and rearing small-bodied coregonids, such as bloater. As a result, it is difficult to predict and assess post-release behaviour and survival of bloater needed to inform their restoration potential.

Acoustic telemetry is a tool well suited to address questions about bloater ecology and the viability of stocking as a method to re-establish a self-sustaining population of deepwater ciscoes in Lake Ontario. Passive acoustic telemetry is a method of tracking that provides a unique opportunity to continuously track identifiable individuals and overcome some of the existing challenges imposed by gear avoidance (Clemens and Crawford 2009; Hussey et al. 2015). An electronic transmitter is fitted to an organism and emits ultrasonic sounds to be detected, decoded, and recorded by submerged acoustic receivers at fixed locations, allowing for continuous spatial and temporal monitoring. Acoustic transmitters can also be equipped with sensors that provide additional information, such as the water temperature and pressure (depth) at the time of detection (Hussey et al. 2015). In this study, we aimed to examine the initial post release survival, 3D movement, and behaviour of hatchery-reared bloater stocked in Lake Ontario using acoustic transmitters with pressure (depth) sensors. Our specific objectives were: (1) to conduct a preliminary assessment of survival, (2) to identify immediate patterns in movement following release, (3) to evaluate horizontal and vertical space use, and (4) to assess the occurrence of schooling behaviour. Due to the high initial mortality (>50%) that is sometimes associated with stocked fish (e.g., Hanson and Margenau 1992; Aprahamian et al. 2004) in combination with the challenges of acclimating to a new environment, we predicted high initial mortality (>50%) and that survival of remaining live fish will increase through time. Given the preference of bloater for deeper, colder water, we predicted that if dispersal was rapid, movement would follow the deeper bathymetry surrounding the study site. As several instances of DVM have been observed in bloater, we predicted that bloater would begin to exhibit DVM shortly after release. Finally, the formation of shoals by other coregonid species (Röusch 1987; Ptak et al. 1998) led us to predict that bloater will exhibit schooling behaviour shortly after release.

3.2 Methods

Study site and acoustic receiver array

The study was conducted in the St. Lawrence Channel near the Canada-USA border of eastern Lake Ontario (43°55.307' N, 76°31.715' W) (Fig. 3.1). The St. Lawrence Channel is a bathymetric feature that is approximately 4 km wide and 20 km long with depths of 50-60 m along its axis bordered by shallower (~20 m) water on either side. We selected this location as it offers habitats that we anticipated bloater would favour (i.e., channel areas >50 m) while also constraining movement for observations in the otherwise vast expanse (>19,000 km^2) of Lake Ontario. An array of 85 acoustic receivers (69-kHz VR2W receivers, Vemco Inc., Bedford, Nova Scotia, Canada) was initially deployed in October 2015 for the first stocking of tagged bloater and was expanded to 101 receivers following the first download and redeployment of the array in May 2016. Four additional receivers were added to the array in May 2017 following the second download and redeployment for a total of 105 receivers. The receiver array was specifically designed to ensure a high certainty of detecting the initial stocking and movements of bloater post-release as well as to detect movement into shallower or deeper water should the bloater exit into surrounding shallow areas or the open lake. Receivers were spaced ~1 km apart based on the expected detection efficiency of 80% at 600 m for the transmitters that would be implanted into bloater (see Chapter 2). The stocking site in the center of the array was encircled by an inner ring of 10 receivers to detect initial movement of bloater and a larger ellipse of 40 receivers that defines the limits of our core study area (84.7 km^2, 17.2 linear km of channel). Additional receivers spanned the width of the larger ellipse to detect directional movement of bloater following the contours of the channel. A horseshoe-shaped north gate that extends approximately 5 km from the outer bounds of the core array permits describing the trajectory of movement should bloater emigrate from the study site into shallower water north and east of the core area (<20 m). A double line southern gate of receivers was situated along the sill separating the shallower eastern basin from the main lake to detect movement of bloater exiting the array into deeper water (>50 m). Receiver moorings were constructed following the methods described in Chapter 2 with the receiver hydrophone pointing upwards suspended ~2 m above the lake bottom.

Bloater tagging and stocking

The bloater used in this study were reared at the Ontario Ministry of Natural Resources and Forestry (OMNRF) White Lake Fish Culture Station (Sharbot Lake, Ontario) from fertilized bloater eggs that were collected from northern Lake Michigan in previous years by the U.S. Fish and Wildlife Service. Bloater tagging took place over three periods during which a total of 42 bloater were tagged: fall 2016 (n = 6), spring 2017 (n = 8), and fall 2017 (n = 28) (Table 3.1). Fish were placed in an anaesthetic solution of buffered tricaine methanesulfonate (MS-222; 400 mg/L); immersion times varied but generally required 100-180 s in order to achieve stage III anaesthesia (Summerfelt and Smith 1990). Fork length (FL) was measured to the nearest 1 mm, and wet mass was recorded to the nearest 1 g. Anesthetized bloater were placed in a cradle, where their gills were irrigated with a maintenance dose of MS-222 (80 mg/L). An incision of approximately 20 mm in length was made immediately adjacent to the linea alba and a V9TP-2x 69-kHz transmitter (nominal delay 120 s, estimated battery life 582 d; Vemco Inc., Bedford, Nova Scotia, Canada) equipped with a pressure (depth) and temperature sensor was inserted into the body cavity. The incision was closed with three interrupted, independent sutures (Ethicon Coated VICRYL Plus antibacterial suture, size 5-0, with RB-1 tapered needle) tied with a 2-1-2 surgeon’s knot. All surgical equipment was disinfected in a betadine solution (1 part betadine:9 parts water) prior to each surgery. Procedures lasted approximately 120-180 s from the time the fish were placed in the cradle to the time of placement in the recovery tank.

Fish were monitored daily by hatchery staff as part of routine tank inspections for ~2 weeks following surgery to ensure good recovery and overall fish health. Tagging resulted in negligible mortality and no tag loss consistent with the findings of Klinard et al. (2018). Tagged fish were hand netted into a stocking truck equipped with oxygenated tanks along with ~10,000 to 30,000 untagged individuals for transport to Lake Ontario following MNRF Fish Culture transportation guidelines. Upon arrival at the lake, fish were hand netted off the stocking truck to aerated holding tanks supplied with a continuous flow of lake water on the vessel which transported the fish to the release location. At the release location, tagged bloater were hand netted for release. Underwater videography during transport and release suggested that all tagged fish were healthy and exhibited no signs of stress.

Data analysis

To examine initial post-release space use and decrease the likelihood that data collected represented the location, movements, or behaviour of a predator that had consumed a tagged bloater, detections that occurred after a two-week period (i.e., 14 full days after the date of release) following the release date were removed for analyses. For all analyses, only detections of individuals that were considered alive at the time of detection were included to avoid detections of dead fish biasing results. Instances of mortality were identified during exploratory analyses by visual assessment of depth sensors, with the portion of data that was assessed as dead removed. Detection data were considered to have originated from a dead fish when the depth of the fish was constant and consistent with the bottom depth at the location that the fish was being detected. It should be noted that some fish could have swam out of the array and thus be counted as dead but there was no evidence for this. Statistical significance was assumed at $\alpha \leq 0.05$ and all analyses were completed in R version 3.5.2 (R Core Team 2018).

24-hr post-stocking behaviour

To examine initial post-release movement of tagged bloater, we selected the first 24 hours of detection data following the release date and time for each individual. A principal component analysis (PCA) was used to explore affinities among individuals and identify similarities in detection metrics based on the first 24 hours of movement. The variables considered were the number of detections, minimum depth, maximum depth, range of depth use, maximum distance from release site, and number of receivers. Minimum depth was not included in the PCA due to high collinearity with the range of depth use (pairwise cc = -0.96) and all data were checked for normality (PCA used a correlation matrix).

Bloater detections were assigned a specific location that was randomly estimated within 600 m of the receiver that the detection was recorded on. Random positions were estimated to account for the uncertainty associated with the actual location of the tagged individual due to the detection range of the receivers. A distance of 600 m was selected based on previous detection range testing performed in the study system from November 2015 to May 2016 that indicated a detection efficiency of ~80% for V9 tags at depth (see Chapter 2). Location estimates were then calculated using a 30 min mean position algorithm to derive centers of activity (COAs) following the methods described in Simpfendorfer et al. (2002). A 30 min timestep was selected as it would ensure a sufficient amount of detection data were incorporated into each location estimate to produce more accurate positions while maximizing the number of positions within a day (i.e., possible 48 positions per day) for the two-week period of analysis. To assess initial direction and distance of movement, we selected COAs for 24 hours post-release for each individual and plotted the angle and distance from release of the first and last position of the fish within the selected time period.

Horizontal space use

Horizontal autocorrelated kernel density estimates (AKDE) representing the core activity space (50%) and activity space extent (95%) of individuals were calculated from 30 min COAs of live detections for the full two-week period using the *akde* function in the R package 'ctmm' (Fleming et al. 2015). We chose to use AKDEs as opposed to the conventional kernel density estimation (KDE), which explicitly assumes that location data are independent and identically distributed and often results in KDEs that underestimate activity space areas (Fleming et al. 2015; Fleming and Calabrese 2017; Noonan et al. 2019). AKDE estimates the correlation structure in the data by fitting continuous-time movement models and selecting the best fitting model based on the approximate small sample size corrected Akaike Information Criterion (AIC) to address the stronger autocorrelation that is associated with the ever-finer sampling of movement paths (Kays et al. 2015; Calabrese et al. 2016; Noonan et al. 2019).

We determined patterns in horizontal space use among individuals by examining the areas of overlap of the 50% and 95% AKDEs of all individuals within each release group. To evaluate possible drivers of horizontal space use among individuals, we considered the release period, fork length, number of days detected, and number of COAs. We assessed collinearity of these variables using Pearson's pairwise correlation coefficient to verify independence prior to inclusion in additional analyses. The number of days detected and the number of COAs were highly collinear (pairwise cc = 0.9) and thus, were considered as a single covariate represented by number of days detected in further analyses. The *lm* function in the R package 'stats' was used to fit a linear model (LM) to examine trends in 95% AKDE size (km^2) as a function of the release period, fork length, and number of days detected for each individual (R Core Team 2013). The numerical data of days detected and fork length were centred and scaled following z-transformation prior to modelling.

To identify schooling behaviour among tagged bloater, we conducted a proximity analysis using the COAs of the fish from the largest release group (fall 2017; n = 22). One individual was removed from analysis due to insufficient data for calculating proximity. The following analyses were performed on the remaining 21 fish using COAs from the first 24 hours following release as well as using all COAs. A proximity index was calculated for every pair of individuals using the *Prox* function in the R package 'wildlifeDI' (Long 2014). The *Prox* function determines the proportion of simultaneous fixes that are proximal based on a selected distance threshold to evaluate positions through space and time. We selected a timestep of 30 minutes to complement the 30-minute interval of the COAs and conducted a sensitivity analysis to select an appropriate distance threshold at which fish would be considered proximal. Because COAs were derived from detections with positions randomly assigned within a 600 m radius of the receiver they were recorded on, we ran ten iterations of COA calculations each for select individuals using new randomized detection positions each time. We compared iterations of COAs within an individual by calculating the proximity index among iterations at a select distance threshold. The process was repeated for several distance thresholds and individuals to determine the minimum distance that provided a >0.95 proximity index among all iterations of each individual. Sensitivity analysis revealed 800 m as the most appropriate distance threshold at which to calculate proximity index for every pair of individuals. This method of proximity analysis includes only comparable timesteps (timesteps in which both fish in a pair were detected) as a conservative approach to evaluate schooling behaviour of fish as absence of a detection does not guarantee absence from the study site. Furthest neighbour clustering was implemented using the proximity indices to determine whether pairings with high proximity exhibited similar relationships with other fish.

Vertical space use

Depth values associated with each detection were grouped into 30 min intervals by individual and an average depth was calculated for each timestep. A linear mixed-effects model (LMM) was applied to determine whether release period, fork length, number of days detected, and time of day influenced depth use with transmitter ID as a random effect. The *lme* function in the R package 'nlme' was used to fit the LMM as it allowed for inclusion of a first-order auto-regressive correlation structure (AR1) to account for temporal autocorrelation between depths for adjacent timesteps nested within each transmitter ID (Pinheiro et al. 2018). The numerical data of days detected and fork length were centred and scaled following z-transformation prior to modelling. A post-hoc Tukey's test determined which time periods differed when they significantly influenced depth use.

Diel patterns

To further explore diel patterns in space use, daily sunrise and sunset times were used to classify the 30 min COAs as day (after sunrise and before sunset) or night (after sunset and before sunrise) based on the date and time of the position estimate. For each individual, all of the COAs that occurred during the day were pooled together and all of the night COAs were pooled together. The *kernelUD* function in the R package 'adehabitatHR' was used to calculate the day and night kernel utilization distributions (KUDs) representing the core activity space (50%) and activity space extent (95%) of individuals (Calenge 2006). A smoothing parameter (h) of 600 was used to estimate KUDs based on an estimated detection efficiency of ~80% at 600 m for the acoustic receivers in our study system (see Chapter 2). Individuals with less than 5 total detections during either the day or night period were removed from KUD calculations as a minimum of 5 relocations are required to calculate a KUD using the *kernelUD* function. A paired t-test was performed to compare day/night differences in horizontal space use within individuals.

Fate of tagged bloater

The fate of all 42 bloater that were tagged and stocked throughout the study period was assessed to determine if spatial and temporal patterns in mortality and survival among individuals were evident. For fish that were assessed as dead, the location of their death was examined in relation to the number of days with live detections prior to mortality. For fish that were still alive at the time of their last detection, their last known COA was examined in relation to the number of days they had been detected in total.

3.3 Results

Detection summary

Of the 42 bloater that were tagged and released in northeastern Lake Ontario from November 2016 to November 2017, 38 fish (90%) were detected; the four that were never detected came from the fall 2017 release group. The influx of tags being released into the system during stocking and the resultant influx of tag transmissions likely decreased ability of receivers in the inner ring to record all transmissions being emitted from tags immediately after stocking. The fall 2017 fish were released with 80 other tagged bloater that had been fitted with different tag models but were also emitting transmissions at the same rate as the pressure sensor tagged bloater. It is probable that these four fish died shortly after release and sank to the bottom where they were beyond detection range of the receivers without any detections being recorded. Given the detection range of the tags (>600 m at 80%, see Chapter 2) and the distance between receivers, it is unlikely that a live fish could swim out of the array without being detected.

Of the 38 individuals that were detected, 10 were removed entirely from analyses due to depth sensors indicating short term (<1 hr) mortality evident by detections at a consistent depth for a prolonged period of time that were distinctly different from live fish movements (Table 2). Thorough examination of the remaining 28 fish that exhibited live detections revealed 14 that experienced mortality at some point in their detection duration and all detections following mortality were removed from further analyses. The number of days detected alive for the 28 bloater that were used in analyses ranged from 1 to 15 with a mean ± SE of 4 ($n = 1$), 7.4 ± 2.2, and 5.5 ± 0.9 for the fall 2016, spring 2017, and fall 2017 release groups, respectively (Table 3.2). Two individuals were detected within the array for longer than two weeks following the date of release (i.e., 14 full days after release date) but these additional detections were removed for consistency of analysis. Both individuals were from the fall 2017 release group and were detected for an additional 1 day and 4 days beyond the two-week cut-off that was implemented for analyses.

24-hr post-stocking movement

The first two dimensions of the PCA accounted for 67.9% of the variance in the data (eigenvalues for dimensions one and two were 2.22 and 1.18, respectively; Fig. 3.2). The individual in the fall 2016 release group was characterized by a higher number of detections on numerous receivers, a large maximum depth and range of depth, and a large maximum distance at which it was detected, relative to most other individuals. The spring 2017 and fall 2017 release groups exhibited minimal overlap on the PCA with the spring 2017 fish often having a larger number of detections and lower maximum depth and distance detected. In contrast, the fall 2017 fish were less discriminant with most of the points and the ellipse centered around the middle of the plot, although they generally displayed higher maximum depths and distances than fish from other groups.

Initial position estimates (<1 hr) following release revealed the majority of fish headed south with a focus on the southeast quadrant of the array (Fig. 3.3a). Most individuals were detected within 1 to 2 km from the release location with few being detected up to 4 km away. Final position estimates 24 hours post-release revealed strong preference for the northeast quadrant of the array with 18 fish (64%) detected in the northeast direction at distances ranging from 1 to 6 km away (Fig. 3.3b). In contrast to the first position, few fish were detected in the southern half of the array. Trajectories of the initial position estimates appeared more dispersed than the trajectories of position estimates 24 hours post-release that showed stronger preference for the northeastern direction.

Horizontal space use

The core activity space of all bloater (50% AKDE) ranged from 2.8 to 99.3 km^2, while the activity space extent (95% AKDE) ranged from 11.5 to 386.1 km^2 (Table 3.2). Overlap in horizontal space use was similar between release groups with the greatest degree of overlap in 50% and 95% AKDEs occurring in the inner ring of the receiver array (Fig. 3.4). Individual activity space estimates tended to follow the deep channel bathymetry although there were several individuals with activity spaces that also encompassed shallow water areas. While most activity spaces occurred in the core area of the array, the fall 2016 and spring 2017 activity spaces were more focused around the southern part of the array whereas the fall 2017 activity spaces extended into the northern and western areas beyond the extent of the array. One individual in the fall 2017 release group was last detected on receivers from another telemetry project that were northwest of our array. The number of days detected was the only explanatory variable that had a significant impact on overall 95% AKDE size of tagged bloater (LM: $F_{1,23} = 6.4$, $p < 0.05$; Fig. 3.5). An increase in the number of days that an individual was detected was associated with an increase in the size of their activity spaces extent.

Proximity analysis revealed few individuals that would be considered schooling on the basis of a proximity index ≥0.5 denoting attraction (Long 2014). A total of 7 pairs had a proximity index ≥0.5 within the first 24 hours following release but decreased to two instances of attraction when examining the entire time period (Fig. 3.6). Furthest neighbour clustering indicated that pairs with high proximity indices during either time period were generally not part of the same final cluster (Fig. 3.7). However, fish that exhibited similar overall proximity relationships with all other individuals often grouped out into a cluster (e.g., fish 1682 and fish 1648 both had a strong relationship with fish 1684; Fig. 3.6a).

Vertical space use

Investigation of the effect of release period, fork length, number of days detected, and time of day on the depth use of bloater identified time of day (LMM: $F_{3,3698} = 138.9$, $p < 0.0001$) and number of days detected (LMM: $F_{1,3698} = 88.8$, $p < 0.0001$) as significant variables. A post hoc Tukey's test revealed that all time periods except for 6-12 h and 12-18 h differed significantly with 0-6 h and 12-18 h being significantly different at $p < 0.01$ and all other groups being significantly different at $p < 0.001$. Bloater exhibited the shallowest depth use during 18-24 h and the largest change in depth use between the 12-18 h and 18-24 h periods (Fig. 3.8). Depth use remained consistent and was deepest during the 6-12 h and 12-18 h periods. Further examination of individual depth use revealed strong DVM during which bloater remained at depth near the bottom during the day, ascended to shallow waters within metres of the surface shortly after sunset, and descended back down to depth before sunrise (Fig. 3.9).

Diel patterns in horizontal space use

Of the 28 fish that had live detections, 25 had a sufficient amount of detections (≥ 5) during both the day and night periods to calculate an autocorrelated kernel density estimate. Comparing day and night 95% AKDE revealed no significant difference (t-test: $t_{24} = -0.67$, $p = 0.50$) in horizontal space use within each individual.

Fate of tagged fish

Within the two-week period that bloater movements were examined, individuals were detected for a range of 1 day to the full 15-day period (Fig. 3.10). A total of 13 fish out of the 38 detected (34%) were considered alive at the time of their last detection. The majority of fish were detected for less than one-week post-release, however, there were several individuals that remained within the array longer. Final locations of tagged bloater tended to be in deeper waters but aside from this, there were no other evident overall spatial or temporal patterns in distribution of individuals or by release group. Of the fish that were considered alive at the time of last detection, the three that were detected the longest were last located at the north gate of the receiver array and northwest of the array on other receivers. Several of the fish that were deemed alive at the time of their last detection had final positions around the inner area of the array.

3.4 Discussion

Understanding the movement and behaviour of bloater in Lake Ontario broadens our limited existing knowledge of bloater ecology while also providing findings that can be applied to the adaptive management of bloater reintroduction efforts. Bloater play an important role throughout the Great Lakes as a native species in the offshore prey fish community that links deep benthic production with the upper trophic levels (Baldwin 1999; Favé and Turgeon 2008). Successful reintroduction of bloater in Lake Ontario will help restore historic energetic pathways in the food web, increase biodiversity, improve ecological integrity and resilience, and serve as a basis for the management of other native species in the Great Lakes. Passive acoustic telemetry allowed for the monitoring of bloater movements at spatial and temporal scales that have never before been observed for this species. This study demonstrated that following release, adult bloater tended to disperse fairly quickly with a general preference for deeper waters and underwent extensive diel vertical migration (DVM) from lake bed to within metres of the surface. Despite overlap in the activity space of many individuals, there was no evidence of schooling behaviour. While initial survival was low, there is the possibility that several bloater exited the array and survived elsewhere in the lake, suggesting survival and proliferation of reintroduction stocking individuals. Six bloater have been captured in Lake Ontario bottom trawls since 2015 (two in 2015, one in 2017, four in 2018) at maximum distances of 203 km from the stocking location (unpublished data). These fish were caught between depths of 60 to 95 m with a mean ± SE of 82 ± 6 m. The size range of the six bloater was 96 to 240 mm (FL) with a mean ± SE of 134 ± 22 mm.

The distance and direction of movement of bloater within 24 hours following release revealed a general change in trajectory and dispersal from the initial release until the end of the first day. The greater dispersal of initial position estimates may be a result of fish moving around more as they explore and orient themselves while trying to get accustomed to a new environment. A majority of position estimates in the northeast direction within the array after 24 hours suggests preference of bloater for the deeper waters of the St. Lawrence Channel compared to the shallower water to the southeast and northwest. The directional movement of bloater in deep waters (>50 m) several kilometers from the release point is consistent with findings from other studies that have shown that they tend to prefer depths of >35 m (Jobes 1949; Wells 1968; Brown et al. 1985). The greater maximum depths and distance travelled within the first 24 hours following release for the fall 2017 fish relative to the spring 2017 fish may indicate seasonal differences in bloater movement and activity. Research on the movement and depth use of bloater is limited seasonally with most studies occurring in the fall and summer and few during the spring, but studies have shown they occupy deep offshore waters in the fall (Koelz 1929; Wells and Beeton 1963; Brandt et al. 1991).

Autocorrelated kernel density estimates representing the horizontal activity space of bloater showed a wide range in space use with a mean extent of activity space of >80 km^2 across all release groups. The highest degree of overlap in bloater activity space occurred around the release location and north of it. While a high overlap in activity space is expected at the location that fish are released, the decrease in overlap further away from the release point may indicate that fish stayed closer to the release area. High AKDE overlap at the release location may also be influenced by a shorter detection period for the fish that either died or left the array shortly after release. A significant positive relationship between the number of days detected and 95% AKDE size may indicate that the longer bloater are detected in the array, the more new space they are using each day, resulting in a larger cumulative activity space.

The fall 2017 fish that was detected on receivers from another array northwest of ours supports the idea that bloater may be leaving the array and moving elsewhere in Lake Ontario. During this time of year, the lake is isothermal so it is possible that bloater are expanding their space use into shallower waters because of the greater extent of habitat that is within their range of thermal preference. Detections of two individuals from the spring 2017 release group on the southern gates of receivers may also suggest that bloater are leaving the array through the south and moving into the open lake.

Although bloater within each release group exhibited a high degree of overlap in horizontal space use, they did not appear to aggregate and form schools within the array. Higher proximity indices in pairs of bloater within 24 hours following release relative to the entire detection period was likely an artifact of fish being closer together due to release at the same location. Other coregonids have been shown to exhibit schooling behaviour revealed through acoustic observations (Rösch 1987; Eckmann 1990), which suggests that bloater may also display schooling. It is possible that due to the short period of time that many fish were detected in the array and this potentially being a period of acclimation, we did not witness schooling behaviour. The smaller number of surviving fish may also have impacted schooling behaviour, and as the fish acclimate and find each other after stocking, schooling may occur. Given we know so little about bloater, it may also be possible that they school at different times of the year related to spawning and lake conditions (thermal stratification).

Tagged bloater underwent strong DVM that has never before been observed at this frequency and amplitude in this species. Gear avoidance has previously played a large role in restricting the ability to examine the depth distribution and vertical migration of bloater (Clemens and Crawford 2009). As a result, existing research has infrequently observed bloater at depths less than 10 m. In our study, we revealed multiple instances where bloater ascend to depths within a few metres of the surface during DVM, suggesting that the extent of DVM is greater than previously perceived. Mehner et al. (2007) witnessed a consistent DVM in two coregonid species (*C. albula* and *C. fontanae*) throughout the entire year in a lake in Germany independent of season. Despite the bloater tagged in the present study being raised in a hatchery from eggs that originated in

Lake Michigan, they still performed DVM immediately upon release. Several hypotheses exist to explain why bloater and other vertically migrating fishes undergo DVM. The optimal foraging-antipredation (OFA) hypothesis suggests that fish stay within light levels that maximize foraging while minimizing predation risk as they migrate vertically in the water column (Clemens and Crawford 2009). Hrabik et al. (2006) concluded that data from hydroacoustic surveys in Lake Superior suggest ambient light levels and siscowet lake trout (*Salvelinus namaycush siscowet*) controlled DVM in deepwater ciscoes, including bloater. The metabolic efficiency hypothesis proposes that depth of residence is a result of maximization of metabolic efficiency that occurs in cool, well-oxygenated, hypolimnetic waters during the nighttime (Mehner et al. 2007). Although there are many instances in which DVM of bloater has been examined, hydroacoustic and trawl surveys in Lakes Michigan and Superior have revealed that not all bloater undertook DVM (Fabrizio et al. 1997; Eshenroder et al. 1998; TeWinkel and Fleischer 1999; Yule et al. 2007). Diel patterns in space use appeared to be limited to vertical movement as the size of each individual's 95% AKDE was not significantly different between day and night.

Tagged bloater survived following release with several individuals last detected alive in the receiver array. Survival of bloater was low initially with ten individuals dying within a short period after release (<1 hr). The initial mortality of bloater is consistent with what would be expected due to the stress associated with stocking and acclimating to a new environment. Stocked bloater are released in a location with a maximum depth of 53 m and thus, are exposed to depths and pressures that they have never experienced in a hatchery setting and may have difficulty acclimating to. Despite high mortality, we observed 13 individuals of the 38 detected (34%) that appeared to be alive at the time of their last detection. Of these individuals, 10 of them were located near the outer receivers in the array, which could indicate that they left the array without further detection and are alive elsewhere in the lake. The five live individuals last detected beyond the outer ring of the array were all located in areas where depth reached 30 to 40 m. This may suggest that bloater prefer these depths in isothermal conditions, which is consistent with existing research that states the upper range of their preferred depth is 36 m (Jobes 1949; Wells 1968; Brown et al. 1985; Eshenroder et al. 1998), but may also be a function of most receivers being in the 30-40 m depth range. The three bloater that were deemed alive at the time of their last detection and had final positions around the inner area of the array may have died and sank to the lake bottom beyond the detection range of the receivers. Due to the positioning of receivers in the array that is designed to detect directional movement entering and exiting the array and the known detection range of the receivers, it is unlikely that these three individuals exited the array without detection on additional receivers.

Individuals that were alive for several days prior to dying may suggest that the fish experienced a delayed natural stocking mortality, difficulty acclimating to a new environment post-stocking, predation and subsequent tag expulsion, or tag loss. Based on a lab study conducted by Klinard et al. (2018) that evaluated tag retention in bloater and revealed 100% retention over a 6-month period, it is unlikely that the tag was dropped. The strong diel vertical migrations characteristic of bloater that were exhibited until the last live detection of the fish leads us to believe the fish died of causes other than predation. A possible explanation is that we are witnessing delayed mortality associated with stocking or acclimation to a new environment. Considering bloater are a prey fish and the specimens in this study were reared in a hatchery and stocked into a foreign environment, a survival of 34% is auspicious. Over several years of stocking bloater annually, survival of bloater beyond 2 weeks is promising for bloater proliferating and establishing a self-sustaining population in Lake Ontario as demonstrated by the six bloater caught in bottom trawls in recent years.

This study used acoustic telemetry to reveal movement and behaviour of bloater that has never been observed before at this resolution, produced results valuable to management of a reintroduced species, and demonstrated the value of acoustic telemetry in stocking and restoration efforts. The findings from this study not only contribute to our understanding of the fundamental ecology of bloater and deepwater ciscoes as a whole, but they also address existing knowledge gaps about the fate of fish post-stocking. The implementation of acoustic telemetry in this study allowed us to identify mortality events, estimate survival, and track live fish movements in 3D, demonstrating the type of information that can be produced to inform restoration management practices.

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Table 3.1 Summary of characteristics of bloater (*Coregonus hoyi*) tagged and released into eastern Lake Ontario over three periods in fall 2016, spring 2017, and fall 2017. Mean ± SE (range) are shown for mass (g) and fork length (mm).

Release group	Tagging date	Release date	*n*	Mass (g)	Fork length (mm)
Fall 2016	2016-10-27	2016-11-08	6	285 ± 26 (179–362)	269 ± 6 (245–285)
Spring 2017	2017-03-20	2017-04-10	8	336 ± 16 (267–402)	306 ± 3 (297–320)
Fall 2017	2017-10-23	2017-11-07	28	284 ± 8 (210–409)	262 ± 3 (235–285)

Table 3.2 Summary of detections for all tagged bloater (*Coregonus hoyi*) from Lake Ontario that were used in analyses. Mean ± SE (range) is shown for days detected, 50% AKDE (km^2), 95% AKDE (km^2), and number of detections. Day 1 corresponds to the day of release and day 15 corresponds to a full two weeks following the release date.

Release group	*n* (tagged)	*n* (analyzed)	Days detected	50% AKDE (km^2)	95% AKDE (km^2)	Number of detections
Fall 2016	6	1	4	36.0	138.0	777
Spring 2017	8	5	7.4 ± 2.2 (3–15)	36.5 ± 9.5 (12.4–65.1)	140.7 ± 35.9 (46.4–239.3)	688.4 ± 134.3 (396–1002)
Fall 2017	28	22	6.0 ± 0.9 (1–15)	21.0 ± 5.3 (2.8–99.3)	88.3 ± 20.2 (11.5–386.1)	549.0 ± 139.4 (6–2380)

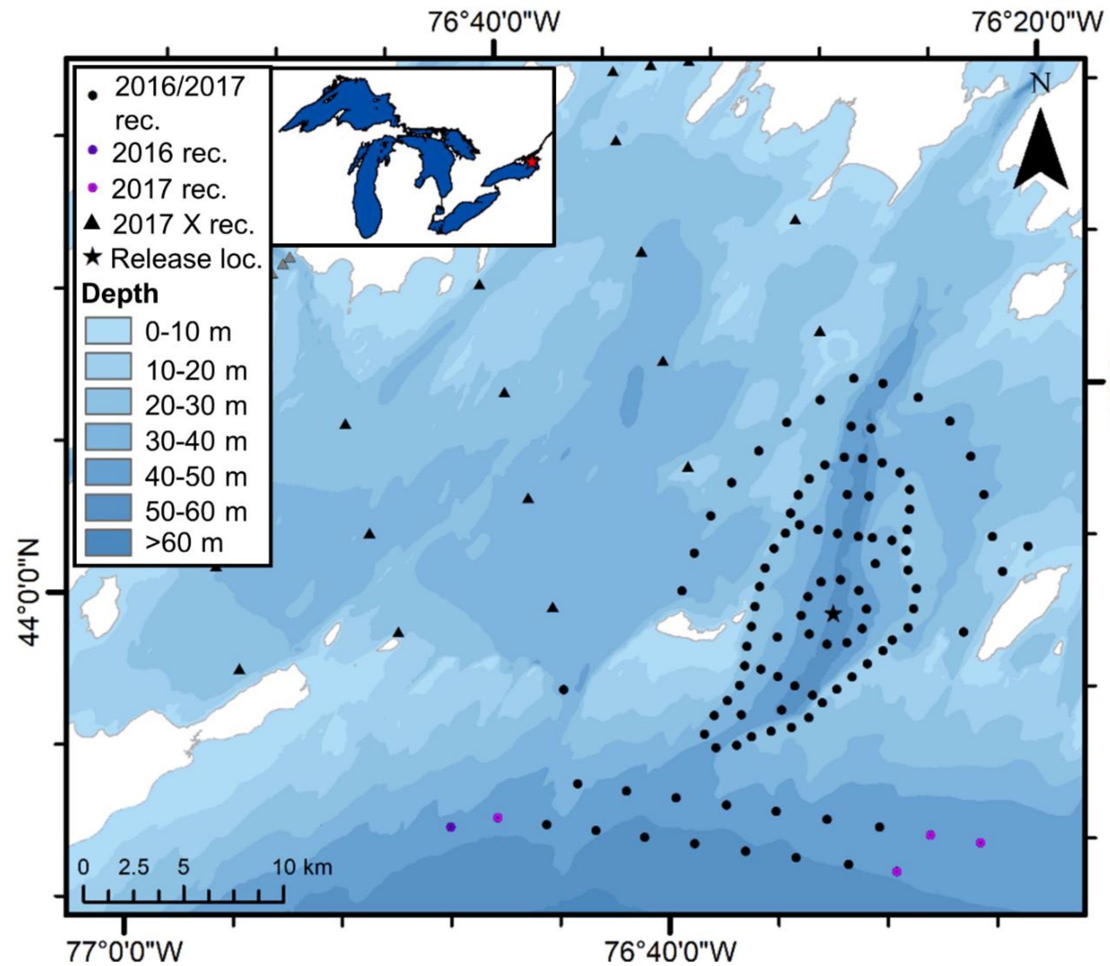

Figure 3.1 Bathymetry and location of receiver moorings in northeastern Lake Ontario. Red star in map inset illustrates location of the study site within the Laurentian Great Lakes. Black, purple, and pink circles signify receivers deployed throughout the entire study period, from June 2016 to June 2017, and from June 2017 onwards, respectively. Black triangles signify receivers from another telemetry study deployed in April 2017. Black star indicates the release location where all bloater were stocked.

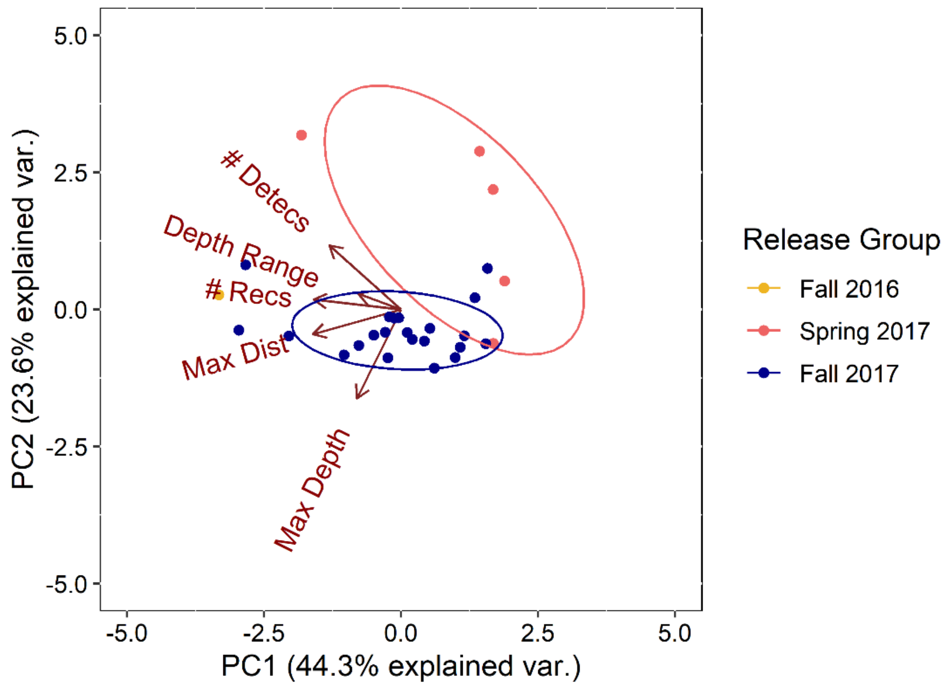

Figure 3.2 Principal component analysis output demonstrating individual variation of tagged bloater (*Coregonus hoyi*) relating to several detection metrics in the first 24 hours following release. PC1 (eigenvalue 2.22) and PC2 (eigenvalue 1.18) are presented (accounting for 67.9% of variation) and individuals are coloured by release group (ellipse to highlight grouping differences).

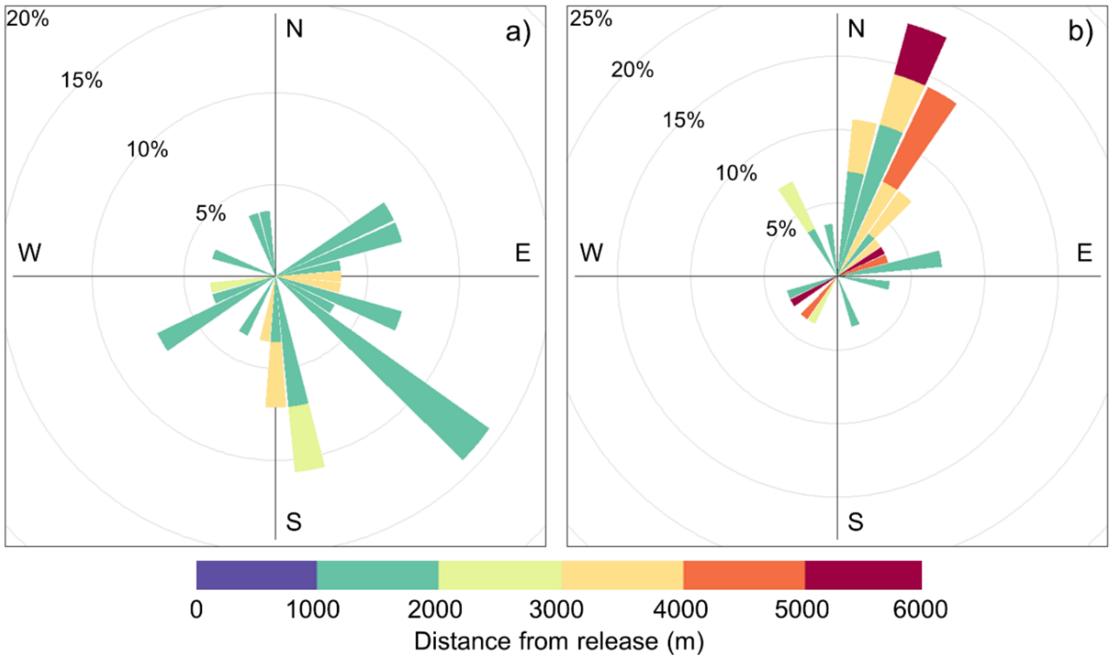

Figure 3.3 Distance and direction of movement of all live tagged bloater (*Coregonus hoyi*) (n = 28) for: (a) the first center of activity (COA) after release and (b) the last COA in the 24-hour period following release. Length of wedge corresponds to the number of individuals and percent contours indicate the percentage of the sample size that constitutes a wedge.

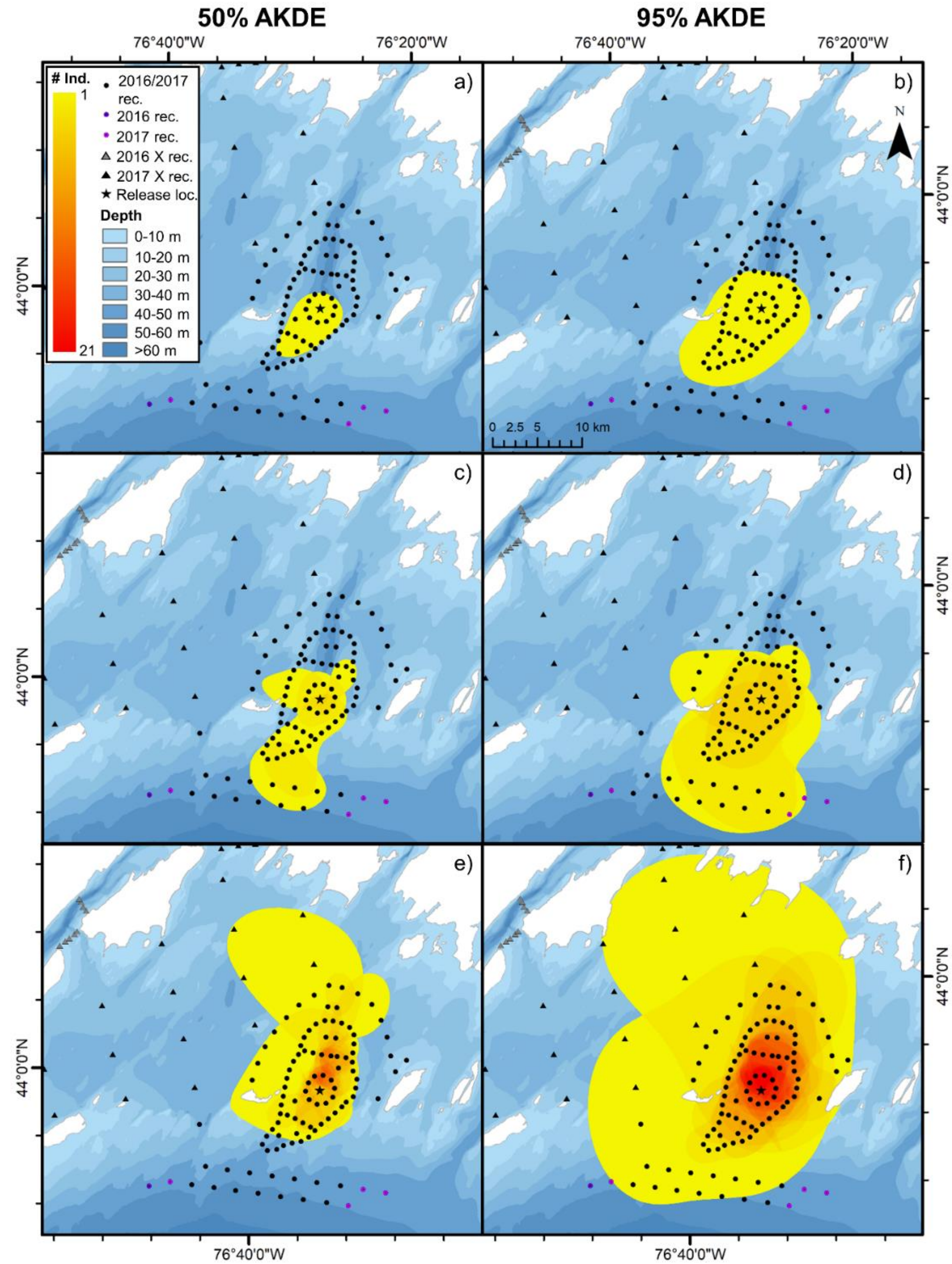

Figure 3.4 Overlapping horizontal autocorrelated kernel density estimates (AKDE) representing the core activity space (50%) and activity space extent (95%) of each tagged bloater (*Coregonus hoyi*) in northeastern Lake Ontario. Colour gradient signifies the number of individuals with overlapping activity space in a location. Activity space estimates are shown by release group and AKDE type; (a) 50% AKDE and (b) 95% AKDE for fall 2016 fish (n = 1); (c) 50% AKDE and (d) 95% AKDE for spring 2017 fish (n = 5); (e) 50% AKDE and (f) 95% AKDE for fall 2017 fish (n = 22). Black, purple, and pink circles signify receivers deployed throughout the entire study period, from June 2016 to June 2017, and from June 2017 onwards, respectively. Black and grey triangles signify receivers from another telemetry study deployed in April 2017 and in May 2016, respectively. Black star indicates the release location where all bloater were stocked.

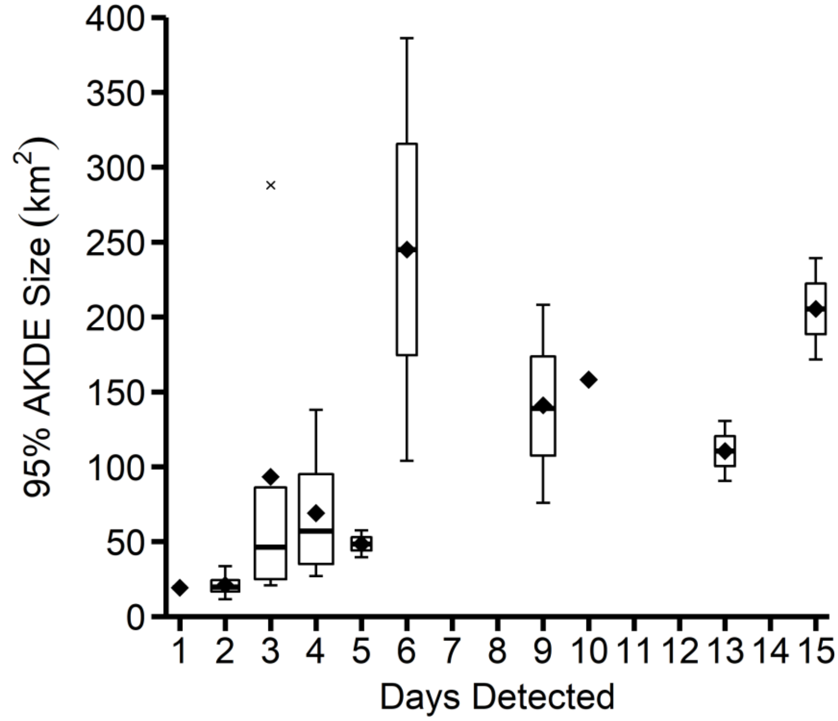

Figure 3.5 Effect of number of days detected on 95% autocorrelated kernel density estimate (AKDE) size of tagged bloater (*Coregonus hoyi*) from a linear model. Boxes are the 25th and 75th percentiles; whiskers represent 10th and 90th percentiles; solid midline indicates the median; diamond signifies the mean; and an x represents an outlier. Box widths are proportional to the square-roots of the number of observations in the groups.

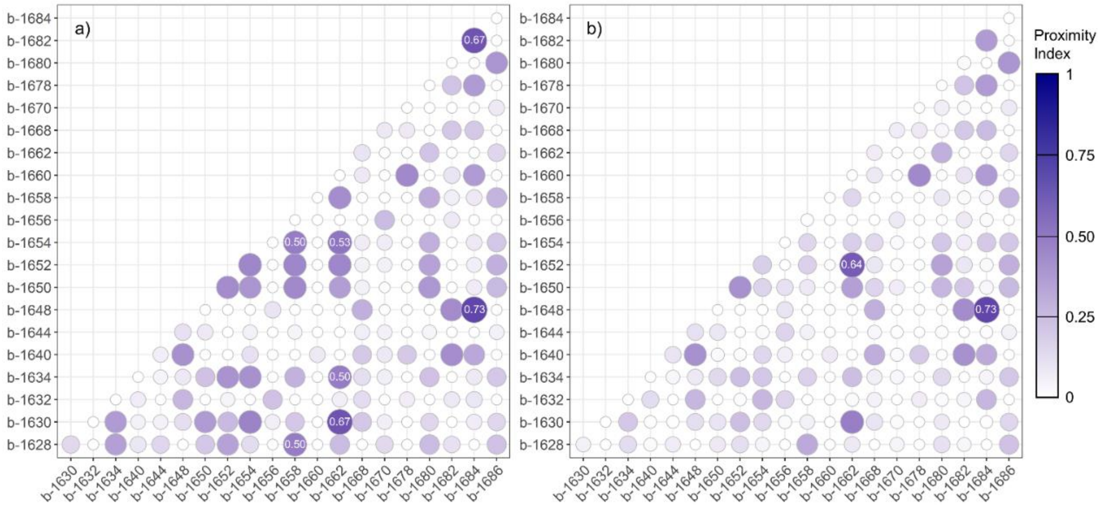

Figure 3.6 Correlograms illustrating the proximity index between each pair of tagged bloater (*Coregonus hoyi*) from the fall 2017 release group used in analysis (n = 21) for: (a) the first 24 hours following release and (b) the entire detection period of each fish. Individual fish IDs are listed along the axes. Circle colour and size correspond to the proximity index. Proximity index is written for pairs that have a proximity index ≥0.5.

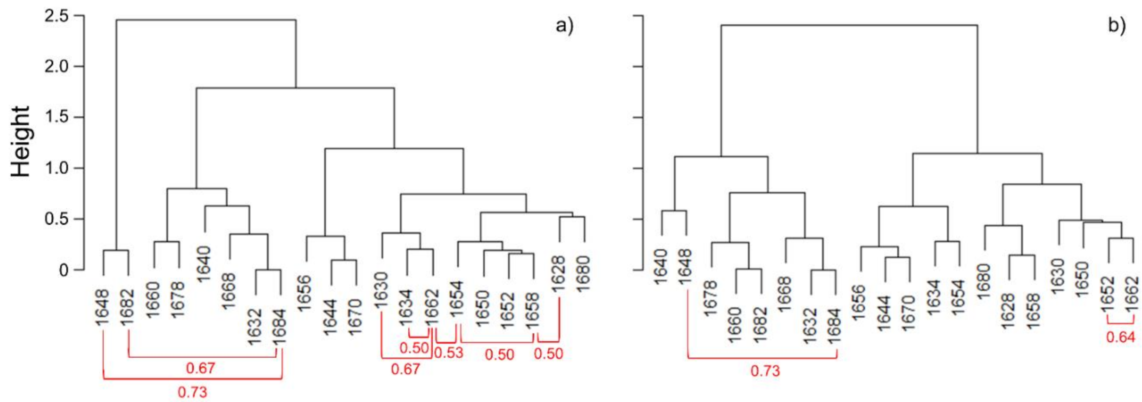

Figure 3.7 Dendrograms illustrating furthest neighbour clustering of proximity indices for each pair of tagged bloater (*Coregonus hoyi*) from the fall 2017 release group used in analysis (n = 21) for: (a) the first 24 hours following release and (b) the entire detection period of each fish. Red linkages and values signify pairs with proximity indices ≥0.5.

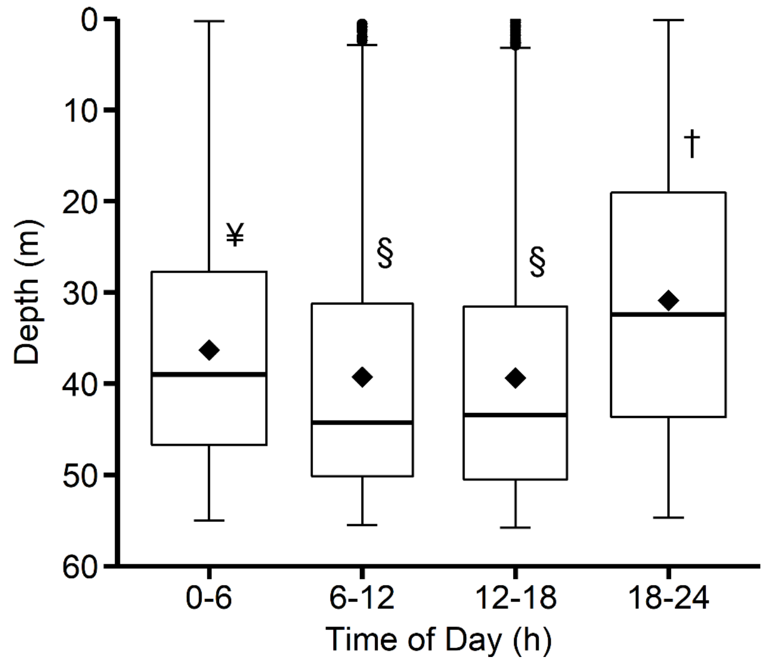

Figure 3.8 Significant effect of time of day on depth use of tagged bloater (*Coregonus hoyi*) from linear mixed effects model. Boxes are the 25th and 75th percentiles; whiskers represent 10th and 90th percentiles; solid midline indicates the median; and the diamond signifies the mean. Box widths are proportional to the square-roots of the number of observations in the groups and symbols above each plot represent statistically different time periods based on contrasts following the mixed effects model.

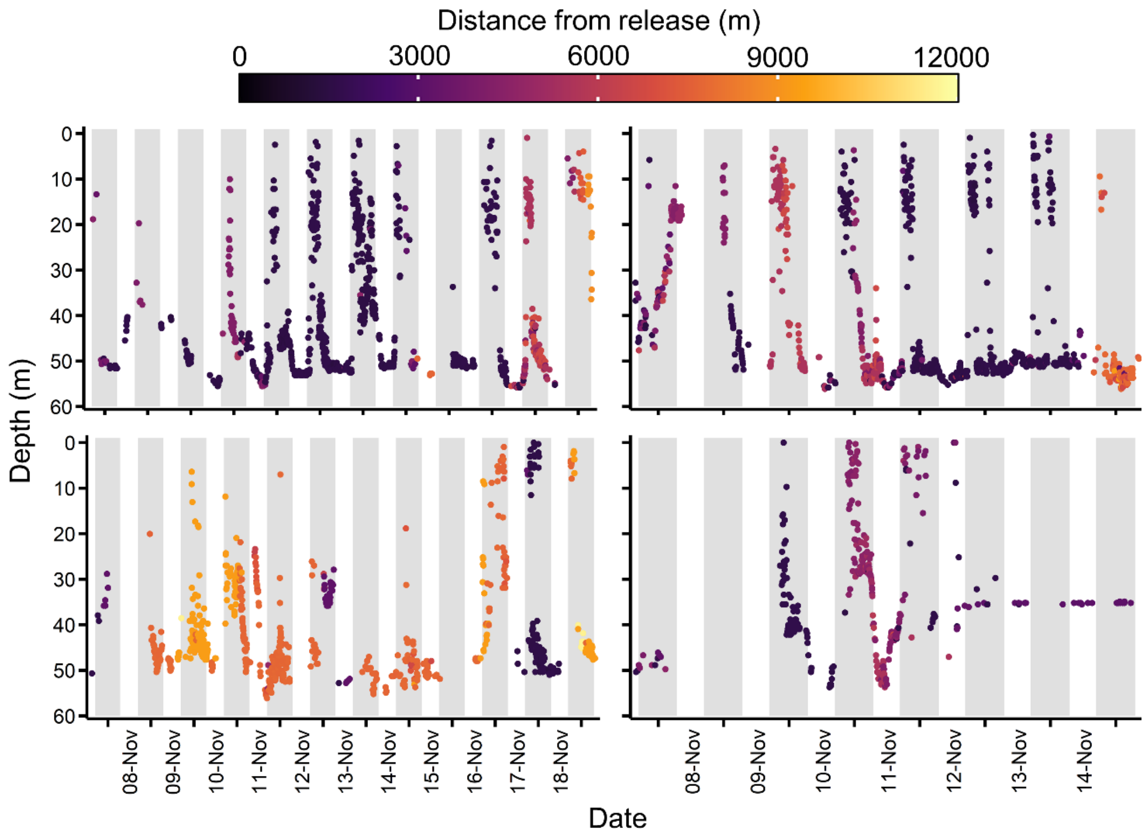

Figure 3.9 Depth profiles of four bloater (*Coregonus hoyi*) that were released and detected in November 2017 showing diel vertical migration (DVM) displayed by tagged individuals. Each circle represents a single detection and the colour of the circle corresponds to the distance from the release site (m) at time of detection. Grey shaded areas indicate night periods based on daily sunrise and sunset times.

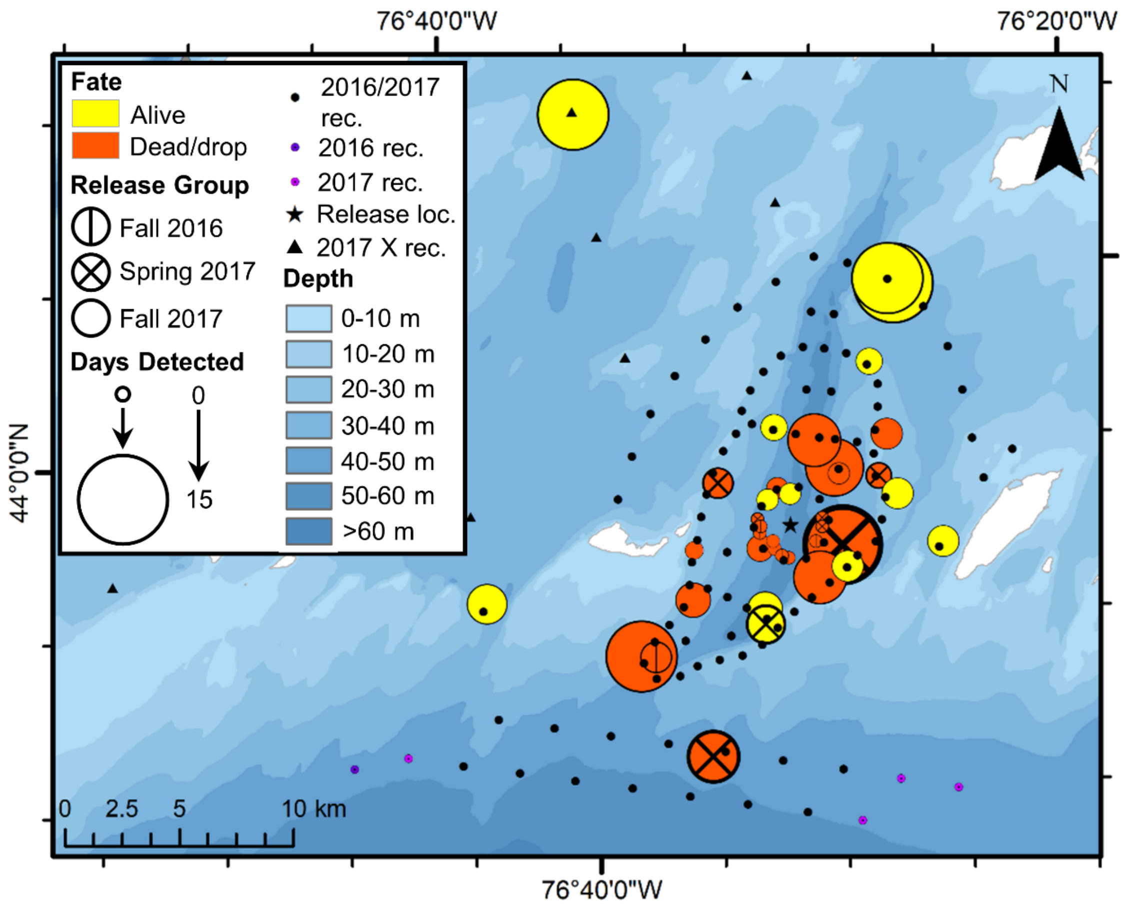

Figure 3.10 Fate of all tagged bloater (*Coregonus hoyi*) stocked and detected (*n* = 38) in northeastern Lake Ontario in fall 2016, spring 2017, and fall 2017. Yellow symbols signify the last center of activity (COA) for live fish whereas orange symbols signify the location of death for fish that were assessed as dead based on depth data. Symbol type denotes release group and symbol size corresponds to the number of days detected prior to last detection for live fish (yellow) and prior to death for dead fish (orange) with zero days indicating apparent death shortly after release (<1 hr) and day 1 corresponding to the date of release. Black, purple, and pink circles signify receivers deployed throughout the entire study period, from June 2016 to June 2017, and from June 2017 onwards, respectively. Black and grey triangles signify receivers from another telemetry study deployed in April 2017 and in May 2016, respectively. Black star indicates the release location where all bloater were stocked.

CHAPTER 4

GENERAL DISCUSSION

4.1 Summary

Fish stocking occurs worldwide in freshwater and marine systems to supplement naturally occurring wild populations, create recreational and commercial fishing opportunities, and re-establish extirpated species (Cowx 1994; Worm et al. 2009; Halpern et al. 2012). Despite the importance and prevalence of fish stocking today, challenges still exist in evaluating the success of stocking and determining what happens to fish post-release due to difficulty monitoring them. More than 20 million native and non-native fish species are stocked in the Great Lakes annually yet relatively little is known about the post-stocking ecology and fate of many of these species, especially forage fishes (Zimmerman and Krueger 2009; Mandrak and Cudmore 2010; Bunnell et al. 2014). Acoustic telemetry is a method of tracking that allows for passive continuous monitoring of tagged individuals and can provide insight into some of the unknowns of post-stocking fish ecology such as movement, behaviour, and survival (Hussey et al. 2015). Implementing acoustic telemetry in stocking programs throughout the Great Lakes provides a unique opportunity to contribute to our understanding of the fundamental ecology of Great Lakes fishes while also providing invaluable data to inform restoration management and fisheries practices.

The main objective of this thesis was to use acoustic telemetry to examine the post-stocking ecology of bloater (*Coregonus hoyi*) in Lake Ontario and provide information relevant to restoration stocking efforts. More specifically, my thesis entailed: (1) understanding the influence of dynamic environmental interactions on detection efficiency of acoustic transmitters in Lake Ontario, and (2) determining the movement and behaviour of acoustically tagged bloater following release into the lake. The first objective addressed the assumptions and limitations associated with the variable performance of telemetry in different environments and how biotic and abiotic factors impact detection efficiency, and was a necessary and important step for the second objective of my thesis. It is important to comprehend the relationship between detection efficiency and different factors in a telemetry study to understand the quality of information obtained, enable more accurate interpretation of telemetry data, and ultimately, to make stronger inferences about the ecology of the study organisms. Evaluating the performance of acoustic telemetry in Lake Ontario produces findings valuable to current and future telemetry studies in the Great Lakes and other large, deep, freshwater lakes. The second objective pertained to addressing knowledge gaps in bloater ecology and gaining insight into the immediate post-stocking movements of a reintroduced forage fish that is the focus of binational restoration efforts in the Great Lakes. Establishing a self-sustaining population of bloater will help restore fish native to Lake Ontario, thus increasing biodiversity, improving ecological integrity and resilience, and serving as a basis for the reintroduction and management of other native species throughout the Great Lakes (Favé and Turgeon 2008; Eshenroder et al. 2016).

In Chapter 2, I used an extensive telemetry dataset in a system that is underrepresented in acoustic telemetry to demonstrate that the probability of a receiver detecting a transmission from an acoustic tag in Lake Ontario varies both spatially and temporally and is influenced by environmental conditions. While many studies examine the effects of individual environmental variables and focus on quantifying these effects, in this chapter I illustrated the complex and dynamic relationship that exists between detection efficiency and the environment. Chapter 2 revealed a maximum detection distance of 9.3 km in Lake Ontario and a higher detection efficiency at greater tag-receiver distances than many previously published telemetry studies in marine environments where detection range is generally <1 km (e.g., Cagua et al. 2013; Hazel et al. 2013; Jossart et al. 2017). By comparing tags of different power outputs at different depths, I showed that shallower tags have a lower detection efficiency than deep tags of the same power output and that the effects of close proximity detection interference are variable across tag powers and depths. I also observed temporal variation in detection efficiency, which revealed winter months as a period of decreased detection relative to the fall and spring. I demonstrated that generalized additive mixed models provide many advantages over the variety of linear and non-linear models that are typically used in range studies to describe detection efficiency. Finally, although distance between the tag and receiver was the primary factor that influenced detection efficiency, I displayed the varying impact of each environmental variable on detection efficiency. Overall, this chapter demonstrated the complexities of understanding detection efficiency of acoustic telemetry in a heterogeneous freshwater environment.

In Chapter 3, I used data from 42 acoustically tagged bloater in Lake Ontario to reveal previously unobserved horizontal and vertical space use of bloater, provide preliminary estimates of post-stocking survival, and demonstrate the value of acoustic telemetry in stocking and restoration efforts. In this chapter, I used a variety of exploratory and statistical analyses to address different questions regarding the post-stocking ecology of bloater. I showed rapid dispersal of stocked bloater following release with a general preference for deeper waters and a high degree of overlap in horizontal space use, but no evidence of schooling behaviour. Chapter 3 also showed that bloater underwent extensive diel vertical migration (DVM) where bloater ascended nightly to much shallower depths than previously believed (TeWinkel and Fleischer 1999; Clemens and Crawford 2009). Finally, I provided preliminary estimates of the post-stocking survival of bloater and showed that while initial survival was low, survival of remaining individuals increased through time and suggested movement out of the receiver array and into other areas of the lake.

4.2 Conclusion

In this thesis, I used acoustic telemetry to address existing knowledge gaps in the ecology and post-stocking movement of bloater while also evaluating one of the main challenges encountered when conducting a telemetry study. Although range testing and implementing telemetry to study an organism were presented in separate chapters of my thesis, they are complementary because the quality of acoustic telemetry data and accuracy of the conclusions that can be drawn from these data rely heavily on the performance of telemetry in the study system. The detection efficiency and range estimates that I have produced in my thesis encompass various tag power outputs and depths in Lake Ontario and can be applied to telemetry studies throughout the Great Lakes and other large, freshwater lakes. Understanding the performance of acoustic telemetry in a specific environment is an important aspect of study design and determining spacing for receivers to achieve the desired resolution of detection data.

The high detection range and spatial and temporal variability in range that I observed in Lake Ontario have large implications for how telemetry data in the Great

Lakes are analyzed and the scale and accuracy at which we can draw conclusions. In addition to providing information useful for current and future telemetry studies in large, freshwater lakes, the results from my thesis reiterate the variable performance of acoustic telemetry in different environments and the value of performing range testing concurrent with animal studies. Here, I have demonstrated the value of retrospective range analysis to determine changes in detection efficiency and assess how range should be incorporated into analyses of detection data. Results from this range testing study were incorporated into the present analysis of bloater data and will further contribute to refining future analysis of data from bloater and other species in Lake Ontario that utilize this array (e.g., Chinook salmon (*Oncorhynchus tshawytscha*) and lake trout (*Salvelinus namaycush*)). In future analyses, the spatial and temporal changes in detection efficiency observed in this study will be used to inform the probability of detecting a fish at individual receivers through time.

Bloater and other deepwater ciscoes have never before been studied using acoustic telemetry. The continued development of telemetry technology and the miniaturization of tags in particular has permitted the tagging of smaller fishes. Successful use of telemetry on a forage fish that is notoriously susceptible to handling stress in this study has pushed the boundaries of telemetry applications and demonstrated the potential for further studies on bloater and similar species. The application of acoustic telemetry in this study permitted observation of more fine-scale movements than traditional monitoring methods, such as mark-recapture, hydroacoustic surveys, and using genetic markers to track stocked fish. Traditional monitoring methods often provide general location data that may be limited by sampling time, sampling location, or gear avoidance. Future reintroduction efforts could use acoustic telemetry in combination with more broad-scale monitoring methods to further inform on the survival, movement, and behaviour of reintroduced individuals.

The data presented here have corroborated pre-existing knowledge of bloater ecology, such as DVM, but have also expanded on this knowledge and provide evidence that suggests alternate conclusions from what was previously believed. The preference of bloater for deeper waters, rapid dispersal following release, and moderate survival are all valuable for informing future studies and management practices. Understanding the space use of stocked bloater is important for management agencies that aim to locate and quantify surviving individuals from stocking events and helps mitigate the effects of gear avoidance. The horizontal space use of bloater and how it changes throughout the year can inform what locations should be targeted during acoustic surveys and trawls while the vertical space use informs what depths should be targeted. For instance, since bloater tend to remain at depth during the day as part of their DVM, sampling that occurs during daylight hours should target deeper waters. Survival estimates derived from telemetry data can also aid in determining the number of bloater that are required to be stocked in order to provide a population large enough that individuals will reach sexual maturity and reproduce. Future studies on bloater using telemetry should focus on expanding coverage of the array into surrounding areas to acquire longer periods of detection data and determined long-term survival and behaviour to further inform management.

The behaviour of bloater that was observed in this study may also inform stocking practices, such as the method, location, and time at which stocking occurs. Diel vertical migration of bloater is thought to be driven by optimizing feeding, avoiding predation, or a combination of both. The preference of bloater for deeper water during daylight hours may indicate that stocking at night, when bloater are already often in shallow water and may be avoiding visual predators, may reduce the stress and vulnerability of bloater during stocking. The rapid mortality of several individuals following release could suggest that the stress associated with transport or stocking contributes to low survival. As a deepwater forage fish that is reared in a hatchery in shallow tanks and then stocked into a large lake, bloater may experience disorientation or difficulty acclimating to new depths and pressures, making them more vulnerable to predation. Alternate stocking methods, such as soft release in net pens, may provide bloater with the time necessary to acclimate to their new environment and increase survival following release (Brown and Day 2002).

The bloater observed in this study were reared in a hatchery and may not be representative of wild individuals. A challenge in understanding the ecology of a reintroduced species is the behavioural differences that may be present between hatchery raised and wild fish. It is assumed that gear avoidance is the primary reason for the differences in the ecology of bloater that has been observed in other Great Lakes and the bloater tagged and released in the present study. Although there may be challenges associated with the tagging of wild bloater as they must be brought to the surface for surgery, future studies are encouraged to tag wild caught bloater to facilitate a comparison between hatchery raised and wild fish to better inform management practices for both types of fish.

Although this research focused specifically on studying bloater in Lake Ontario, it has larger implications for the lake since bloater restoration contributes to improving ecological integrity and food web stability by restoring original energetic pathways. Re-establishing a population of bloater in Lake Ontario is important for the restoration of native top predators in the lake and reducing and controlling the impacts of non-native species. The successful use of telemetry to examine the post-stocking movement, behaviour, and survival of a reintroduced species in Lake Ontario can be used as a framework for other restoration studies in the Great Lakes and other systems.

In conclusion, this thesis presents novel information on bloater ecology that helps inform reintroduction practices, demonstrates the value of acoustic telemetry in restoration studies, and addresses one of the major assumptions associated with the performance of telemetry in different environments. The findings of this thesis are applicable to several different highly relevant areas of study and contribute to improving research in Great Lakes and the future of Lake Ontario.

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