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Quantifying survival and behaviour of hatchery-reared juvenile bloater stocked across bathymetric depths in Lake Ontario

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Quantifying survival and behaviour of hatchery-reared juvenile bloater stocked across bathymetric depths in Lake Ontario

By

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Quantifying survival and behaviour of hatchery-reared juvenile bloater (*Coregonus hoyi)* stocked across bathymetric depths in Lake Ontario

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ABSTRACT

Over 20 million native and non-native fishes are stocked into the Great Lakes annually as part of restoration initiatives and to support commercial and recreational fisheries. Bloater (Coregonus hoyi), a deep-water planktivore that was extirpated from Lake Ontario in the 1980s, has been consistently stocked in the lake since 2012 by Canadian and American natural resource agencies with the goal of producing a self-sustaining population. Previous research has highlighted challenges with stocking such as poor survival, attributed to high predation, potential maladaptive behaviour and barotrauma resulting from introducing a hatchery-reared species into a foreign environment. To address these survival challenges, bloater in this study were tagged with acoustic predation tags and stocked over three bathymetric depths in Lake Ontario (5, 50, and 100 m) to assess survival, behaviour, and to quantify sources of mortality at each depth. Coupling high resolution receivers (HR2) with predation tags permits fine-scale auto-estimation of predation-related mortality, in turn improving detailed survival estimates of stocked fish, specifically juveniles. Time-to-event modeling indicated a low survival rate (12%) in the first three-weeks post-stocking for individuals within the study area. Initial data suggested that predation played a dominant role in shallower depths, while mortality at deeper depths could be linked to barotrauma, although, no statistical differences were found in survival between the three depths. Relative position estimates demonstrated rapid dispersion of bloater post-release, with movement rates suggesting a tendency to migrate towards deeper waters. Continued investigation into the movement and predation of bloater post-release will be used to determine the survival of the stocked population. This enhanced understanding of the movement and mortality of stocked fish will play a crucial role in refining stocking strategies and assessing the overall restoration potential for bloater in Lake Ontario.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

GENERAL INTRODUCTION

1.1 Study System

The Laurentian Great Lakes are composed of five post-glacial lakes (Lakes Superior, Michigan, Huron, Erie, Ontario), forming the world's largest freshwater ecosystem (Magnuson et al. 1997, Weaver et al. 1997; Great Lakes Commission 2022). Over 40 million people are dependent on the Laurentian Great Lakes (*hereafter* Great Lakes) for water supply, recreational and commercial fisheries, essential inland shipping routes, and sustaining more than 1.5 million jobs, which highlights the important ecological and economic roles they play (Great Lakes Commission 2022). The multitude of connecting channels and lakes create a unique ecosystem to support a wide variety of plant and animal species, over 150 of which are fish (Manny et al. 1988; Landsman et al. 2011).

Lake Ontario, the 13th largest lake in the world, is 245 m deep with a surface area of 19,000km^2, yet it is the smallest by surface area of the five Great Lakes (Stewart et al. 2013). The biodiverse lake is home to over 120 fish species, including non-native top and meso-predators such as Chinook salmon (*Oncorhynchus tshawytscha*) and rainbow trout (*Oncorhynchus mykiss)*, and forage fish, alewife (*Alosa pseudoharengus*) and round goby (*Neogobius melanostomus*). The native top predators are Atlantic salmon (*Salmo salar*) and lake trout (*Salvelinus namaycush*), which are currently undergoing rehabilitation through stocking of hatchery-reared fishes (LOTC, 2022; Stewart et al. 2017). Additionally, the stocking of hatchery-reared juvenile bloater (*Coregonus hoyi)* has been an ongoing effort since 2012 with the aim of re-establishing the native species to the lake (Weidel et al. 2022).

1.2 Stocking of fish in the Great Lakes

Global stressors that have an influence on fish stocks include invasive species, overfishing, climate change, and overdevelopment (Cowx et al. 1994; Halpern et al. 2012; Ullah et al. 2018). These stressors can lead to dwindling fish populations, unstable ecosystems, and depleted food webs. Fish stocking is a global practice aimed to compensate for these stressors by supplementing naturally occurring populations, introducing non-native species for recreation or management, or re-establishing extirpated species (Pace et al. 1999; Cowx 1994). More than 20 million fish have been stocked annually into the Great Lakes since the late 20th century. As a result, fish stocking in the Great Lakes supports world-class recreational fisheries, aids in the restoration of native species, and maintains the ecological stability and integrity of the lakes (Zimmerman and Krueger 2009; Bunnell et al. 2014). Despite this long history, the fate of fishes post-release is largely unknown due to difficulty monitoring them. Mark-recapture, hydroacoustic surveys and netting data are methods that provide fundamental information on survival and movement but lack the fine scale tracking, behaviour and fate of fishes post-release. The development of various types of aquatic telemetry has allowed for new insights into animal movements and interactions post-release.

1.3 Deepwater coregonids in the Great Lakes

Deepwater coregonids have a rich history in the Great Lakes where they once played a vital ecological role (Bunnell et al. 2012). As forage fishes that migrate throughout the water column, they link deep benthic production with higher level piscivores, creating an energy rich connection within food webs (Fave & Turgeon 2008; Zimmerman & Kruger 2009). Prior to European settlement, each of the Great Lakes supported a complex assemblage of nearshore and offshore coregonids. There were a total of seven deepwater coregonid species (*C. hoyi, C.*

reighardi, C. alpenae, C. zenithicus, C. johannae, C. kiyi, C. nigrippinis) across all five lakes, each home to several taxa (Bunnell et al. 2012; Eshenroder et al. 2016). Early fisheries targeted the spring feeding migrations and autumn spawning migrations of the nearshore coregonids using beach seines (Eshenroder et al. 2016). However, as fishing expanded and the demand for coregonids grew, fishing efforts shifted towards harvesting the deep-water forms. The late 1800s marked the start of the deep-water coregonid fisheries, with a focus on the largest form, *C. reighardi* (Eshenroder et al. 2016). The high demand for deep-water coregonids and the expansion of fishing efforts contributed to the depletion of several coregonid populations by the late 1900s and many were eventually extirpated from the Great Lakes (Christie 1972; Owens et al. 2003). Today, most deep water coregonines have suffered local extirpations due to invasive species, habitat loss, and commercial exploitation (Anneville et al. 2015; Eshenroder et al. 2016). An exception to this is bloater which is currently extant in Lakes Huron, Michigan, and Superior.

1.4 Bloater Ecology

Bloater are a small (<30 cm) forage fish that typically inhabit deep waters and play a unique role in large, oligotrophic lakes, serving as prey for native piscivores, such as lake trout (Fratt et al. 1997; Weidel et al. 2021). Current knowledge of bloater within the Great Lakes is documented from Lakes Huron, Michigan and Superior with a major focus on their depth distribution and their physiological ability to exploit deep sections of large lakes (Hrabik et al. 2006; Jensen et al. 2006; Clemens and Crawford et al. 2009).

Historically, bloater were abundant in Lake Ontario until the 1950s, when their population experienced a significant decline, which was primarily attributed to overharvesting and the introduction of invasive species (rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*)) (Wells 1969; Christie 1974). The last bloater caught in bottom trawl surveys in Lake Ontario was in 1983, suggesting that the population had been extirpated (Christie 1972; Owens et al. 2003). Today, alewife dominate the community biomass and diets of most large piscivores in Lake Ontario, and alewife consumption has been linked to thiamine deficiency resulting in early mortality and negative impacts at multiple life stages of native salmonids, such as lake trout and Atlantic salmon (*Salmo salar)* (Brown et al. 2005; Honeyfield et al. 2005; Mumby et al. 2018; Futia et al. 2019). Although alewife serve as an alternative prey fish for piscivores, they are restricted to the meta- and epilimnetic layers during periods of thermal stratification (Adkinson and Morrison 2014), and thus cannot fully replace the ecological niche that bloater once occupied Research has utilized hydroacoustic and trawl surveys to identify and confirm the presence of bloater at specific depths, providing insights into their vertical space use (Hrabik et al. 2006; Clemens and Crawford 2009; Klinard et al. 2020). Telemetry studies found substantial predation on stocked fish (Klinard et al. 2020), suggesting restoration may be slowed by low post-release survival. Due to the lack of individual tracking following release, our understanding of the extent of initial survival of hatchery-reared juvenile bloater following stocking remains limited (Bunnell et al. 2023).

1.5 Bloater Restoration

The availability and abundance of bloater play a significant role in sustaining the health and vitality of higher trophic level species. Today, much of the impetus for restoration of native coregonines stems from the desire to restore native lake trout and Atlantic salmon (Weidel et al. 2022). Historically, lake trout and Atlantic salmon, amongst other predators, relied on bloater as a crucial energy source, contributing to their growth, reproduction, and overall population dynamics. The loss of bloater in Lake Ontario has resulted in a disruption of the natural trophic interactions and energy flow within the lake's food web (Christie 1973).

To address the loss of bloater and native prey fish community, a bi-national restoration effort has been established to restore a self-sustaining population, increase prey fish diversity, benefit the native predator restoration, and offer greater resilience to invasive species and a changing climate (Weidel et al. 2022). As a hatchery-reared, deep-water prey species, it is difficult to predict bloater survival after introduction into the recipient lake (Brown et al. 2002). Past bloater research has been limited to gillnet, bottom trawl, and hydroacoustic survey data with the last documented catch in 1983 (Owens et al. 2003). From the beginning of the restoration effort in 2012 until 2021, 1,028,191 bloater have been stocked into Lake Ontario (Great Lakes Fishery Commission 2022). In both the U.S. and Canada, bloater were stocked at surface over varying bathymetric depths. U.S. stocking locations were predominantly over ~100 m depths near Oswego, NY, but shallower stocking sites (~50 m depths) were selected in 2019. The Canadian stocking locations were more dispersed throughout the entire lake over depths of ~50m.

Since the restoration effort began, 10 bloater have been caught in bottom trawl surveys with the first caught in 2015 (Holden et al. 2021; Weidel et al. 2022). The depth of captured bloater was similar to that of historic depth distributions with the highest historic catch occurring in depths ranging between 55 and 110m (Pritchard et al. 1931; Stone 1947). In Lakes Superior and Huron bloater densities peak at the 50-90m depths suggesting deeper water preferences (Gorman et al. 2012; Riley and Adams 2010). Preferences for deeper water (>50m) may explain low survival and rapid movement of acoustically tagged fish (Klinard et al. 2020; Weidel et al. 2022).

The initial release of hatchery-raised fish into the wild is a well-known period of vulnerability, with most mortality attributed to predation during the first 48-hours (Brown and

Day 2002). Recent research using acoustic telemetry and hydroacoustics has shown that hatchery-raised bloater quickly descend to the lake bottom where >40% fail to move again, characteristic of mortality potentially associated with compression barotrauma (Klinard et al. 2020). This was demonstrated in Lake Ontario where acoustic telemetry studies reported 66% of hatchery-reared juvenile bloater died within the first 14 days post-release, with most mortalities occurring within the first two days; predation accounted for 81% of the observed mortalities (Klinard et al. 2020; Klinard et al. 2021). For hatchery-raised fish which have not experienced changes in water pressure prior to release, rapid compression could cause significant stress. An experimental study using a hyperbaric apparatus to test the impacts of pressure on hatchery-reared juvenile bloater, demonstrated significant negative effects of barotrauma at 5 m depth (0.5 atm), and greater than 20% mortality at a 50m depth (5 atm) (O'Gorman et al., *unpublished data)*. Thus, the current deep-water stocking practices intended to minimize predation effects on survival may be less effective than previously thought.

1.6 Acoustic telemetry

The movements and habitat uses of fishes influence the structure and function of aquatic ecosystems (Hussey et al. 2015). Technological advancements in telemetry have made it feasible to study movements and interactions of fish, and influence of the environment at fine and coarse spatial scales. (Cooke et al. 2004). Acoustic telemetry has long been established as a valuable approach to monitoring aquatic spatial and behavioural ecology (Hussey et al. 2015; Hellström et al. 2016), where individuals of aquatic species are externally or internally equipped (*hereafter* tagged) with transmitter devices (*hereafter* tags). Tags can be programmed to emit data-encoded soundwaves at different frequencies (e.g., Innovasea's 69, 180, or 307 kHz) that contain unique identification codes for each individual tagged. Receivers of the same frequency detect the transmitted signals, decode, timestamp, and log the transmissions until retrieval (Kessel et al. 2014). The receivers are strategically moored throughout the study area either in a gated array to detect tagged fish swimming by or in a gridded array to quantify the time a tagged fish remains in a certain area (Cooke et al. 2013). Passive acoustic telemetry is a common tracking method as it allows for minimal disturbance to the study site, multiple individuals can be tracked simultaneously, and data can be collected for long periods of time given transmitters and receivers are active and individuals are within detection range (Kessel et al. 2014; Hussey et al. 2015).

Identifying predation of tagged individuals is key for properly assessing acoustic telemetry data. There are a variety of acoustic transmitters that contain sensors that measure physical parameters, including temperature and depth or can detect biological events, predation of a tagged prey fish (Halfyard et al. 2017) or acceleration to aid in data interpretation. The transmitters used in this study are predation transmitters (hereafter predation tags) V5D-180 kHz (estimated battery life of 45 days; 12.7mm x 5.6mm; 0.68g in air) from Innovasea (Bedford, Nova Scotia, Canada). To detect a predation event, these tags have a small magnet covered in a calcium carbonate resin (i.e., a biopolymer) which relies on the acidic conditions of a predator's stomach for digestion. Once the biopolymer is digested, the magnet is released triggering an internal sensor to change the transmitter's identification code (Halfyard et al. 2017; Weinz et al. 2020). The predator will continue to be detected until the tag is expelled from the digestive tract (~6 hours) or until the tag reaches its battery life (Halfyard et al. 2017; Klinard et al. 2019). There is a delay between predator consumption and transmitter identification switch, however these transmitters allow for identification of alive and deceased detections of the tagged individual (Lennox et al. 2021; Halfyard et al. 2017; Weinz et al. 2020).

1.7 Thesis Objectives

There is a need to better understand the sources of mortality to stocked bloater in the Great Lakes, specifically in the initial phase following release. The goal of this thesis is to quantify sources of mortality and behaviour of hatchery-reared juvenile stocked bloater across bathymetric depths in Lake Ontario using acoustic telemetry. The objectives of my research are to: i) quantify the post-release survival rate of hatchery-reared bloater stocked across three bathymetric depths (5, 50, 100m); and ii) quantify behaviour and movement of bloater post-release, and iii) quantify sources of mortality post-release. To address these objectives, acoustically tagged, hatchery-reared juvenile bloater will be stocked at three bathymetric depths (5, 50, and 100 m) in Lake Ontario to determine if mortality is associated with depth of release or predation. Bloater behaviour will also be assessed to provide insights into depth choices (i.e., do bloater released at shallower depths move towards deeper water?). This study will contribute to our fundamental knowledge of bloater stocking behaviour and survival post-release into a Great Lake. Determining the sources of mortality and quantifying behaviour post-release will inform the restoration project and assist in broad scale fishery management decisions regarding the stocking of coregonines in the Great Lakes.

More specifically, my research chapter utilizes fine-scale acoustic telemetry and time-to-event analysis to estimate survival of hatchery-reared bloater in eastern Lake Ontario. Specifically, I aim to examine the initial post-release survival, predation, and possible barotrauma of hatchery-reared bloater stocked at three depths in Lake Ontario using acoustic transmitters with predation sensors. Stocked fish sometimes exhibit high initial mortality (>50%) associated with maladaptation to a new environment (Aprahamien et al., 2004). As the fish are to be released at surface, over three varying bathymetric depths, I predict high initial natural mortality at the deeper sites due to compression barotrauma as bloater are typically released over deeper water characteristic of their wild distribution. Given the preference of bloater for deep, colder water, I predict that fish released into shallow water will disperse toward deeper water but demonstrate less compression related altered behaviour. Finally, I predict that the fish stocked at shallow depth will experience higher predation than deeper stocked fish.

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CHAPTER 2

Quantifying survival and behaviour of hatchery-reared juvenile bloater (*Coregonus hoyi*) stocked across bathymetric depths in Lake Ontario

2.1 Introduction

Global stressors affecting fish stocks include climate change, overfishing, invasive species, and urbanization, which can lead to diminished food webs and unstable ecosystems (Cowx et al. 1994; Halpern et al. 2012; Ullah et al. 2018). Fish stocking, the addition of hatchery fish to an ecosystem, is a global practice to supplement declining or low natural populations, introduce non-native species for recreation or management, or for re-establishing extirpated species (Pace et al. 1999; Cowx 1994). Fish stocking in the Laurentian Great Lakes (hereafter Great Lakes) has occurred since the 1800s, and today, more than 20 million fishes are stocked annually to supplement valuable commercial and recreational fisheries and to mitigate ongoing ecological changes (Todd 1986; Zimmerman and Krueger 2009; Bunnell et al. 2014). Despite this long history of fish stocking, identifying the fate of fishes post-release is poorly quantified due to difficulty monitoring them until they get to an age and size vulnerable to capture gears. Little to no information is available in the period after release, which is a vulnerable period associated with high mortality (Brown and Day 2002). Indeed, recent work in Lake Ontario has shown high mortality in the first 14 days after release of bloater (*Coregonus hoyi*), which has been attributed to predation and unknown stress (Klinard et al. 2020). Mark-recapture, hydroacoustic surveys and netting data are common methods that provide initial information on survival and movement but lack the fine scale tracking, behaviour and fate of fishes post-release, particularly for smaller bodied species preyed upon by larger piscivores.

Bloater (*Coregonus hoyi*), a small bodied coregonid native to the Great Lakes, is an important prey species that has and does support commercial fisheries. In Lake Ontario, bloater were one of several coregonid species that supported commercial fisheries in the early 20th century (Eshenroder et al. 2016). Their extirpation resulted in a disruption of the natural trophic interactions and energy flow within the lake's food web. Today, alewife are the dominant prey species of piscivores in Lake Ontario (Brandt 1986; Mumby et al. 2018). Bloater would provide native top predators (e.g., lake trout and Atlantic salmon) a prey fish alternative to alewife, as alewife have high thiaminase activity, a thiamine-degrading enzyme linked to reproduction deficiencies in salmonines (Ketola et al., 2000; Honeyfield et al., 2005; Futia et al. 2019). To address the loss of bloater, Ontario and American natural resource agencies have partnered to restore self-sustaining populations of bloater through stocking of juveniles, with a goal of increasing prey fish diversity for the benefit of native predator populations and offering greater resilience to the negative impacts of invasive species and a changing climate (Weidel et al. 2021; Stewart et al. 2017; Baldwin 1999).

Acoustic telemetry is a technology well suited to inform bloater restoration. Small transmitters can be surgically implanted into hatchery reared bloater and other small fishes with negligible effects on survival and behaviour (Klinard et al. 2018; Gatch et al. 2022; Gorsky & Sweka *unpublished data*). Specialized acoustic transmitters can identify habitat use (e.g., depth, temperature occupied), behaviour (e.g., accelerometers), and quantify and differentiate sources of mortality (Klinard et al. 2020; Villegas-Rios et al. 2020). High residence (HR) receivers have made it possible to release large numbers of acoustically tagged fish in a small area while maintaining maximal detection efficiency for a short period of time. Identifying predation of tagged individuals is key for properly assessing acoustic telemetry data. Predation tags contain a biopolymer that dissolves in the stomach of a predator which results in a change in transmission ID that can be subsequently decoded by receivers. Coupling tags with predation sensors with HR-180 kHz high residence systems permits fine-scale auto-estimation of predation-related mortality, in turn improving survival estimates of stocked fish, specifically juveniles (Halfyard et al. 2017; Lennox et al. 2017). Acoustic telemetry networks (e.g. GLATOS, Krueger et al. 2017) have greatly increased collaboration, making it feasible to study movements and interactions of fish and the influence of the environment at fine and coarse spatial scales across the Great Lakes (Marsden et al. 2016; Krueger et al. 2017).

The initial release of hatchery-raised fish into the wild is a well-known period of vulnerability, with high mortality, particularly predation, occurring in the first days after release (Brown and Day 2002). Offshore stocking practices are believed to increase survival of stocked fish given the lower density of predators (Lantry et al. 2011), however, in Lake Ontario, recent acoustic telemetry studies showed that 66% of juvenile bloater died within the first 14 days after release, most within the first two days, and 81% of the mortalities were associated with predation (Klinard et al 2020; Klinard et al. 2021). Many bloater were also observed to swim quickly to the bottom with limited subsequent movement, suggesting a maladaptation to the environment they are released into (Klinard et al. 2020). Subsequent experiments with hatchery-raised bloater using a hyperbaric apparatus showed significant negative impacts of compression barotrauma on bloater behavior at 0.5 atm (5 m depth) and > 20% mortality at 5 atm (50 m depth) (O'Gorman et al., *unpublished data)*. Thus, the presumed advantages of deep offshore release of stocked fish to minimize predation may be less effective than thought (Lantry et al. 2011).

There is a need to better understand and quantify the sources of mortality in stocked bloater, and other fish, in the Great Lakes, specifically in the initial phase following release. To address this, acoustically tagged, hatchery-reared juvenile bloater at relevant stocking-sizes (~11-25 g) were released over three bathymetric depths (5, 50, and 100 m) in Lake Ontario to quantify survival and assess potential sources of mortality associated with depth of release or predation, or both. These chosen sites are located within the same area where New York State Department of Environmental Conservation (NYSDEC) stocks bloater which will allow mark-recapture modelling to be applied to multiple detections of individual fish to estimate survival, behaviour, and predation. This depth range likely provides a gradient for assessing predation and barotrauma related mortalities. The shallow depth (5 m) will minimize barotrauma effects while maximizing predation (*cf* Lantry et al. 2011), the centre depth (50 m) reflects the approximate release depth of stocked bloater with a mix of predation and barotrauma, while the deepest depth (100 m) encompasses the current release depth of stocked bloater that minimizes predation and maximizes potential barotrauma. Bloater behaviour will also be assessed to provide insights into depth choices (i.e., do bloater released at shallower depths move towards deeper water?). By addressing stocking depths and predation, this project directly addresses the key management action (i.e., stocking) used to restore extirpated populations and maintain predator-prey balances, assuming stocked fish survive to contribute to fisheries and/or survive to support natural reproduction. Smaller acoustic telemetry tags and systems (V5D tags; 180 kHz) are used to determine sources of mortality and quantify behaviour post-release to inform the restoration potential and assist in broad scale fishery management decisions regarding stocking of coregonines in the Great Lakes.

2.2 Methods

Study site and acoustic receiver array

The study was conducted in the southeastern basin of Lake Ontario near the Port of Oswego (43.482863, -76.582074) (Fig. 1). The study site is a bathymetric feature that sees depth increasing from 5m to 100 m within 10 km of shore, offers habitats that bloater would favour (i.e., depths > 50m), and is a traditional stocking site for production bloater and other species in US waters of the lake. An array of 108 acoustic receivers (66 VR2W-180 kHz and 42 HR2-180 kHz, Innovasea, Bedford, Nova Scotia, Canada) was deployed in April of 2022 and tagged juvenile bloater were released May 10, 2022. Receivers form a larger rectangle (~9 km^2) extending about 9 km offshore with stocked fish released in the middle of depth specific triangles (Figure 2.1.). The receiver array contained 42 HR2 receivers in the center of the array to ensure high certainty of detecting the initial stocking and movements of bloater post-release at a fine scale. An additional 66 VR2W receivers were spaced around the central HR2's to extend the array as well as to detect movements into shallower or deeper water. High residency acoustic receivers operate at 180 kHz and decode transmissions of both traditional Pulse Position Modulation (PPM) and High Residence (HR) transmission coding systems. The traditional PPM transmission transmits a series of 8-10 pulses and each series represents the tag's unique identification code. PPM transmission generally require 3-5 seconds to transmit where all pulses must be heard to generate a detection on the receiver, followed by a signal delay period of 30 seconds to 3 minutes to allow for surrounding tags to transmit. With a longer transmission period, PPM transmissions are susceptible to signal collisions and tag delay. Alternatively, HR transmission require a few milliseconds to transmit, greatly reducing potential signal collisions and allow for shorter tag delays as well as many more tags to be released into a study system. The HR2 receivers were spaced at ~500m and the VR2W receivers were spaced at ~750 m apart. This dense array ensures numerous detections to record fine-scale movements upon initial release as well as detect predation events as instantaneously as possible. Receivers were moored approximately 1 m off lake bottom within cement rounds, and consisted of a short piece of rebar affixed to a cement base and where the receivers were attached (either one VR2W-180 kHz or HR2-180 kHz and one VR2W-69kHz or VR2AR-69 kHz; the 69 kHz receivers provided information for separate studies).

Bloater tagging and stocking

To monitor the movements of juvenile bloater, 120 juvenile bloater (113-148 mm total length) reared in captivity at the U.S Fish and Wildlife, Northeast Fishery Center (Lamar, Pennsylvania) were surgically implanted with acoustic tags on April 20th and 21st, 2022. Individuals were held in a hatchery rearing tank containing ~1,800 age-1 (yearling) bloater, reared from the Lake Michigan (Blo-Lm strain). We had to select the larger individuals of the general population to ensure tagging survival. For tag insertion, fish were anesthetized in a buffered solution of tricane methanesulfonate: sodium bicarbonate (MS-222:$NaHCO_3$; 0.4g/0.8g) for 90 – 120 s to reach stage III anesthesia (Summerfelt and Smith 1990). Wet mass was recorded to the nearest 1 g and total length was recorded to the nearest 1 mm, and anesthetized bloater were placed into a cradle with their gills irrigated with hatchery water. An incision of ~10 mm in length was made adjacent to the linea alba and a V5D-180 kHz transmitter (5.8 mm width, 12 mm length, wt. in water = 0.38 g, power output = 143 dB, nominal delay 5/30 sec for HR/PPM, est. 95% battery life, Innovasea, Bedford, NS, Canada) equipped with a predation sensor was inserted into the coelomic cavity. Acoustic tags were programmed to transmit signals at 180 kHz in random intervals from 3 s (HR) to180 s (PPM) and operate for up to 31 days. The incision was closed with a single interrupted suture (Sharpoint polydioxanone monofilament antibacterial suture, size 5-0) tied with a 2-1-1-1 surgeon’s knot. All surgical equipment was disinfected in a diluted chlorohexidine solution prior to each surgery. Surgical procedures lasted 95 - 105 s from the time the fish was placed in the cradle to time of placement in recovery tank.

Following surgery tagged bloater were sequentially placed in three quarantined holding tanks (n = 40 per tank) separate from untagged juvenile bloater and monitored for signs of post-surgery stress and mortality. After 14 days, all 120 bloater retained the tags, had resumed normal feeding behaviour, and appeared visibly healthy. Sutures were removed following a14-day recovery period as rapidly growing juveniles tend to tear sutures prior to healing, causing injury, additional stress, and or mortality (Sweka and Gorksy, *unpublished data*).

On May 10, 2022, bloater were transported ~364 km from the fish hatchery to Oswego, NY, in hatchery transport vehicles equipped with aeration tanks, along with ~19,000 conspecifics. Upon arrival, bloater were hand-netted off the transport truck into holding tanks on a vessel equipped with aeration device, and were released mid-day offshore over the three bathymetric depth treatments. At each stocking site, bloater were released first at 100 m (n=40), then 50 m (n=40) and 5 m (n=39; one tagged fish died in transit and was not released), along with ~6,300 conspecifics by hand-netting for surface release. Acoustic receivers were retrieved in late August 2022 and detection data were uploaded to the GLATOS database.

Data Analysis

The first step in the statistical analysis was to identify dead fish, which was performed by visual assessment of detection histories for each individual, with the portion of data that was assessed as dead removed. Instances of mortality were identified during exploratory analysis by visual assessment of horizontal movement and predation sensors, with the portion of data assessed as dead removed. An individual bloater that was continuously detected on a single receiver (or neighbouring receivers due to proximity) for the entire study duration without movement within the array was interpreted as a mortality. Cessation of bloater detections from the array were recorded as emigration and not mortality because individuals could still be alive but in areas of the lake without 180 kHz receiver coverage.

Of the 119 fish stocked, a total of 12 individuals were removed from analyses because their transmitters had reported a false positive predation event, i.e., the predation tag switched to the predation ID before the fish were released. Individuals that had emigrated the array or were suspected of avian predation were censored at their last known detection as having an unknown fate. Censoring of individuals refers to an incomplete observation time and occurs for one of two reasons: 1) they migrated out of the study area or 2) they were no longer located within the array but also not confirmed dead (e.g., suspected avian predation). In both cases, the time of censoring was the date on which the last location was made in the array. To account for the suspected avian predation events, the survival analysis was run two ways to give the best representation of the overall survival. First, individuals suspected of avian predation were given a censored fate, and second, they were included as dead at the time of suspected avian predation.

For all statistical analyses, only detections of individuals that were considered alive at the time of detection were included and were completed in R version 4.2.2 (R Core Team 2023) and statistical significance was set at $\alpha \leq 0.05$.

Survival Analysis

Kaplan-Meier survivorship functions were estimated for each depth separately to assess if there was a difference in rate of mortality over time when comparing the three stocking depths. The Survival, SurvMiner, and KMsurv packages in R (version 4.2.2) were used to calculate the Kaplan-Meier survivorship function (Kaplan and Meier 1958; Pollock et al. 1989a; Krebs 1994) to determine the survival of bloater over the entire study period and the first 12- and 24-hours post-stocking. The Kaplan-Meier survivorship function calculates the likelihood that an individual will survive for t units of time after the study's start using:

$$\hat{S}_t = \prod_{i:\ t_i \le t} \left(1 - \frac{d_i}{n_i}\right) \quad (1).$$

And variation around the estimate was quantifying using:

$$\widehat{\mathrm{Var}}\left(\widehat{S}(t)\right) = \widehat{S}(t)^2 \sum_{i:\ t_i \le t} \frac{d_i}{n_i(n_i - d_i)} \quad (2).$$

Where $\hat{S}_t$ is the survival probability over time period t, d_i is the number of deaths recorded at time i, and n_i is the number of individuals alive and at risk of death at time i. The Kaplan-Meier survival function allows for censorship of individuals that have an unknown fate, allows for a staggered entry design, and does not assume distribution of data, unlike the alternative parametric Weibull and Exponential survival models (Zhang 2018; Friedman 1982). A Cox proportional hazards model was used to test the effects of covariates on bloater survival (Cox1972; Pollock et al.1989b). The instantaneous rate of death conditional on survival time is the hazard function using:

$$h(t|z) = h_0(t)\exp\{\beta' z\},$$

where $h_0(t)$ is the baseline hazard, z is the covariate vector, and β' is a vector of parameter. The survival data of all treatment depths combined was first analyzed and a Cox proportional hazards model was used to determine if there was a difference in survival among depths. Cox proportional hazards models were then used to determine if the covariates of treatment depth, fish size (weight, 11.0 - 23.0 g), and movement rates influenced survival. Hazard models were evaluated for each covariate independently. A Shapiro-Wilk test was used to assess normality of data and Kruskal-Wallis was used to determine differences among bloater implanted with acoustic transmitters in terms of treatment depth (5, 50, and 100 m) and size. Importantly, the survival analysis is limited to individuals remaining within the study area. Upon emigration from the array, the number of individuals included in the survival analysis decreases therefore limiting the overall survival of stocked bloater.

Dispersal and Behaviour

To determine dates of dispersal from the array and estimate mortality rates of tagged juvenile bloater, detections were false filtered using custom scripts based on location to determine where and when bloater were detected. A Spearman's rank-order correlation test (r_s) was used to determine whether bloater size and emigration date were correlated, with bloater total length and emigration day (i.e., hour since stocking) as model variables. Spearman's rank-order correlation test was used as the data did not meet assumptions (normality of residuals) for a parametric correlation test (e.g., Pearson product moment test).

The total distance traveled for each fish was measured for the entire study period post-stocking to describe the spatial patterns of bloater movement within the array. To more accurately measure distance travelled, a center of activity (COA) was calculated when individual transmitters were detected by multiple receivers. Location was approximated from the acoustic tag detections of each individual using centers of activity (hereafter, 'CoA'; Simpfendorfer et al. 2002) at three intervals, 10-min, 15-min, and 20-min (i.e., the 'average' position based on all receiver detections within each 10-min period). The 10-min timestep was selected as it would ensure a sufficient amount of detection data were incorporated to maximize movement over time of individuals with short detections histories and it most accurately reflected movement rates of bloater in the wild. For the 10-min timestep, COAs were calculated two ways, first utilizing all HR detections, and second, utilizing all PPM detections. Due to the greater number of detections for HR than PPM, COAs were calculated separately to avoid HR detections biasing position estimates. The total distance traveled within a timestep was calculated by summing all distance measurements on receivers (VR2W and HR2 separately) within the determined timestep for an individual bloater. Notably, the distance traveled is not the distance from the stocking site, rather the distance between two COAs. Relative movement rates were calculated based on the COAs by summing the total distance traveled (km) for each bloater detected in the array for their individual detection histories. A non-parametric Kruskal-Wallis was used to determine whether the average total distance traveled by bloater were different between the three depth treatments. Relative movement rates were calculated for each individual on both PPM and HR array and were compared across depths. The relative movement rates on HR were log-transformed to represent a normal distribution to meet the assumptions of a one-way analysis of variance (ANOVA) given the large inter-individual variances in movement rate. If significant, a Tukey *post hoc* test was computed to compare pairs of depth treatments.

2.3 Results

The size of the tagged juvenile bloater was 127.0 ± 7.4 (mean ± 1 S.D.) mm in total length and 14.7 ± 2.7 g in wet weight, and the tag mass: fish mass ratio ranged from 1.6 – 3.4% (2.67% ± 0.44; mean ±1 S.D.) (Table 1). There were no tagging mortalities. None of these variables were significant between stocking depths (length: ANOVA; $F_{(2, 104)} = 2.23$, $p = 0.11$; weight: $\chi^2 = 0.53$, df = 2, $p = 0.76$; tag:fish ratio: ANOVA; $F_{(2, 104)} = 0.54$, $p = 0.5$).

Detection summary

Of the 119 total stocked individuals, twelve were removed due to the false predation switch. The remaining 107 tagged bloater were detected following release into southeastern Lake

Ontario, producing 568,654 detections from May 10 – June 6, 2022, of which 558,940 were HR and 9,714 were VR2W detections (Figure 2.4). The 107 individuals had a mean of 4,788 ± 7,538 (mean ± 1 S.D.) detections each (HR and VR2W combined), ranging from 149 to 58,888, and were detected for a mean of 25.3 ± 66.8 hours, ranging from 0.9 – 611.7 hours. A total of 19 predation events, i.e., the transmission signal of the tag switched to predation identification, were detected (17.7% of tagged bloater, Table 2.1) between 1.5- and 130-hours post-stocking. Predation rates between depth treatments varied significantly (ANOVA; $F_{(3,107)} = 4.67$, $p = 0.01$), with the 5 and 50 m treatments combined accounting for 18 of the 19 predation events. Of the 35 tagged individuals stocked at the 5 m depth, 28.6% (n = 10/35) were predated within 6 days following release, with majority (63%) of events occurring within the first 2 days (Figure 2.4). From the total 19 predation events, 18 had predators detected in the array for hours to days following predation.

Survival Analysis

Total cumulative post-stocking mortality over the 27 days of detections was determined to be 36.4%. All 107 fish detected were included in the survival analysis but was limited to each individual remaining within the array. For the first survival analysis, a total of 68 individuals were censored: 24 from the 5 m, 21 from the 50 m, and 23 from the 100 m treatment groups. These 68 censored individuals did not signal predation and are presumed to have emigrated from the array or had an unconfirmed fate. A total of 39 individuals (36.4%) were interpreted to have died, i.e., 11 from the 5 m treatment group, 15 from the 50 m treatment group, and 13 from the 100 m treatment group. The two deeper depths, 50 and 100 m, had the highest number of interpreted mortalities within the first four-hours following stocking (n = 7 and n = 8 respectively) compared to the 5 m treatment (n = 4) (Figure 2.2b). The highest number of mortalities for the 50 and 100 m treatment depths occurred within the first eight-hours following stocking, while the 5 m treatment depth had fewer initial mortalities with most occurring after twelve-hours after release. For the second survival analysis, the 18 individuals that were suspected of being avian predated were interpreted to have died, totaling 57 mortality events (53%) throughout the study period: 16 from the 5 m treatment, 21 from the 50 m treatment, and 20 from the 100 m treatment.

The first Kaplan-Meier survivorship estimate (i.e., probability of survival) for all depths combined for the first 12-hours and 24-hours was 0.71 (95% CL 0.62 – 0.81) and 0.62 (0.52 - 0.75), respectively, and over the entire study period (May 10 to June 6, 27 days) was 0.16 (0.05 - 0.51) (Figure 2.2a). The second survival estimate for all depths combined was 0.12 (0.04 – 0.38) for the overall study period, and 0.58 (0.49 – 0.69) and 0.49 (0.39 – 0.61) for the first 12-hours and 24-hours, respectively. The Cox proportional hazards model indicated no statistical difference in survival between the three depth treatments for either survival estimate (first and second survival analysis; $\chi^2 = 0.23$, df = 2, p = 0.8 and $\chi^2 = 1.2$, df = 2, p = 0.5).

Neither covariate of depth nor fish size had significant influence on bloater survival. Survival at 5 m after 12- and 24-hours was 0.90 (0.80-1.00) and 0.80 (0.65 – 0.98), respectively, and the last mortality was five days following stocking. The highest censorship of individuals occurred ~ 3 hours following release for the 5 m treatment group. Survival in the 50 m treatment group decreased faster than both the 5 and 100 m treatment groups from May 10 to May 15 (Figure 2.2b). The 50 m survival after 12- and 24-hours was 0.59 (0.43 – 0.81) and 0.51 (0.33 – 0.78), respectively. The first eight hours showed a steady decline in survival of individuals released at the 50 m treatment, at which mortalities plateaued for a short period while individuals emigrated from the array. All interpreted mortalities occurred within 51 hours of release for all depths combined. The highest survival of the three treatment groups throughout the entire study duration was the 100 m group, which was 0.29 (0.07 – 1.00). The highest number of censored individuals occurred after 4 days for this group, and most of the mortality occurred within the first twelve hours 0.64 (0.49 – 0.84) followed by a slight decrease in survival to 0.59 (0.42 – 0.81) by 24-hours. The first interpreted mortality occurred within 2 hours following stocking and the last interpreted mortality was 19 hours after stocking. The majority of interpreted mortalities across all depths occurred in the first 12 hours post-release, during which bloater were also emigrating the array, after emigration, the fish were unlikely to be detected and estimates of mortality became more conservative.

Dispersal and behaviour

A total of eight individuals were removed from subsequent behavioural analysis due to confirmed mortality. Emigration began within the first hour following stocking (May 10) and by 72-hours post-stocking, 46.7% of the bloater (n=50) had emigrated from the array. Of the 50 bloater that emigrated from the array, 62% (n = 31/50) re-entered and exited the array before the end of the 31-day study period, the majority of which returned within the first 48-hours following stocking. There was no correlation between bloater size and timing of emigration (r_s = -0.092, p = 0.342).

When determining the direction of movement, the difference in receivers included in the analysis influenced the overall direction following stocking. The HR2s provide fine scale directional movement while the PPM show broadscale directional movement between the three depths. Bearings between successive points based on the mean-position algorithm were relatively northward across the three depths. The mean direction of travel was most variable for the 5 m depth on both PPM and HR arrays (mean ± SE; PPM: -6.02 - 45.08°; HR: -0.20 – 98.89°). There was no significant difference in the mean direction of travel between the three depths on the PPM array ($F_{(2, 104)} = 1.44$, $p = 0.24$) or the HR array ($F_{(2, 104)} = 0.48$, $p = 0.62$ (Table 2.2.).

The total distance traveled by bloater following release varied by individual and by depth, however there were no significant differences on either the PPM array ($\chi^2 = 0.23$, df = 2, p = 0.89) or the HR array ($\chi^2 = 0.51$, df = 2, p-value = 0.78) (Table 2.2.). On the PPM array, the total distance traveled by bloater following release was the longest for the 100 m treatment with a mean distance traveled of 7.67 ± 16.8 km and a range of 0.37 – 98.56 km (Figure 2.5) over a timeframe of 23.97 ± 90.50 hrs (range of 0.17 – 516.83 hrs). Conversely, on the HR array, the average total distance traveled by tagged bloater was longest for the 5 m treatment, with a mean distance traveled of 6.43 ± 7.97 km and a range of 0.39 – 32.25 km (Figure 2.6) over 12.80 hrs (0.33 – 69.17 hrs).

The average movement rate of bloater across all depths combined for the PPM and HR was 0.25 m/s (± 0.01) and 0.18 m/s (± 0.01), respectively.

The relative movement rates did not differ significantly on the PPM array (ANOVA; $F_{(2, 95)} = 2.14$, $p = 0.12$), but did vary significantly between the three depths on the HR array (ANOVA; $F_{(2, 96)} = 4.04$, $p = 0.021$), with the individuals stocked at the 5 m treatment having the highest movement rate (Table 2.2). Comparisons between treatment depths using a Tukey's *post hoc* test revealed differences between the 5 and 100 m and the 50 and 100 m treatments (p = 0.03; p = 0.05) but no statistical difference between the 5 and 50 treatments (p = 0.9).

2.4 Discussion

Passive acoustic telemetry utilizing PPM and HR transmissions allowed for the quantification of bloater movement and survival after stocking over three bathymetric depths in Lake Ontario. Survival estimates for all treatment groups were low and did not significantly vary between stocking depths. Trends in mechanisms of mortality were distinct between the three depths, with increasing mortality from the shallowest to deepest stocking depths (29% for the deepest (100 m), 20% for the middle depth (50 m), and 16% for the shallowest (5 m), and estimates were all lower when avian predation events were included. The fate of bloater that left the array is unknown but were determined to be alive at the time of their last detection. Predation was the predominant source of mortality at the shallow stocking depth, whereas non-predation mortality was the predominant source at the deeper depths, which is presumed to be related to stress and potentially barotrauma. A majority of bloater were detected for <24 hours in the array and the last detection of a non-predated individual was 27 days after release. Bloater dispersed quickly from the release sites northward towards deeper waters (>40 m), at relatively consistent movement rates (0.21 m/s ± 0.02 for the 5 m; 0.28 m/s ± 0.03 for the 50 m; 0.26 m/s ± 0.02 for the 100 m) on the PPM array. The movement rates calculated on the PPM array did not differ between depths but did based on the HR array, with the 5 m depth having the highest movement rate (0.20 m/s ± 0.02) out of the three. The results of this study provide evidence that stocking depth can influence the source of mortality.

Low survival following stocking is consistent with a previous study on bloater, where Klinard et al. (2020b) found only 32% of acoustic-tagged bloater age-2 survived longer than 12 days in the St. Lawrence Channel of Lake Ontario. Similar to our study, Klinard et al. (2020b) also found high initial mortality, 58% over 12 days, a majority associated with predation. High mortality following stocking of hatchery fish has been observed across many species. For example, Jepsen et al. (1998) used radio telemetry that revealed a 3-week mortality rate of 90% for post-stocking mortality of juvenile Atlantic salmon (*Salmo salar*) smolts stocked in the Danish River Gudenå watershed, with fish predation accounting for 56% and avian predation accounting for 31% of the total. Other tagging studies have also experienced high initial mortality of stocked salmon smolts (Holbrook et al., 2011; Huusko et al., 2018; Thorstad et al. 2011; Thorstad et al., 2012), however there are limited studies that examine the post-release survival of bloater or other deep-water coregonids.

The maximum number of bloater at risk of death was at the time of release (n=107). After release, the number of fish remaining in the study declined rapidly as individuals either emigrated from the array or experienced mortality. After 130 hours following stocking, only three individuals were left at risk of death within the array. Although stocking survival was not statistically different between the three depths, there were notable differences in timing of death and sources of mortality. There were three quantified sources of mortality in this study, fish predation (18%), avian predation (17%), or stress related (19%). Fish predation is the most definitive given the telemetry tags that were used, these have been shown to have a low false positive rate (Halfyard et al. 2017). Avian predation cannot be confirmed but appears likely as these fish disappeared from within the middle of the array shortly after stocking and birds were observed foraging in the direct vicinity immediately after release of the fish. Stressed related mortality was defined by the lack of horizontal movement of individuals between receivers shortly following release with detections occurring at a single receiver for the entire study duration.

The occurrence of 19 predation events is consistent with a similar study in northern Lake Ontario on tagged bloater where 13 bloater (were predated within *c*. 2 weeks following release (Klinard et al. 2020b). Further, the 13 predation events observed by Klinard et al. (2020b) from bloater stocked over a depth of *c.* 50 m is similar to the 8 observed predation events in our study at the same depth and the 10 events at the shallower 5 m depth. The size of tagged bloater used in Klinard et al. (2020b) were age-2 (mean weight of 253 g; 259 mm (FL)), over double the size of our bloater. The bloater use in our study were smaller than those of Klinard et al. (2020b) and most comparable in size to the tagged bloater in Klinard, Halfyard, et al. (2019), supporting the idea that smaller bloater are more vulnerable to predation. Given the size of the juvenile bloater stocked, there are a number of potential fish predators, including lake trout *Salvelinus namaycush* and other piscivorous salmonids (e.g., Atlantic salmon (*Salmo salar*), as well as avian predators (e.g., *Larus spp*. and *Phalacrocorax auratus*). Using machine learning techniques and retention of predated tags in the stomach of the predator, Klinard et al. (2021) estimated that these species, along with brown trout (*Salmo trutta*), chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), and rainbow trout (*Oncorhynchus mykiss*), consumed the stocked bloater. The higher predation at the 5 and 50 m depths is consistent with the depths these species use in May during this experiment. For example, Raby et al. (2020) found that Chinook salmon occupy depths of 14.4 ± 2.5 m while Atlantic salmon were reported occupying depths of 22.0 ± 4.6 m during the spring period (Larocque et al. 2022). Similarly, brown trout tend to stay nearshore (<2 km) year-round and spend the spring and summer near the thermocline (mean (±SD) depths of 14.6 ± 6.7 m) at warmer temperatures (13.4 ± 3.7 °C; Nettles et al., 1987; Olson et al., 1988).

A total of 18 individuals from the censored group were suspected of avian predation and occurred between midday to early evening hours (12:00-17:00). Avian predation cannot be confirmed but appears likely, given that these fish disappeared from the array shortly after stocking and birds were observed foraging after release of the fish. Plus, given the density of receivers surrounding stocking locations, it is more likely that an individual was avian predated in the center of the array than it is for the fish to swim 5-6 km undetected. Additionally, cessation of movement in the center of the array from individuals that demonstrated movement typical of a live individual is more likely related to avian predators removing the tag from the system. Since the fate cannot be confirmed, these individuals (17%) have been censored at their last known detection timestamp. Censoring an individual assigns an unknown fate to that individual but removes them from the at risk of death category. This is different from assigning a known fate (i.e., mortality) as it assumes the individual is still alive. To account for the avian predation events, the survival analysis was run both ways to provide the most realistic representation of survival. Comparably, Jensen et al. (2009) found up to 12% of the tags from hatchery-reared Atlantic salmon smolts in the River Eira (Norway) were found immediately after release in sea gull pellets, *Larus spp*.. Similarly, Fielder et al. (2023) assessed the spatial and temporal extent of predator movements in Lake Huron and found that double-crested cormorants were the first potential predator to arrive at a stocking site, out-competing two top predators, walleye (*Sander vitreus*) and lake trout (*Salvelinus namaycush*).

For hatchery-reared fish that have not experienced changes in water pressure prior to release, rapid compression could cause a significant stress. The proposed mechanism for this stress related mortality is compression induced barotrauma. Eight bloater died from non-predation causes within four hours of release, most of these (n = 5) were from the 100 m stocking depth. The cause of these deaths cannot be confirmed but could be related to stress of transport and stocking, poor acclimation, and/or stress associated with compression at depth. Current stocking protocols for bloater involve releasing fish at depths > 50 m, where they descend rapidly immediately upon release (Klinard et al. 2020). In hatchery settings, tanks are typically less than two meters deep and the bloater’s innate response when stressed is to dive down, however in the wild, they are not restricted to a shallow tank. Upon release, they exhibit similar behavioural responses by descending rapidly, exposing themselves to one atmosphere of pressure for every 10m depth. Such rapid compression could be a source of stress and physical trauma for fish which have only experienced ~0 atm of pressure (relative to sea level) in the hatchery. Similar behaviour was observed by Klinard et al. (2020) where 16 tagged individuals released over depths of *c.* 50 m were removed from analysis as their depth data suggested rapid mortality (<1 hr). Accompanying laboratory experimentation with hatchery-raised bloater using a specially designed hyperbaric apparatus to study the effects of pressure on fish, demonstrated significant negative impacts of barotrauma on bloater behaviour at 0.5 atm (5 m depth) and > 20% mortality at 5 atm (50 m depth) (O'Gorman et al., *unpublished data*). As little as 1 atm of pressure caused bloater to experience abnormal behaviour, and at much greater pressures associated with 100 m depths, significant mortality (O'Gorman et al., *unpublished data).* Knowledge of possible effects of barotrauma on juvenile hatchery-reared fish could refine objectives for restoration stocking strategies or provide suggestions for alternative stocking practices. Understanding the effects of compression barotrauma on acoustically tagged fish will also inform other telemetry research occurring throughout the Great Lakes, including hatchery-raised deep-water fish.

After consideration of a range of COAs based on past research on fish (Gatch et al. 2022; Klinard et al. 2020b; Simpfendorfer et al. 2002), the 10-min timestep was considered the best, generating total distance travelled and relative movement rates of bloater compared to other Coregonus species (Gjellard et al. 2004; Rudstam et al. 1984). The 10 min timestep was selected as it represented the relative movement rate of bloater across both PPM and HR while incorporating sufficient distance between two COAs. The longer 15- and 20-minute timesteps generated too few COAs and movement rate estimates, and thus failed to describe individuals that had experienced mortality or emigrated from array within an hour. A smaller COA resulted in an overwhelming number of estimates without any travel distance, thus overestimating the movement rates. The 10-min COA estimates were ideal to use in this situation as they most accurately reflected movement rates of wild bloater and other Coregonus species without compromising the individuals that migrated out of the array quicker than other individuals (Thorstad et al. 2012; Rudstam et al. 1984).

The distance and direction of movement of bloater following release showed dispersal from the three release sites and a general northward trend in trajectory towards deeper water. The direction of dispersal from initial stocking locations is likely a result of fish moving and orienting themselves while acclimating to a new environment. A large proportion of individual bloater had COA estimates along the northeast and northwest edges of the array within 12-24-hours following release. After moving towards deeper depths bloater dispersed laterally from the 50 and 100 m array, suggesting a preference for this depth range, consistent with findings from previous studies that have observed bloater at depths greater than 35 m (Klinard et al. 2020; Gorman et al. 2012; Brown et al. 1985; Wells 1968). The 100 m individuals had the shortest distance to travel to emigrate from the array northward, and the majority of bloater stocked at the 100 m site remained in the vicinity following release.

The average movement rate of bloater across all depths for the PPM and HR remained consistent throughout the first few days following stocking. These movement rates are relative estimates of movement rates rather than absolute swim speeds, although they are consistent with past studies on coregonids. Gjellard et al. (2004) used hydroacoustics to determine the influence of light on swim speeds of pelagic whitefish (*Coregonus lavaretus*) and vendace (*Coregonus albula*) in subarctic lakes in northern Norway. They determined average swimming speed was highest in periods with low incident light or crepuscular light (0.16–0.18 m/s) and lowest in darkness (0.08–0.10 m/s). Similarly, Rudstam et al. (1984) reported routine swimming speed for 0.15 m bloater swimming at a mean speed of 0.186 m/s in tanks around 09:00 in June. This is similar to our estimates for relatively the same size fish in crepuscular or daylight, with values typically around 0.20 m/s. Although the short-term tracking of bloater movements in this study may not be representative of long-term behaviour, there is limited data for hatchery-reared juvenile bloater of this size class to compare to within the Great Lakes. Likewise, the spatial coverage of our receiver array only covers a fraction of Lake Ontario (*c.* 10 km^2 of *c.* 19,000 km^2). Despite this, the high number of detections within our array and initial survival estimates are fitting with previous survival estimates and trawl surveys of stocked juvenile bloater (Klinard et al. 2020; Weidel et al. 2022).

The relative location of the different stocking sites influenced the outcome of the bloater fate. The highest number of individuals censored were from the 100 m treatment group (n=23/68) and were also censored earlier than the 5 and 50 m treatment groups. This contributed to the 100 m stocking depth having the highest survival estimate, but this could be biased because these fish were close to the open lake where a lack of 180-kHz receivers would prevent their detection relative to the longer path of receivers that individuals stocked at the shallower depths would encounter (*c.* 5-8 km vs 2 km).

Other mortality factors could include tagging effects, but these tags were not expected to cause high mortality as studies have shown no or little negative effects of similar surgical implants (Klinard et al. 2018; Jepsen et al.2008). Moore et al. (2000) recommended that tags be <5% of the fish's mass to minimize effects on behaviour and survival of Atlantic salmon post-smolts. Similarly, Darcy et al. (2019) compared a variety of response metrics relative to tag burden in juvenile lake trout and rainbow trout and found no statistically significant effects of tag burden. Further, there was low variability in hatchery bloater size in our study and there was no statistical difference in tag:fish ratios between the fish that were interpreted as dead and those that were interpreted to have survived, suggesting tag weight did not affect survival. In the present study, tag weight of body weight (2.67% ± 0.44; mean ±1 S.D.) was well below both mentioned studies tag effect means. Thus, tag failure is an unlikely explanation for the differences in sources mortality among groups, as these tags have earlier proven to be reliable (Klinard & Matley 2020).

Tracking the behavior and survival of individual bloater that have experienced different stocking depth treatments into an open lake provides the opportunity to understand which factors most strongly influence mortality. Bloater recaptured in bottom-trawl surveys revealed that stocked fish use similar habitats and food resources as historical populations, but the low number of recaptures (n=10) over the past decade (2012-2022) indicates low survival of stocked fish (Weidel et al. 2022) or that too few fish are being stocked to generate sufficient returns. Each bloater captured in trawls was a solitary individual, supporting our rapid dispersal observation and suggesting bloater are not forming dense schools following release. Low survival of a stocked prey species is not surprising given that over 48 million predatory individuals were stocked into Lake Ontario over the same period one million bloater were stocked (Weidel et al. 2022; Connerton 2020; Klinard et al. 2019; Lake 2018).

Expanding the receiver coverage of the 180-kHz system could aid in determining the sources of mortality and allow for more fine-scale behaviour and movement between the three depths beyond the current array. Weidel et al. (2022) noted that bloater restoration in Lake Ontario could benefit from identifying the environmental conditions that contribute to successful bloater reproduction in the upper Great Lakes as well as seeking to improve post-stocking survival through predator and food acclimation in the hatchery or acclimating stocked fish in the lake prior to release. Given that salmonids occupy a large portion of the Lake Ontario water column during the spring when stocking occurs, and avian predators are largely limited to surface waters, it could be beneficial to expose juvenile hatchery-reared bloater to predators prior to release in a 'soft release' fashion. Since bloater are reared in a hatchery setting, they may not develop the appropriate predator avoidance cues that wild conspecifics have. A soft release would hold the fish in underwater pens for several days to weeks to acclimate to their new environment and provide the opportunity to be accustomed to predators without direct exposure which could in turn reduce initial predation rates. Brown and Day (2002) reviewed stocking practices and suggested that predator and food acclimation as well as soft release procedures have potential to improve released fish survival. Such practices have doubled survival rate of stocked salmonines in Lake Ontario (Connerton 2021); these practices could be applied to bloater restoration to potentially improve the survival of bloater.

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Table 2.1. Size, number and fate of bloater acoustically tagged and released into southeastern Lake Ontario over three depth treatments in May 2022. Mean ± 1 SE are shown for mass (g) and total length (mm).

Depth Treatment (m)	N	Mass (g)	Total Length (mm)	Confirmed Deaths	Number Censored (Survival analysis 1)	Number Censored (Survival analysis 2)	Predation Events	Suspected Avian Predation	Stress Related Mortality
5	35	15.43 ± 0.59	129.60 ± 1.39	11	24	19	10	5	1
50	36	14.73 ± 0.44	127.17 ± 1.33	15	21	15	8	6	7
100	36	14.41 ± 0.32	125.97 ± 0.94	13	23	16	1	7	12
Total	107	14.85 ± 0.27	127.56 ± 0.72	39	68	50	19	18	20

Table 2.2. Summary of the total distance traveled and movement rates of acoustically tagged bloater on the HR and PPM array released over three depth treatments in Lake Ontario May 2022. Mean ± SE are shown for total distance traveled (km) and movement rates (m/s). Direction of dispersal is compass bearing (i.e., north = 0°).

Array	Depth	Total Distance Traveled (km)	p-value	Movement Rate (m/s)	p-value	Direction of Dispersal (°)	p-value
HR	5	6.43 ± 1.41	0.78	0.199 ± 0.017	0.05	5.97 ± 3.65	0.62
	50	5.36 ±1.21		0.195 ± 0.016		5.99 ± 2.09	
	100	5.06 ± 1.34		0.144 ± 0.011		3.26 ± 1.82	
PPM	5	5.44 ± 0.97	0.89	0.214 ± 0.020	0.12	3.48 ± 1.67	0.24
	50	5.33 ± 0.94		0.282 ± 0.026		1.33 ± 0.77	
	100	7.67 ± 2.94		0.264 ± 0.024		0.26 ± 1.39	

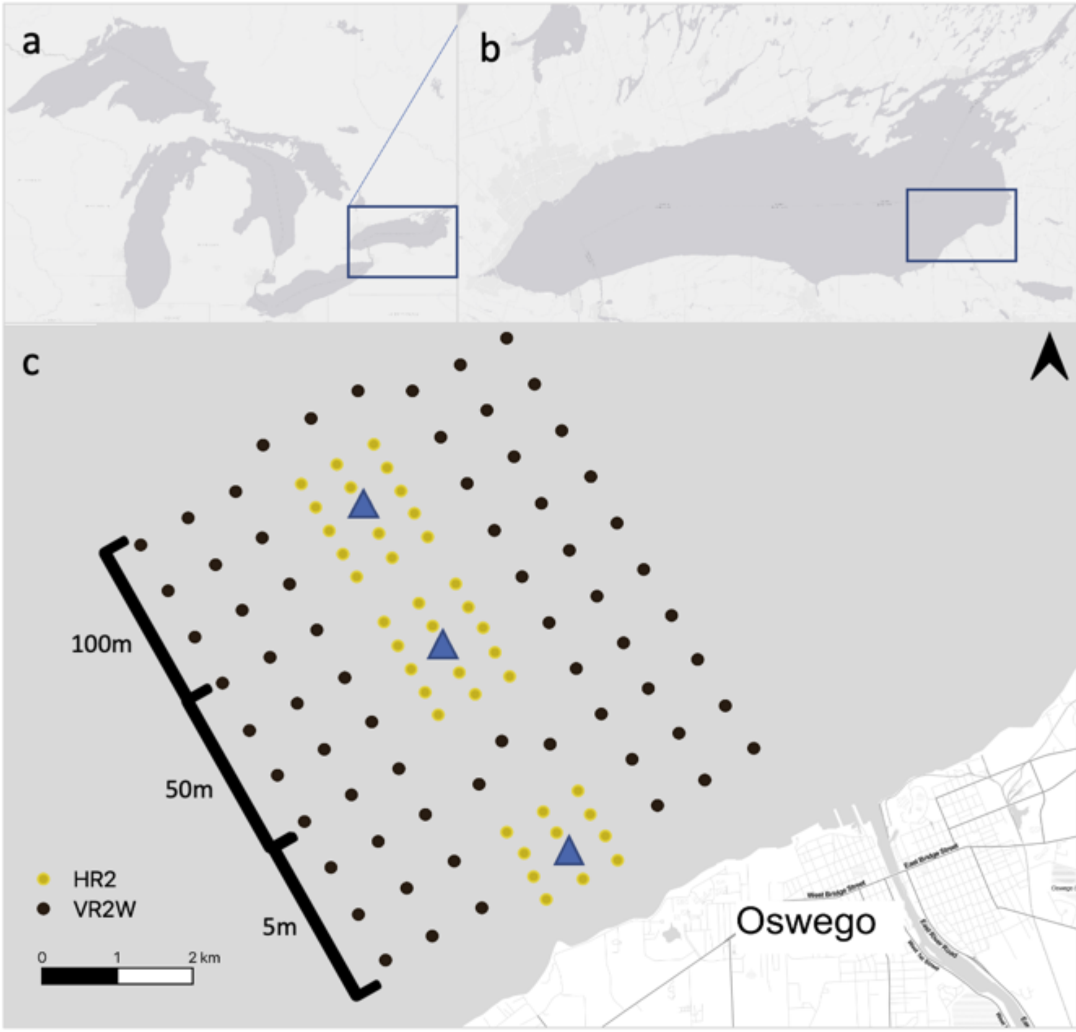

Figure 2.1. a) Location of the study site within the Great Lakes. b) A closer look at the study site within the southeastern basin of Lake Ontario. c) The distribution of the receivers within the study site (black indicates the VR2W-180 kHz receivers, yellow indicates the HR2-180 kHz receivers, blue triangles indicate stocking sites).

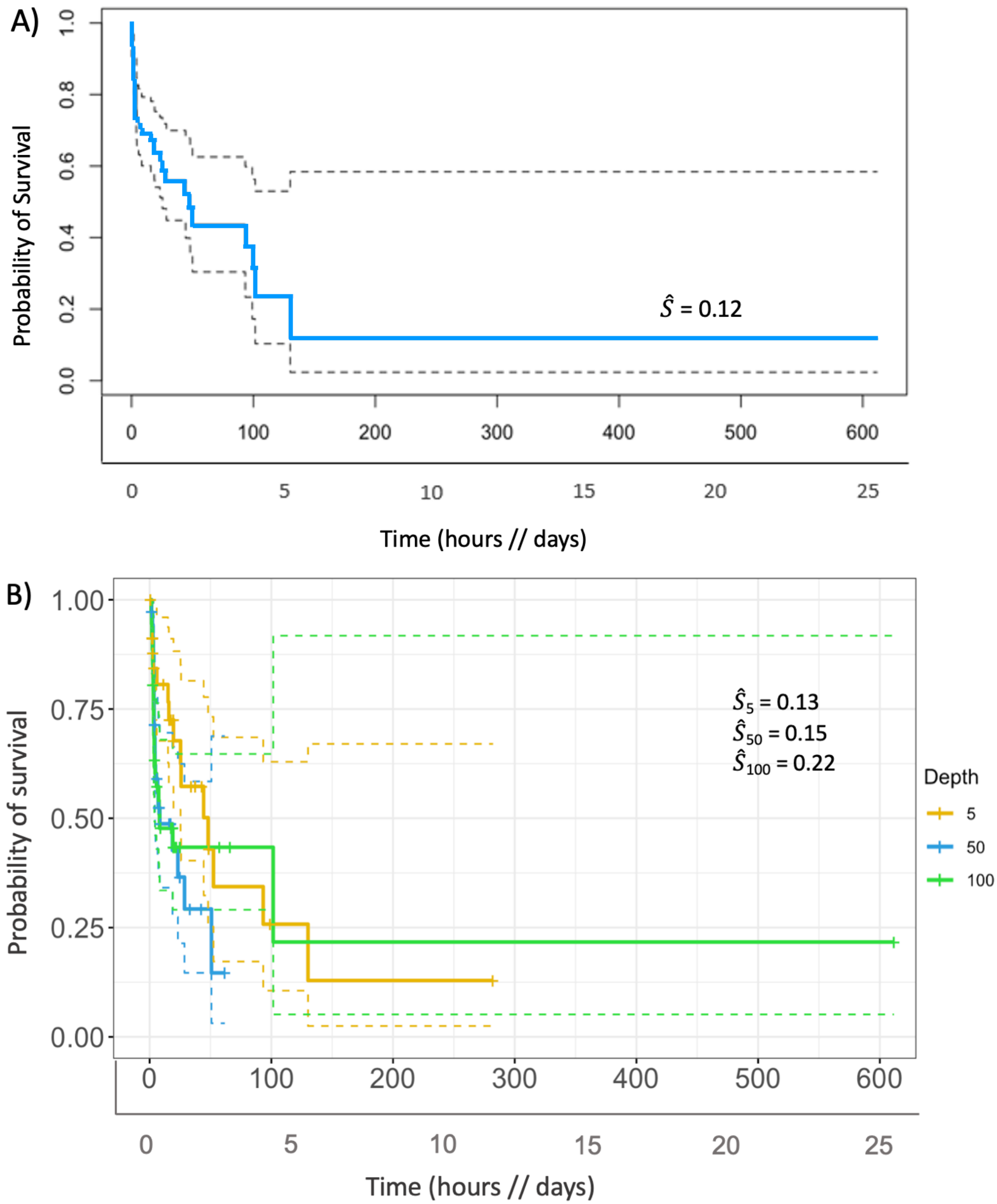

Figure 2.2. A) Kaplan-Meier survivorship estimates for acoustically tagged bloater released in southeastern Lake Ontario. The dashed lines represent 95% confidence intervals. B) Kaplan-Meier survivorship estimates for bloater released across three bathymetric depths in southeastern Lake Ontario. Depth treatments are coded by colour, orange indicates 5 m treatment, blue

indicates 50 m treatment, and green indicates 100 m treatment. The dashed lines represent 95% confidence intervals.

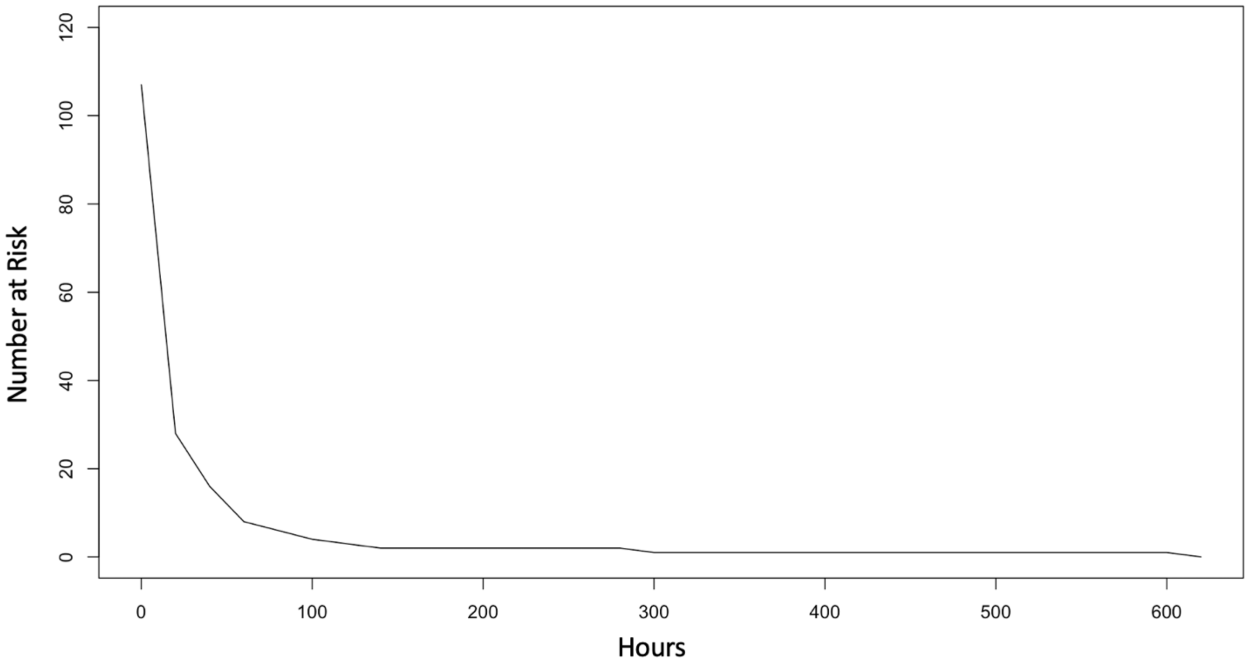

Figure 2.3. Number of bloater at risk of death in southeastern Lake Ontario over the duration of the study (May 10 – June 6, 2022). The number at risk at a specific hour reflects the number of individuals removed from the study due to mortality or censored individuals with unknown fates.

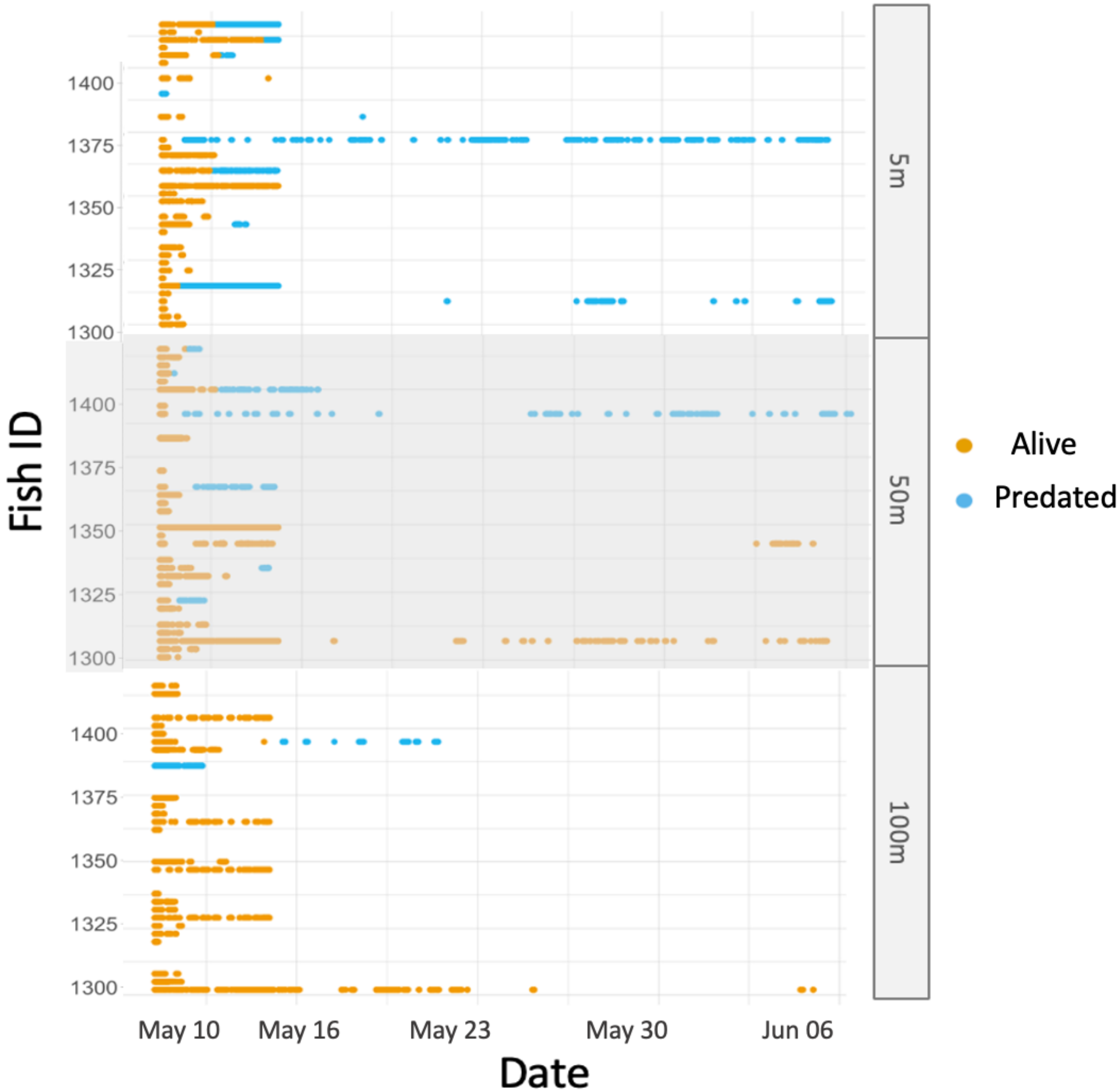

Figure. 2.4. Acoustic detections of hatchery-reared juvenile bloater released from three depths within the Oswego array in southeastern Lake Ontario from May 10, 2022, to June 6, 2022. Colours represent alive or predated detections.

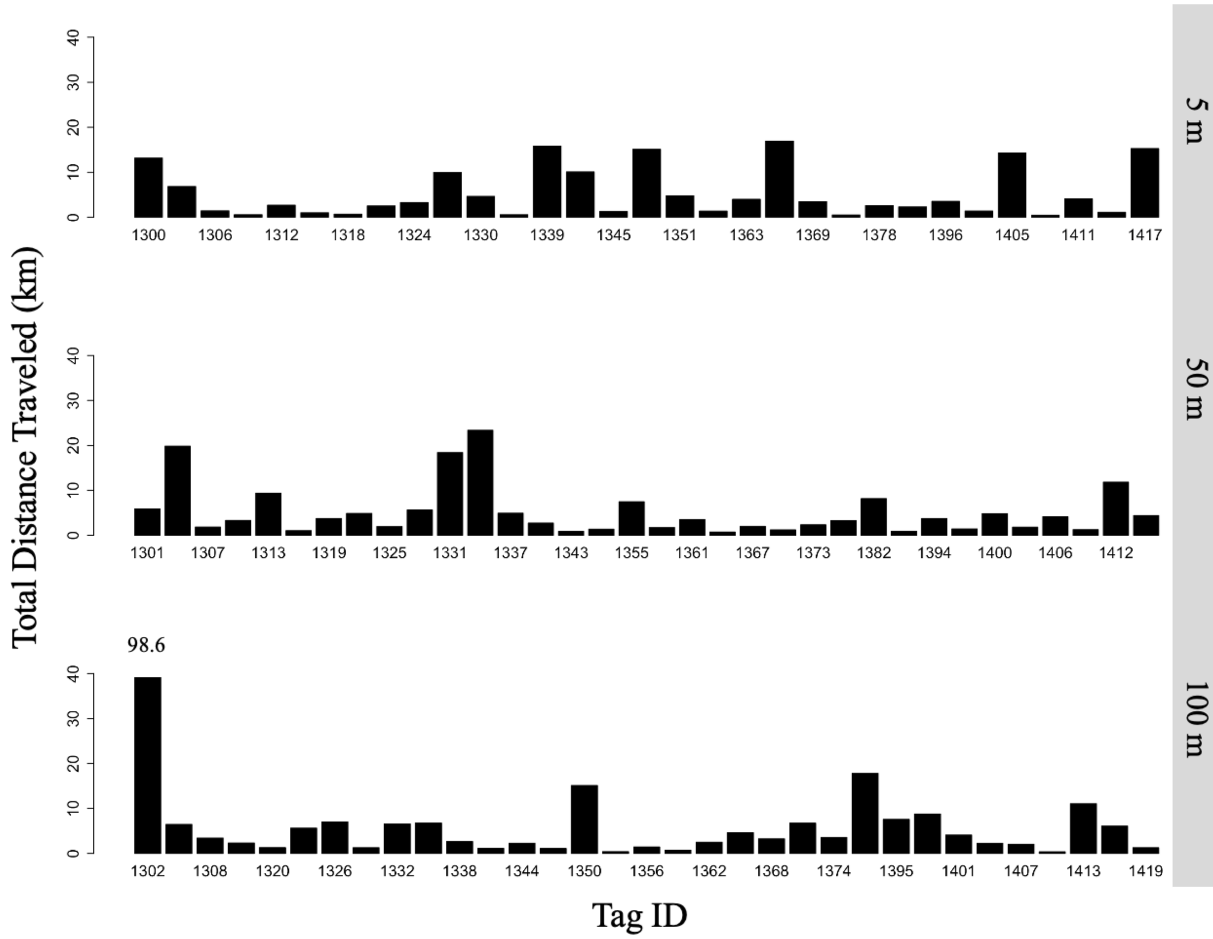

Figure 2.5. Total distance traveled (km) by individual acoustically tagged yearling bloater for duration of study period with PPM detections. Yearling bloater were released between 12:00 and 14:00 on May 10, 2022 into the acoustic receiver array in southeastern Lake Ontario. Individual movements were summed for each bloater to determine total distance traveled.

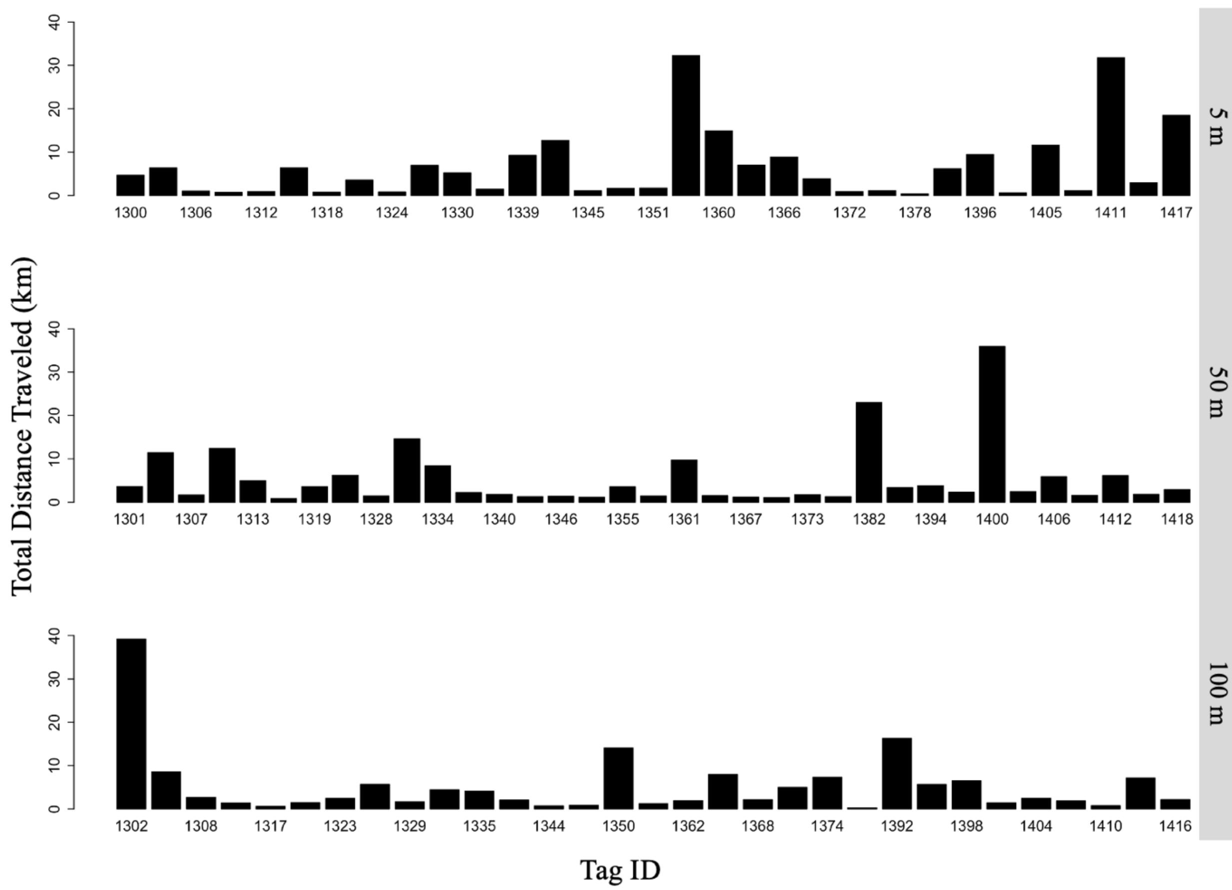

Figure 2.6. Total distance traveled (km) by individual acoustically tagged yearling bloater for duration of study period with HR detections. Yearling bloater were released between 12:00 and 14:00 on May 10, 2022 into the acoustic receiver array in southeastern Lake Ontario. Individual movements were summed for each bloater to determine total distance traveled.

CHAPTER 3

GENERAL DISCUSSION

3.1 Summary

More than 20 million native and non-native fish species are stocked into the Great Lakes annually to support commercial and recreational fisheries, supplement naturally occurring populations, and for restoration efforts to re-establish native species associated with ecological and economic benefits (Spraker 1992; Stewart et al., 2017). These benefits are closely linked as a healthy biodiverse ecosystem is more resilient to changes (Costanza et al. 1992). Despite this long history, the post-stocking ecology and fate of fishes post-release is largely unknown due to difficulty monitoring them, especially for small fishes (Zimmerman and Krueger 2009; Mandrak and Cudmore 2010; Bunnell et al. 2014). Acoustic telemetry is a common tool in the Great Lakes used to study the post-stocking ecology of fishes by passive continuous monitoring of tagged individuals (Espinoza et al. 2011; Klinard et al. 2020b). The development of the high residence (HR) telemetry system has allowed researchers to monitor and position multiple tagged individuals with sub-meter accuracy using both the HR and pulse position modulation (PPM) transmission system. The HR system operates at a frequency of 180 kHz which encompasses a smaller rang of tags permitting the study of small forage fishes, a feature not possible on the larger, more common 69 kHz tags. Coupling HR receivers with predation tags permits fine-scale estimation of predation-related mortality, in turn, improving detailed survival estimates of stocked fish, specifically juveniles. Knowledge gained through studies of aquatic animal movement aids in the management and conservation of fish while contributing to our fundamental ecological knowledge of the stocked species.

The overall aim of this thesis was to use acoustic telemetry and time to event modeling to determine if bathymetric depth influences survival and behaviour of hatchery-reared juvenile bloater (*Coregonus hoyi*) stocked into Lake Ontario to provide information relevant to restoration stocking efforts. More specifically, my thesis entailed: 1) quantifying the post-release survival of bloater across and within three depths (5, 50, and 100 m); 2) identifying the sources of mortality at each depth; and 3) determining the movement and behaviour of bloater following release across each depth. Addressing these objectives expands on our fundamental knowledge of bloater ecology and provide insight into the immediate post-stocking movements of a reintroduced forage fish. Understanding the post-stocking movement ecology of bloater is crucial as they are the focus of a binational restoration effort in Lake Ontario, with the goal of re-establishing a self-sustaining population in the lake. A self-sustaining population of bloater in Lake Ontario restores a native fish population, thus increasing the biodiversity and providing a framework for reintroduction and management efforts of other native species (Favé and Turgeon 2008; Eshenroder et al.2016). Additionally, bloater would provide ecologically and economically important salmonids (e.g., lake trout *Salvelinus namaycush*, Chinook salmon *Oncorhynchus tshawytscha*, and Atlantic salmon *Salmo salar*) a prey fish alternative to alewife, as alewife have high thiaminase activity, a thiamine-degrading enzyme linked to reproduction deficiencies in salmonines (Ketola et al., 2000; Honeyfield et al., 2005; Futia et al. 2019). Continued investigation into the movement and predation of bloater post-release will be used to determine survival of the stocked population. This enhanced understanding will play a crucial role in refining stocking strategies and assessing the overall restoration potential for bloater in Lake Ontario.

To address these objectives, 107 acoustically tagged hatchery-reared juvenile bloater were released into Lake Ontario to quantify the survival, sources of mortality, and behaviour post-stocking across three bathymetric depths. Time-to-event modelling revealed low survival

(12%) during the first three weeks post-stocking with initial data suggesting mortality in shallower depths was dominated by predation while mortality at deeper depths was related to compression barotrauma, however no statistical differences were found in survival between the three depths. Relative position estimates indicated bloater dispersed rapidly following release and exhibited relative movement rates towards deeper waters within hours (> 12hours) following stocking. Poor survival and rapid dispersal from the stocking site are consistent with previous findings of hatchery-reared juvenile bloater (Klinard et al. 2020b); however trends in sources of mortality were indicated between the different stocking depths. Despite low survival and bloater emigrating the array quickly following stocking, the HR system provided fine-scale movement and behaviour of bloater, generating over a half million detections, majority of which were within the first 48 hours after release, demonstrating the value of high residence telemetry systems in stocking and restoration efforts.

3.2 Conclusions and Future Directions

Majority of the information provided on the post-stocking ecology of bloater using acoustic telemetry has been observed in recent studies (e.g., Klinard et al. (2019; 2020a; 2020b). The development of smaller acoustic tags and high residence receivers has allowed for the successful use of telemetry to study small fishes, which often generate shorter detection periods as they are especially susceptible to handling and stocking stress. Acoustic telemetry in this study improved our understanding of the post-stocking survival, behaviour, and sources of mortality across a variety of depths, all important information for the management and restoration efforts for this species and other reintroduced species across the Great Lakes. Utilizing fine-scale high residence receivers permitted detailed behavioural analysis and the estimation of predation related mortality. This study highlighted the significant and novel value of using high residence acoustic telemetry in restoration studies and determining the post-release ecology of stocked fishes. Although there were no significant differences in survival across the three depths, the data presented here provided a closer look into the differences in the mechanisms of mortality at each depth, providing valuable information pertinent to the methods and timing of future stocking practices. Most of the mortality at the 5 m site was attributable to fish predation, while roughly equal proportions were assigned to fish predation, avian predation, and stress related at the 50m site. Given that salmonids occupy a large portion of the Lake Ontario water column during the spring when stocking occurs, and avian predators are largely limited to surface waters, it could be beneficial to expose hatchery-reared juvenile bloater to predators prior to release in a 'soft release' fashion. Since bloater are reared in a hatchery setting, they may not develop the appropriate predator avoidance cues that wild conspecifics have. A soft release could provide the time needed to acclimate to their new environment and provide the opportunity to be accustomed to predators without direct exposure which could in turn reduce initial predation rates (Brown and Day 2002).

At 100m, fish predation was not a notable source of mortality, but stress related mortality accounted for over half of all mortality at this depth. For hatchery-reared fish which have not experienced changes in water pressure prior to release, rapid compression could cause a significant amount of stress on individuals. The proposed mechanism for this stress related mortality is compression barotrauma. This compression barotrauma has been previously observed by Klinard et al. (2020b), which showed similar results where bloater descended quickly to bottom without subsequent movement, suggesting that hatchery-reared juveniles are not well-suited for deep, offshore release. To alleviate this issue, bloater could be stocked in shallower water where they can slowly descend along a bathymetric gradient towards deeper water, reducing pressure impacts.

This study focuses on data from spring 2022, year one of three, and therefore requires further investigation. A second year of data from spring 2023, which coincided with a federal cormorant shooting the week prior to stocking, could have reduced the presence of avian predators as none were observed during stocking. Aligning future stocking events of bloater with cormorant shooting could alleviate a large predation stressor. The logistics associated with offshore stocking can often be difficult to coordinate, leading more agencies to consider onshore stocking practices. Typically referring to <30 m from shore, onshore stocking could lessen stress and vulnerability associated with depth. Furthermore, it has been documented that bloater undergo diel vertical migrations to optimize feeding and avoid predators (Klinard et al. 2020b). Bloater preference for deeper water during daylight hours may indicate that stocking at night, when bloater are already in shallow water, could reduce stress and predation during stocking (Johnson et al., *unpublished data)*.

This research focused on bloater in Lake Ontario as their restoration is key in diversifying the offshore prey community and re-establishing historic energy pathways, increasing food web stability. The binational effort to re-establish a self-sustaining population of bloater will also aid in the restoration of native salmonids and off-set impacts from non-native prey fish.

In conclusion, understanding the movement and mortality of stocked fish will aid in refining stocking strategies and informing restoration potential for the species. Although there were no significant differences in survival among the three depths, quantifying the sources of mortality across depths and the factors driving them is important as it provides researchers and managers with different variables to target when determining future stocking success. Altering the time of stocking could increase bloater survival following stocking. Given the preference of bloater for deeper water during daylight hours, stocking offshore during the night when bloater are already in shallow water may reduce stress associated with offshore stocking but also reduce the pressures from visual fish and avian predators during stocking, potentially increasing their restoration potential.

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