The Contribution of Fish Movement to Ecosystem Function in Lake Superior

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Lakehead University, Thunder Bay, ON
October 2023

A dissertation submitted in partial fulfillment of the requirements of the degree of
Doctor of Philosophy

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Thesis Abstract

Ecosystems are complex, highly interconnected systems in which organisms interact with their physical environment. Often, to simplify our understanding of their function, populations within ecosystems are treated as either spatially ubiquitous or discrete and fail to fully consider the costs and benefits of organism movement within and across ecosystems. This is especially prevalent in considering the ecosystem function of large aquatic systems like Lake Superior. Though most fishes in Lake Superior are known to exhibit large scale movements to spawn in the fall or spring, the costs and benefits resulting from this interconnectedness and daily behaviours of fish undergoing these movements are poorly characterized. This knowledge gap is due, in part, to limitations of current survey and assessment methods (i.e., mobile down-looking sonar surveys), which are costly, have known biases that underestimate fish populations, and are inadequate for detecting fine scale fish movements. To combat these gaps, I first used a new stationary acoustic platform to improve the accuracy of fish density estimates in the upper water column compared to traditional down-looking surveys and provide insight into ship avoidance behaviours and temporal migration patterns. I then applied this technology to describe inter-annual, regional, and diel differences in fish behaviour across Lake Superior. Finally, I examined the productive Lake Superior Shoals lakemount and found strong evidence of a deep chlorophyll maxima and of diel-vertical migration behaviour in the fish and *Mysis* at the shoals, both of which are key components for evaluating current-dependent hypotheses for elevated shoal production. However, I conclude that this shoal system would benefit from the use of the stationary acoustic platform as the current standard sampling methods were unable to provide substantial direct support for these hypotheses. Insights gained from these investigations can be

applied by government agencies to better manage the integral recreational, commercial, and First Nations fisheries within the Great Lakes of North America.

Lay Summary

Lake Superior is one of the largest freshwater lakes in the world and supports substance, commercial, and recreational fishing for millions of people in the US and Canada. In order to continue to protect this resource for generations to come, we need to continue to grow our understanding of it and the fish that call it home. Using new technology, I sought to provide a better understanding of both the numbers of fish and their behaviors in different regions across the lake. I focused on using this technology first to directly improve abundance estimates of the lake herring fishery in Thunder Bay, Ontario, then to better understand fish movement across the lake, and finally to highlight an excellent opportunity to use this technology to grow our understanding in the future at the unique and understudied underwater mountain range that is the Lake Superior Shoal.

Acknowledgements

I would first like to thank God, who’s strength and mercy I relied upon daily throughout my graduate studies. I am extremely grateful to my advisor Dr. Michael Rennie for his guidance, support, and mentorship throughout my graduate experience. I would also like to thank my internal committee members Dr. Rob Mackereth and Dr. Brian Shuter, my external defense committee member Dr. Lars Rudstam, and external thesis proposal examiner Dr. Connie O’Connor for their contributions and advice in the process of completing my thesis. Additionally, I would like to thank Captain Dave Montgomery and the crew of the MNRF R/V Superior Explorer, Captain Joe Walters and crew of the USGS R/V Kiyi, and Captain Raul Lee and the crew of the LLO R/V Blue Heron for all their help in equipment deployment and data collection. I would also like to thank Eric Berglund and Fritz Fisher for their aid and support in deploying my equipment alongside the MNRF surveys as well as their contribution of down-looking acoustic and netting data. I am also grateful to Dan Yule for his support throughout my project, and for including me and the platform in the great Acoustic-palooza. I am also thankful to Dr. Thomas Hrabik for the guidance, acoustics experience, and data from the Lake Superior Shoals he provided, which I was able to carry forward into my doctorate. I am also grateful to my family; my parents, Ruth and Chris Grow, my wonderful fiancé Lara Besselt, my siblings, Kevin and Sarah Grow, my extended family, and friends for their continued encouragement throughout my graduate career; their love and support was invaluable throughout the whole of my education. I am also thankful to the CEELab students and faculty for their camaraderie and support in my time at LU, especially my fellow doctoral students Haley McLeod and Alex Ross. I also thank LUCF, One TBYA, and FWBC for being caring and compassionate communities that I have been honored to be a part of during my time in Thunder Bay. I am grateful to RAEON for providing the stationary up-looking platform and other associated equipment for deployment and retrieval. I thank Brandon Greenaway and Nadine Elmehriki at LU for their help in benthic organism counts. Finally, I would like to thank Lakehead University and the Ontario Graduate Scholarship for providing assistantships and funding throughout my thesis project.

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Thesis Introduction

The field of ecosystem ecology seeks to understand the structure and function of ecosystems including interactions between organisms and their environments. Much work to attempt to explain ecosystem function has focused on breaking large and complex systems down into specific abiotic or biotic ecosystem processes and looking at the role of specific drivers on function (Humbert and Dorigo, 2005; Tilman et al., 1997). These processes typically include decomposition, production, nutrient cycling, and energy flow within a given system (Carpenter and Lodge, 1986; Díaz and Cabido, 2001; Tilman et al., 1997). However, organism movement on both fine and broad scales can also be significant drivers of ecosystem function by spatially integrating nutrient cycling pathways, fundamentally driving energy flow through food web interactions, and contributing to productivity hotspots through habitat usage (Jones and Mackereth, 2016; Stockwell et al., 2014). Despite the potential importance of characterizing organism movement and spatial distributions, technological, financial, and logistical constraints often limit the prioritization of assessing organismal movement patterns in ecological surveys (McIntyre et al., 2015; Polis and Strong, 1996). Additionally, anthropogenic stressors such as climate change, habitat loss, and invasive species can all threaten ecosystem function (Hautier et al., 2015; Vitousek, 1990), especially in aquatic ecosystems (Carpenter et al., 2011; Edwards and Richardson, 2004; Hoegh-Guldberg and Bruno, 2008).

The overall goal of my research was to improve our basic understanding of the contribution that fish movement and distribution makes to broader ecosystem function, which can be applied across freshwater ecosystems, particularly The Great Lakes. The main objectives of my thesis were to: 1) test the viability of stationary up-looking platforms as a novel fish survey tool in freshwater systems, 2) improve our understanding of how daily fish movements differ spatially across Lake Superior using autonomous stationary up-looking acoustic platforms, and 3) examine the energy flow pathways and specific food web dynamics at the productivity hotspot of the Lake Superior Shoals system using biological data and hydroacoustic survey methods.

In my first chapter, I aimed to overcome the technical limitations of down-looking acoustic surveys by using stationary up-looking platforms that may be capable of more accurately and efficiently accessing fish density and fine scale/seasonal movements. Currently, hydroacoustic fisheries surveys are typically accomplished via ship-based down-looking surveys, which are an important tool for fisheries researchers and managers to quantify and monitor the status and trends of populations (Kubečka et al., 2009; Simmonds and MacLennan, 2005). They have many advantages, including the deployment of fish estimation surveys over broad, spatially diverse areas and allow for sampling in areas where traditional netting methods are impractical (Qiao et al., 2006; Warner et al., 2012; Yule et al., 2007). Despite the several positive attributes of acoustic surveys, limitations exist. The surface dead zone, which consists of a portion of the water column closest to the transducer, and vessel avoidance, which occurs when fish exhibit avoidance, diving, or herding behaviour in response to the presence of a large survey vessel, are among the most pressing limitations as they ultimately lead to an underestimation of pelagic fishes, particularly those that occupy the upper portion of the water column (DuFour et al., 2018; Guillard et al., 2010; Parker-Stetter et al., 2009). Regardless of these drawbacks, standard mobile down-looking acoustic surveys are currently employed to provide density estimates and help set quotas for commercially important pelagic fish species like cisco (*Coregonus artedi*) in Lake Superior (Fisch et al., 2019a; Pratt et al., 2016; Yule et al., 2012). One promising method currently being used to correct for the issues with down-looking surveys are up-looking acoustic surveys (De Robertis et al., 2018; Elliott et al., 2021; Grow et al., 2020). Up-looking surveys can be mobile, using tow bodies, or deployed from moored stationary platforms equipped with upward facing acoustics (De Robertis et al., 2018; Elliott et al., 2021; Grow et al., 2020). In my first data chapter, I aimed to deploy a stationary up-looking survey in conjunction with the typical cisco survey in Thunder Bay, ON to explore the potential benefits to be gained compared to traditional down-looking surveys.

Cisco are a cold-water pelagic fish found in many North American lakes and are threatened across their range by increasing water temperatures from climate change and declining oxygen levels due to eutrophication in their inland lake habitats (Grow et al., 2021; Jacobson et al., 2010; Magnuson et al., 1997; Stefan et al., 2011). In Lake Superior, cisco are ecologically and economically important due to their participation in offshore and nearshore food webs and active movements both vertically (Ahrenstorff et al., 2011) and horizontally among seasons (Stockwell et al., 2014). They also serve as prey for top-level predators (Kennedy et al., 2018; Sierszen et al., 2014) and support large-scale commercial fisheries with annual yields of over 1,000 metric tons (Pratt et al., 2016). Cisco populations are not evenly distributed spatially in Lake Superior (Yule et al., 2009) and typically stay more nearshore relative to other coregonines (Schmidt et al., 2011). Recent studies show that Lake Superior cisco recruitment is sporadic and decreasing for unknown reasons (Vinson et al., 2016). Additionally, Lake Superior cisco populations have been facing challenges associated with a targeted commercial roe and fillet fishery that consists of multiple bi-national and inter-state/provincial management jurisdictions as well as additional inter-nation treaties with various tribal organizations (Pratt et al., 2016). These challenges make accurate monitoring of cisco population dynamics crucial to their conservation and management.

In my second chapter, I investigate how fish movement patterns vary across spatial and temporal conditions by deploying the stationary acoustic platform in a diversity of regions throughout Lake Superior. Organism movement on both fine and broad scales can be a significant driver of ecosystem function by spatially integrating nutrient cycling pathways, allowing for rapid responses to new available resources from large recruitment or spawning events, and fundamentally driving energy flow through food web interactions (Jones and Mackereth, 2016; Stockwell et al., 2014). Within large complex ecosystems such as Lake Superior, the daily movement patterns of organisms can contribute to nutrient usage, cycling, and dispersion (Polis et al., 1997; Welch et al., 1992).

Lake Superior is the largest freshwater lake in the world by surface area and is one of the most pristine of the Laurentian Great Lakes in terms of native species presence and water quality standards (Harvey and Kitchell, 2000; Shuchman et al., 2017). However, it is an ecosystem threatened by major anthropogenic stressors; Lake Superior is acutely affected by climate change, warming significantly faster than the global average and warming disproportionately to surrounding terrestrial areas (Austin and Colman, 2008; O'Reilly et al., 2015). There are currently more than 90 non-native or invasive species within Lake Superior, many of which have the potential to alter life histories of fish and divert energy flow pathways (Minnesota Sea Grant, 2017). Additionally, the damming of many Lake Superior tributaries has severely impacted the life history strategies of several native and naturalized fish species, altering their habitat usage, breeding success, and food web interactions (Bond and Jones, 2015; Burtner et al., 2011; Wilson et al., 2007). This fine balance between "pristine" condition and potential impacts of the anthropogenic stressors listed above emphasizes the importance of understanding what drives and shapes ecosystem processes within large complex ecosystems, like Lake Superior.

In Lake Superior, there are several well documented ecosystem subsidies that result from movement patterns of species (Ahrenstorff et al., 2011; Jones and Mackereth, 2016; Stockwell et al., 2014). Despite the potential importance of characterizing organism movement and spatial distributions, technological, financial, and logistical constraints often limit the prioritization of assessing organismal movement patterns in ecological surveys (McIntyre et al., 2015; Polis and Strong, 1996). The extent and degree to which either broad or fine-scale (i.e., day/night diel scale) movement patterns vary across parts of Lake Superior for different fish species is not yet well known. Regional variability in movement patterns within a given species might reflect differences in energy habitat coupling among regions, and if there are substantial differences in swimming speeds there may be implications for life history outcomes. Alternatively, the resource use by a given fish species within a region may affect the overall efficiency of energy transport within the region, of which fish movement can be a component. The application of my stationary up-looking acoustic survey in regions across Lake Superior was designed to provide a better understanding of how fish movement speeds and behaviours varies across the broad geographical area represented by Lake Superior.

In my third chapter I focus on testing a suite of hypotheses attempting to explain the processes underway at the productive Lake Superior Shoals Complex using acoustic survey methods and biological sampling. The function of many freshwater and marine pelagic food webs across the globe are controlled by interactions between benthic and pelagic ecosystems (Angel, 1993; Griffiths, 2010; Vadeboncoeur et al., 2008, 2002; Vander Zanden and Vadeboncoeur, 2002). These large, deep-water systems are punctuated by small, relatively shallow areas of high productivity; namely, sea mounts in marine systems, and shoals or reefs in freshwater systems (Rogers, 2018). In these areas, the food web dynamics between the pelagic and benthic zones change due to the lake bottom reaching the photic zone, making large invertebrates vulnerable to predation, and enabling benthic algal production to exceed bacterial production (Huxel and McCann, 1998).

The Lake Superior Shoals system covers an area of 52 km^2 and is in the northern central region of Lake Superior where the depth of the lake bottom rises to 6 m at its shallowest and is bordered by depths of 300 m (Manson and Halls, 1991). Similar to oceanic seamount ecosystems which host high levels of productivity and biodiversity, prior research on shoal systems in Lake Superior found increased productivity in the form of increased population diversity and density of pelagic fishes such as lake trout (*Salvelinus namaycush*) and coregonines (Schram et al., 1995). However, very little is known about the ecological processes operating at the Lake Superior shoals. One proposed mechanism for the elevated secondary productivity observed on freshwater shoal systems is the Topographic Blockage Hypothesis proposed by Houghton et al. (2010). On a Lake Michigan shoal, researchers proposed that *Mysis diluviana* preforming diel vertical migrations move up in the water column at night and slowly drift over the shoal by way of weak surface currents, then in the morning when they try to migrate back down to avoid daytime predation are stranded on the shallow shoal, thus becoming easy prey for fish (Houghton et al., 2010). Other processes observed in marine systems may be involved with increased production on freshwater shoal; the increased productivity at the Lake Superior Shoals could be due to the shallow conditions providing an increase in Benthic Algal Production on the shoal system, effectively concentrating the amount of food available for zooplankton and secondary detrital consumers as seen in marine reefs (Haas et al., 2011). Alternatively, Leeward Eddy Retention (LER) is a process also known to marine systems that predicts the retention and deposition of suspended material down current of reefs (Limer et al., 2020; Shulzitski et al., 2018; White et al., 2008); however, this has yet to be examined on freshwater reef analogues. The Lake Superior Shoals offer a unique opportunity to explicitly assess these hypotheses in a freshwater setting and demonstrate how movement of organisms can influence energy flow pathways that drive ecosystem function.

This work will help to advance the basic understanding of the contribution that fish movement makes to broader freshwater ecosystem function. Ultimately, this research may help to improve management quotas by explicitly recognizing fish movement, and ultimately better protecting fisheries while preserving the livelihoods and well-being of many Ontario and US residents.

Chapter I: A stationary up-looking platform as a novel fish survey tool for pelagic fishes in Lake Superior

Abstract

Mobile hydroacoustic surveys using ship-based down-looking transducers are widely used to estimate densities for ecologically and economically important pelagic fishes; however, this method may underestimate some population sizes due to biases introduced by the acoustic surface dead zone and ship avoidance behaviours. My objective was to compare pelagic fish density estimates of cisco (*Coregonus artedi*) acquired by a standard down-looking acoustic survey to estimates obtained by a novel stationary up-looking platform. I deployed both systems concurrently during the fall cisco spawn in Thunder Bay, Lake Superior over the course of three years. The up-looking acoustic platform density estimates were on average 6.7 times higher in the upper water column (~1 – 10 m) and 2 times higher for the whole water column (~1 – 45 m). I also found clear evidence of ship avoidance behaviour by cisco in the upper (<10 m) water column during mobile acoustic surveys; median cisco densities of ~36 fish/ha measured in the upper water column by the platform immediately before and after ship passage fell to only ~9 fish/ha when the ship passed over platform. When used to estimate commercial fishing quotas, the acoustic platform provided higher quota estimates than the mobile down-looking survey in 2020 and 2022 but estimates from different acoustic collection methods were not significantly different in 2021. The platform also indicated a better ability track migration patterns, where it detected a progressive increase each night of a three-day deployment, while this relationship would be missed by a one-night pass over a given region (typical of ship surveys). These findings have major implications for typical acoustic surveys and management of pelagic fishes

in the Great Lakes, as many managers rely on accurate acoustic estimates to help inform commercial fishing quotas and monitor the overall population trends of Great Lakes fishes.

Introduction

Mobile hydroacoustic fisheries surveys are an important tool for fisheries researchers and managers to quantify and monitor the status and trends of populations (Kubečka et al., 2009; Simmonds and MacLennan, 2005). Acoustic surveys are used to estimate fish densities over broad, spatially diverse areas and allow for sampling in areas where traditional netting methods are impractical due to size of the ecosystem or concern over sampling mortality on sensitive species (Qiao et al., 2006; Warner et al., 2012; Yule et al., 2007). When deployed as mobile surveys, acoustic surveys can sample large spatial scales much faster than standard net-based surveys (Yule et al., 2009). The use of acoustics for fisheries surveys relies on the emission of high frequency sound pulses from a transducer that can both transmit and receive pulses and measure received pulses in decibels (dB), returning echoes of sound from targets like fish and solid surfaces like the lakebed (Haslett, 1969). The swim bladder of fishes is a critical feature for sound to resonate from (based on density differences between air and water), and because swim bladder volume scales with fish length, their echoes can be used to estimate fish size (Foote, 1980; Love, 1971). In the Laurentian Great Lakes, mobile down-looking surveys have been used to follow the status and trends of pelagic fishes (Parker-Stetter et al., 2009; Yule et al., 2012). For example, acoustic surveys are employed to provide density estimates and help set quotas for commercially important pelagic fish species like cisco (*Coregonus artedi*) in Lake Superior (Fisch et al., 2019a; Pratt et al., 2016; Yule et al., 2012). Lake Superior cisco management has faced challenges on multiple fronts as their recruitment is sporadic and in decline (Vinson et al., 2016). Cisco are mainly targeted commercially for their roe, with annual yields of over 1,000 metric tons of fish biomass, across many state/provincial management jurisdictions and various tribal organizations (Pratt et al., 2016).

Due to large scale management and sustainability challenges like that of cisco in Lake Superior, acoustic methods have become commonly deployed in the Great Lakes to monitor the population status and trends of fishes region wide. Their widespread use is mainly due to their ability to minimize biases related to gear efficiency and fish availability (Davison et al., 2015; Hoffman et al., 2009) in a non-destructive manner (Guillard and Vergès, 2007). Gear efficiency is a bias metric based on what percentage of fish that encounter a sampling method and are successfully captured by it; for example, a fish species encountering a trawl net that is better able to evade the net than other species in the survey would cause the trawl net to have a low efficiency at capturing that species, resulting in biased catch estimates (Davison et al., 2015). Fish availability is a bias metric based on what fish are vulnerable to the sampling technique; for example, if a trawl net is built of material with a mesh spaced wider than the body diameter of small fishes, it would fail to capture these fish, resulting in a strong availability bias against smaller sized fish in the survey. Acoustic surveys reduce error and bias from both concerns of efficiency and availability bias as sound waves do not discriminate among different sizes or speeds of fish and cannot be visually or physically detected/avoided by fish, which functionally removes the typical concerns around net-based surveys. As a result, acoustic methods are thought to provide less biased estimations of a total biomass for the sampled area than traditional net-based collection methods (Stockwell et al. 2007; Yurista et al. 2014). However, acoustic surveys can also be subject to encounter efficiency bias if fish density is so high that some fish are obscured by the bodies of others, which can result in density underestimation. This concern is considered negligible in comparison to net-based efficiency biases (Barange et al., 1996), especially when applied to moderate- to low-fish density ecosystems like Lake Superior (Stockwell et al., 2007).

Despite the several positive attributes of acoustic surveys, limitations exist. Acoustic measures of fish density may be readily available, but determination of species composition is generally only achievable in conjunction with net sampling. Additionally, there are two known acoustic dead zones (DZ) in traditional down-looking acoustic surveys that introduce availability bias; the bottom DZ and the surface DZ. The bottom DZ is the area near the bottom of a given acoustic survey where slope and roughness of bottom bathymetry obscures fish from the survey. This zone has been well studied (Mello and Rose, 2009; Totland et al., 2009), and can be addressed with correction factors, as in the case for walleye pollock (*Theragra chalcogramma*) in the bottom DZ of the Bering Sea (Kotwicki et al., 2013). The surface DZ consists of a portion of the water column closest to the transducer and is present due to a combination of near field exclusion zones, deployment vessel draft interference, transducer deployment depth, and surface bubble interference (Parker-Stetter et al., 2009; Totland et al., 2009). Additionally, some fish species may be disturbed by the presence of a large ship and exhibit avoidance, diving, or herding behaviour introducing additional availability bias to the surface DZ, with both processes ultimately leading to an underestimation of fish density of certain species that tend to occupy the upper portion of the water column (DuFour et al., 2018; Guillard et al., 2010). Partially due to these complications and due to the lack of tools able to assess it, the surface DZ has received less attention in the acoustic literature than the bottom DZ.

One method currently being used to correct for the limitations associated with down-looking surveys is the increasing use of up-looking acoustic surveys (De Robertis et al., 2018; Elliott et al., 2021; Grow et al., 2020). Up-looking surveys can be done actively using tow bodies or passively from moored stationary platforms equipped with upward facing acoustics (De Robertis et al., 2018; Elliott et al., 2021; Grow et al., 2020). These survey methods can generate fish density estimates across spatially diverse areas and, in the case of stationary acoustics, can be used to detect fish movement patterns (De Robertis et al., 2018; McKee, 2019). A recent study on pelagic fishes in Lake Superior utilizing a multi-directional acoustic tow body discovered that density estimates for pelagic fish species may be 2.5 times higher than previously thought due to the loss of the upper DZ in traditional down-looking surveys (Grow et al., 2020). Similar studies utilizing up-looking acoustic technology have been deployed in Lake Ontario and discovered that there were 2 times as many alewife (*Alosa pseudoharengus*) than traditional down-looking acoustic methods were estimating, and that these alewife were exhibiting previously undocumented diel vertical migration (DVM) patterns (Elliott et al., 2021; Riha et al., 2017). These findings highlight the need for improved acoustic survey methods to accurately investigate fish movement patterns in aquatic ecosystems that account for near-surface distributions of fishes.

In this chapter, I assess the viability of a stationary up-looking platform as a novel fish survey tool in freshwater systems. This stationary platform deployment may provide more accurate fish density estimates in surface waters specifically, which are generally not well characterized by traditional sonar methods. If down-looking acoustics are underestimating fish density in Lake Superior particularly in the upper water column, I would expect to see higher fish density estimates from the up-looking surveys compared to down-looking surveys, especially in the upper section of the water column, while seeing little difference between methods for the lower portions of the water column. In addition, if any underestimation observed is due to ship avoidance behaviours, I expect to see fewer fish in the upper water column with the up-looking survey when the down-looking survey ship passes over or near the up-looking platform. These potential issues with down-looking surveys could have significant impacts on cisco quota determination as they are a pelagic species that are vulnerable to surface DZ and ship avoidance-based biases. I also evaluate fish density at a single location over the course of several days using the stationary platform to better understand temporal differences in cisco spawning migrations. Where typical mobile surveys only provide a brief snapshot of the density at a given location/area, and identical regions are rarely surveyed consecutively in the interest of achieving greater spatial coverage.

Methods

Survey design

Description of acoustic surveys

Both acoustic systems were deployed from the research vessel (R/V) Superior Explorer, operated by the Ontario Ministry of Natural Resources and Forestry (OMNRF) between October 29 – November 23 during 2020-22. The stationary up-looking platform (‘acoustic platform’ hereafter), manufactured by The Oceanscience Group Ltd. (Poway, CA, USA), was equipped with an upward-aimed 121 kHz 8° circular split-beam transducer operated with a BioSonics, Inc. (Seattle, WA, USA) DT-X Sub (Fig. 1.1), powered by 2 to 4 DEEPSEA (San Diego, CA, USA) 12V batteries (Fig. 1.2). The ship acoustic system consisted of a single downward facing 70 kHz 5° circular split-beam transducer deployed off the starboard side of the ship via a pole mount to a depth of 1 m below the lakes surface, connected to a separate BioSonics DT-X system and laptop. These two frequencies have been shown to provide similar results (see review in Yule et al., 2009), and are recommended by the Standard Operating Procedures for Fisheries Surveys in the Great Lakes (Parker-Stetter et al., 2009). Acoustic data were collected with acquisition thresholds set at -100 dB (dB), pulse durations set at 0.4 ms and realized ping rates of 2 pings per second for the ship and 5 pings per second for the acoustic platform. Acoustic platform deployment locations were determined similarly to methods in De Robertis (2018), using previous (2018) down-looking mobile fall cisco surveys to identify areas of representative fish density in Thunder Bay as well as their proximity to current survey transects for the given year (Fig. 1.3). For both survey methods, each night of sampling began after twilight and ended before sunrise, lasting approximately seven hours and twenty minutes of sampling per night. The acoustic platform was deployed from one to three nights at each location in each year (Table 1.1). For the ship, each transect was approximately 80 km long and ship speed was approximately 11 km/h. A water temperature profile was collected with a HOBO mini logger (ITM Instruments INC., Toronto, ON, CAN) at each acoustic platform deployment location to provide an accurate sound speed and absorption coefficient to the acoustic data (Parker-Stetter et al., 2009). For each night of the ship survey, I recorded when the ship passed closest to the acoustic platform along its transect (range of 180 m – 370 m) in order to directly examine any ship avoidance behaviour exhibited by the fish, as recorded by the acoustic platform.

Pelagic gillnet survey

Concurrent to acoustic sampling, 28 pelagic gillnet sites were sampled between October 29 – November 23 during 2020-22 along acoustic transects (Fig. 1.4). The suspended gillnets were 10 ft by 100 ft panels of 1.5” – 6” clear monofilament graded stretch mesh. All nets fished for < 24 hours (overnight sets). The gillnets were suspended (canned) 10 m below the water’s surface regardless of bathymetric depth.

Data analyses

Data processing and preparation

The data from the two acoustic survey methods were processed with Echoview Software Ver. 11 (Echoview Software Pty. Ltd., Hobart, TAS, Australia). Field calibrations of the ship and acoustic platform echosounders were carried out using a 38 mm tungsten carbide sphere and applied following Foote et al. (1987). I created near-field and bottom exclusion lines and removed regions of bad data in the ship and acoustic platform echograms (Parker-Stetter et al., 2009). For the acoustic platform, the surface line was adjusted to eliminate obvious noise from wave action and entrained air bubbles, which is equivalent to adjusting the bottom exclusion zone in down-looking surveys. The ship-based down-looking transducer's surface exclusion depth was set at 6.6 m, while the acoustic platform's surface exclusion zone varied across deployments and with surface conditions (Table 1). The bottom exclusion zone was set to 0.5 m off the bottom or at a maximum of 45 m (MNDNR and OMNRF acoustic cisco survey SOP) for the down-looking survey and was equal to the deployment depth minus the sum of the 1.2 m nearfield exclusion and the 1 m transducer mount depth for the stationary up-looking survey (Table 1.1). In order to focus the analyses on cisco primarily, I used a minimum target strength (TS) detection threshold of -41.20 dB (within single target detection method 2 in Echoview) to identify single targets and eliminated any targets > -31.48 dB based on the size of the largest cisco sampled by the OMNRF gillnets (496 mm). It follows that the applied -41.20 dB threshold eliminated macroinvertebrates, smelt, and any young-of-year (YOY) coregonines but retained all adult cisco (>165 mm; Rudstam et al., 2003). This dB threshold is in line with the MNDNR and OMNRF acoustic cisco survey SOP considering adult cisco to be those fish targets greater than 165 mm. Additionally, this survey takes place during the season that cisco are known to congregate in Thunder Bay to spawn and the concurrent OMNRF gill nets caught nearly exclusively cisco (see results). Therefore, all fish density estimates I derived from the acoustic data were assumed to be cisco density estimates. The minimum and maximum range-dependent threshold of dB was also applied to the volume backscattering strength (S_v) echogram to ensure that density estimates were calculated from cisco sized targets (Parker-Stetter et al., 2009). The S_v is defined as the ratio of intensity of sound scattered back in the direction of the transducer by a unit volume to the intensity of the incident plane wave and expressed in dB units (Iida et al., 1996). Each mobile transect or stationary deployment was divided into 20-minute intervals (for the mobile survey, 20 min at ~11 km/h is ~3700 m cells) to ensure that each cell was an independent sample as suggested in Hrabik et al., (2006) while targeting a reasonable number of single echo detections or SED's.

In order to prepare the stationary up-looking and ship-based data for statistical analyses and comparisons between methods, the data for the whole water column (~1 m – 45 m) were initially examined as a single unit to reflect current standard practice of obtaining cisco density estimates for management purposes. Subsequently, the data from the entire water column were split into two depth layers and reanalyzed. The upper water column layer was defined as ~1 – 10 m based on the recommendation of Yule et al. (2012) to improve cisco density estimates in this layer during spawning periods, 10 m being a typical measurement increment in the Lake Superior acoustic surveys (Rudstam et al., 2009) and a similar split (~4 – 9 m) in recent up-looking acoustic work (Grow et al., 2020). The lower water column layer was defined as that ranging from 10 – 45 m to examine how the stationary up-looking unit performed within the portion of the water column that is adequately sampled by standard down-looking acoustics.

For each analysis of up-looking and down-looking data (i.e., whole water column as well as separate water layers), cisco density ($D_{i,t,k,m}$) for each individual 20-minute cell i, each paired stationary acoustic deployment and down-looking transect location t, water column layer k, and survey method m were calculated with the echo integration method by:

$$D_{i,t,k,m}(\text{number/ha}) = 10{,}000 * ABC_{i,t,k,m}\sigma_{i,t,k,m}^{-1}. \qquad \text{(eq 1.1)}$$

where ABC is the area backscattering coefficient for each combination of i, t, k, and m that provided greater than 20 SEDs available within each cell (Parker-Stetter et al., 2009). The ABC (in m^2) was calculated by multiplying the mean thickness of the beam (in m) being integrated by the mean volume backscattering coefficient of the domain (s_v,, in m). By convention, S_v is equal to $10^{sv/10}$, where S_v is the mean linearized volume backscattering strength then converted to decibels (dB). The respective ABCs were scaled by σ (in m^2); their respective mean backscattering cross sections ($\sigma_{i,t,k,m}$), which was calculated by $10^{TS/10}$, where TS is the mean linearized target strength of the SEDs then converted to the domain in dB. Finally, I applied a 10,000 multiplier to convert fish/m^2 to fish/ha. When fewer than 20 SEDs (but greater than 0) were available in a cell, I altered equation 1.1 so that the mean TS for each layer used for scaling was the average for the entire transect/deployment. When fewer than 20 SEDs were available in a layer/transect combination, I used a global estimate of TS based on averaging TS in that layer over all seven deployments/transects. If there were no SED's in a cell it was assigned a density of 0 fish/ha.

I also examined the upper water column cisco density detected by the acoustic platform in the 20 min cell in which the ship passed closest to it and compared that density to those of the cell 20 min before and after the pass to access any possible boat avoidance effects. Additionally, I examined the cisco density detected by the ship in the upper water column to the cells before and after the pass to ensure that the area near the acoustic platform is not an area of significantly lower cisco density.

In order to relate the data obtained from both survey methods more directly to management applications, cisco density estimates for the whole water column were converted to spawner biomass $B_{i,t,k,m,y,w,s}$ for each method across survey years, y, by multiplying cisco density by the mean cisco weight w in kg from the gillnet survey and the ratio of females from the gillnet survey s:

$$B_{i,t,k,m,y,w,s}(kg) = D_{i,t,k,m,y} * w_y * s_y. \qquad \text{(eq 1.2)}$$

I then estimated quota for the Thunder Bay region (in kg/ha) by multiplying mean spawner biomass ($B_{i,t,k,m,y,w,s}$) by the surface area of Thunder Bay (~66,600 ha) and a value of 0.1 which is based on the current management practice of setting the quota to 10% of the spawner biomass (Fisch et al., 2019b; Stockwell et al., 2009; D. , Yule et al., 2006). Finally, in order to better understand the impacts of only sampling a given area once (as is typically done during mobile down-looking acoustic surveys during the cisco spawning period), I examined temporal variation across sample night on the whole water column mean cisco density estimates obtained by the acoustic platform across three nights *n* at station TB3 in 2020 and the typical single night estimate obtained by the ship survey during a 3-night deployment using eq 1 to calculate fish density/ha each night.

Statistical analyses

The layers of the water column sampled by the acoustic platform were compared to the ship-based down-looking survey to determine whether there were significant differences in density estimates across acoustic survey methods. Due to the non-normal distribution of residuals, all cisco density data were square root transformed prior to the statistical tests in order to better meet the assumptions of normality and homogeneity of variance. First, a three-way ANOVA testing the effects of survey method m, each paired stationary acoustic deployment and down-looking transect location t, and survey year y on square root-transformed cisco densities ($D_{i,t,k,m,y}$) for each individual 20-minute cell *i* was applied to the whole water column comparison by:

$$\sqrt{(D_{i,t,m,y})} \sim m_i * t_i * y_i. \qquad \text{(eq 1.3)}$$

When this resulted in significant differences between survey methods, a separate three-way ANOVA was performed on each water column layer. For all three-way ANOVA's (n = 3) I used an α = 0.017 (after Bonferroni correction 0.05/3 for each separate three-way ANOVA) for significance testing among factor levels to account for the family-wise error rate of 0.05 and reduce the chance of a Type I error (false positive). A Tukey HSD test was applied post hoc to examine which deployments/transects contained significant differences between the ship and acoustic platform survey.

Due to the relatively low occurrence of events where the ship passed closest (within 370 m) to the acoustic platform (N = 7), I used two permutation tests for the comparison between the median cisco densities near and during the ship passing the acoustic platform. The first test was conducted on the calculated difference between median cisco densities detected in the upper water column by the acoustic platform while the ship passed over the platform and the median cisco densities of the adjacent 20 minute cells (Permutation Test, iterations = 100,000, α = 0.05), and the second test was on the difference between median cisco densities detected in the upper water column by the ship survey while it passed over the platform and the median cisco densities of the adjacent 20 minute cells (Permutation Test, iterations = 100,000, α = 0.05).

Cisco quota estimates were examined using one-way ANOVA tests (α = 0.05) comparing the two survey methods within each survey year. To examine the effect of sample night on the mean cisco density estimates obtained by the acoustic platform across three days and the typical single night estimate obtained by the ship survey at TB3 in 2020, I also used a one-way ANOVA test ($\alpha = 0.05$) to compare mean cisco densities detected each night. All statistical tests were conducted in the R Program version 3.4.0 (R Core Team, 2020).

Results

Gillnet Catch

A total of 518 fish were caught in the 28 gillnet samples over all years. The catch was almost exclusively adult cisco (N = 517) that were all between 217 mm and 496 mm in total length (Table 1.2); other species in gill net catches were represented by a single lake trout (711mm) captured in 2020.

Whole Water Column Comparisons

A three-way interaction between acoustic method, location, and year was not significant for cisco densities across the whole water column (three-way ANOVA, $F_{2,615} = 2.02$, $p = 0.134$; Table 1.3). However, all three two-way interactions were significant for whole-water column cisco densities: the interaction of survey method and location ($F_{2,615} = 29.06$, $p < 0.001$), survey method and year ($F_{2,615} = 15.50$, $p < 0.001$), and location and year ($F_{2,615} = 56.47$, $p < 0.001$; Table 1.3). Based on a Tukey HSD test, mean cisco densities obtained from the acoustic platform were significantly higher ($p < 0.017$) than the traditional down-looking acoustic survey at TB1 in 2020 and 2021, and at TB3 in 2020 and 2022, but at TB2 in 2021 the ship obtained significantly higher cisco densities than the acoustic platform (Fig. 1.5). Cisco densities were not statistically different among methods across the rest of the locations and years included in the study ($p > 0.017$; Fig. 1.5).

Depth-Specific Comparisons

I observed significant variability in the differences between methods depending on depth strata. A three-way interaction between method, location, and year was not significant for cisco densities across the whole water column (three-way ANOVA, $F_{2, 627} = 3.54$, $p = 0.030$, $\alpha = 0.017$; Table 1.3). The same three two-way interactions were significant for differences in cisco densities for the upper water column (Table 1.3), the interaction of survey methods and location ($F_{2, 627} = 6.50$, $p = 0.002$), survey method and year ($F_{2, 627} = 11.69$, $p < 0.001$), and location and year ($F_{2, 627} = 41.25$, $p < 0.001$). Cisco density in the ~1 – 10 m layer was significantly higher in the acoustic platform-based survey compared to the ship-based survey for every transect ($F_{1, 627} = 224.48$, $p < 0.001$), although based on the Tukey HSD test the difference varied across location and sample year (all $p < 0.001$; Fig. 1.6A).

For the deeper 10 – 45 m layer, the three-way interaction between method, location, and year was significant ($F_{2, 633} = 6.60$, $p = 0.002$). Based on a Tukey HSD test, mean cisco densities obtained from the traditional down-looking acoustic survey were significantly higher ($p < 0.05$) than the acoustic platform at TB2 and TB3 in 2021 but not significantly different at any deployment location in 2020 or 2022 ($p > 0.0017$; Fig. 1.6B).

Ship Avoidance Comparisons

I observed a significant decrease in the median cisco density estimates for the acoustic platform within the upper water column in the 20 min cell closest to the ship's passage compared to the two adjacent 20 minute cells compared to what would be expected from random (permutation test, iterations = 100,000; $T = 48.70$; $p = 0.034$; Fig. 1.7). In the nearby 20-minute cells, fish density estimates were ~36 fish/ha in upper water column, but when the ship passed over platform, they fell to ~9 fish/ha. By comparison, the ship detected significantly higher median cisco density estimates in the upper water column in the 20 min cell closest to its passage over the acoustic platform compared to adjacent 20 minute cells (iterations = 100,000; $T = 23.61$; $p = 0.032$; Fig. 1.7), with median cisco densities of ~24 fish/ha in the 20 minute cell passing over the stationary acoustic platform compared to ~0 fish/ha in the adjacent 20 minute cells, suggesting that the decrease in upper water column cisco density detected by the acoustic platform when the ship was passing closest to it was not simply an artefact of lower fish densities over the location where the platform was deployed.

Spawner Biomass Estimates

Based on whole water column estimates, there was a significant interaction between survey method and year for cisco spawner biomass estimates (Two-way ANOVA, $F_{2, 623} = 9.79$, $p < 0.001$; Table 1.4). The follow up Tukey test found that cisco spawner biomass estimates were significantly higher from the acoustic platform survey compared to those from the ship in 2020 ($p < 0.001$), but there was no significant difference between estimates in 2021 ($p = 0.76$) or 2022 ($p = 0.21$; Fig. 1.8).

Temporal Comparisons

There was a significant effect of sample night on the mean cisco density estimates at TB3 in 2020 (One-way ANOVA; $F_{2, 105} = 3.80$, $p = 0.026$). A follow up Tukey test found that the platform recorded significantly higher mean density estimates on night three compared to night one ($p = 0.02$) and the platform recorded significantly higher densities on night one, two, and three compared to the ship densities recorded on night one ($p < 0.001$; Fig. 1.9).

Discussion

The stationary acoustic platform provided significantly (6.7 times) higher estimates of cisco density compared to the traditional ship-based down-looking survey in the upper water column across all survey sites, and in two of the three sites surveyed for the whole water column. Further, estimated cisco densities obtained by the acoustic platform were 6.7 times higher than those obtained by the traditional ship-based survey for all seven transects within the upper ~1 – 10 m of the water column. I found that average cisco density estimates for the whole water column were approximately 2-fold greater (or 41 fish/ha on average) when using the acoustic platform across all sites compared to the traditional ship-based down-looking survey method, consistent with other up-looking acoustic surveys in the Great Lakes (Grow et al., 2020; Riha et al., 2017). In the most extreme case, TB1 in 2020, the acoustic platform detected 4.3 times more fish per hectare than the ship-based system. However, there was a lack of difference and even a potential reversal in trends observed at the TB2 site that may reflect differences in sampling effort. Notably, the TB2 acoustic platform deployment location had the least nights sampled (3 nights) compared to other sites (4 nights at TB1 and 6 nights at TB3).

Beyond consistent and significant differences in fish densities observed in the upper water column, ship avoidance behaviour by cisco in the upper (<10 m) water column was more directly observed in this study by examining changes in cisco densities in the time preceding and following the ship passing over the acoustic platform; platform-based median cisco densities experienced a 5 times decrease when the ship passed directly over the platform (close to the aforementioned 6.7 times difference observed across both whole surveys) compared to adjacent 20 minute cells where the ship was not present. In examining the down-looking data obtained by the ship, I was able to confirm that this difference was not based on the platform's location itself having lower cisco densities, as the down-looking survey detected substantially higher cisco densities while passing directly over the platform compared to the densities in the areas right before and after it passed the platform (but comparable to other areas along the transect). These findings are supported by other recent work in the Great Lakes that have suggested that boat avoidance behaviours of pelagic fishes are especially notable in surface waters under large vessels (the R/V Superior Explorer is ~17 m in length; (DuFour et al., 2018); also observed in a similar mobile up-looking survey by Grow et al., 2020). This has major implications for typical acoustic surveys and management of pelagic fishes in the Great Lakes, as fisheries managers rely on accurate acoustic estimates to help inform quotas and monitor the overall population trends of Great Lakes fishes. If fish are indeed avoiding surveys as they are typically conducted (e.g. from mobile ships under steam), then quota estimates could be significantly underestimated.

Similarly, the acoustic platform either provided higher quota estimates or matched the traditional down-looking survey in its quota estimates, and did so more efficiently in terms of use of available resources and time in the field. Typical surveys are conducted over a ~6-hour period at night, navigating in darkness, and require multiple nights of ship time, during typically adverse November weather conditions, to collect sufficient data to generate cisco density estimates. By contrast, the deployment and retrieval of an acoustic platform (or array of acoustic platforms) can be done at any time of day, allowing for the work to be done in the safest conditions possible, in a much shorter amount of ship time and demand on field staff. Deploying/retrieving the acoustic platform takes less than 20 minutes, thus an array of three or four units could easily be deployed or retrieved over the course of a single field day in good conditions after collecting data for one to several nights. These platforms can each be programed to record data on a set schedule and could remain deployed for weeks at a time depending on battery capacity and deployment scheduling. In the present study, I recorded 85 hours of non-stop acoustic data off a four-battery deployment, which could easily be programed to be spread out over multiple weeks (recording discrete periods of data several times daily). For instance, De

Robertis et al. (2018) were able to deploy a three-unit array of stationary up-looking acoustic platforms for ~70 days in the Bering Strait and obtained comparable walleye pollock spawning density estimates to ship based surveys by scheduling the platforms to turn on for ~1.5 minutes at the top of every hour. Though not the focus of the current study, data collected from this study could easily be used to determine the optimal sampling schedule required to provide adequate fish density estimates for a given fish population. Integrating acoustic platforms into fisheries management practices has the potential to not only provide less biased fish density estimates but also save a considerable amount of hazardous and expensive ship time hours by resource management staff.

Another drawback of current ship-based acoustic methods is that they trade temporal detail for increased spatial coverage. In other words, ship-based surveys are done in a relatively short time window (e.g., just two to three nights in November), and as such could easily miss spawning aggregations and finer temporal behaviours exhibited by the fish of interest, ultimately limiting our full understanding of the true standing stock available for safe harvest, which has significant implications for quota estimates. An array of multiple (3-4) stationary platforms could help address this issue as they could address both spatial coverage and could be deployed over a longer period to provide a better estimate of peak spawn numbers and/or provide a more representative estimate of density in a particular area. In the present study, this was evident in my three-night deployment at TB3 in 2020 (Figure 6), where each night the stationary acoustic platform recorded progressively higher cisco densities as the spawn likely began to reach its peak while the ship only sampled the first night resulting in a much lower estimate.

More research is necessary before prescribing lake wide correction factors to traditional mobile down-looking acoustic survey fish density estimates, but for the present location, study species, and vessel, I would recommend applying a 6.7 multiplier to cisco density estimates obtained in the upper 10 m of the water column from ship-based acoustics to better account for standard survey biases, assuming the difference in density estimates between the two methods is not simply a function of spatial variability. This assumption is reasonable as I am integrating the stationary estimates across multiple locations and nights. Similar methodology was deployed to estimate a population of spawning fish over a much larger area, which demonstrated that relatively few sample locations (3 – 5) were necessary to provide fish density estimates comparable to standard mobile surveys (De Robertis et al. 2018). Additionally, recent mobile up-looking surveys over a large region in Lake Superior saw similar magnitude of differences in detected fish densities in the upper water column between standard down-looking and up-looking surveys as those reported here (Grow et al., 2020) Aside from the need to test this survey method in other locations and for different species before making large scale corrections, other studies have shown that for some fish species, transducer orientation may also differ on backscatter readings. In a recent study on caged European whitefish (*Coregonus lavaretus* L.) of known size classes, their up-looking unit obtained consistently greater TS values than paired down-looking transducers (Wanzenböck et al., 2020). However, when the authors calculated the estimated total lengths of single targets via linear regression, they found that the up-looking TS values produced predicted lengths much closer to the actual fish lengths of fish included in the experiment. This observation provides additional support for up-looking acoustics to be utilized for obtaining accurate fish density estimates, especially when there is interest in knowing the size structure of the fish community.

One drawback of the up-looking acoustic survey is that the main DZ of concern is expected to shift to the bottom of the water column; however, this impact is already present to some degree in down-looking acoustic estimates. In my study within the 10 – 45 m/lakebed layer, estimates between the platform and down-looking surveys were more similar. Overall, the trend of the acoustic platform detecting higher cisco density estimates reversed, with the ship estimates being 1.8 times higher on average than the acoustic platform estimates, but this relationship was only significant for two locations (TB2 and TB3) in a single year (2021). This higher density in the lower water column in down-looking vs. up-looking surveys could be due to the biases introduced by the transducers near-field exclusion zone being transferred to the bottom of the water column with this acoustic arrangement. However, in Lake Superior, cisco inhabit waters of 20 m on average at night (Rosinski et al., 2020) and are targeted by commercial nets in waters < 10 m during their November spawning period (Yule et al., 2012). As such, the impact of this bias would be expected to be lower than the biases introduced by the upper water column DZ in traditional down-looking surveys when considering pelagic species like cisco, but could be something to consider for attempting to survey more benthic species like lake whitefish. As expected, in the present study focusing on pelagic species the density of cisco in the lower water column was only significantly lower in the platform survey in two out of seven deployments.

The evidence from this study suggests that the benefits provided by stationary up-looking surveys have the potential to outpace the uncertainties associated with the method with further development. With further study and modifications around platform-based survey design, stationary up-looking surveys could provide low-cost and low-effort acoustic surveys of pelagic fishes in freshwater ecosystems compared to current mobile acoustic methods. Up-looking platforms appear to better characterize the upper water column than current mobile acoustic methods, with very little loss of info at greater depths.

Tables

Table 1.1. Year, latitude, longitude, mean surface exclusion depth, bottom exclusion depth (Bottom depth – 1.2 m nearfield exclusion plus 1 m from platform height) and nights deployed each year for all fall acoustic platform deployments in Thunder Bay, Lake Superior.

Location	Year	Latitude	Longitude	Mean Surface Exclusion Depth (m)	Bottom Exclusion Depth (m)	Nights Deployed
TB1	2020	48.47091	-88.96392	3.5	29.8	2
TB2	2020	48.43092	-89.09435	1.5	38.1	2
TB3	2020	48.34828	-89.11034	3.4	34.2	3
TB2	2021	48.43966	-89.07544	2.5	38.8	1
TB3	2021	48.30215	-89.08254	5.4	23.6	2
TB1	2022	48.4706	-88.96368	2.2	30.4	2
TB3	2022	48.34992	-89.11034	4.3	33.4	1

Table 1.2. Summary of cisco gillnet data across years (total number of cisco caught, percentage of catch female, mean cisco weight and harvest) and mean cisco quota estimate (kg) by acoustic survey method in Thunder Bay, Lake Superior. Harvest provided by the Ontario Ministry of Northern Development Mines Natural Resources and Forestry (Upper Great Lakes Management Unit Lake Superior, 2022).

Year	# Cisco	Percent Female	Mean Weight (kg)	Method	Harvest (Thousands of kg)	Mean Quota Estimate (Thousands of kg)
2020	240	45%	0.373	Ship	122.1	42.5
				Platform		123.0
2021	165	61%	0.484	Ship	123.1	151.7
				Platform		134.8
2022	112	44%	0.376	Ship	-	30.4
				Platform		58.7

Table 1.3. Three-way ANOVA results for acoustic cisco density estimates for the whole water column and the two water column layers. The effects of acoustic platform or ship survey method, location, year, and an interaction between them all was tested in the models. For all ANOVA's, a Bonferroni α value of 0.017 was used to access significance.

Water Column Layer (m)	Model Factor	df	Mean Squares	F-Ratio	P-value
~1 – Lakebed	Method	1	456	34.99	<0.0001
	Location	2	557	42.68	<0.0001
	Year	2	165	12.66	<0.0001
	Method*Location	2	379	29.06	<0.0001
	Method*Year	2	202	15.50	<0.0001
	Location*Year	2	736	56.47	<0.0001
	Method*Location*Year	2	26	2.02	0.1340
	Residuals	615	13	-	-
~1 – 10	Method	1	2867	224.48	<0.0001
	Location	2	566	44.28	<0.0001
	Year	2	582	45.58	<0.0001
	Method*Location	2	83	6.50	0.0016
	Method*Year	2	149	11.69	<0.0001
	Location*Year	2	527	41.25	<0.0001
	Method*Location*Year	2	45	3.54	0.0297
	Residuals	627	13	-	-
10 – Lakebed	Method	1	536	69.49	<0.0001
	Location	2	108	13.96	<0.0001
	Year	2	90	11.71	<0.0001
	Method*Location	2	98	12.68	<0.0001
	Method*Year	2	367	47.59	<0.0001
	Location*Year	2	93	12.06	<0.0001
	Method*Location*Year	2	51	6.60	0.0015
	Residuals	633	8	-	-

Table 1.4. Two-way ANOVA results for acoustic cisco spawner biomass (kg) for the whole water column in 2020, 2021, and 2022. For all ANOVA's, a Bonferroni α value of 0.05 was used to access significance.

Independent Variable	Model Factor	df	Mean Squares	F-Ratio	P-value
Cisco Spawner Biomass (kg)	Method	1	6.33	18.107	<0.0001
	Year	2	10.21	29.206	<0.0001
	Method*Year	2	3.42	9.788	<0.0001
	Residuals	623	0.35	-	-

Figures

Figure 1.1. Picture of the acoustic platform deployment with a two-battery arrangement.

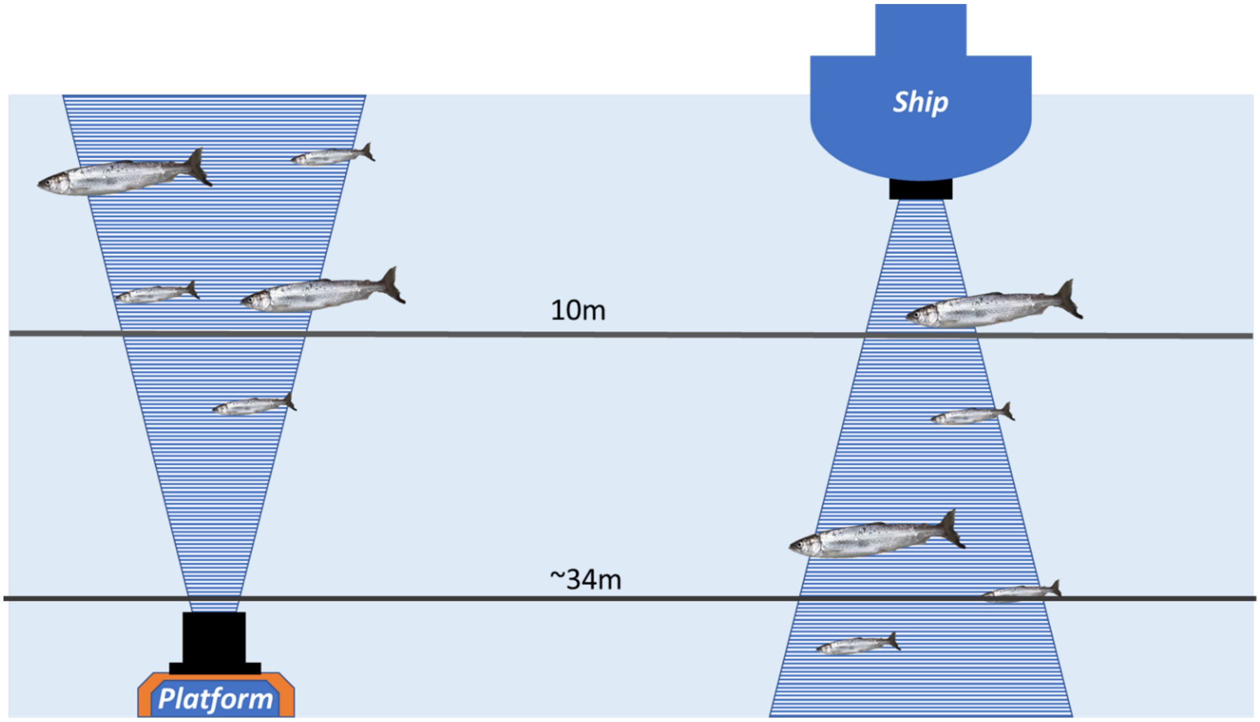

Figure 1.2. Diagram of acoustic survey methods. The typical ship-based down-looking survey method is shown on the right and the up-looking platform based acoustic survey method is on the left. The platform was deployed at 34 m of depth on average. The two water column analysis sections (upper and lower water column) are displayed with their approximate depths. The fish pictured are cisco (*Coregonus artedi*).

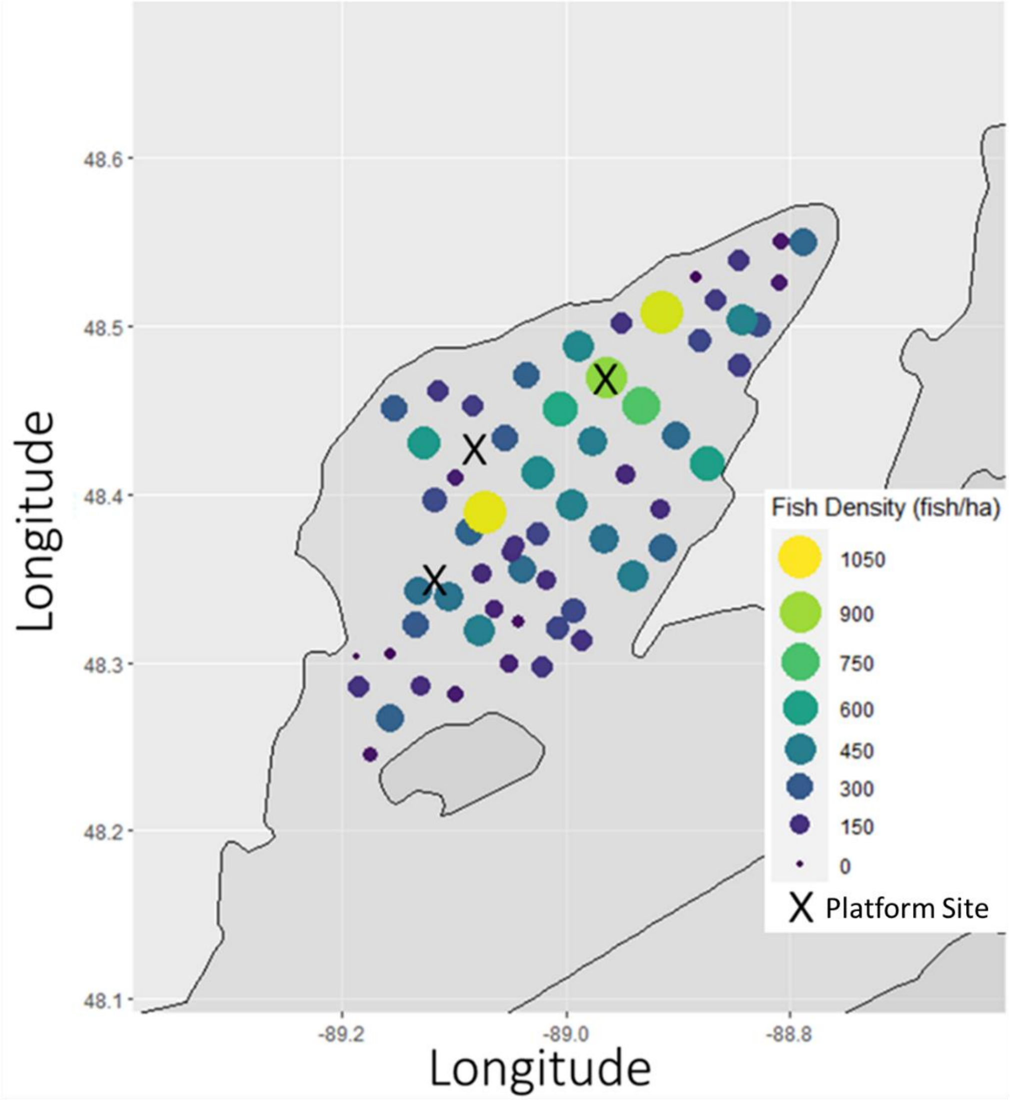

Figure 1.3. Map of fish > 250mm density from the Thunder Bay MNRF 2018 fall cisco survey used in informing potential acoustic platform deployment locations.

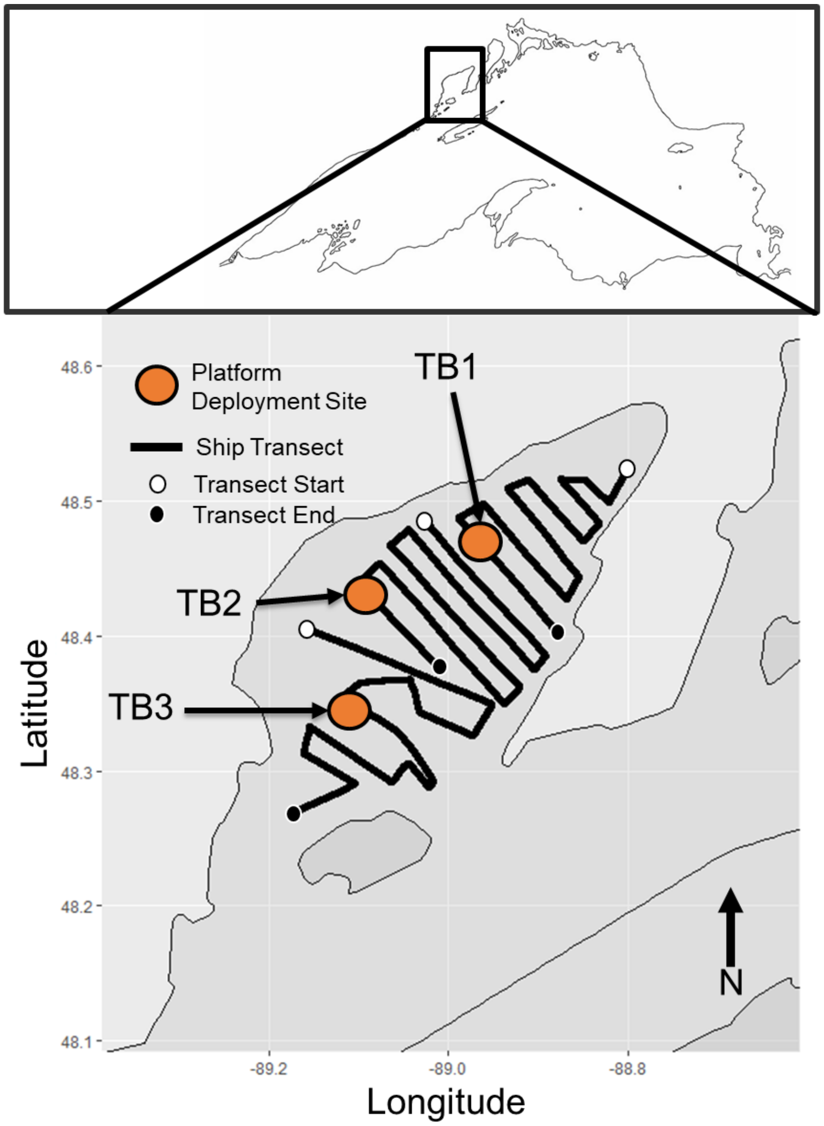

Figure 1.4. Map of acoustic platform deployment locations and concurrent Thunder Bay MNRF fall cisco survey transects. Each transect (shown in black lines) was approximately 80 km in length. All transects were sampled between October 29 – November 23 in 2020-22. Circles indicate approximate locations of cocurrent acoustic platform deployment locations sampled. The three locations/transects are Thunder Bay 1 (TB1), Thunder Bay 2 (TB2), and Thunder Bay 3 (TB3) and are abbreviated in subsequent figures. The 28 gillnets were deployed following a random sample design along each ship acoustic transect.

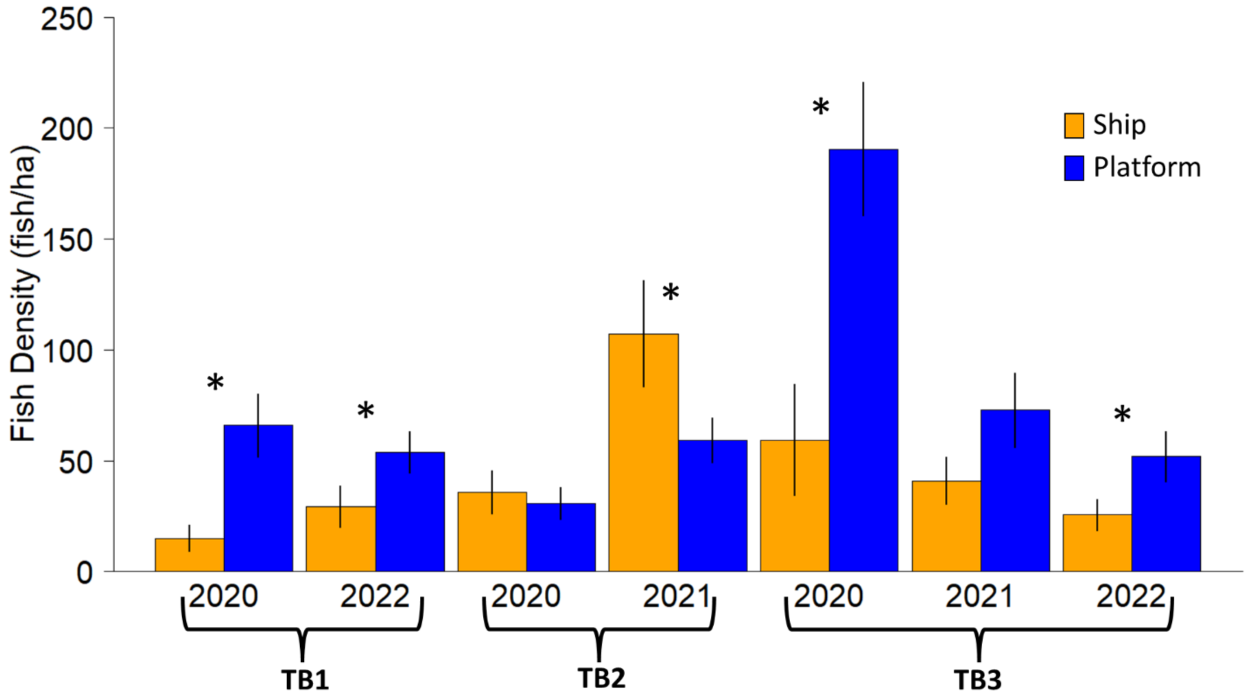

Figure 1.5. Acoustic platform vs ship whole water column (~1 – 45 m/lakebed) mean cisco density across location and year. Bars show mean cisco density from ~20 different 20-minute-long sections of the water column on the seven Thunder Bay sampling locations/transects from each night of sampling (all ship transects include one night of sampling refer to Table 1 for number of nights sampled for each acoustic platform deployment). The three locations/transects are defined in Figure 1.3. Asterisks represent significant differences ($p < 0.05$) between the two survey methods for individual deployments/transects as determined by a Tukey HSD test. Error bars indicate 95% confidence intervals around each mean.

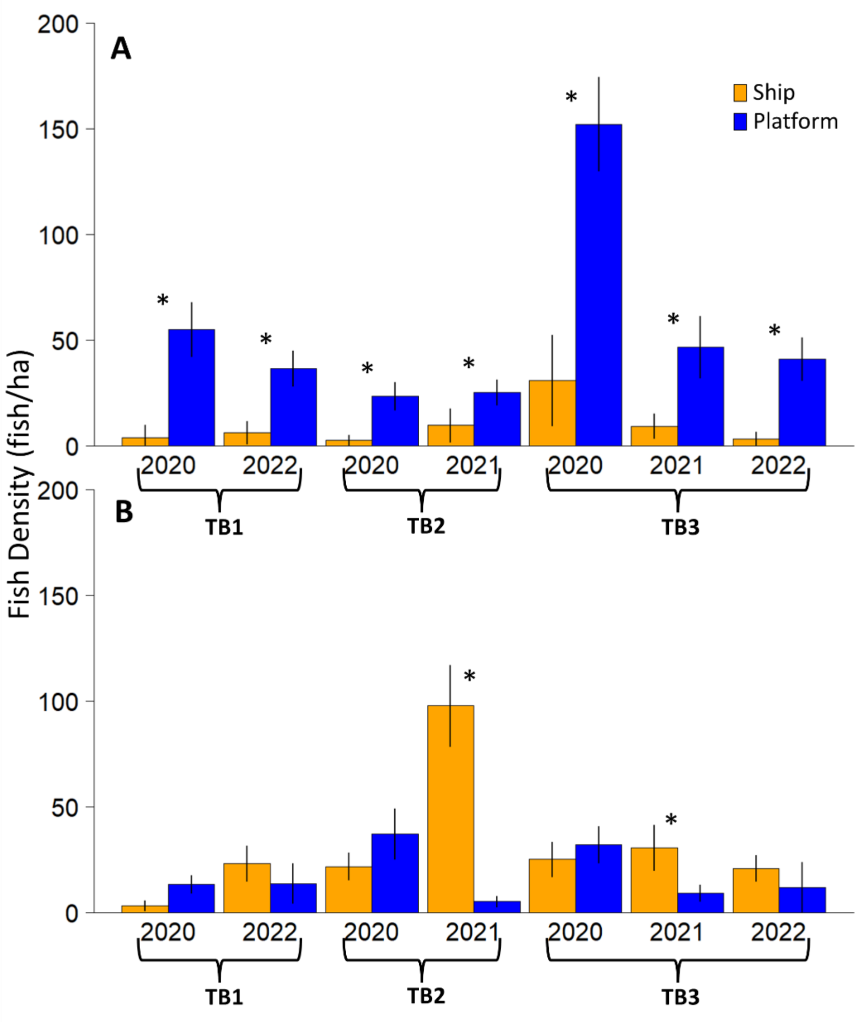

Figure 1.6. Acoustic platform vs ship upper (~1 – 10 m) water column (A) and lower (~10 – 45 m/lakebed) water column (B) cisco density across location and year. Bars show mean cisco density from ~20 different 20-minute-long sections of the water column on the seven Thunder Bay sampling locations/transects from each night of sampling (all ship transects include one night of sampling refer to Table 1 for number of nights sampled for each acoustic platform deployment). The three locations/transects are defined in Figure 1.3. Asterisks represent significant differences ($p < 0.05$) between the two survey methods within a given year and transect for individual deployments/transects as determined by a Tukey HSD test. Error bars indicate 95% confidence intervals around each mean.

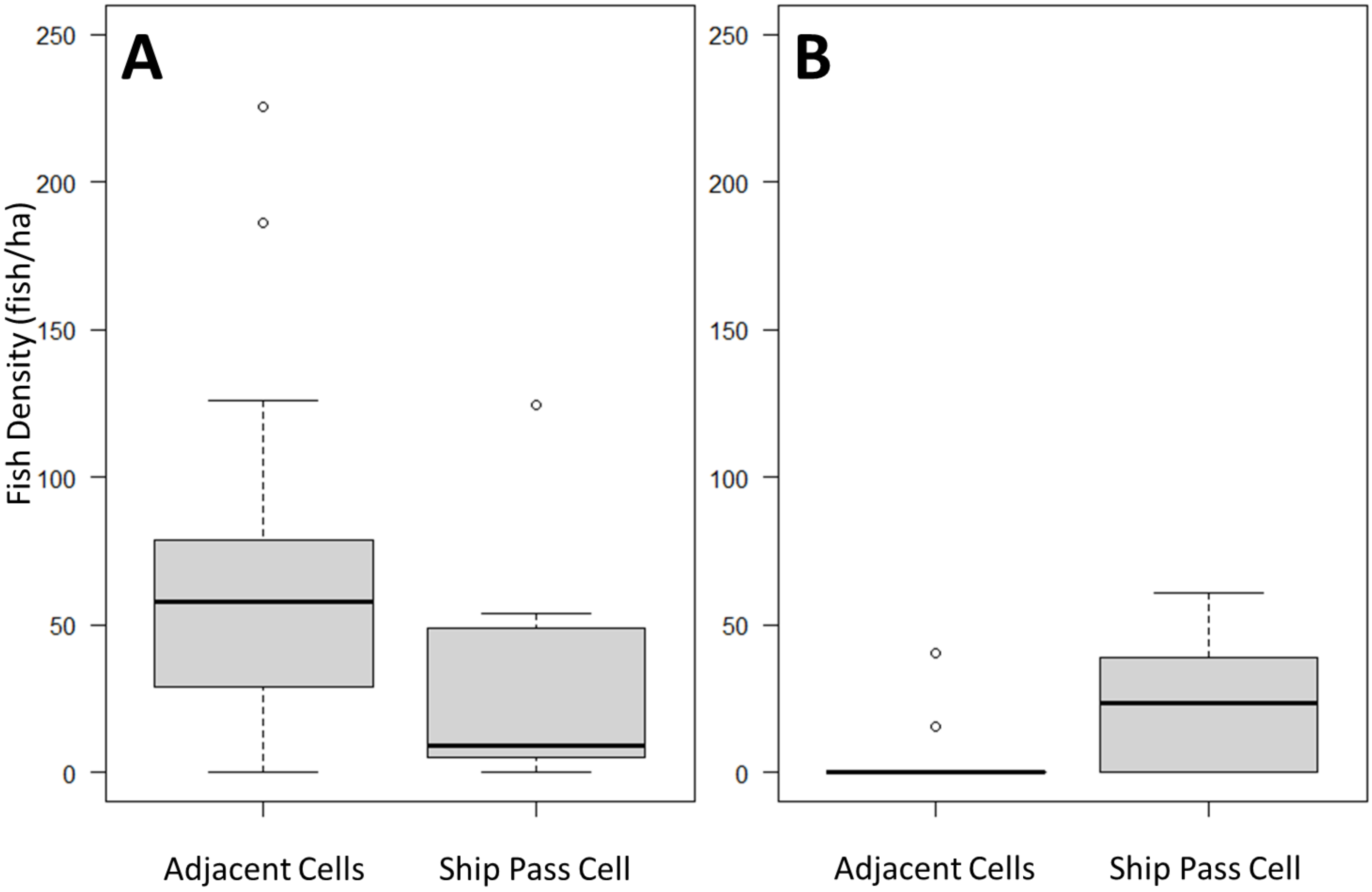

Figure 1.7. Median upper water column (~1 – 10 m) cisco density in the 20 min cell during and cells adjacent to the ship passing the acoustic platform. Bars show median cisco density in the upper water column detected by the acoustic platform (A) and the ship (B) from all years and locations/transects sampled in Thunder Bay.

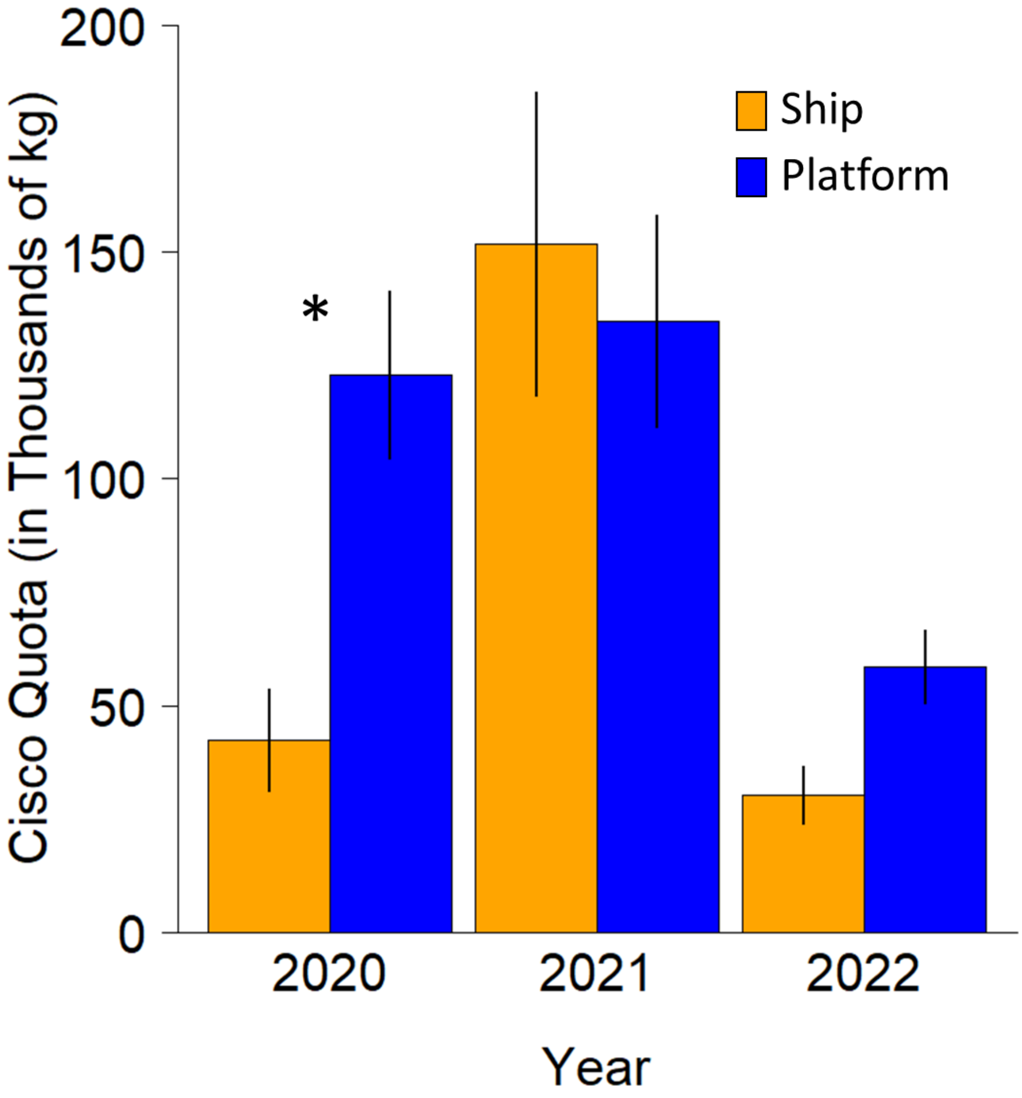

Figure 1.8. Acoustic platform vs ship whole water column (~1 – 45 m/lakebed) cisco quota biomass estimate (in Thousands of kg) each year in Thunder Bay, based on whole water column estimates of cisco density. Bars show the mean estimated cisco quota based on applying an exploitation rate of 10% spawner biomass across years. Asterisks represent significant differences ($p < 0.05$) between the two survey methods for each year as determined by a Tukey HSD test. Error bars indicate 95% confidence intervals around each mean.

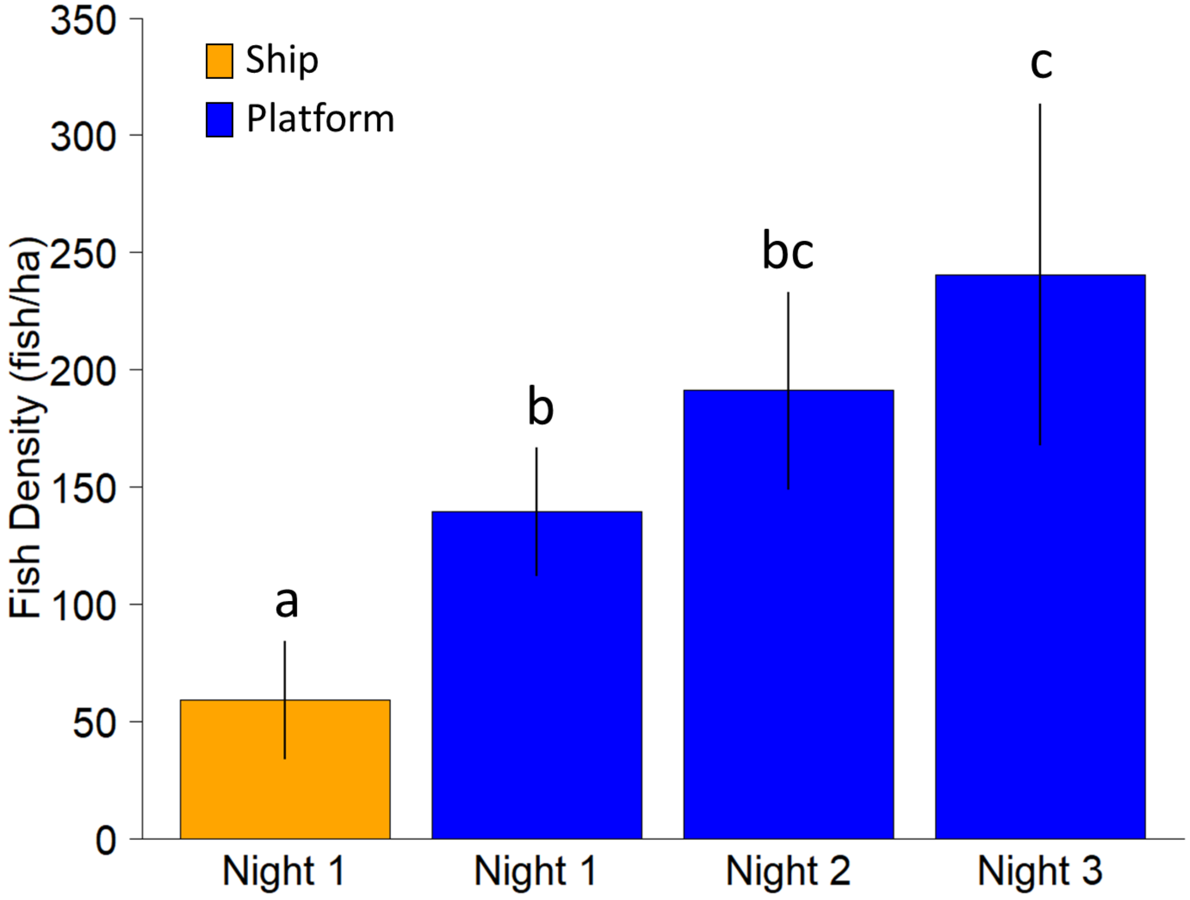

Figure 1.9. Acoustic platform and ship whole water column (~1 – 45 m/lakebed) cisco density across sample nights at TB3 in 2020. Bars show mean cisco density from ~20 different 20-minute-long sections of the water column on the seven Thunder Bay sampling locations/transects from each night of sampling. Lowercase letters represent significant differences ($p < 0.05$) between the mean density estimates as determined by a Tukey HSD test. Error bars indicate 95% confidence intervals around each mean.

Chapter II: Spatial variation and trends of fish movement patterns in Lake Superior

Abstract

Freshwater fish in large lake ecosystems undergo movement behaviours that vary across species, diel cycle, spatially distinct regions, and years, which can have major impacts on ecosystem function through the delicate balance of individual energy expenditures and inputs, scaled to the population level. However, there have been relatively few studies that measure these movement patterns directly. I sought to combat this knowledge gap by deploying an autonomous stationary up-looking acoustic platform in various regions of Lake Superior in 2021 and 2022, allowing for detailed temporal measurements of fish swim speed and depth occupancy. I found strong inter-annual differences in fish behaviour between 2021 and 2022 across all regions in Lake Superior, with 2022 having generally higher movement speeds than 2021, likely in response to shifts in the community structure of pelagic prey (e.g., the presence of a strong year class of young-of-year coregonines in 2022). Further, regional differences in relative fish movement speeds were observed across the lake. Whitefish Bay (near the Lake's outflow) had consistently slower speeds than other regions and Nipigon Bay and the Western Arm (areas of high water input) had consistently faster speeds than other regions. Although fish density estimates acquired by the platform examining the whole water column did display a clear increase in fish density in nighttime hours compared to daytime, consistent with diel-vertical migration (DVM), unexpected regional differences in fish depth occupancy were also observed across diel cycles, with few areas and size classes of fish being found higher in the water column at night vs the day, as expected with conventional DVM behaviour. Ultimately, the up-looking acoustics platform allowed for new direct insights into fish movement behaviours in Lake Superior and

indicates great potential for expanded use in improving our understanding of regional behavioural variation in large ecosystems to aid in fisheries management decisions.

Introduction

Organism movement on both fine and broad scales can be a significant driver of ecosystem function by spatially integrating nutrient cycling pathways, allowing for rapid responses to new available resources from large recruitment or spawning events, and fundamentally driving energy flow through food web interactions (Jones and Mackereth, 2016; Stockwell et al., 2014). Within large complex ecosystems such as Lake Superior, the daily movement patterns of organisms can contribute to nutrient usage, cycling, and dispersion (Polis et al., 1997; Welch et al., 1992). These movement patterns allow the connection of different spatially independent nutrient sources that can ultimately alter the overall production of the system (Polis et al., 1997).

In Lake Superior, there are several well documented ecosystem subsidies that result from movement patterns of species. For example, offshore benthic and riverine systems are connected through seasonal spawning runs by white sucker, (*Catostomus commersonii*; (Jones and Mackereth, 2016), offshore pelagic and nearshore regions are connected via coregonine spawning (Stockwell et al., 2014), and diel-vertical migration movements (DVM) by *Mysis* integrate benthic and pelagic systems in Lake Superior (Ahrenstorff et al., 2011). Diel bank migration , movement towards and away from shore, has also been observed for juvenile fish in the Apostle Islands using acoustics and netting (Gorman et al., 2012a), as well as in nearshore areas lake wide via bottom trawling (Gorman et al., 2012b). Despite the potential importance of characterizing organism movement and spatial distributions, technological, financial, and logistical constraints often limit the prioritization of assessing organismal movement patterns in ecological surveys (McIntyre et al., 2015; Polis and Strong, 1996).

There has been some recent advancement in overcoming difficulties in studying fish movements. A recent study demonstrated spatial differences in activity estimates by fish communities across Lake Superior with respect to the usage of nutrients from benthic and pelagic energy pools, deriving their estimate of fish activity from a combined methylmercury and bioenergetic mass-balance model (Wegher, 2019). This trend was also observed in a study by Grow et al., (2020), utilizing new multi-directional acoustic technology to demonstrate that fish densities vary spatially within Lake Superior, specifically with the upper water column, indicating differential spatial concentrations that may be related to biological requirements of fishes (e.g., feeding, spawning, etc.). However, the extent and degree to which either broad or fine-scale (i.e., diel) movement patterns vary across parts of Lake Superior for different fish species is not yet well known. Regional variability in movement patterns within a given species might reflect differences in habitat coupling among regions, and substantial differences in swimming speeds could have implications for life history outcomes. Alternatively, the resource use by a given species within a region may affect the transfer of energy within a region. The application of a stationary up-looking acoustic survey in Lake Superior can provide a better understanding of how spatial variation impacts fish movement speeds and DVM behaviours.

In order to better understand large freshwater ecosystem dynamics, I seek to improve our understanding of daily, regional, and annual variation in fish movement across Lake Superior using an autonomous stationary up-looking acoustic platform. This stationary platform deployment allows for detailed temporal measurements of fish swim speed and depth occupancy by size class, which are generally not characterized by traditional sonar methods. The current understanding of DVM driving deep water pelagic energy flow in Lake Superior has yet to be tested on a spatially explicit basis using direct acoustic observation (Ahrenstorff et al., 2011; Gorman et al., 2012b; Stockwell et al., 2010). If the current understanding of DVM is consistent lake wide and there are no substantial differences in prey subsidies across years, I would expect to see fishes of all size classes move shallower in the water column at night regardless of site or year, and typically slow down as schools of fish disperse. However, I expected to see considerable variation in overall fish density and average swim speeds depending on the relative dependence that location has on benthic vs pelagic resources (Wegher, 2019). Further, if the activity estimates modeled by Wegher (2019) are accurate, I would expect strong correlations across survey region between my direct movement estimates and theirs.

Methods

Survey design

Description of acoustic deployments

The stationary acoustic system was deployed from several vessels on Lake Superior. The research vessel (R/V) Superior Explorer, operated by the Ontario Ministry of Natural Resources and Forestry (OMNRF) conducted deployments between June 24 – September 21 in 2021-22 in Nipigon Bay and Whitefish Bay; the R/V Blue Heron, operated by the Large Lakes Observatory at the University of Minnesota, Duluth conducted deployments between August 19 – 31 2021 at one Western Arm site (near Bark Point, WI), and the R/V Kiyi, operated by the United States Geological Survey (USGS), conducted deployments between August 18 –September 7 in 2022 at the remaining Western Arm and Keweenaw Peninsula sites (Table 2.1, Fig. 2.1).

The stationary up-looking platform (‘acoustic platform’ hereafter), manufactured by The Oceanscience Group Ltd. (Poway, CA, USA), was equipped with an upward-aimed 121 kHz 8° circular split-beam transducer operated with a BioSonics, Inc. (Seattle, WA, USA) DT-X Sub, powered by 2 to 4 DEEPSEA (San Diego, CA, USA) 12V batteries (Fig. 2.2). During the R/V Kiyi deployments in 2022, an additional upward-aimed 208 kHz 11.3° circular split-beam BioSonics transducer was added. These two frequencies have been shown to provide similar results (see review in Yule et al., 2009) and are recommended by the Standard Operating Procedures for Fisheries Surveys in the Great Lakes (Parker-Stetter et al., 2009). Acoustic data were collected with acquisition thresholds set at -100 dB (dB), pulse durations set at 0.4 ms and realized ping rates of 5 pings per second. A DST compass magnetic logger (Star-Oddi hf., Garðabær, Iceland) was also attached to the platform to provide a compass direction correction for the acoustic data.

Deployment locations were determined based on the areas examined in Wegher (2019) as well as their proximity to gillnet/mid-water trawl survey transects for the given deployment vessel (Fig. 2.1). The acoustic platform was deployed from one to three nights at each location in each year (Table 2.1). A water temperature profile was collected during each deployment, varying with deployment vessel to provide a thermocline depth for each region and a mean temperature estimate of the whole water column to calculate accurate sound speed and absorption coefficients for acoustic data (Parker-Stetter et al., 2009). For R/V Superior Explorer deployments, a HOBO mini logger (ITM Instruments INC., Toronto, ON, CAN) was slowly lowered through the water column, recording measurements every second and pausing every 5 m to record stable data until the bottom was reached. For R/V Kiyi and Blue Heron deployments, an electronic bathythermograph (SBE19plus profiler, SeaBird, Bellevue, WA, USA) was used to establish thermal conditions in the water column near each deployment location.

Gillnet and Trawl surveys

Concurrent to acoustic sampling, 18 gillnets were deployed across the Nipigon Bay and Whitefish Bay regions between June 24 – September 21 in 2021 by the R/V Superior Explorer as part of the OMNRF Lake Superior community index netting survey. The bottom-set gillnets were 10 ft by 100 ft panels of 1.5” – 6” clear monofilament graded stretch mesh. Consequently, this method results in very low catchability of fish < 12cm, however we were limited to the vessels standard operating procedures (Rudstam et al., 1984). Bathymetric deployment depths target four depth strata (0 – 30 m, 30 – 60 m, 60 – 90 m, and > 90 m) with 6 deployments at each stratum across the given region. All nets fished for < 24 hours (overnight sets).

As a part of the USGS Cooperative Science and Monitoring Initiative (CSMI), mid-water trawl surveys were deployed across all of Lake Superior from the R/V Kiyi in August 18 – October 4 in 2022 (N = 64). These surveys were concurrent to the acoustic platform deployments in the Apostle Islands, the Western Arm, and at the Keweenaw Peninsula. Mid-water trawls had 15.2 m headrope and footrope lines and 13.7 m breast lines. The mesh graduated from a stretch measure of 152 mm at the mouth to 13 mm at the cod end (further description of the trawl can be found in Yule et al., (2013). Mean fishing depths ranged from 0 m to 65.2 m with speeds around 4.4 km/h. All trawls were either fished for ~30 min (N = 29; i.e., approximately 1.25 km) or 20 min (N = 35; i.e., approximately 1 km).

Data analyses

Data processing and preparation

Stationary acoustic data were processed with Echoview Software Ver. 11 (Echoview Software Pty. Ltd., Hobart, TAS, Australia (Parker-Stetter et al., 2009; Rudstam et al., 2009). Field calibrations of the acoustic platform echosounders were carried out using a 38 mm tungsten carbide sphere and applied following Foote et al. (1987). I created near-field and bottom exclusion lines and removed regions of bad data in the acoustic platform echograms (Parker-Stetter et al., 2009). For the acoustic platform, the surface line was adjusted to eliminate obvious noise from wave action and entrained air bubbles and varied across deployments and with surface conditions (Table 2.1). I used a minimum target strength (TS) detection threshold of -55.00 dB (within single target detection method 2 in Echoview) to identify single targets. This threshold eliminated macroinvertebrate and most larval stage fish targets (< 30mm) while retaining most young-of-year (YOY) coregonines and all adult fishes (Rudstam et al., 2003). This minimum range-dependent threshold of dB was also applied to the volume backscattering strength (S_v) echogram to ensure that no targets smaller than 30 mm were included in the dataset (Parker-Stetter et al., 2009).

Length (L_d, in mm) from the mean TS of a given fish track d as calculated by the echoview software for the up-looking transducers was predicted using the many fishes dorsal-ventral equation:

$$L_d = 10^{\frac{TS_d-(0.9\times LOG\left(\frac{c}{f}\right))+62.3}{19.2}} \times 10. \qquad \text{(eq 2.1)}$$

where c is the speed of sound in freshwater in m/s, f is the frequency of the transducer in Hz (Table 2.1), and TS_d is the mean σ transformed to TS of the fish track d in dB (Love, 1971; Parker-Stetter et al., 2009). For a fish track to be accepted, a minimum of 5 pings and single targets per track with a maximum gap between single targets of 50 pings were required, and then visually inspected and adjusted manually where necessary to ensure no tracks contained multiple fish. I then split the fish targets (i.e., all those identified from acoustic tracks) by their estimated length (L_d) into small -55.0dB – -41.2dB (30 – 155 mm), medium -41.2dB – -31.24 dB (155 – 510 mm), and large fish size classes -31.24dB – -24.40dB (510 – 1,150 mm). I set the maximum allowable large fish size to 1,152 mm and removed any larger targets from the dataset (Yule et al., 2013). Fish tracks provided individual speeds in m/sec, fish detection depth (m), and movement direction (°) for each target. I converted m/sec swim speeds to body lengths/sec by dividing the mean swim speed by the estimated body length obtained from equation 2.1 for each individual target to control for the impact of size on fish swim speed (Ware, 1978). I converted the fish detection depth to relative detection depth (RDD), calculated as [(bottom depth - detection depth)/ (bottom depth - thermocline depth)] for fish below the thermocline and {[(thermocline depth - detection depth)/ (thermocline depth)] + 1} for fish above the thermocline (Grow et al., 2021). Therefore, fish detected on the lake bottom, thermocline, and lake surface have RDD values of 0, 1, and 2, respectively.

Additionally, to allow for broader comparisons to other acoustic surveys, fish density for the whole water column during the day (sunrise to sunset) and night (sunset to sunrise) was calculated by dividing ABC by σbs for each 20 min grid cell at each deployment region following the same procedure as described in Chapter 1.

Statistical analyses

Acoustic data were compared across year, region, and diel cycle to determine whether there were significant differences in movement estimates across these variables. Due to the non-normal distribution of residuals, fish movement speed data were converted to body lengths per second and square root transformed prior to the statistical tests to better meet the assumptions of normality and homogeneity of variance. First, to investigate the impact of survey year on fish movement, I applied a three-way ANOVA on the three regions that were surveyed both years (the Western Arm, Nipigon Bay, and Whitefish Bay). The three-way ANOVA tested the effects of year (2021 and 2022), region, and size class (small, medium, and large) on mean fish movement speeds (day and night combined; Table 2.2). There was a significant interaction between year, region, and size class on mean fish movement speeds for the three regions that I surveyed both years (the Western Arm, Nipigon Bay, and Whitefish Bay, Three-way ANOVA, $F_{4, 6697} = 17.28$, $p < 0.001$; Table 2.2). The three size classes (small, medium, and large) as defined were meant to represent different species (rainbow smelt *Osmerus mordax*, cisco *Coregonus artedi*, and lake trout *Salvelinus namaycush*) in Lake Superior, and are therefore independent of one another, so were considered separately in terms of movement patterns for further analysis. Further, the magnitude of annual differences in movement appeared to vary with size class (based on the observed size-by-year interaction, Fig. 2.3) though generally, 2022 movement appeared to exceed that of 2021 for all locations and size classes examined (Fig. 2.3). One of my major interests was in regional differences in swimming speeds across Lake Superior (rather than inter-annual differences), so I corrected for these annual differences in swimming speeds (across all regions, including those sampled only in 2022) by subtracting size-class specific annual mean speeds (i.e., mean across all regions within a size class) from all individual fish observations in all regions surveyed in 2021-2022 (the Western Arm, Nipigon Bay, Whitefish Bay, the Keweenaw Peninsula, and the Apostle Islands); this resulted in a dataset with mean-adjusted swimming speeds that allowed for the assessment of day/night and regional differences in movement among fish within each size class across all regions surveyed in both years, relative to the mean movement speeds observed for that year. These data were examined within each size class to assess both regional and diel movement patterns using a series of two-way ANOVAs (Table 2.3).

To further my investigation into the impacts of diel cycle on fish behaviour across region and size class, I also examined these effects on mean fish relative detection depths (RDD). To better understand annual variation in this response variable, I first used a four-way ANOVA that tested the effects of year (2021 and 2022), diel cycle (day and night), region, and size class (small, medium, and large) on mean fish RDD for the three regions that I surveyed both years (the Western Arm, Nipigon Bay, and Whitefish Bay; Table 2.4). There was a significant interaction between year, diel cycle, region, and size class on mean fish movement speeds (4-way ANOVA, $F_{3,\,6680}= 18.08$, $p < 0.001$; Table 2.4). Due to the nature of my RDD calculation, I was unable to correct for year effects as was done for movement speeds. As such, and to better aid in interpretation, the analyses were split by year and size-class into six two-way ANOVAs examining the effects of region and diel cycle on each size class and each year separately (Table 2.4).

Finally, a three-way ANOVA was applied to fish density estimates from the whole water column across regions and diel cycle comparison. Due to the non-normal distribution of residuals, all fish density data were log transformed after 0.01 was added to each observation to prevent zeros from interfering with this transformation. Fish density ($D_{i,r,n,y}$) was estimated for i individual 20 min cells, and the model tested the effects of region r (5 regions), diel cycle n (two levels, day or night), survey year y (2021 or 2022), and the interactions between r, n, and y (Table 2.5):

$$LOG(D_{i,r,n,y} + 0.01) = r_i * n_i * y. \qquad \text{(eq 2.2)}$$

Tukey HSD *post hoc* tests were applied whenever significant interactions were detected to determine differences among group means for main effects or interactions where appropriate. All statistical tests were conducted in the R Program version 3.4.0 (R Core Team, 2020). For all ANOVA tests and post hoc Tukey HSD tests, I started with an $\alpha = 0.05$ for significance testing and applied a Bonferroni correction ($\alpha = 0.025$) when considering differences among fish movement speeds and RDD to prevent errors using multiple ANOVA tests (after having initially tested the data with more complex four- and three-way ANOVAs and then following up with simpler two-way ANOVAs).

Results

Netting Catch

Mid-water trawl samples supported my dB cutoff for small fish sizes in my analysis; a total of 9,725 fish were caught in the 64 mid-water trawl samples across Lake Superior in 2022. There were 187 fish < 30 mm comprised mostly of YOY rainbow smelt (N = 164) that did not meet the target threshold of -55 dB. Fish in the small category range (30 – 155 mm, N = 9,080) were predominately rainbow smelt (N = 5,104; 56.2%) and YOY coregonines (N = 3,908; 43.0%), where other fish made up <1% of the rest of the catch (N = 68; Table 2.6). Fish in the medium category range (155 – 510 mm, N = 373) were mostly cisco (N = 181; 48.5%) and kiyi (*Coregonus kiyi*, N = 147; 39.4%), followed by other coregonines (N = 21, 5.6%), rainbow smelt (N = 17;4.6%), and <2% other fish species (N = 7; Table 2.6). Trawling captured only one fish in the large category range (510 – 1,150 mm), a 750 mm siscowet lake trout. Although there was a lack of captures of fish in this size range, I can be confident that most fish in this size range are lake trout. In mid-water trawl surveys of Lake Superior conducted by the U.S. Geological Survey from 2000 – 2018, 90% of fish caught ≥ 510 mm (N = 21) were lake trout (U.S. Geological Survey 2019, Great Lakes Research Vessel Operations 1958 – 2018. [ver. 3.0, April 2019], https://doi.org/10.5066/F75M63X0).

A total of 579 fish were caught in 18 gillnet sets across Lake Superior in 2021. As expected, the gillnets did not capture any fish in the small category range (30 – 155 mm) since they are designed to target larger fish (Table 2.6). Fish in the medium category range (155 – 510 mm, N = 460) were mostly lake whitefish (*Coregonus clupeaformis*, N = 171; 37.2%), bloater (*Coregonus hoyi*, N = 110; 23.9%) and lake trout (N = 107; 23.3%), followed by cisco (N = 46, 10.0%), burbot (*Lota lota*, N = 19, 4.1%), and 1.5% other fish species (N = 7; Table 2.6). Fish in the large category range (510 – 1,150 mm, N = 119) were mostly lake trout (N = 87; 73.1%) followed by lake whitefish (N = 26; 21.8%), burbot (N = 4; 3.4%) and 1.7% other fish (one lake sturgeon *Acipenser fulvescens* and coho salmon *Oncorhynchus kisutch*; Table 2.6).

Fish movement speed comparisons

There was a significant interaction between region and diel cycle on mean year-adjusted residual movement speeds for the small (Two-way ANOVA, $F_{4,\,7435}$= 17.64, $p < 0.001$) and medium (Two-way ANOVA, $F_{4,\,1500}$= 4.35, $p < 0.001$) sized fish, but not for large fish (Two-way ANOVA, $F_{4,\,770}$= 2.58, $p = 0.04$; $\alpha = 0.025$). Large fish had significant main effects of region (Two-way ANOVA, $F_{4,\,770}$ = 23.49, $p < 0.001$) and diel cycle (Two-way ANOVA, $F_{1,\,770}$= 20.29, $p < 0.001$; Table 2.

3). Based on a Tukey HSD test following the significant interaction, the mean year adjusted residual movement speeds obtained from the acoustic platform for small sized fish were significantly faster during the day than the those during the night in the Western Arm (Day, -2.39 ± 0.72 adjusted body lengths/sec; Night +4.41 ± 0.20 adjusted body lengths/sec) and Keweenaw Peninsula (Day, -1.57 ± 4.50 adjusted body lengths/sec; Night +3.51 ± 0.26 adjusted body lengths/sec; $p < 0.001$), but not significantly different in the other sites ($p > 0.025$; Fig. 2.4A). The medium sized fish year adjusted residual movement speeds obtained from the acoustic platform during the day were not significantly different than those during the night in any region (*p* > 0.025; Fig. 2.4B). The main effect for the large sized fish was that mean year adjusted residual movement speeds obtained from the acoustic platform during the day (-0.33 ± 0.07 adjusted body lengths/sec) were significantly higher than the those during the night (+0.21 ± 0.08 adjusted body lengths/sec) across all regions, but due to there being no interaction present, a Tukey HSD was not performed examining diel cycles by region (Fig. 2.4C).

A Tukey HSD test evaluating the main effect of region indicated that fish in the small size class had the highest mean year adjusted residual movement speeds in the Western Arm (+3.92 ± 0.19 adjusted body lengths/sec), Keweenaw Peninsula (+3.42 ± 0.27 adjusted body lengths/sec), and Nipigon Bay (+4.56 ± 0.57 adjusted body lengths/sec), followed by Whitefish Bay (-2.96 ± 0.34 adjusted body lengths/sec), and then the Apostle Islands (mean -5.33 ± 0.24 adjusted body lengths/sec; Fig. 2.4A). The medium size class were much more similar overall across regions, but the Western Arm (+0.37 ± 0.12 adjusted body lengths/sec) and Nipigon Bay (+0.17 ± 0.22 adjusted body lengths/sec) had significantly higher year adjusted residual movement speeds than medium-sized fish from Whitefish Bay (-0.89 ± 0.24 adjusted body lengths/sec), with the Keweenaw Peninsula (+0.00 ± 0.22 adjusted body lengths/sec) and Apostle Islands (+0.55 ± 0.41 adjusted body lengths/sec) regions being intermediate and not significantly different from any of the other regions (Fig. 2.4B). For large fish, Nipigon Bay (+0.38 ± 0.09 adjusted body lengths/sec) had significantly higher mean year adjusted residual movement speeds than the Keweenaw Peninsula (-0.02 ± 0.09 adjusted body lengths/sec) but both sites were not significantly different from the Western Arm (+0.06 ± 0.13 adjusted body lengths/sec), or the Apostle Islands (+0.31 ± 0.18 adjusted body lengths/sec) and all regions had significantly higher speeds than Whitefish Bay (-1.01 ± 0.11 adjusted body lengths/sec) (Fig. 2.4C).

Fish RDD Comparisons

For all three size classes and in both survey years, I found a significant interaction between diel cycle and region with respect to fish RDD ($p < 0.001$; Table 2.4). Based on a Tukey HSD test following the significant interaction, the mean small-sized fish RDD obtained from the acoustic platform in 2021 during the day were significantly shallower than the those during the night in Nipigon Bay and Whitefish Bay ($p < 0.001$) and were significantly deeper during the day than those during the night in the Western Arm ($p < 0.001$; Fig. 2.5A). These relationships were similar in 2022, as the mean small sized fish RDD obtained from the acoustic platform in 2022 during the day were significantly shallower than the those during the night at the Apostle Islands ($p < 0.001$) and Whitefish Bay ($p < 0.001$), significantly deeper during the day in the Western Arm than the those during the night ($p = 0.003$), but not significantly different in respect to diel cycle in the other regions ($p > 0.81$; Fig. 2.5B). The mean medium and large sized fish RDDs obtained from the acoustic platform in 2021 were not significantly different between day vs the night at any region ($p > 0.5$; Fig. 2.6A&2.7A). Differing slightly from 2021 trends, the mean medium sized fish RDD obtained from the acoustic platform in 2022 during the day were significantly shallower than the those during the night in Whitefish Bay ($p < 0.001$), but not significantly different in any other region ($p > 0.10$; Fig. 2.6B). Similarly, but in the opposite direction, the mean large sized fish RDD obtained from the acoustic platform in 2022 during the day were significantly deeper than the those during the night at a single site (Nipigon Bay, $p = 0.001$), but not significantly different in the other sites ($p > 0.05$; Fig. 2.7B).

Whole Water Column Density Comparisons

A significant interaction between geographical region, diel cycle, and year on the density of fish detected across the entire water column was observed (Three-way ANOVA, $F_{2,\ 1260}=$

19.96, $p < 0.001$; Table 2.5). The Tukey HSD found all mean fish densities obtained from the acoustic platform at night were significantly higher ($p < 0.001$) than the mean fish densities obtained from the acoustic platform during the day, except for in the Apostle Islands ($p = 0.73$; Fig. 2.8).

Discussion

Inter-annual differences in movement between survey years were the main differences in fish movement patterns from my initial analysis, and primarily associated with the small fish size class. Across all regions sampled both years, small fish mean movement speeds were significantly elevated in 2022 in comparison to 2021 (increased from 7 to 17 body lengths/sec). Based on the USGS trawl netting data, the elevated movement speeds of the small size class is likely due to 2022 being a large recruitment year for YOY coregonines (Vinson et al., 2022). Cisco are known to exhibit infrequent recruitment in Lake Superior, previously having a more cyclical once every three-year boom cycle, but in recent years have become more irregular and less frequent (up to seven years between pulses with smaller pulses; Vinson et al. 2022). Juvenile and adult rainbow smelt are known to be less active swimmers in comparison to coregonines (Ray et al., 2007; Savitz and Bardygula, 1989), thus a year class dominated by juvenile coregonines would be expected to have greater swimming speeds compared to one without. Additionally, adult rainbow smelt are known to prefer temperatures < 10 °C (Gaeta et al., 2012; Lantry and Stewart, 1993), which were only attainable below the thermocline in the present study. Unfortunately, there is not a published temperature preference for YOY cisco in Lake Superior but the closely related YOY lake whitefish are known to have a thermal optima of 16.8 °C (Edsall, 1999), temperatures found exclusively above the thermocline in the present study;

thus, a year class dominated by juvenile coregonines could be expected to be observed above the thermocline as I saw in 2022.

Based on this diel pattern of densities, I would expect larger fish to generally slow down at night as they disperse, and smaller fish to speed up as they no longer form schools for protection from predation (de Kerckhove et al., 2015; de Kerckhove and Shuter, 2022). Consistent with this expectation, there were significant differences in fish movement speeds across the diel cycles for the small and large fish in the directions predicted; large-sized fish slowed down significantly at night across all regions, seemingly only needing to outpace the nighttime speeds of their prey. Conversely, small fish sped up significantly at night in the Western Arm and Keweenaw Peninsula and trended in a similar direction at the other sites (except for Whitefish Bay). Medium-sized fish showed little difference in mean swim speeds between day and night cycles.

Standardizing movement to the mean annual swimming speed also allowed for inter-regional comparisons. Fish across all size classes typically had the highest mean year adjusted residual movement speeds in areas with high water input from tributaries (the Western Arm, and Nipigon Bay), and lower speeds near the Lake's outflow (Whitefish Bay). These differences were much stronger for fish in the small size class +3.92 ± 0.19 adjusted body lengths/sec in the Western Arm and +4.56 ± 0.57 adjusted body lengths/sec in Nipigon Bay compared to -2.96 ± 0.34 adjusted body lengths/sec in Whitefish Bay), which could be due to compositional differences in the species assemblages regionally. In Lake Superior, tributaries are known to have a strong regional influence on available nutrients, with larger tributaries having greater impacts (Marcarelli et al., 2019; Yurista and Kelly, 2009). My study provides a possible link between these regional influxes of nutrients and fish behaviour.

Generally, observed movement patterns showed some similarities to other work which estimated regional differences in movement indirectly from bioenergetic model assessments (Wegher 2019), but primarily among small and large fish. For small sized fish (YOY coregonines and rainbow smelt in this study and rainbow smelt in Wegher 2019), I saw some correspondence between studies. In both studies, small fish in Whitefish Bay had low activity/movement rates, and high activity/movement rates in the Keweenaw Peninsula, a magnitude of approximately 3 times faster in both studies (Wegher, 2019). However, in the current study, small fish activity in the Western Arm and Nipigon Bay were similar to the Keweenaw Peninsula, whereas these two sites were intermediate to the other sites using bioenergetic assessments (Wegher 2019). I also acknowledge that some differences between the small fish movement speeds may be influenced by the large year class of YOY coregonines I sampled in 2022, however the year mean adjustment should account for that influence. For large fish, both the Keweenaw Peninsula and Western Arm had similarly high swimming speeds, significantly higher than Whitefish Bay, similar to Wegher (2019). However, in my study the magnitude difference between these regions was ~2 times faster, compared with just ~1.1 times faster mean activity rates in Wegher (2019). By contrast, in my study Nipigon Bay large fish had significantly higher speeds than the Keweenaw Peninsula (~1.2 times faster mean movement speeds), and both these regions were not significantly different from the Western Arm or the Apostle Islands, while Nipigon Bay and Whitefish Bay grouped with the lowest activity rates (~1.1 – 1.2 times slower mean activity rates) in Wegher (2019). I chose not to directly compare the medium size class between studies. While both studies consider coregonines in this size class, the majority of the medium fish in my study were cisco, which are pelagic feeders in Lake Superior (Gamble et al. 2011), Wegher (2019) reported bioenergetic estimates for lake whitefish, typically a more nearshore benthic feeding fish in Lake Superior whose activity may be more dependent on variations in bathymetric depth and substrate type than cisco (Rennie et al. 2015; Fera et al. 2017). Overall, some degree of difference between my activity estimations and those from previous studies is to be expected as my activity rates are directly measured but are only from 1 – 3 nights of sampling mid-summer. Derived activity estimates integrate a broader time period, modelling fish activity over an entire year and using methods that are generally unable to separate day and night energetics or speeds (Rennie et al., 2005a; Wegher, 2019). Additionally, bioenergetic estimates are derived from mass balance models vs. direct observations, even though there is evidence that activity multipliers do correspond to direct swimming observations (Rennie et al., 2005b).

The mean swimming speeds observed in this study are largely congruent with the literature for the large (2 body lengths/sec) and medium (4 body lengths/sec) size classes (laboratory and in situ ranges 1 – 8 body lengths/sec for fish 155mm – 872mm: Bernatchez and Dodson, 1985; Dunlop et al., 2010; Feldman and Savitz, 1999; Rudstam et al., 1994). Benefits from outlier pruning may be negligible for the current study, as only 10% of the medium fish and just 0.5% of the large fish exceeded these thresholds. The mean swimming speeds for the small size class were higher than expected in this study (12 body lengths/sec) compared to published in situ expected movement speeds for small fish (1 – 7 body lengths/sec for fish 28mm – 155mm; Bernatchez and Dodson, 1985; Dabrowski, 1986), however laboratory studies of 80mm rainbow smelt and coregonines have recorded predation escape speeds well above our mean observed speeds (36 – 53 body lengths/sec; Feldman and Savitz, 1999). As with medium and large fish, just 4% of the small fish observed in the present study exceeded the low end of the laboratory burst speeds (36 body lengths/sec), suggesting a stricter outlier cutoff is unlikely to effect the data. Similar stationary acoustic work has observed that split-beam acoustics can be prone to biasing small fish movement speeds higher than is realistic (Arrhenius et al., 2000). However, for the main goals of this study of comparing fish movement speeds across years, regions, and diel cycles these biases are less of a concern as they are methodological and/or equipment based, both of which were held constant across the study and therefore should not influence the magnitudes of the differences observed.

The most common pattern in RDD among regions for small fish was to move closer to the surface during daytime hours compared to night, rather than the expected DVM pattern of retuning to greater depths near the lakebed during the day. I only observed the expected DVM response (e.g., deeper in the day) in the Western Arm (sample depths > 50 m) for small fishes in both years. Large sized fishes only displayed this behaviour in Nipigon Bay (sample depths > 50 m) in 2022. This lack of clear DVM in my data could be partially explained by diel bank migration movements occurring for fish within my small size class, as it has been shown previously that fish within this size class often undergo diel bank migration rather than DVM at sites < 50 m in Lake Superior (Gorman et al., 2012b). Additionally, it is possible that I was mainly sampling a behavioural strategy utilized by only a minority of small fishes (411 total small fish detected during the day vs 7,034 detected at night), whereas the rest of the small fish may have moved into nearshore areas that offer the possibility of protective habitat structures during the daytime hours (Gorman et al., 2012b). My fish movement direction data lends some support to this idea; at sunrise hours in 70% of my sample sites, most small fish were moving horizontally towards shallower water and in the sunset hours at 60% of my sample sites, most small fish moved horizontally towards deeper waters. While large fish consistently moved towards deeper water during diel transition times (sunrise and sunset), very few fish of any size moved parallel to the nearest shoreline (Table 2.1). Additionally, due to the nature of how fish are detected withing the spreading acoustic beam (causing the sample volume at the surface to be higher than the lakebed) the RDD data may be biased against detecting fish deeper in the water column. However, I believe this effect to be negligible in the current study. If bias against detection of deeper targets were occurring in any significant way, I would expect to see fewer fish deeper in the water column of all sizes in my shallow deployments relative to deployments in deeper water, and this was not the case. In fact, I observed the opposite relationship; in my shallowest deployments (Whitefish Bay), I saw more fish deeper in the water column for the small and medium size classes compared to my deepest deployments (Keweenaw Peninsula) where I saw fewer small and medium sized fish deeper in the water column. The large fish did not have and apparent difference in depths between the shallowest and deepest deployments. This potential bias could be further investigated via a volume-based correction factor, or by examining ratios of fish detected above and below the thermocline across sites, but I believe the aforementioned justification for leaving the data unaltered for the goals of this study to be sufficient.

When looking at my dataset over the whole water column to estimate fish density (fish/ha), as is typical of standard acoustic surveys (Parker-Stetter et al., 2009; Yule et al., 2006; Yule et al., 2009), I observed significantly higher fish densities at night vs the day in all regions across both years (except for in the Apostle Islands in 2022 where there was no difference detected). Managers already adhere to the principle of DVM and conduct all acoustic surveys (and most active trawl net-based surveys) during nighttime hours to ensure good fish density estimates (Yule et al., 2007). This increase in density is consistent with the current understanding of DVM patterns in Lake Superior (Ahrenstorff et al., 2011), however the majority of my RDD results do not display DVM.

The results from this study have several implications for management and commercial harvest using passive gear (e.g., trap nets, gillnets). As passive netting is strongly correlated with fish activity rates (DuFour et al., 2019; Rudstam et al., 1984) regional differences in fish activity can skew netting results towards overestimation of fish population densities in areas of high activity and underestimating population densities in areas with less activity. I observed major differences in activity rates across my sample regions for each size class; In the most extreme case for small fish, I found that fish in Nipigon Bay were moving on average ~4 times faster than the fish in the Apostle Islands, for medium fish I found that fish in the Apostle Islands were moving and average of ~3 times faster than fish in Whitefish Bay, and for large fish I found that fish in Nipigon Bay were moving on average ~2 times faster than the fish in the Whitefish Bay. This implies that studies (such as this) that continue to clearly document regional differences in fish activity make a strong case for fisheries managers to consider activity rates in their gear selectivity estimates when converting catch rates to actual measures of abundance using passive gear.

Variability in regional or local activity rates, such as those observed in this study, may be linked to the long-range dispersal potential of fishes. Large fish in the Great Lakes are known to have the ability to disperse, such as lake trout in Lake Michigan (Schmalz et al., 2002), lake whitefish in Lake Michigan and Huron (Ebener et al., 2010), and walleye in Lake Superior, Huron, and Erie (Hayden et al., 2019; McKee et al., 2022; Wang et al., 2007), and other literature has indicated that there is an influence of regional activity rates on the rate of fish dispersal in freshwater lake systems (Rennie et al., 2012). Broader research on organism dispersal also supports that a higher individual activity rates would likely lead to a higher dispersal potential, making management in high activity zones and bordering regions much more complex than is currently accounted for (Bie et al., 2012; Bonte et al., 2012; Comte and Olden, 2018).

Ultimately, using an up-looking acoustics system, I was able to detect consistent differences in fish movement speeds and RDD across regions and survey years, and surprising and unexpected patterns of DVM in fishes across Lake Superior. These analyses indicate this technology has the potential to improve our understanding of regional behavioural variation in large ecosystems like Lake Superior, as well as significant potential to improve fisheries management by incorporating these regional insights and by providing accurate measures of fish activity rates and diel-vertical movement behaviours when they are completely unimpacted by any vessel based disturbances.

Tables

Table 2.1. Region, research vessel (R/V), deployment date, latitude, longitude, number of nights deployed each year and majority sunset movement direction for small and Medium/Large sized fish for all summer acoustic platform deployments in Lake Superior. The five regions include Nipigon Bay (NB), the Western Arm (WA), Whitefish Bay (WB), the Apostle Islands (AI), and the Keweenaw Peninsula (KP).

Region	R/V	Date	Latitude	Longitude	Nights	Surface Exclusion (m)	Bottom Exclusion (m)	Sunset Direction Small, Med/Large	Sunrise Direction Small, Med/Large	Direction of Deeper Water
NB	Superior Explorer	08/06/2021	48.81942	-87.55290	2	2.1	41.8	W, E	NW, NE	S, E
WA	Blue Heron	08/19/2021	46.87649	-91.23298	4	2.9	52.0	N, N	NW, NE	N, W
WB	Superior Explorer	09/15/2021	46.64268	-84.69337	4	3.6	39.0	SE, S	N, SW	S, W
NB	Superior Explorer	06/25/2022	48.81213	-87.63500	2	3.4	52.2	NE, SW	W, W	S, E
WB	Superior Explorer	08/04/2022	46.65057	-84.69685	2	1.9	37.0	NE, SW	N, SE	S, W
AI	Kiyi	08/18/2022	46.80302	-90.43480	1	2.4	63.3	N, E	SW, E	N, E
WA	Kiyi	08/21/2022	46.92470	-91.11687	1	2.3	61.5	NW, N	NE, N	N, W
WA	Kiyi	08/24/2022	46.89361	-91.86266	1	5.2	70.0	W, SE	SW, S	S, E
KP	Kiyi	09/04/2022	47.29233	-88.75366	2	3.0	72.8	SE, E	S, SE	N, W
KP	Kiyi	09/06/2022	47.24103	-88.94493	1	2.7	70.4	N, N	SE, N	N, W

Table 2.2. Three-way ANOVA test and results for mean speed (body length/s) and year adjusted residual mean speed estimates (body length/s) examining effects and interactions between year, region, and fish size classes. An α value of 0.025 was used to access significance.

Independent Variable	Model Factor	df	Mean Squares	F-Ratio	P-value
Fish speed (body length/s)	Year	1	689.9	521.39	<0.0001
	Region	2	936.6	707.88	<0.0001
	Size	2	1756.2	1327.29	<0.0001
	Year*Region	2	441.9	333.96	<0.0001
	Year*Size	2	33.1	25.05	<0.0001
	Region*Size	4	17	12.87	<0.0001
	Year*Region*Size	4	22.9	17.28	<0.0001
	Residuals	6697	1.3	-	-

Table 2.3. Two-way ANOVA tests and results for year-adjusted residual mean speed estimates (body length/s) examining effects of region and diel cycle. For all ANOVA's, a α value of 0.025 was used to access significance.

Independent Variable	Model Factor	df	Mean Squares	F-Ratio	P-value
Small fish speed (body length/s)	Region	4	315.7	233.91	<0.0001
	Diel	1	135.2	100.20	<0.0001
	Region*Diel	4	23.8	17.64	<0.0001
	Residuals	7435	1.4	-	-
Medium fish speed (body length/s)	Region	4	0.7	4.83	<0.0001
	Diel	1	0.0	0.05	0.8328
	Region*Diel	4	0.7	4.35	0.0017
	Residuals	1500	0.2	-	-
Large fish speed (body length/s)	Region	4	0.6	23.49	<0.0001
	Diel	1	0.5	20.29	<0.0001
	Region*Diel	4	0.1	2.58	0.0361
	Residuals	770	0.0	-	-

Table 2.4. ANOVA tests and results for mean RDD examining effects and interactions between year, diel cycle, region, and fish size classes. For all ANOVA's, a α value of 0.025 was used to access significance.

Independent Variable	Model Factor	df	Mean Squares	F-Ratio	P-value
Fish RDD	Year	1	133.8	1135.11	<0.0001
	Diel	1	0.0	0.20	0.6231
	Region	2	25.7	218.21	<0.0001
	Size	2	5.7	48.46	<0.0001
	Year*Diel	1	14.2	120.04	<0.0001
	Year*Region	2	32.3	273.71	<0.0001
	Diel*Region	2	23.5	199.02	<0.0001
	Year*Size	2	2.2	18.62	<0.0001
	Diel*Size	2	1.3	10.58	<0.0001
	Region*Size	4	0.5	4.23	0.0020
	Year*Diel*Region	2	1.0	8.82	0.0001
	Year*Diel*Size	2	0.5	3.88	0.0207
	Year*Region*Size	4	0.7	5.96	<0.0001
	Diel*Region*Size	4	2.0	16.56	<0.0001
	Year*Diel*Region*Size	3	2.1	18.08	<0.0001
	Residuals	6680	0.1	-	-
Small Fish RDD 2021	Diel	1	10.6	112.00	<0.0001
	Region	3	50.7	536.40	<0.0001
	Diel*Region	3	16.9	179.00	<0.0001
	Residuals	5034	0.1		
Medium Fish RDD 2021	Diel	1	0.3	2.69	0.1020
	Region	3	1.7	18.20	<0.0001
	Diel*Region	3	2.4	25.09	<0.0001
	Residuals	811	0.1	-	-
Large Fish RDD 2021	Diel	1	0.1	1.38	0.2421
	Region	3	0.2	2.18	0.0923
	Diel*Region	2	0.5	5.37	0.0056
	Residuals	148	0.10	-	-
Small Fish RDD 2022	Diel	1	1.0	9.70	0.0019
	Region	4	17.3	174.52	<0.0001
	Diel*Region	4	4.6	46.06	<0.0001
	Residuals	4210	0.1	-	-
Medium Fish RDD 2022	Diel	1	0.3	3.20	0.0739
	Region	4	3.2	30.30	<0.0001
	Diel*Region	4	2.6	25.01	<0.0001
	Residuals	794	0.1	-	-

Large Fish RDD 2022	Diel	1	0.8027	11.03	0.0010
	Region	4	1.4759	20.27	<0.0001
	Diel*Region	4	1.0248	14.08	<0.0001
	Residuals	621	0.0728	-	-

Table 2.5. Three-way ANOVA test for mean fish density (fish/ha) estimates. The three-way ANOVA examined effects and interactions between survey years, regions, and diel cycles on mean fish density. An α value of 0.05 was used to access significance.

Independent Variable	Model Factor	df	Mean Squares	F-Ratio	P-value
Fish density (fish/ha)	Year	1	133	21.16	<0.0001
	Region	4	427	68.03	<0.0001
	Diel	1	7238	1154.42	<0.0001
	Year*Region	2	28	4.53	0.011
	Year* Diel	1	616	98.17	<0.0001
	Region* Diel	4	174	27.69	<0.0001
	Year*Region* Diel	2	125	19.96	<0.0001
	Residuals	1260	6	-	-

Table 2.6. Summary of 2021 MNRF gillnets and 2022 USGS mid-water trawl data across years (total number of cisco caught, percentage of catch female, mean cisco weight, and reported harvest) in Lake Superior. The species caught not explicitly mentioned in the above text caught in relatively low numbers include shortjaw cisco *Coregonus zenithicus*, chinook salmon *Oncorhynchus tshawytscha*, yellow perch *Perca flavescens*, spoonhead sculpin *Cottus ricei*, deepwater sculpin *Myoxocephalus thompsonii*, ninespine stickleback *Pungitius pungitius* and three-spined stickleback *Gasterosteus aculeatus*.

Year	Method	Species	Mean Length (mm)	Min Length (mm)	Max Length (mm)	Total caught
2021	Gillnets	Cisco	261.7	174	394	46
		Lake Whitefish	428.4	196	606	197
		Bloater	241.6	175	305	110
		Kiyi	185	185	185	1
		Lake Trout*	491.4	208	859	194
		Coho Salmon	443.3	297	532	3
		Burbot	413.9	214	644	23
		Shortjaw Cisco	292	287	297	2
		Chinook Salmon	401	401	401	1
		Yellow Perch	258	258	258	1
		Lake Sturgeon	755	755	755	1
2022	Trawls	Cisco**	307.5	132	506	185
		Lake Whitefish	453.3	401	496	7
		Bloater	233.6	202	265	13
		Kiyi	196.8	126	248	160
		YOY Coregonine	73.2	29	122	3910
		Rainbow Smelt	93.0	19	194	5363
		Lean Lake Trout	236.0	121	470	4
		Siscowet Lake Trout	524.0	343	750	3
		Coho Salmon	205.0	200	210	2
		YOY Burbot	19	19	19	1
		Three-spined Stickleback	43.0	32	55	4
		Ninespine Stickleback	57.9	39	79	32
		Spoonhead Sculpin	49.5	37	64	4
		Deepwater Sculpin	30.9	23	69	36

*MNRF did not separate Lean lake trout from Siscowets.

**One 395 mm Unidentifiable Coregonine was also caught in the trawls.

Figures

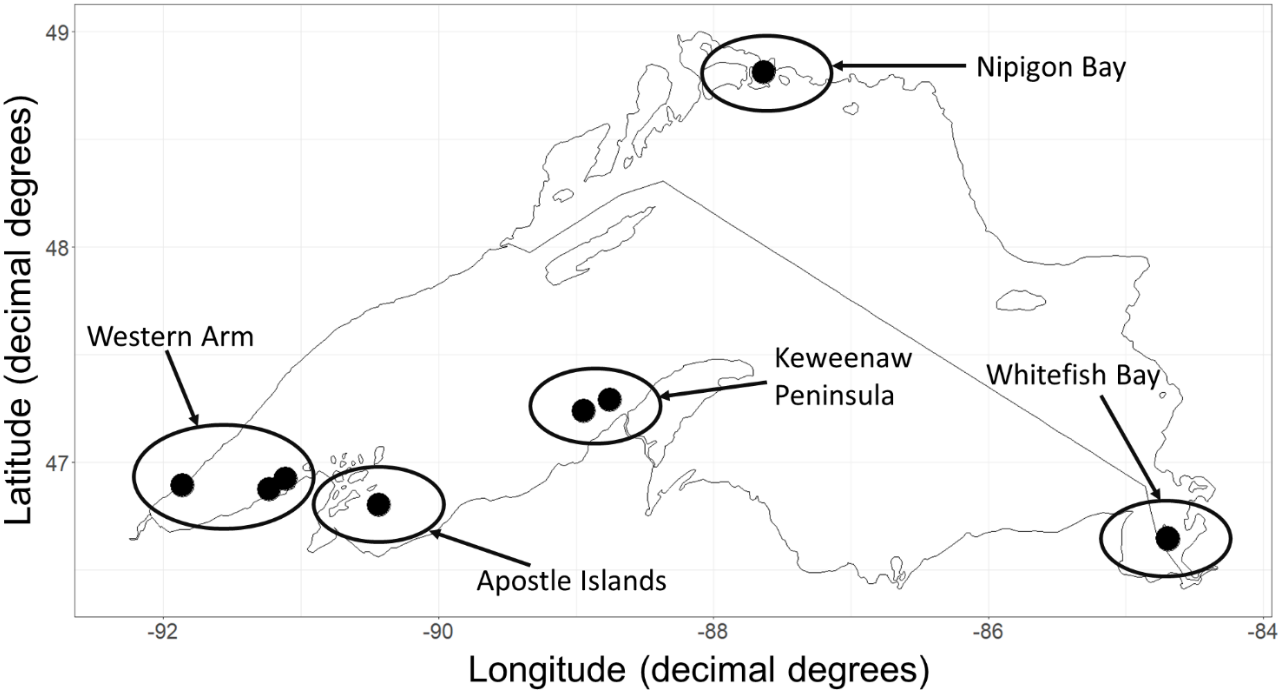

Figure 2.1. Deployment locations and regions for the stationary acoustic up-looking unit. Nipigon Bay, Whitefish Bay, and the Western Arm were surveyed in 2021 and 2022; the Apostle Islands and Keweenaw Peninsula were only survey in 2022. There was a total of 10 deployments.

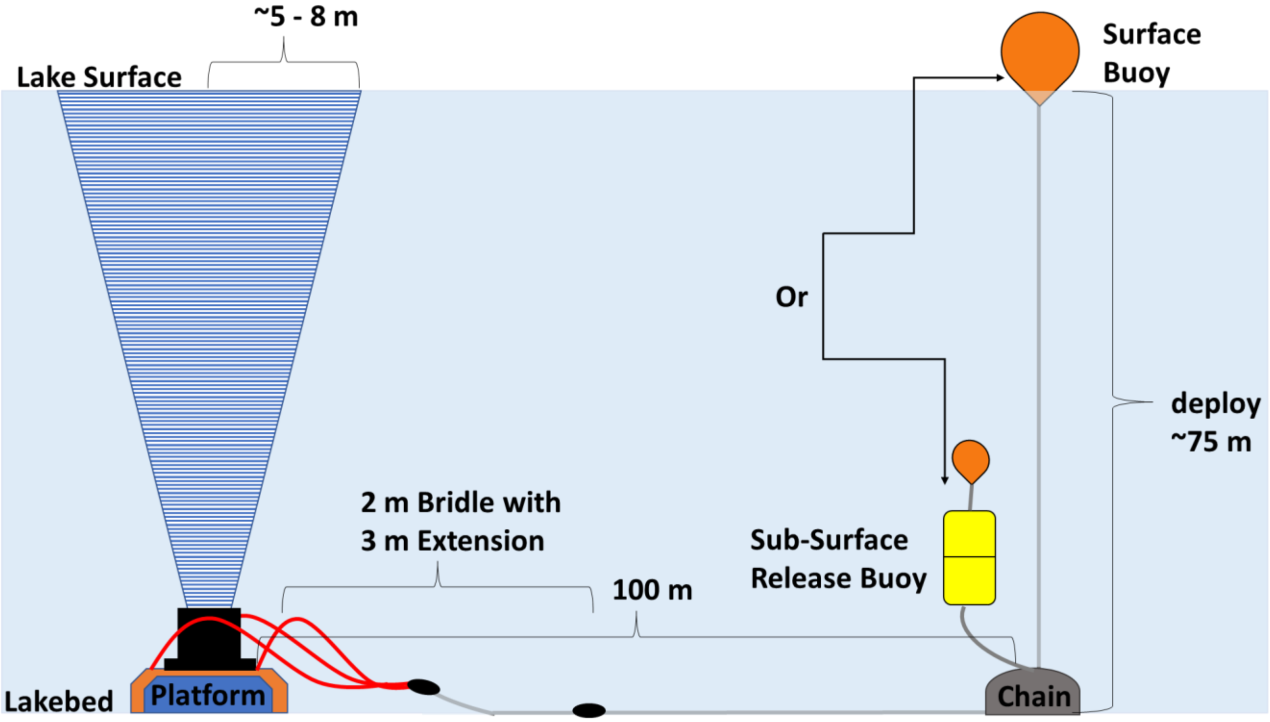

Figure 2.2. Typical deployment configuration for the stationary acoustic up-looking unit. The acoustic platform was deployed with a surface buoy at all locations except for the 2021 Western Arm deployment in which I utilized the sub-surface release buoy.

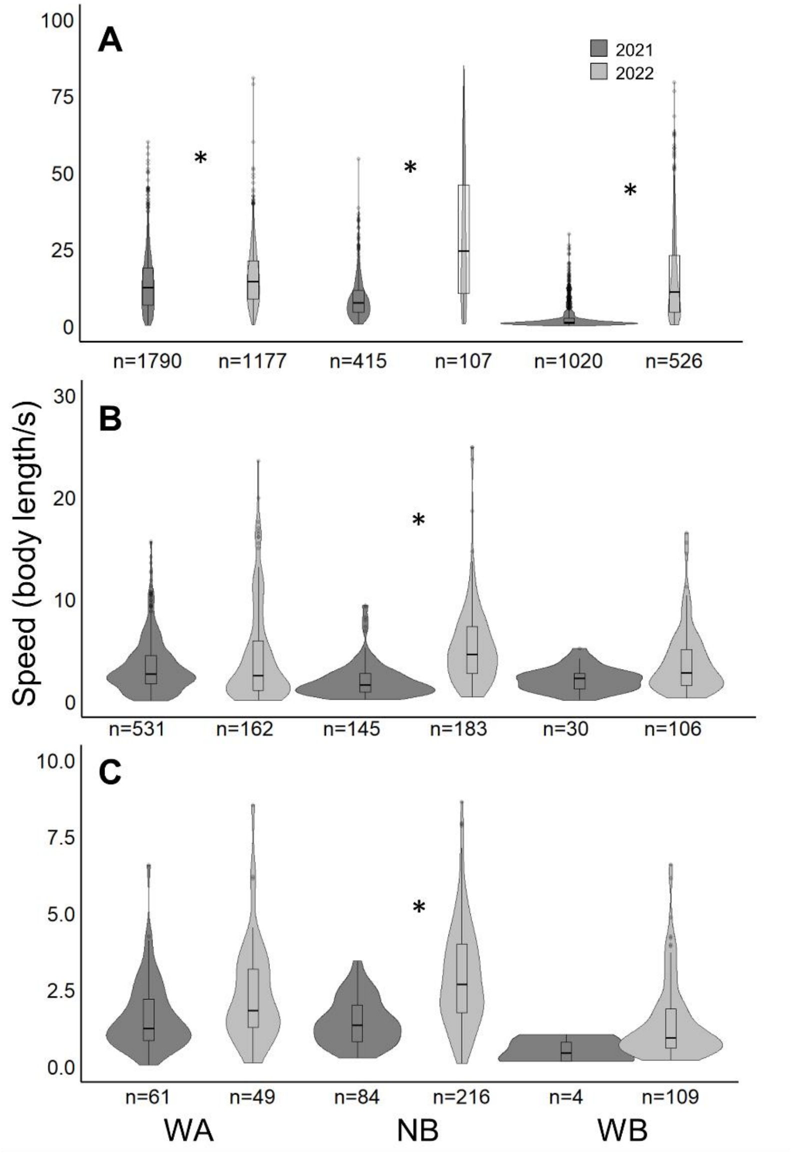

Figure 2.3. 2021 vs 2022 day/night combined fish movement speeds (body length/s) across the Western Arm (WA), Nipigon Bay (NB), and Whitefish Bay (WB) regions by fish size class. Number of fish represented in each violin given by n. Bars show median fish speed of small (A), medium (B), and large fish (C) detected by the acoustic platform survey at a given region across survey years. Asterisks represent significant differences ($p < 0.05$) between mean fish movement speeds across region as determined by a Tukey HSD test.

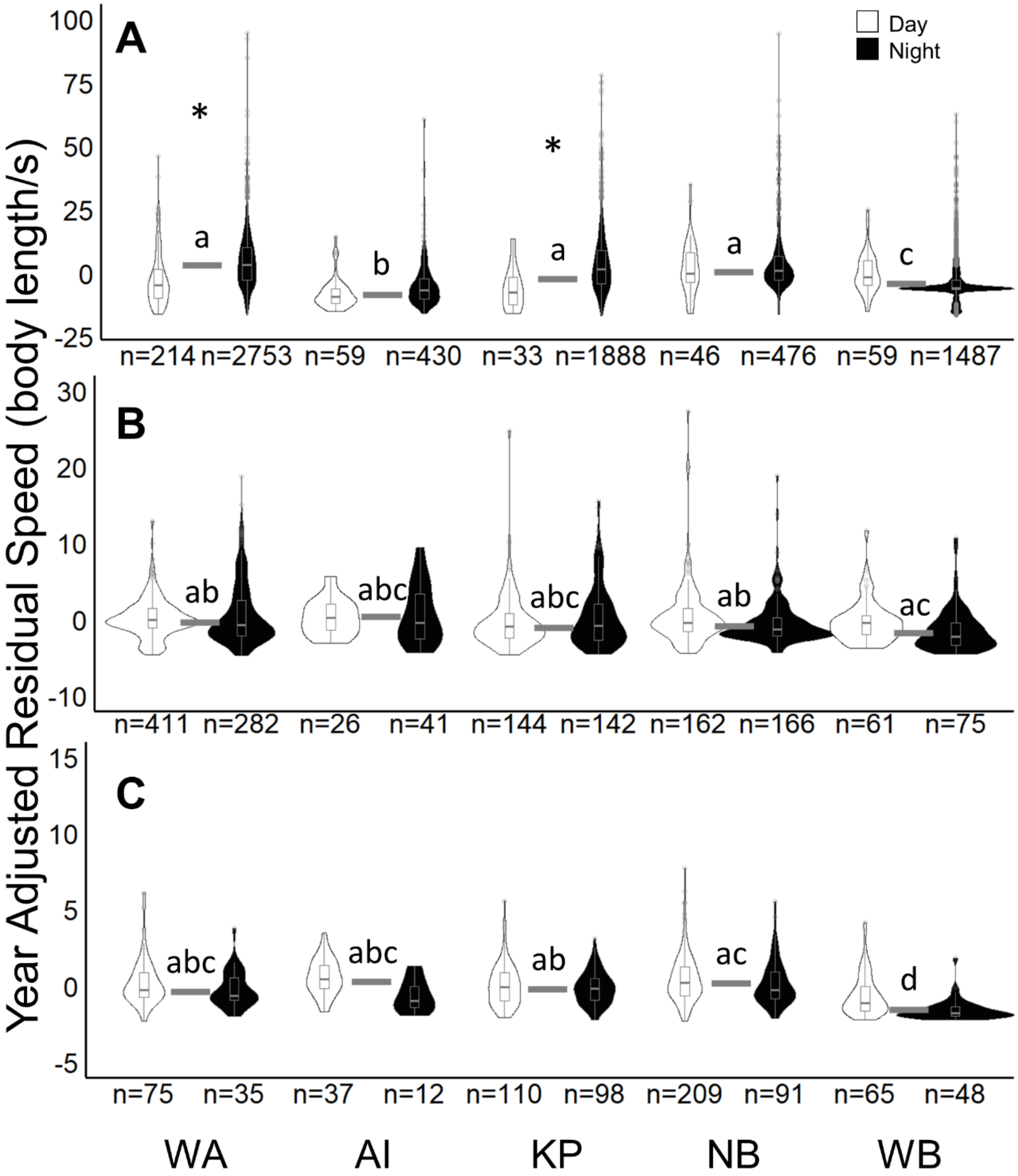

Figure 2.4. Differences in median year adjusted residual movement speeds (body length/s) across the Western Arm (WA), Apostle Islands (AI), Keweenaw Peninsula (KP), Nipigon Bay (NB), and Whitefish Bay (WB) regions by diel cycle (day/night) and diel cycle combined (grey horizontal bars). Thick grey horizontal bars show median year adjusted residual movement

speeds of small fish (A), medium fish (B), and large fish (C) detected by the acoustic platform in each region with day/night combined. Boxplot bars show median year adjusted residual movement speeds of small (A), medium (B), and large fish (C) detected by the acoustic platform survey each day/night the acoustic platform was deployed in a give region in 2022. Number of fish represented in each violin given by n. Asterisks represent significant differences ($p < 0.05$) between mean year adjusted residual movement speeds in the day vs night across region as determined by a Tukey HSD test. Different lowercase letters represent significant differences ($p < 0.025$) between mean year adjusted residual movement speeds across region within each size class determined by Tukey HSD tests.

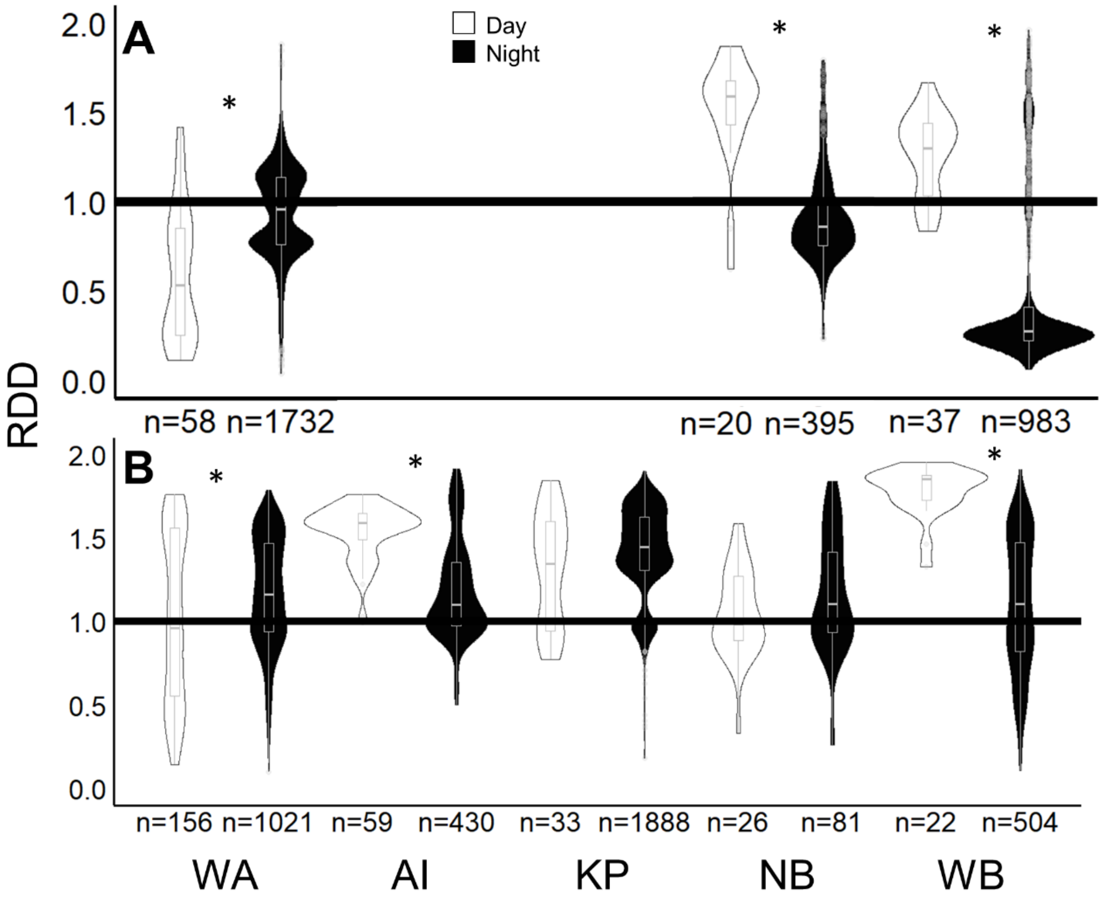

Figure 2.5. Differences in small fish relative detection depth (RDD) across diel cycle by region in 2021 (A) and 2022 (B). Region abbreviation description can be found in Figure 2.4, the Apostle Islands and Keweenaw Peninsula regions were not surveyed in 2021. Bars show mean RDD of small fish detected by the acoustic platform survey each day/night the acoustic platform was deployed in a give region in each year. Number of fish represented in each violin given by n. Asterisks represent significant differences ($p < 0.025$) between mean fish RDD in the day vs night across region as determined by a Tukey HSD test. The horizontal line at 1.0 represents the bottom of the thermocline.

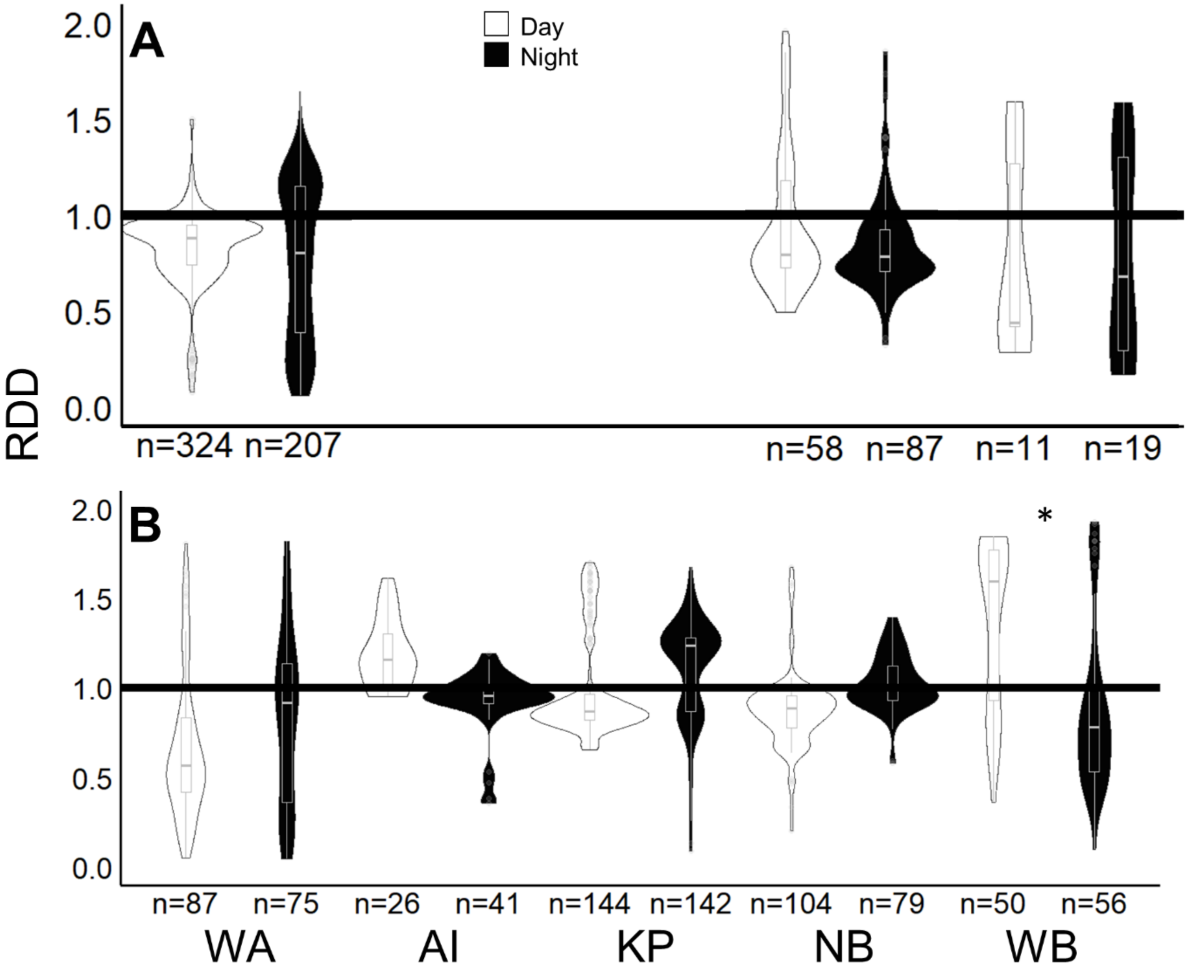

Figure 2.6. Differences in medium fish relative detection depth (RDD) across diel cycle by region in 2021 (A) and 2022 (B). Region abbreviation description can be found in Figure 2.4, the Apostle Islands and Keweenaw Peninsula regions were not surveyed in 2021. Bars show mean RDD of medium fish detected by the acoustic platform survey each day/night the acoustic platform was deployed in a give region in each year. Number of fish represented in each violin given by n. Asterisks represent significant differences ($p < 0.025$) between mean fish RDD in the day vs night across region as determined by a Tukey HSD test. The horizontal line at 1.0 represents the bottom of the thermocline.

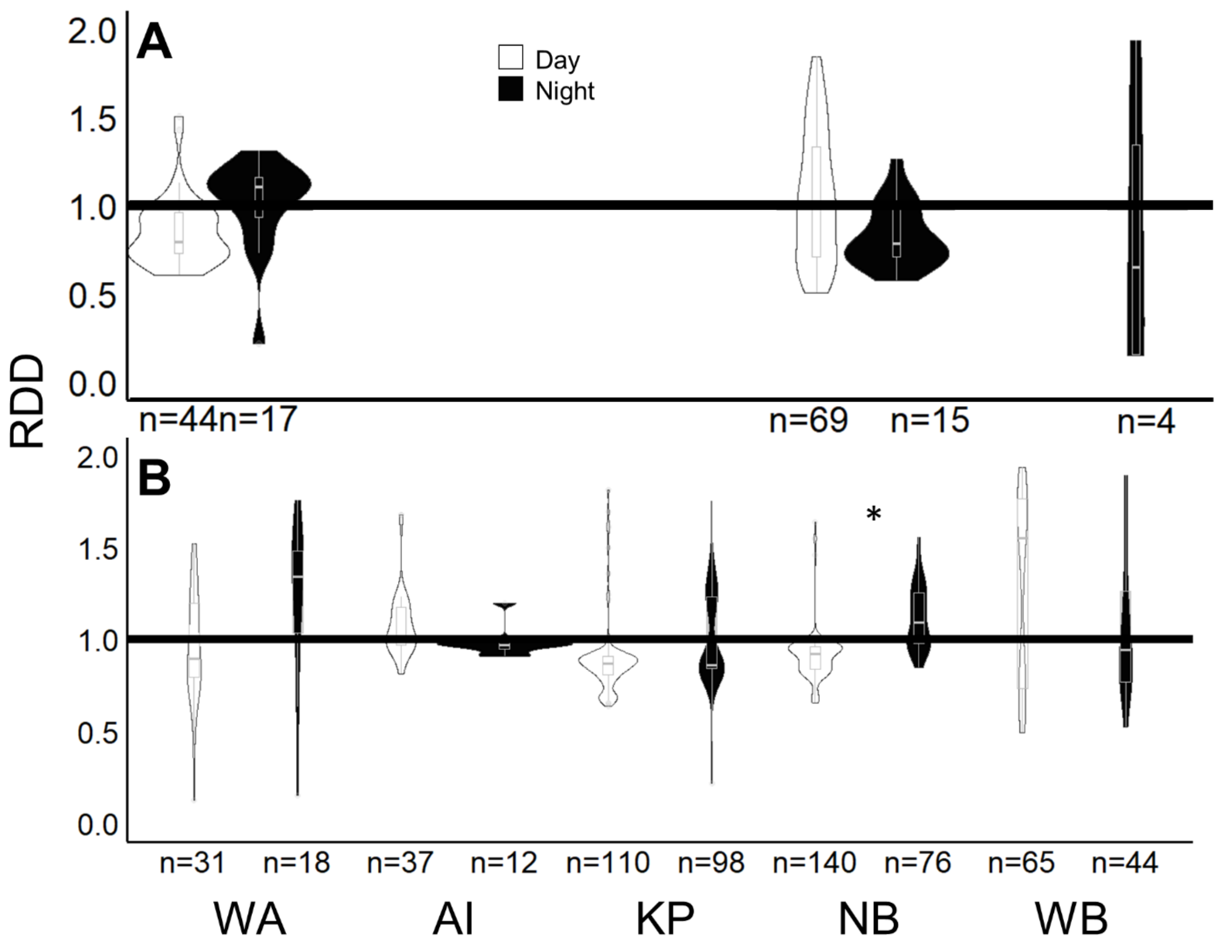

Figure 2.7. Differences in large fish relative detection depth (RDD) across diel cycle by region in 2021 (A) and 2022 (B). Region abbreviation description can be found in Figure 2.4, the Apostle Islands and Keweenaw Peninsula regions were not surveyed in 2021. Bars show mean RDD of large fish detected by the acoustic platform survey each day/night the acoustic platform was deployed in a give region in each year. Number of fish represented in each violin given by n; no large fish were detected during the day at Whitefish Bay in 2021. Asterisks represent significant differences (*p* < 0.025) between mean fish RDD in the day vs night across region as determined by a Tukey HSD test. The horizontal line at 1.0 represents the bottom of the thermocline.

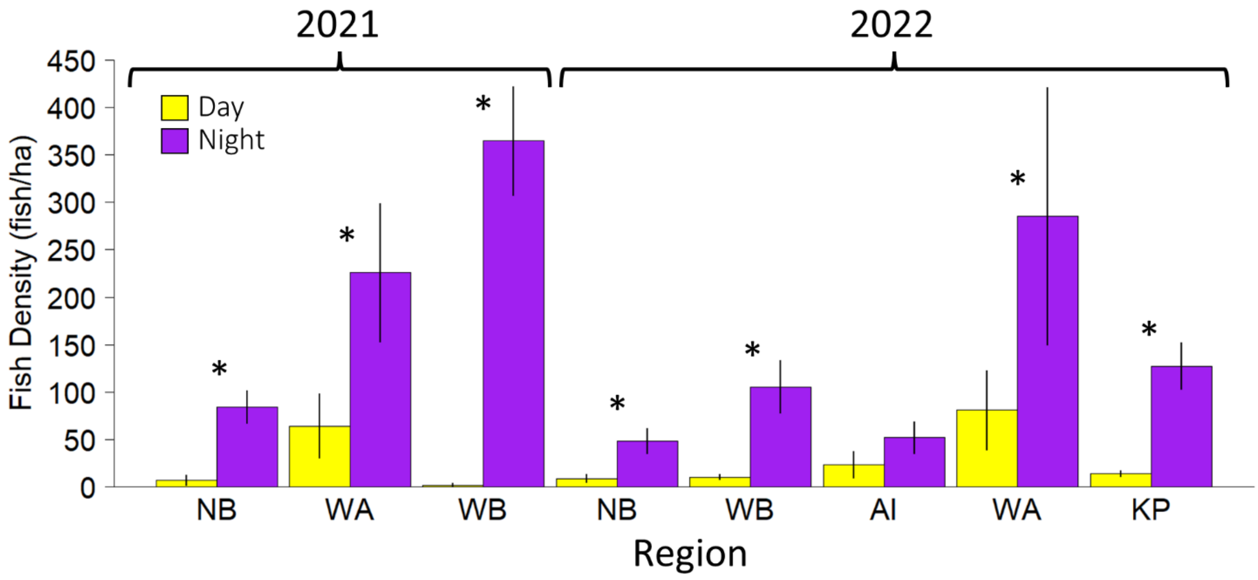

Figure 2.8. Day vs Night fish density (fish/ha) across Lake Superior. Region abbreviation description can be found in Figure 2.4. Bars show mean fish density from 20-minute-long sections of the water column for each day/night the acoustic platform was deployed at the ten sites grouped by region (refer to Table 2.1 for more detail). Asterisks represent significant differences ($p < 0.05$) between fish density detected in the day vs the night for each region surveyed in each year as determined by a Tukey HSD test. Error bars indicate 95% confidence intervals around each mean.

Chapter III: Examining how Diel Movement Patterns Influence Food Web Dynamics of the Lake Superior Shoals lakemount.

Abstract

Freshwater shoals or lakemounts are productive, novel, and understudied systems, which may be analogous to oceanic seamounts in their ecological importance. There are several non-exclusive hypotheses which try to explain the exceptional productivity observed in these unique offshore ecosystems, which propose processes involving the effects of predominant currents on the deposition of nutrients and organisms to shoal-based benthic production. To test and evaluate these hypotheses, mobile down-looking acoustic surveys and biological sampling were deployed at and around the Lake Superior shoal system in the summer of 2017 and 2019. I found strong evidence of a deep chlorophyll maxima and of diel-vertical migration behaviour in the fish and *Mysis* at the shoals, which are required for current-dependent hypotheses of elevated shoal production. However, I found little direct support for any of the main proposed hypotheses, likely due to the slow currents at the shoals during summer and logistical constraints of the sampling procedures as deployed over very brief periods during these surveys (e.g., each lasting only 24-36 hours). My findings point to the pressing need for more targeted research utilizing new autonomous technologies such as stationary acoustic platforms and other moored instrumentation and sampling devices that could allow for longer term observation of the system to provide key insights into the processes at play on the shoals, particularly over times of year when water currents are strongest and when vessel-based sampling in these regions is dangerous if not impossible.

Introduction

The functions of many freshwater and marine pelagic food webs across the globe are controlled by interactions between benthic and pelagic ecosystems (Angel, 1993; Griffiths, 2010; Vadeboncoeur et al., 2008, 2002; Vander Zanden and Vadeboncoeur, 2002). In both marine and freshwater systems, deep water pelagic food web interactions are spread over a large area, dominated by primary producers, fewer primary consumers, and few secondary or higher consumers (Elmgren, 1984; Hairston and Hairston, 1993; Lehodey et al., 2009). The benthic zones derive their main energy source from detritus (pooled mostly from decaying phytoplankton) in the sediment, which is metabolized by bacteria (Mann, 1988). Those bacteria are in turn consumed by secondary detrital consumers (e.g., *Diporeia spp.* in Lake Superior). Detrital energy typically reaches the secondary consumer stage in the pelagic food web through fish consumption, which then cycles back though organism death and metabolic waste products entering the detrital pool (Huxel and McCann, 1998). These large, deep-water systems are punctuated by small, relatively shallow areas of high productivity, namely sea mounts in marine systems, and shoals in freshwater systems (Rogers, 2018). In these areas, the food web dynamics between the pelagic and benthic zones change due to the lake bottom reaching the photic zone, making large invertebrates vulnerable to predation, and enabling benthic algal production to exceed bacterial production (Huxel and McCann, 1998). The large amount of primary productivity that these sea mounts often support also allows for increased organismal community complexity (Clark et al., 2010; Genin et al., 2007; Morato et al., 2010; Rogers, 2018). In large freshwater systems, similar increases in productivity have also been observed in shoal systems (Houghton et al., 2010; Janssen et al., 2006).

The Lake Superior Shoals system covers an area of 52 km^2 and is in the northern central region of Lake Superior where the depth of the lake bottom rises to 6 m at its shallowest and is bordered by depths of 300 m (Manson and Halls, 1991). The shoals are bathymetrically complex, with multiple underwater peaks and valleys (Fig. 3.1). Similar to oceanic seamount ecosystems which host high levels of productivity and biodiversity, prior research on shoal systems in Lake Superior found increased productivity in the form of increased population diversity and density of pelagic fishes such as lake trout (*Salvelinus namaycush*) and coregonines (Schram et al., 1995). However very little is known about the ecological processes underway at the Lake Superior shoals as much of the current collective scientific knowledge at this site can be found in just five publications (Edsall et al., 1991; Goodier, 1981; Hansen et al., 2020; Manson and Halls, 1991; Vinson et al., 2020).

The underwater mountain structures that make up seamounts also physically resemble shoal systems in large lakes, and each break up the usual flow of energy between the pelagic and benthic zones. One proposed mechanism for the elevated secondary productivity observed on freshwater shoal systems is the Topographic Blockage Hypothesis (TBH) proposed by Houghton et al. (Houghton et al., 2010). On a Lake Michigan shoal, researchers proposed that *Mysis diluviana* preforming diel vertical migrations (DVM) move up in the water column at night and slowly drift over the shoal by way of weak surface currents, then in the morning when they try to migrate back down to avoid daytime predation are stranded on the shallow shoal, thus becoming easy prey for fish (Houghton et al., 2010). However, they measured this relationship indirectly through examining slimy sculpin (*Cottus cognatus*) diets and lacked direct estimates of *Mysis* abundance and distribution in and around the shoals. They explicitly called for future use of acoustic survey technology to observe pelagic fish and *Mysis* movements to test this hypothesis directly. There has been recent support for the TBH playing a role in oceanic systems (Aarflot et al., 2019) but little direct evidence connecting it to elevated secondary production on freshwater shoals.

Other processes observed in marine systems may be involved with increased production on freshwater shoals; the increased productivity at the Lake Superior Shoals could be due to the shallow conditions providing an increase in Benthic Algal Production (BAP) on the shoal system, effectively concentrating the amount of food available for zooplankton and secondary detrital consumers. This process has been observed in marine reef complexes but not yet in a freshwater system (Haas et al., 2011). Alternatively, Leeward Eddy Retention (LER) is a process known to marine systems that predicts the retention and deposition of suspended material down current of reefs (Limer et al., 2020; Shulzitski et al., 2018; White et al., 2008); however, that has yet to be examined on freshwater reef analogues.

The Superior Shoals system offers a unique opportunity to explicitly assess these hypotheses in a freshwater setting and demonstrate how movement of organisms can influence energy flow pathways that drive ecosystem function in a chronically understudied system. Determining if fish and *Mysis* are undergoing typical DVM patterns is crucial to testing the TBH hypothesis. Under conventional DVM, I would expect elevated densities of *Mysis* and fish to be detected during the night (compared to densities during the day), both on and off the shoals. If the Lake Superior Shoals are causing a topographic blockage, I would expect *Mysis* and fish density to be higher over the shoals during sunrise hours when *Mysis* are predicted to experience stranding (and therefore feeding by fishes) compared to daytime hours. Further, under TBH, no difference is expected on or off the shoals between other parameters (zooplankton, benthic invertebrate densities, or chlorophyll a concentration [Chl *a*]). If the Lake

Superior Shoals productivity is due to BAP, I would expect to see an increase in zooplankton and benthic invertebrate density and Chl *a* on the shoals versus off the shoals, as well as see a general increase in fish and *Mysis* density over vs off the shoals, which should be more pronounced at night due to known DVM patterns. If the Lake Superior Shoals are experiencing LER, I would expect *Mysis*, fish, zooplankton, and benthic invertebrate density and Chl *a* concentration to be higher on the leeward side of the dominant currents over the shoal versus up current of the shoal. For *Mysis* and fish, this trend would likely be more apparent at night during their DVM.

Methods

General Sample Plan

The shoals were sampled in June 27-28, 2017, and July 27-29, 2019, from the research vessel (R/V) Blue Heron, operated by the University of Minnesota, Duluth Large Lakes Observatory. Hydroacoustic and net based sampling took place at the shoal system (< 120 m depth) and at control "pelagic" sites near the shoals (> 120 m depth; Fig 3.1). The 120 m threshold depth was chosen as it represents the depth at which light levels match the minimum light response level for *Mysis* (1.75×10^{-4} lx; Gal et al., 1999). Depth of light penetration was calculated as the depth to which this light extends in Lake Superior on an overcast day (1,000 lx) using Beer's Law and a light extinction coefficient for Lake Superior provided by Sterner, (2010; 0.13 m^{-1}). Other studies across the Great Lakes have indicated that *Mysis* prefer to inhabit depths greater than 100 m during daytime hours and, due to Lake Superior's exceptional offshore water clarity, it is expected that *Mysis* would occupy slightly deeper daytime depths in Lake Superior than in the other great lakes (Beeton, 1960; Houghton et al., 2010).

Environmental and Biological Survey Methods

To quantify productivity levels and provide a baseline for food web analysis, *Mysis* and zooplankton tows were taken at four separate locations both years, at two shallow sites on the shoals (~50m and ~70m) and two deep sites off the shoals (~125m and ~150m) during both the daytime and nighttime hours. *Mysis* and zooplankton were sampled at each location with two or three replicates of a 1 m diameter by 3 m long, 153 µm Wisconsin plankton net towed 60 m vertically through the water column. Benthic samples were taken at each site with a ponar (sediment grab sampler) with a 12.5” by 13” opening, with 2-3 replicates taken per site. Zooplankton and benthic samples were preserved with 70% ethanol to facilitate later counting. A conductivity, temperature, and depth (CTD) sonde with a fluorimeter was used at each zooplankton/benthic site during the daytime hours to provide a temperature profile for an accurate sound speed and absorption coefficient for acoustic analysis (Parker-Stetter et al., 2009), and provide a measure of Chl *a*, which was used as a proxy for phytoplankton abundance (Yentsch and Menzel, 1963). Chl *a* readings were taken from the upper water column (5 m), mid-water column (deep sites 40 – 45 m, shallow sites 25 – 30 m), and lower water column (deep sites 95 – 100 m, shallow sites 45 – 55 m).

Hydroacoustic Survey Methods

In both 2017 and 2019, the ship acoustic system consisted of a metal tow-fish equipped with downward facing 70 kHz 5° circular split-beam BioSonics, Inc. (Seattle, WA, USA) transducer deployed off the starboard side of the ship to a depth of ~1 m below the lake surface, which was connected to a BioSonics DT-X system and laptop. During 2017 surveys, the 70 kHz transducer was replaced by a 123 kHz 7.2° BioSonics circular split-beam transducer for a few hours during night surveys; however, these two acoustic frequencies are known to provide similar results (Parker-Stetter et al., 2009; Yule et al., 2009). Acoustic data were collected with acquisition thresholds set at -120 dB for the 123 kHz transducer and -75 dB for the 70 kHz transducer, and for both pulse durations were set at 0.4 ms and had realized ping rates of 1 ping per second.

Data analyses

Data processing and preparation

The data from the acoustic surveys were processed with Echoview Software Version 13 (Echoview Software Pty. Ltd., Hobart, TAS, Australia). Field calibrations of the ship echosounders were conducted using appropriately sized tungsten carbide spheres and applied following Foote et al. (1987). I created near-field and bottom exclusion lines and removing regions of bad data in the ship echograms (Parker-Stetter et al., 2009). I used a minimum target strength (TS) detection threshold of -50.00 dB (using single target detection method 2 in Echoview) to identify single targets for the fish density analysis for the 123 kHz and 70 kHz transducers. It follows that the applied -50.00 dB threshold for the fish density estimates eliminated targets < 54 mm, which includes *Mysis*, zooplankton and any young-of-year fishes but retains all adult lake trout and coregonines (Rudstam et al., 2003). The minimum range-dependent threshold of dB was also applied to the volume backscattering strength (S_v) echogram (Parker-Stetter et al., 2009). Each hydroacoustic survey was divided into 1,200 m intervals to ensure that each cell was an independent sample while targeting a reasonable number of single echo detections (SED's; Hrabik et al. 2006). This resulted in 30 total analysis cells (~51 km) in 2017 and 114 (~133 km) total analysis cells in 2019. For the analysis of acoustic data, fish density ($D_{i,y,c,n}$) for individual cell i, sample year y, depth category (on vs off shoal) c, and diel cycle (night, sunrise, or day) n were calculated with the echo integration method per Parker-Stetter et al. (2009) by:

$$D_{i,y,c,n}(\text{number/ha}) = 10{,}000 * \ ABC_{i,y,c,n}\sigma bs^{-1}_{i,y,c,n} \qquad \text{(eq 3.1)}$$

where ABC is the area backscattering coefficient for each combination of i, y, c, and n. The methods listed in chapter one for calculating fish density (briefly: ABC divided by σbs) were then followed. Additionally, to better examine the LER hypothesis, off shoal sites were also classified as North or South of the complex as the direction of prevailing currents over the shoals is North to South.

Statistical analyses

The hydroacoustic fish density estimates on and off the shoals from daytime, sunrise, and nighttime hours were compared to determine whether there were significant differences in density across the two depth regions and diel cycle. Due to the non-normal distribution of residuals, all fish density data were logarithmically transformed prior to the statistical tests to better meet the assumptions of normality and homogeneity of variance. First, a three-way ANOVA test was performed for fish density estimates across depth regions, diel cycle, and year. Fish density ($D_{i,y,c,n}$) for individual cell i was the dependent variable and the model tested the effects of c , n , y and the interaction between c, n, and y:

$$Log\left(D_{i,c,n,y} + 0.01\right) = \ c_i * n_i * y_i. \qquad \text{(eq 3.2)}$$

This yielded no significant year effect via interaction or direct effects, so I then applied a series of two-way ANOVAs across both years of data to examine the effects of diel cycle (day vs night), and region on counted *Mysis* and pelagic zooplankton densities, as well as the effects of species group (*Diporeia*, Oligochaetes, and Other), and region on benthic invertebrate abundance

(Table 3.1). Due to the non-normal distribution of residuals, benthic organism abundance data were square root transformed prior to the statistical tests to better meet the assumptions of normality and homogeneity of variance. I also applied another two-way ANOVA to examine the effects of region and water column sample depth on Chl *a* concentration in 2019. In addition, I used a two-way ANOVA to examine the mean fish density in the off-shoal regions to the North side and South side of the shoals' complex during the night and day. Post-hoc Tukey HSD tests were applied to interpret the main effect of the significant differences between the estimates. All statistical tests were conducted using the statistical program R (R Core Team, 2020). For all statistical tests I used an $\alpha = 0.05$ for significance testing among factor levels.

Results

Fish Density Comparisons

I observed significant differences in fish densities detected over the shoals compared to sites off the shoal system, which also varied between diel hours. There was no significant interaction between region and diel cycle (Two-way ANOVA, $F_{2, 137} = 1.77$, $p = 0.18$; Table 3.1), though significant main effects of region ($F_{1,137} = 88.82$, $p < 0.001$) and diel cycle ($F_{2,137} = 18.26$, $p < 0.001$) on mean fish densities were detected (Table 3.1). A post-hoc Tukey's HSD test revealed that there were significantly higher average fish densities detected off the shoals in water > 120 m than over the shoals. Additionally, there were significantly higher average fish densities detected at night than in the day, both on and off the shoals (Fig. 3.2).

Mysis Density Comparisons

I observed significant differences in *Mysis* densities detected over compared to off the shoal system, which also varied between diel hours. There was not a significant interaction between region and diel cycle (Two-way ANOVA, $F_{1, 31} = 1.54$, $p = 0.22$; Table 3.1). There were significant main effects of region ($F_{1,31} = 11.71$, $p = 0.002$) and diel cycle ($F_{1,31} = 64.38$, $p < 0.001$) on mean *Mysis* densities (Table 3.1). Opposite the pattern with fish densities, there were significantly higher average *Mysis* densities detected on the shoals in water < 120 m than off the shoals, but like fish densities, significantly higher average *Mysis* densities detected at night than in the day both on and off the shoals (Fig. 3.3).

Other Zooplankton and Benthic Organisms Density Comparisons

Pelagic zooplankton tows consisted mainly of copepods (99.8%; Calanoida, and Cyclopoida) with the remaining 0.2% consisting of *Bythotrephes longimanus*, *Mysis*, and *Daphnia*. I observed no significant interaction (Two-way ANOVA, $F_{1, 31} = 1.36$, $p = 0.25$) or main effects differences ($p > 0.27$) between average pelagic zooplankton densities detected over the shoal system versus off the shoal, or during the daytime hours vs the night (Table 3.1; Fig. 3.4).

The benthic organisms were mainly *Diporeia* (55.9%) and Oligochaetes (28.6%) with the remaining 15.5% consisting of Calanoida, Sphaeriidae, Ostrocoda, Chironomidae, and Coelenterata hydra (these latter categories grouped as Other). There was also no difference detected for benthic organism abundance on or off the shoals across both sample years (Fig. 3.5), although there was a significant difference in the average abundance of individual species across sites ($F_{2,48} = 7.94$, $p = 0.001$; Table 3.1). A post hoc Tukey HSD found that the mean abundance of *Diporeia* was significantly greater than the abundance of the other benthic organisms at all sites.

Chlorophyll a Concentration Comparisons

I observed no significant difference between mean Chl *a* concentration detected over the shoal system vs off it across both sample years (Fig. 3.6). There was no significant interaction between water column sample depth and region (Two-way ANOVA; $F_{2,18} = 0.81$, $p = 0.46$), although there was a significant difference among the water column depths sampled ($F_{2,18} = 14.19$, $p < 0.001$; Table 3.1). Based on a post hoc Tukey HSD, the mean Chl *a* concentration in the middle of the water column was significantly higher than those of the upper or lower water column consistent across depth region and years (Fig. 3.6).

LER Fish Density Comparisons

I observed consistent DVM patterns in average fish densities, but no impact of orientation to the shoal (North/South). There was no significant interaction between side and diel cycle (Two-way ANOVA, $F_{1,60} = 0.02$, $p = 0.89$), but there was a significant main effect of diel cycle ($F_{1,60} = 48.91$, $p < 0.001$) on mean fish densities in (Table 3.1). There were significantly higher average fish densities detected at night compared to daytime densities regardless of position on the shoal, consistent with expected DVM patterns (Fig. 3.7).

Discussion

I saw clear evidence of DVM happening in the waters over and near the Lake Superior shoals in the acoustic fish density data and *Mysis* netting samples, as expected from prior work detailing this relationship in Lake Superior (Ahrenstorff et al., 2011; Gorman et al., 2012b; Stockwell et al., 2010). This means that a necessary mechanism of the Topographic blockage hypothesis (TBH) is in place and could enable *Mysis* to be stranded on the shoal during the day, suggesting it could be a potential mechanism of food web enrichment at the shoals.

There were higher *Mysis* densities during both the daytime and nighttime hours over the shoals compared to off the shoals based on the netting, which may provide some evidence that *Mysis* may be getting stranded on the shoals or actively gathering at the shoals. Additionally, the daytime densities were much lower than the nighttime densities on and off the shoal, but based on my fish acoustic data there was not a subsequent increase in fish density over the shoals at any time that would indicate that the fish were taking advantage of increased *Mysis* concentrations over the shoals. The daytime density of *Mysis* was likely not high enough to attract a feeding response that could overcome the increased predation risk planktivorous fish themselves incur in the clear, shallow waters and the higher densities of prey concentrated near the lakebed during daytime hours according to conventional DVM (Ahrenstorff et al., 2011; Beeton, 1960). However, it is curious that the fish did not respond to the higher *Mysis* densities over the shoals at night, perhaps suggesting that the shoals may actually provide some sort of refuge from predation for *Mysis*. Examining acoustic *Mysis* movement data from a higher frequency transducer (208 kHz) deployed during the 2019 survey may yield greater insights into these relationships in future work, however the 2017 dataset (based on 121 kHz) is unlikely to help in this regard due to logistical sampling constraints (it recorded data for only a fraction of the survey at night off the shoals), and I would not expect there to be a major discrepancy between the netting and acoustic data overall. Alternatively, the presence of the sample vessel itself may be enough of a deterrent to fish undergoing their usual feeding behaviours, as vessel avoidance has been shown to impact pelagic fishes in Lake Superior (DuFour et al., 2018; Grow et al., 2020). The observed lack of fish moving to the shoals to feed on *Mysis* may also be seasonal; typical current direction flows from North to South over the shoals, and current speeds peak at 5.6 cm/s in February (when free from ice cover), gradually slowing to 0.3 cm/s through June and July (NOAA/GLERL Great Lakes Monthly depth-averaged currents map; Fig. 3.8). *Mysis* typically swim at a rate of 1 – 2 cm/s (Miller, 2003), which is 3 – 7 times greater than corresponding summer currents of my study period. Since I was only able to sample the shoals in June and July, very slow currents in these months may prevent *Mysis* stranding events at a time when water currents do not exceed *Mysis* swimming capabilities. This indicates a need for sampling earlier in the season (likely not feasible with standard methods as weather conditions are dangerous for research vessels) or use of an autonomous deployment (such as an array of stationary acoustic platforms stationed over and around the shoals) to observe the system when the currents exceed *Mysis* swimming capabilities. From my study alone, there is little direct support for the TBH occurring at Superior Shoals during summer months.

Given results reported here, other suggested hypotheses, Leeward Eddy Retention (LER) and Benthic Algal Production (BAP), also lack support. There was no difference in pelagic zooplankton density or benthic organism abundance on or off the shoals, which might be predicted under these hypotheses. We would have expected the increase in pelagic zooplankton due to nutrient and algal deposition on the leeward side of the shoals and an increase in benthic invertebrates if there was more primary benthic production on the shoals. Though I did not directly sample benthic algae in this study, if there was an increase in primary production, I would expect a proportional increase in the primary consumers (*Mysis*, pelagic zooplankton, and benthic invertebrates) if the system is under bottom up control (e.g., via augmentation from additional benthic production on shoal surfaces). Alternatively, secondary consumers (fish) may proportionally increase over the shoals if the system is under top down control over the shoal (Hillebrand, 2002; Lynam et al., 2017; Rosemond et al., 2001; Smith et al., 2010). Since I did not detect any clear or consistent differences in primary consumers on versus off the shoals (and in fact observed that fish density was consistently lower over the shoals), my data does not appear to provide support for the benthic algal production hypothesis at the Lake Superior shoals.

I also found little support for the LER hypothesis in my study. There was no significant difference in fish densities detected North or South of the shoal along the prevailing current gradient. However, due to logistical and time-based constraints, I was only able to sample environmental conditions at locations on the shoals and North of the shoals. To test this hypothesis more explicitly, future investigations would benefit from retrieving biological samples from both the North and South side of the shoals rather than simply on vs off the shoals as the was the focus of the sampling strategy during these previous brief sampling events. Given the prevailing current flows North to South over the shoals, more extensive sampling of the South side of the shoals will be crucial to understanding whether retention and deposition of suspended material down current of the shoals is occurring as it does in marine reef systems (Limer et al., 2020; Shulzitski et al., 2018; White et al., 2008). Slow summer current velocities may not be sufficient for LER to occur, and may only occur during periods of time with higher current velocities. Although I could provide no support for this hypothesis with the data collected, a more targeted study with emphasis on broader sampling around the shoals, perhaps combined with an ecological tracer analysis like stable isotopes or fatty acids could help shed light on the feasibility of LER and BAP at the Lake Superior Shoals.

Interestingly, we did observe a consistent and significantly greater concentration of Chl *a* at midwater depths in our study, which could be indicative of a deep chlorophyll maximum (DCM) around and over the shoals. The occurrence of a DCM is commonly seen in large marine or freshwater systems across the globe and is known to be an ecologically important driver of nutrient cycles when present (Cullen, 1982; Huisman et al., 2006). Lake Superior commonly shows evidence of DCM throughout the lake and has been documented by several recent studies (Barbiero and Tuchman, 2004, 2001; Sterner, 2010; White and Matsumoto, 2012). The DCM in Lake Superior could serve as an important resource of primary production for primary consumers such as copepods that constitute the majority of summer zooplankton biomass, as well as provide the food base that *Mysis* undergo their DVM to access (Barbiero and Tuchman, 2004; Oliver et al., 2015). As some areas of the shoal would reach depths shallower (< 6 m) than the recorded Chl *a* maxima range in this study (45 – 25 m), a range supported by other recent work (51 – 27 m; Scofield et al., 2020), it could allow for this concentration of production below the thermocline to be accessible to organisms living attached to or on the shoal system. The equipment that we used for sampling benthic invertebrates is specialized for softer substrates and may have been ineffective at sampling on the harder surfaces of the most extremely shallow and rocky shoals. Future forays to the shoals should consider methods for sampling hard surfaces or devices that collect organisms via colonization (e.g., Hester-Dendy samplers), particularly around depths that may encounter regions of high productivity (e.g., the DCM layer) when designing benthic-targeted surveys on the shoals.

In conclusion, my study illustrates the great need for further investigation in the processes driving the ecology of freshwater shoal complexes generally, and the Lake Superior Shoals Complex in particular. Due to its remote location and relatively high density of fish it is likely an important refugia for lake trout populations and provides a stabilizing element to their resiliency in Lake Superior in the face of pressures from invasive sea lamprey and fishing pressure lake wide (Akins et al., 2015; Hansen et al., 1995; Holbrook et al., 2006). This, coupled with the current lack of scientific understanding of the Lake Superior Shoal system, makes improving our understanding of this unique system and others like it with more comprehensive and targeted studies even more important to conservation and restoration efforts for managed fish populations in the Great Lakes system. Remote sampling technology such as the stationary acoustic platform detailed in Chapters I and II has great potential to benefit the enigma of this system by providing more accurate and detailed estimates of fish and *Mysis* behaviour without requiring vessel presence in adverse conditions.

Tables

Table 3.1. Two-way ANOVA tests and results for mean organism and Chl *a* estimates at the Lake Superior Shoals. The first three ANOVA's examined effects and interactions between location (on/off shoal), diel cycles (day/night) for fish density, *Mysis* density, and pelagic zooplankton density. The fourth ANOVA examined effects and interactions between location (on/off shoal) and species (*Diporeia*, Oligochaetes, and Other) for benthic organism abundance. The fifth ANOVA examined effects and interactions between side (North/South of shoal), and diel cycles (day/night) for areas off the shoals. An α value of 0.05 was used to access significance for all ANOVA's.

Independent Variable	Model Factor	df	Mean Squares	F-Ratio	P-value
Fish density (fish/ha)	Location	1	490.6	88.82	<0.001
	Diel	2	100.8	18.26	<0.001
	Location*Diel	2	9.8	1.77	0.175
	Residuals	137	5.5	-	-
Mysis density (#/L)	Location	1	37.7	11.71	0.002
	Diel	1	207.5	64.38	<0.001
	Location*Diel	1	5.0	1.55	0.223
	Residuals	31	3.2		-
Pelagic zooplankton density (#/L)	Location	1	20732	1.26	0.147
	Diel	1	8609	0.52	0.316
	Location*Diel	1	22521	1.36	0.251
	Residuals	31	16515	-	-
Benthic organism abundance (#/m^2)	Location	1	0.0	0.01	0.936
	Species	2	17.7	11.61	<0.001
	Location*Species	2	0.1	0.05	0.948
	Residuals	48	1.5	-	-
Chlorophyll *a* concentration (µg/L)	Location	1	0.0	0.04	0.851
	Column Depth	2	0.1	14.19	0.002
	Location*Column Depth	2	0.0	0.81	0.460
	Residuals	18	0.0	-	-
Fish density (fish/ha)	Side	1	1.8	0.56	0.451
	Diel	1	153.6	48.91	<0.001
	Side*Diel	1	0.1	0.02	0.891
	Residuals	60	3.1	-	-

Figures

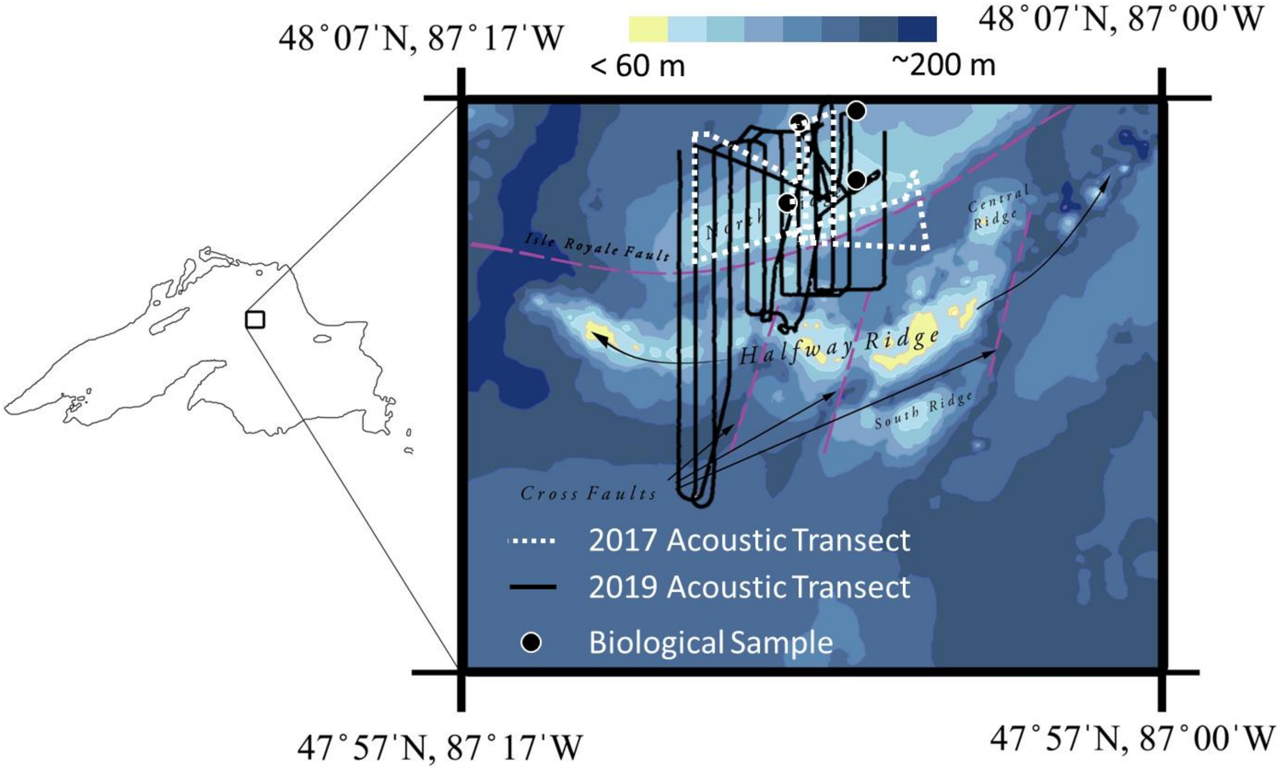

Figure 3.1. Location of Superior shoals' complex, displaying acoustic transects and biological sampling locations. Contour interval 20 m. Adapted from Manson and Halls (1991) and KDS4444 on Wikimedia Commons.

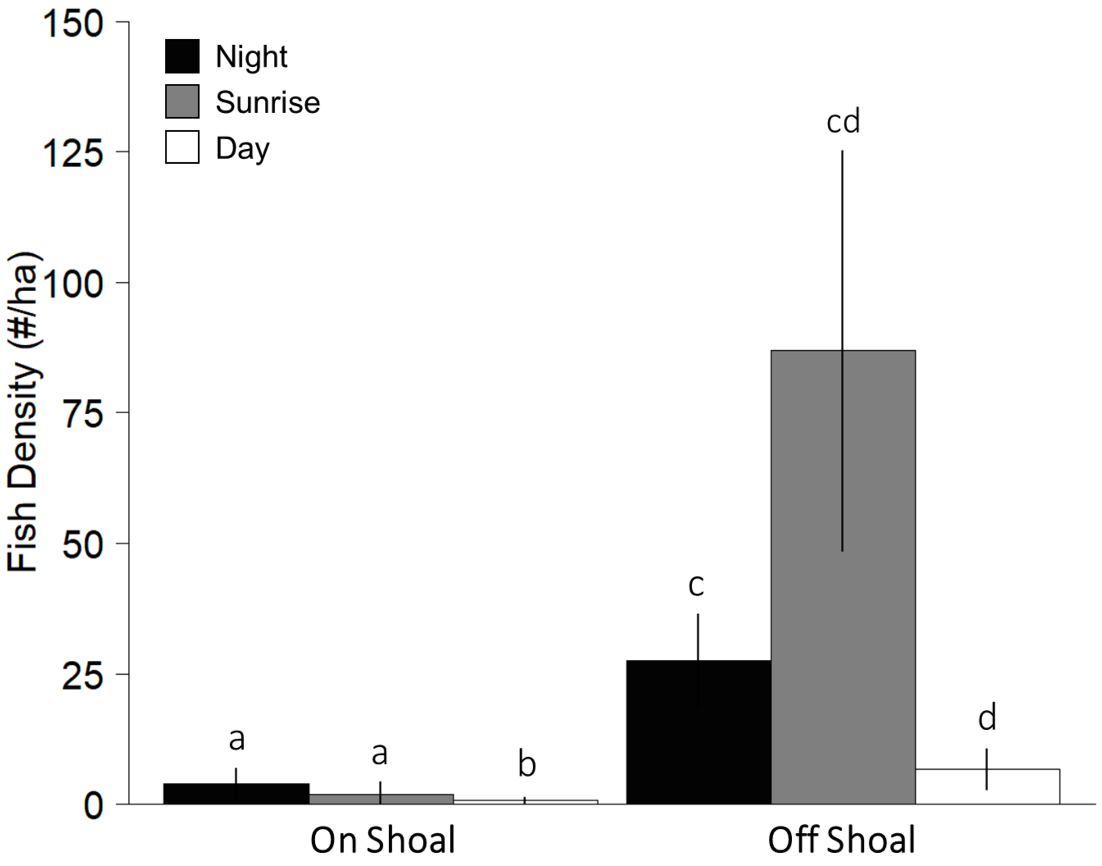

Figure 3.2. Mean fish density (fish/ha) detected by the acoustic survey on (< 120 m) and off the shoals (> 120 m) during the night, sunrise, and day hours in 2017 and 2019. Bars show mean fish density from ~1,200 m sections of the water column for each diel category the acoustic survey was run over the two depth regions in 2017 and 2019. Different lowercase letters represent significant differences ($p < 0.05$) between fish density detected in the day vs the night for each region sampled each year as determined by a Tukey HSD. Error bars indicate 95% confidence intervals around each mean.

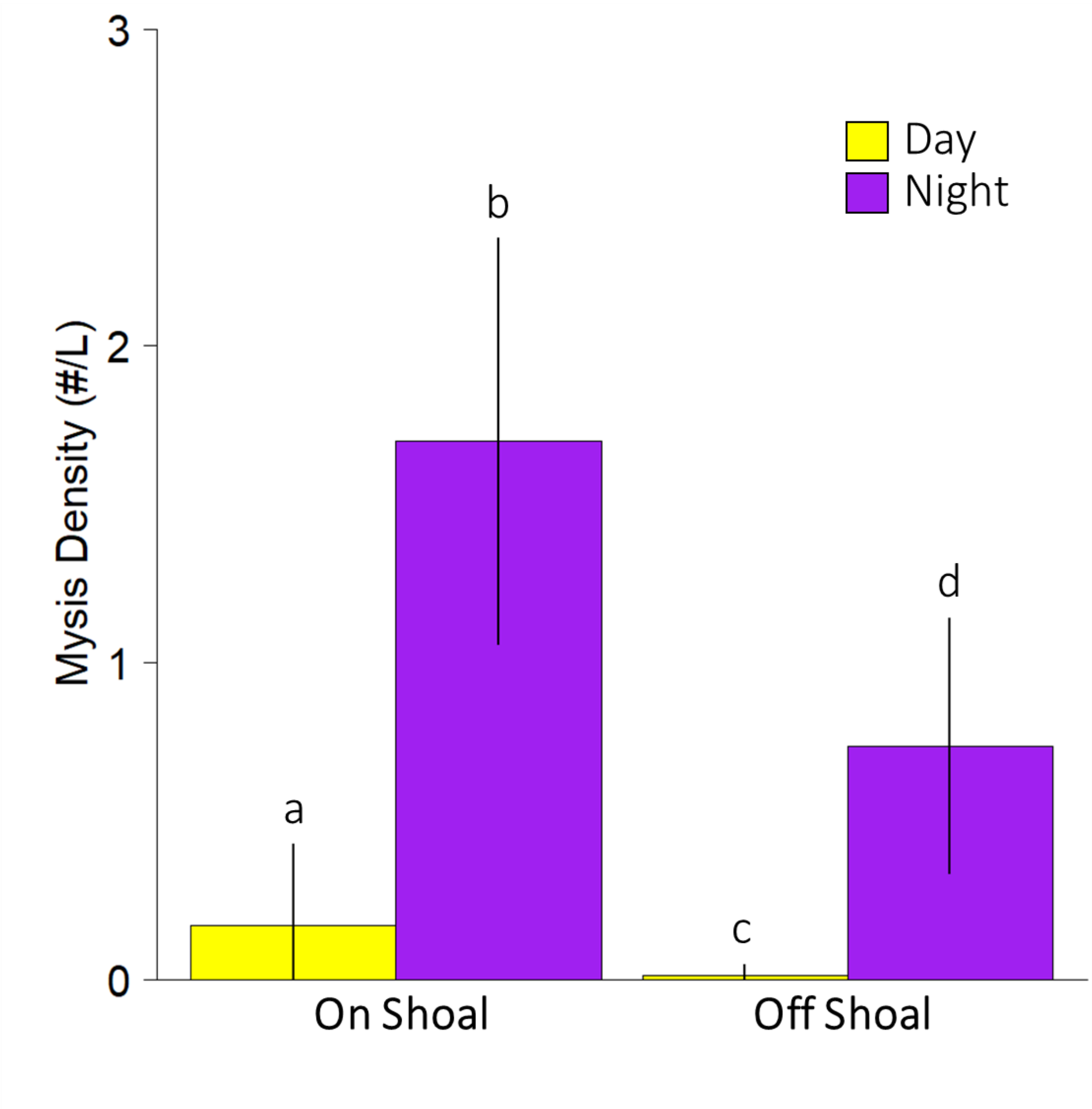

Figure 3.3. Mean *Mysis* density (*Mysis*/L) obtained by the zooplankton net tows on (< 120 m) and off the shoals (> 120 m) during the day and night in 2017 and 2019. Bars show mean Mysis density from 2 – 3 replicates at each biological sampling site during each diel cycle (Day/Night) in shallow (N = 4) and deep (N = 4) areas across both sampling years. Different lowercase letters represent significant differences ($p < 0.05$) between *Mysis* density detected in the day vs the night for each region sampled as determined Tukey HSD tests. Error bars indicate 95% confidence intervals around each mean.

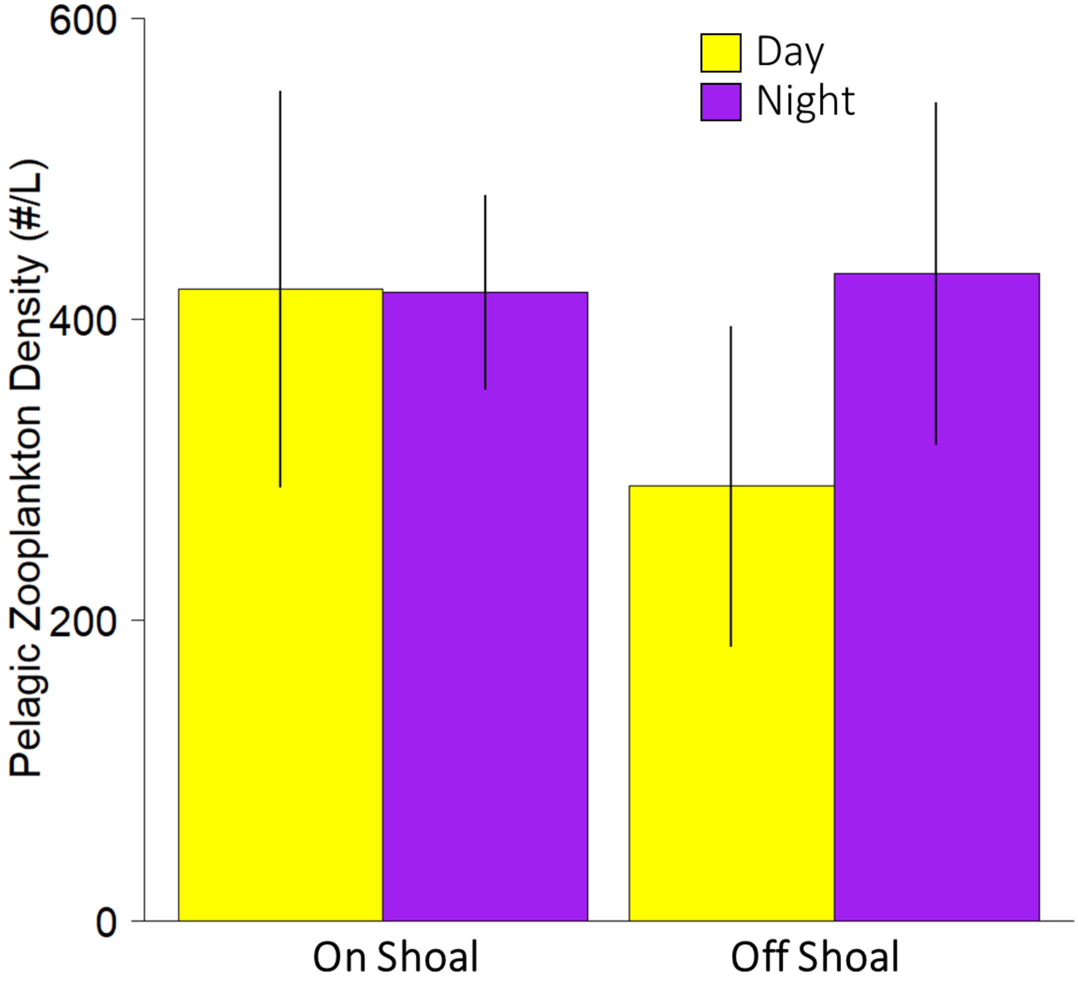

Figure 3.4. Mean pelagic crustacean zooplankton density (#/L) obtained by the zooplankton net tows on (< 120 m) and off the shoals (> 120 m) during the day and night in 2017 and 2019. Bars show mean zooplankton density from 2 – 3 replicates at each biological sampling site during each diel cycle (Day/Night) in shallow (N = 4) and deep (N = 4) areas across both sampling years. Error bars indicate 95% confidence intervals around each mean.

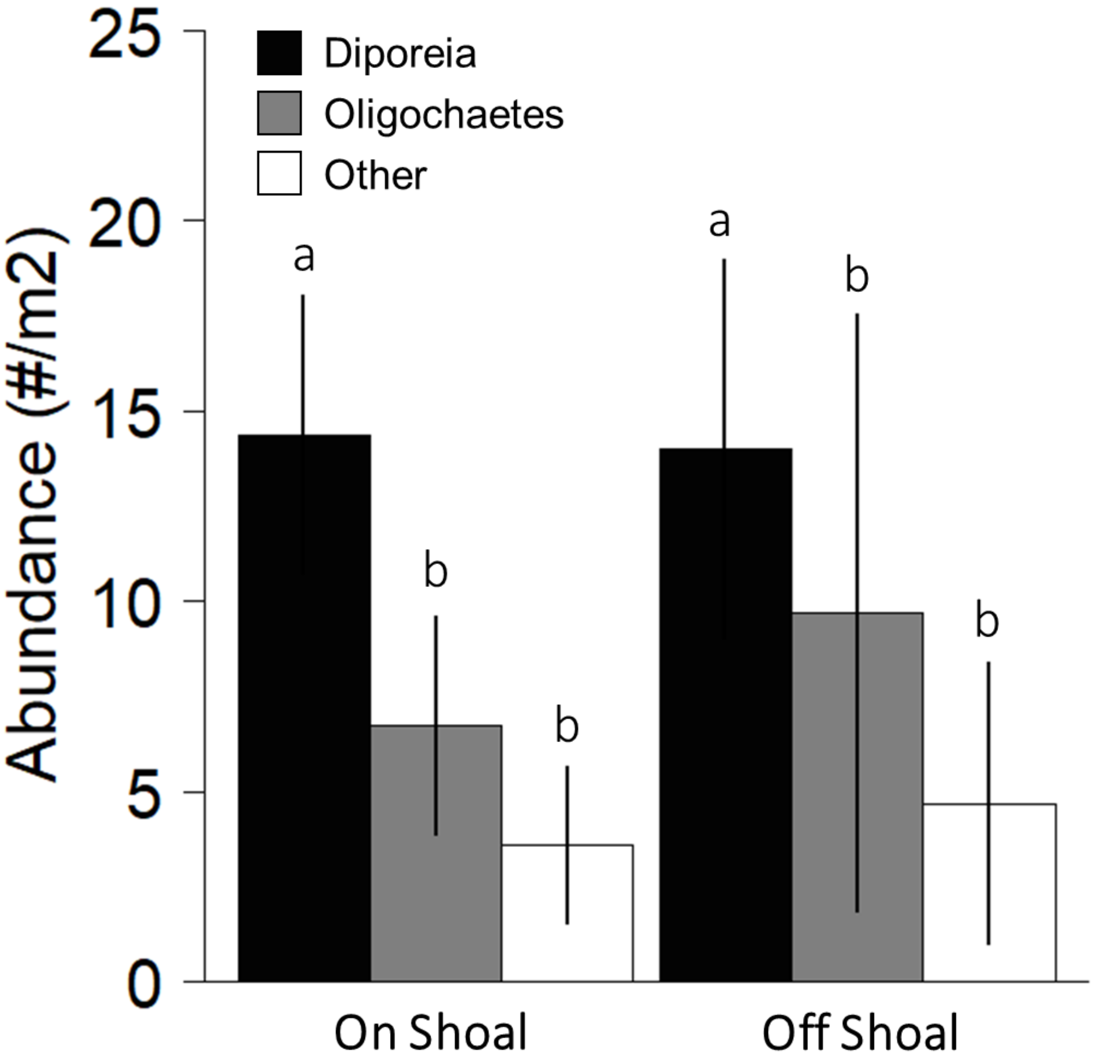

Figure 3.5. Mean benthic organism density (#/m^2) obtained by the ponar grabs on (< 120 m) and off the shoals (> 120 m) during the day in 2017 and 2019. Bars show mean benthic organism density from 2 – 3 replicates at each biological sampling site in shallow (N = 4) and deep (N = 4) water across both sampling years. Different lowercase letters represent significant differences ($p < 0.05$) between density detected in the day vs the night for each region sampled as determined by Tukey HSD tests. Error bars indicate 95% confidence intervals around each mean.

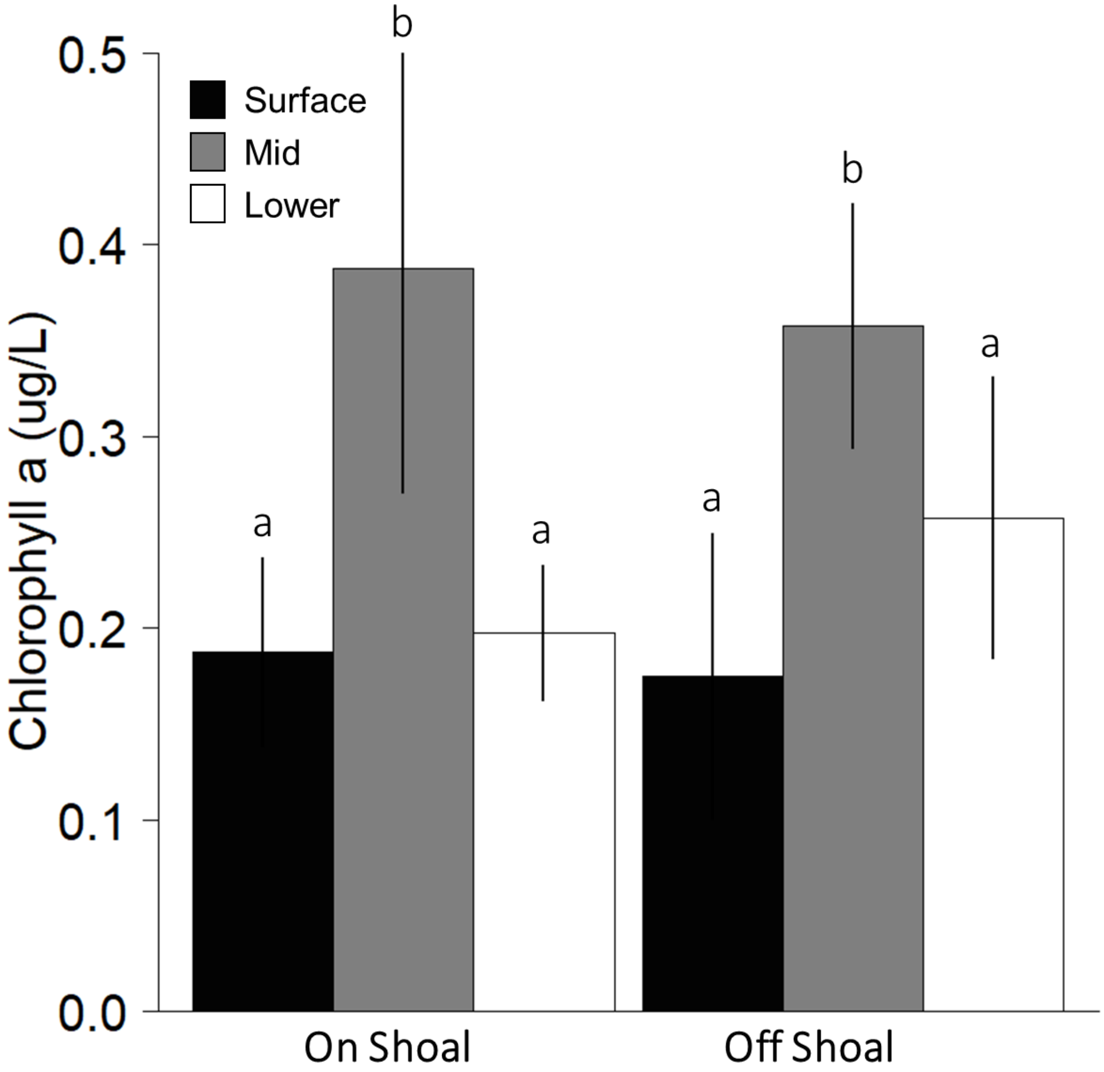

Figure 3.6. Mean chlorophyll *a* concentration (µg/L) obtained by the CTD on (< 120 m) and off the shoals (> 120 m) in 2019. Bars show mean chlorophyll *a* concentration from 2 replicates at each biological sampling site and water column depth category (surface, mid, and lower) sampled in shallow (N = 2) and deep (N = 2) water in 2019. Different lowercase letters represent significant differences ($p < 0.05$) between concentrations measured in the day vs the night for each region sampled as determined by a Tukey HSD. Error bars indicate 95% confidence intervals around each mean.

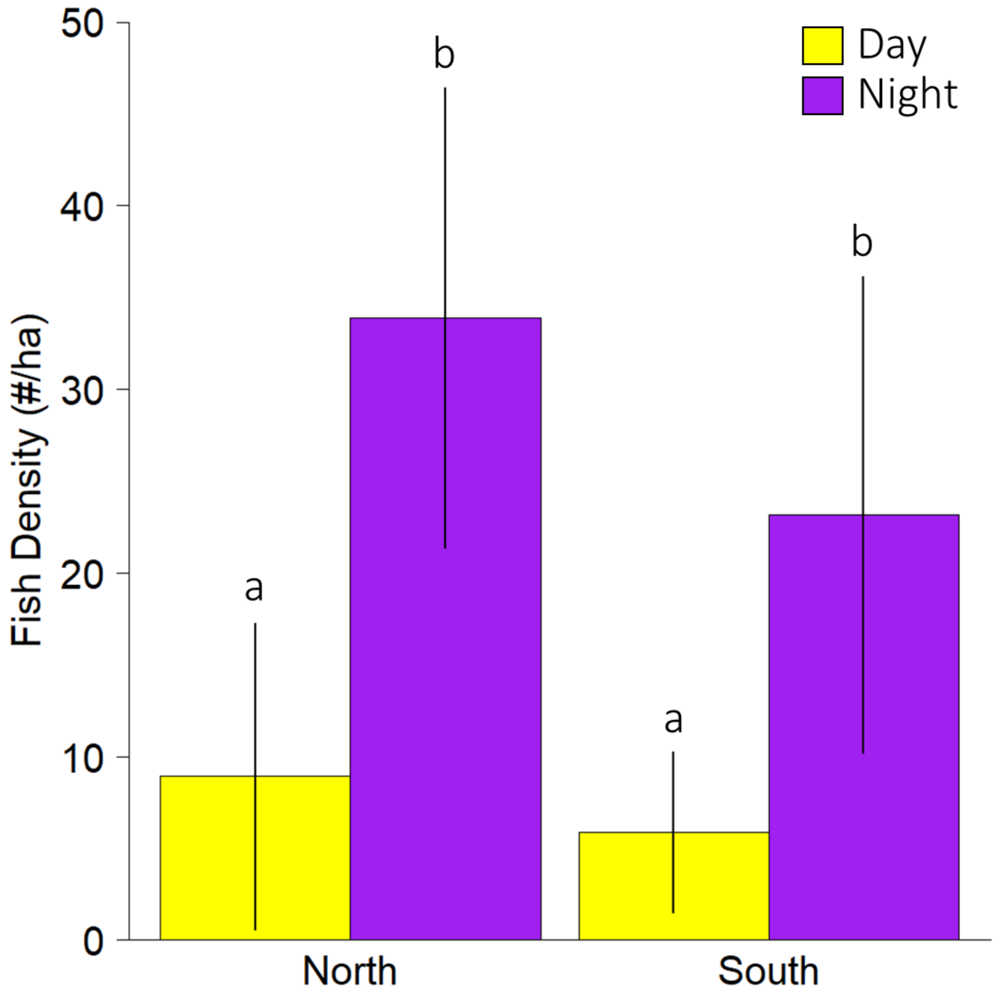

Figure 3.7. Mean fish density (fish/ha) detected by the acoustic survey off the shoals (> 120 m) to the North and South during the day and night in 2017 and 2019. Bars show mean fish density from ~1,200 m sections of the water column for each day/night the acoustic survey was run over sites North and South of the Lake Superior Shoals in 2017 and 2019. Different lowercase letters represent significant differences ($p < 0.05$) between fish density detected in the day vs the night for each region sampled each year as determined by a Tukey HSD. Error bars indicate 95% confidence intervals around each mean.

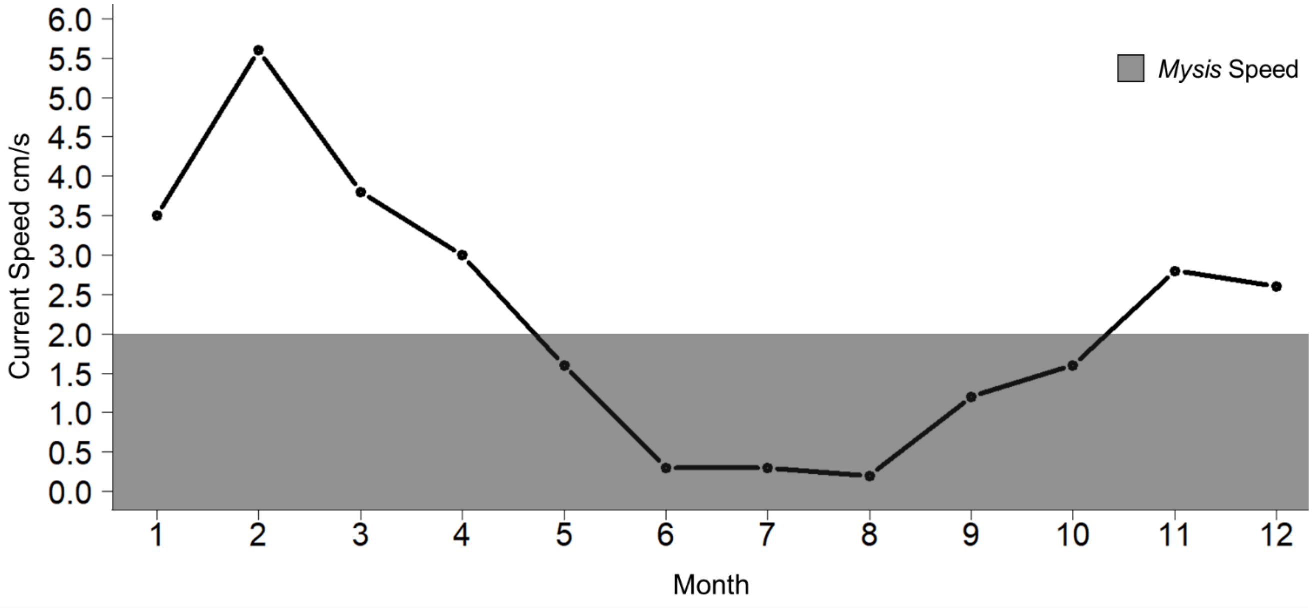

Figure 3.8. Estimated current speeds for each month at the Lake Superior shoals in relation to *Mysis* typical swimming speeds. Points are current speeds that were estimated from NOAA/GLERL Great Lakes Monthly depth-averaged currents map. *Mysis* swim speeds are diel migration speeds from Miller (2003).

Conclusion

Through this dissertation, I have demonstrated several unique applications of acoustic technologies (i.e., up-looking stationary deployments), or applications of traditional acoustic technologies to unique environments (i.e., Superior Shoals), all of which demonstrate the promise these applications have in improving our understanding of fish populations and ecology. Specifically, the updating and supplementing current survey techniques with stationary up-looking surveys has allowed me to provide new insights into the ecologically and commercially important cisco density patterns within the upper water column in Thunder Bay, ON. Deploying the stationary platform alongside summer netting surveys has allowed me to examine impacts that regional, diel, and inter-annual effects have on fish activity and behaviour across Lake Superior. I also highlight how a novel system that would benefit enormously from use of this autonomous up-looking survey method at the Lake Superior shoals complex. Through these studies I was able to build our general knowledge of the ecological processes related to fish density and movement that are applicable to current management practices, and fill scientific knowledge gaps that have large scale ramifications for aquatic fish and wildlife conservation in large freshwater ecosystems.

The key findings in my first chapter were that the stationary acoustic platform provided 6.7 times higher estimates of cisco density compared to the traditional ship-based down-looking survey in the upper water column across all survey sites. Additionally, when the cisco density estimates obtained from the whole water column were compared across sites, the acoustic platform detected significantly more fish than the traditional ship-based down-looking survey method overall. I also measured ship avoidance behaviour exhibited by cisco in the upper water column, with platform-based median cisco densities experiencing a 5 times decrease as the ship passed over the stationary unit. These findings are supported by other recent work in the Great Lakes that has suggested boat avoidance behaviours of pelagic fishes (DuFour et al., 2018; Grow et al., 2020). This has major implications for typical acoustic surveys and management of pelagic fishes in the Great Lakes; if fish are avoiding typical boat-mounted acoustic surveys, then quota estimates could be underestimated, calling into question the accuracy of acoustic estimates managers rely on to help inform quotas and monitor the overall population trends of Great Lakes fishes. Additionally, I found that integrating acoustic platforms into fisheries management practices has the potential to not only provide less biased fish density estimates but also save a considerable amount of hazardous and costly ship time hours. With further study and modifications around platform-based survey design, stationary up-looking surveys could provide low-cost and low-effort acoustic surveys of pelagic fishes in freshwater ecosystems with similar or better accuracy compared to current mobile acoustic methods.

Directly building on these insights, in my second chapter I discovered that inter-annual differences in movement and relative detection depth (RDD) between survey years were the main difference in fish behaviour at multiple locations in Lake Superior, and primarily associated with the small fish. This likely had the ecological explanation of 2022 being a large recruitment year for YOY coregonines which have elevated movement speeds and higher thermal optima (leading to shallower habitation depths) than other small fishes in Lake Superior such as rainbow smelt (Edsall, 1999; Lantry and Stewart, 1993; Ray et al., 2007; Savitz and Bardygula, 1989; Vinson et al., 2022). There were also significant differences in fish movement speeds across the diel cycles for the small and large fish in the directions predicted; large-sized fish slowed down significantly at night across all regions. Conversely, small fish sped up significantly at night in most of my study regions (with Whitefish Bay being the only exception). I also found distinct spatial patterns among the different size classes regarding movement speed. Variability in regional or local activity rates, such as those observed in this study, may be linked to the long-range dispersal potential of fishes. Broader research on organism dispersal supports the notion that a higher activity rate would likely lead to a higher dispersal potential, making management in high activity zones and bordering regions much more complex than is currently accounted for (Bie et al., 2012; Bonte et al., 2012; Comte and Olden, 2018). I also saw differences in RDD among regions, most commonly small fish moved closer to the surface during daytime hours compared to night rather than the expected DVM pattern of returning to greater depths near the lakebed during the day. It is possible that I was mainly sampling a novel behavioural strategy utilized by only a minority of small fishes, whereas the rest of the small fish may have either moved further offshore during the day to achieve greater depths (DVM) or moved into nearshore areas that offer the possibility of protective habitat structures (DBM; Gorman et al., 2012) during the daytime hours. These analyses indicate stationary up-looking platforms have the potential for understanding regional behavioural variation in large ecosystems (like Lake Superior), as well as significant potential to improve fisheries management by incorporating these regional insights.

Finally, I applied traditional acoustic methods in a novel environment, and provided insight into how this system would benefit greatly from future use of the stationary acoustic platform technologies detailed in this thesis. I examined the enigmatic Lake Superior Shoals system and sought to test the current hypotheses associated with the ongoing ecological processes driving production there, the Topographic Blockage hypothesis, the Benthic Algal Production hypothesis, and the Leeward Eddy Retention hypothesis. I found strong evidence of a deep chlorophyll maxima and diel-vertical migration behaviour in the fish and *Mysis* at the shoals, which are important building blocks for the TBH and LER hypotheses. However, I found little direct support for any of the three hypotheses, likely due to the slow currents at my time of sampling and logistical constraints to the sampling procedures. My findings point to the pressing need for more targeted research utilizing new autonomous technologies such as a stationary acoustic platform survey that will allow for longer term observation of the system and provide key insights into the processes at play on the shoals.

To summarize, I have advanced our understanding of the role that organism movement plays in energy flow, and therefore ecosystem function, through examining how fish movement patterns change in response to spatial and environmental variation and contribute to productivity hotspots. All my investigations can also be applied to better inform resource management and improve our basic understanding of fish ecology in large aquatic systems like Lake Superior. Specifically, the information from my study could help government organizations identify areas to create aquatic refuges for fish species preservation and set sustainable fisheries quotas that account for fish movement patterns explicitly. The findings of this study also benefit the general public through the lake management knowledge gained that will help maintain, or improve, Lake Superior's billion-dollar fisheries and tourism industries that rely on healthy lake ecosystems.

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