Examining the natural and disturbed behaviours of Alewife (*Alosa pseudoharengus*) using hydroacoustic surveys in Lake Ontario

By

Connor W. Elliott

A thesis submitted to the Department of Biology

in conformity with the requirements for the

degree of Master of Science

Queen's University

Kingston, Ontario, Canada

August 2018

Abstract

In Lake Ontario, Alewife are the primary prey for salmonids, which provide a popular and socio-economically important recreational fishery. There is concern with regards to whether the Alewife population has the ability to support the predatory demand in Lake Ontario after a crash in the Alewife and predator populations occurred in Lake Michigan. To avoid such a crash, it is imperative that agencies working on Lake Ontario have accurate methods of assessing fish populations. Mobile hydroacoustic surveys of the lake began in 1991 as a method to assess the Alewife population, however, there is growing concern about the accuracy of these estimates. Fish in hydroacoustic surveys can appear to be smaller when oriented off-axis, as is common with fish displaying boat avoidance behaviour. The mobile assessment estimates are made using size thresholds to classify targets in the survey and Alewife which are diving may be appearing too small to be correctly classified. Using information from mobile, as well as stationary up-looking surveys, this study assesses how Alewife react to the survey vessel, and how the reactions may be impacting their observed target strength. The results indicate that Alewife are observed at smaller sizes in the mobile survey than would be expected. The mobile survey observed fish at deeper depths and the behaviour of the fish was indicative of boat avoidance. Fish from the mobile survey swam faster and more linearly than fish from the stationary survey. Consecutive targets in tracks from the mobile survey also increased in depth with a more negative track tilt. There were no strong predictors of changes in target strength tested with linear models which could be used as correction factors in the current dataset. In future studies, analysis of variables such as the true orientation of the fish may provide appropriate correction factors for this

type of data. The current survey approach provides a valuable index of “relative” Alewife abundance from year to year, however, additional research will be required to provide more accurate estimates of the absolute abundance of Alewife in Lake Ontario.

Acknowledgements

I would like to thank Dr. Bruce Tufts for providing me with not only the opportunity to work on this project, but also to be a member of the Freshwater Fisheries Conservation Lab. Over the last few years I have been exposed to many different areas of fisheries research, and these experiences have fostered exciting opportunities for me. His guidance along the way has been very helpful and will continue to benefit me in the future.

I would also like to thank Jeremy Holden and Michael Connerton for all their guidance and time that went into the planning and development of this thesis. Their work, along with the individuals at the Lake Ontario Management Unit (Ontario Ministry of Natural Resources and Forestry) and the New York State Department of Environmental Conservation, produced much of the data used for this thesis.

I would like to acknowledge my committee members, Dr. Paul Blanchfield, Dr. Bill Nelson and Dr. Mel Robertson, for their input and recommendations with regards to my thesis. I would also like to thank the members of the Freshwater Fisheries Conservation Lab, specifically Randy Lindenblatt for the time he spent preparing for field work, as well as Sean Bridgeman for his input and support.

This research was funded by the Greenberg Family Fund at Queen’s University. Their desire to support fisheries conservation in Canada is very much appreciated and made this project a possibility.

Finally, I would like to give a big thanks to my family and friends for all of their support and encouragement.

Table of Contents

List of Tables

List of Figures

List of Abbreviations

EMS – Early Mortality Syndrome

LOMU – Lake Ontario Management Unit

NYSDEC – New York State Department of Environmental Conservation

OMNRF – Ontario Ministry of Natural Resources and Forestry

Chapter 1: Introduction and Literature Review

Recreational fisheries in North America provide a wide range of cultural and economic benefits. With an annual economic value of over 40 billion dollars, recreational fisheries have a greater economic impact than both commercial fisheries and aquaculture combined within North America (Tufts et al. 2015). To ensure recreational fisheries can be sustained for current and future demand, they must be properly managed. This task often falls upon governmental agencies. In the case of Lake Ontario, which is bordered by both Canada and the United States, there are multiple agencies making managerial decisions, for example, Canada's Lake Ontario Management Unit (LOMU) of the Ontario Ministry of Natural Resources and Forestry (OMNRF), and the United States of America's New York State Department of Environmental Conservation (NYSDEC). To ensure the sustained health of the entire lake, there must be co-operation and collaboration among agencies when making managerial decisions regarding topics such as the stocking of fish into the system. For fisheries managers working on Lake Ontario's popular recreational salmonid fisheries, it is imperative that they have a reliable estimate of the current forage base, as this is largely what determines the stocking targets for these large predatory fish. For almost 50 years, Alewife (*Alosa pseudoharengus*) have been recognized as one of the most important forage fish in Lake Ontario (Smith 1970). The Alewife populations in Lake Ontario are monitored annually through various assessment methods by both Canadian and American governmental agencies. Since 1991, joint mobile hydroacoustic surveys have been conducted by both the OMNRF and the NYSDEC to assess the abundance, biomass and distribution of Alewife throughout the pelagic zone of Lake Ontario.

Alewife

Alewife are a small-bodied fish (average length of 152 mm) which have a deep, laterally-compressed body shape, and an overall silvery colouration (Scott and Crossman 1973). They are a schooling species that primarily occupy the pelagic zone of water-bodies. During the day, Alewife can be found concentrated at the bottom of the water column, however, at night, they typically migrate upward to the base of the thermocline to feed (Janssen and Brandt 1980). Their diet is composed primarily of zooplankton, including copepods, cladocerans, ostracods, and mysids (Scott and Crossman 1973). Alewife growth is usually rapid during the early stages of their life, and decreases with the onset of maturity at age 2 for males and age 3 for females (Graham 1956). Females have faster growth rates than their male counterparts and attain greater overall sizes than males (Pritchard 1929).

Alewife are an anadromous species which were historically found primarily along the east coast of North America (Scott and Crossman 1973). Alewife are also known to use coastal freshwater streams to spawn. Over time, populations of Alewife have migrated inland and become landlocked in several lakes throughout south-eastern Ontario (Toner 1934). Alewife which have become landlocked are known to inhabit the deep, open regions of the lake for the majority of the year. At spawning times, they migrate into shallow areas and ponds. The spawning movements of Alewife begin in April and peak around mid-June, with some variation depending on location and water temperature (Graham 1956). Odell (1934) reported freshwater females depositing up to twelve thousand eggs over sandy or gravelly bottom substrate. The time it takes for the eggs to hatch typically depends on the mean water temperature, ranging from 3 days at 22.2 ºC, to 6 days at 15.6 ºC (Mansueti and Hardy 1967). Once hatched, the fry remain on the spawning grounds until the late larval stage and then slowly move to the deeper waters (Graham 1956). It was also reported that the adults return immediately to deeper water after spawning. Smith (1907) found that the young-of-year Alewife reach a mean size of 50-75 mm by the fall.

Perhaps the most important inland invasion of Alewife was into the Laurentian Great Lakes. The Great Lakes' invasion of Alewife began with Lake Ontario, where it was the first marine invasive species to become successfully established within the lake (Smith 1892). Alewife were first recorded in Lake Ontario during the spring of 1873, although there remains some disagreement about the exact mechanism behind their introduction (Bean 1884, Scott and Crossman 1973). Early researchers theorized that Alewife fry may have been accidentally stocked along with Atlantic Shad (*Alosa sapidissima*) in 1870 (Bean 1884). This theory is unlikely as the fraction of survivors from that stocking event would not have had enough time to mature and reproduce to the numbers observed by the spring of 1873 (Smith 1970). Another possibility is that Alewife naturally migrated up the St. Lawrence River, however, this is also unlikely as there were large sections of the river where Alewife were described as absent up until 1878, 5 years after the Lake Ontario establishment (Bean 1884). It is most likely that Alewife gained access to Lake Ontario through the Erie Canal (Smith 1970). The canal linked the Atlantic Ocean to the Lake Ontario drainage basin through the Oneida-Oswego River system. Both Cayuga and Seneca Lakes were observed to have large numbers of Alewife during the 1860s, which could have been producing substantial numbers of juveniles (Bean 1884, Smith 1892). These juveniles would have had access to Lake Ontario through the adjoining rivers. This theory is the most widely accepted mechanism of introduction since this timeline would account for the large numbers of adults discovered in Lake Ontario by 1873.

The Alewife population that became established in Lake Ontario was able to rapidly expand due to favourable habitat and a lack of predation. At the time, there was a top-predator void in the system because native predator populations in Lake Ontario had experienced severe declines. Atlantic Salmon (*Salmo salar*) and Lake Trout (*Salvelinus namaycush*) were the lakes' major piscivores and had historically occupied the shallow and deep areas of the lake until they were subject to sharp population declines in the 1860s (Smith 1892). The declines in these predator populations were the result of intensive habitat alteration, commercial over-harvesting, and parasitism by Sea Lamprey (*Petromyzon marinus*) (Crawford 2001). The Sea Lamprey was thought to have been introduced to Lake Ontario in a similar manner to the Alewife, through the Erie Canal, either swimming from its native habitat in the Atlantic drainage or attached to the hulls of boats (Mills et al. 1993). Therefore, the major piscivores, which may have historically inhibited entrance of Alewives using natural routes into the lake, were experiencing declining or greatly reduced populations. This was occurring at the same time as the large influx of Alewives was entering the lake from the Erie Canal in the 1860s (Smith 1970).

With no natural predators and a favourable environment, the Alewife population rapidly expanded in Lake Ontario and had several negative consequences on the ecosystem. Some species native to Lake Ontario, such as the Yellow Perch (*Perca flavescens*), were directly affected by Alewife. It has been observed that Alewife prey upon the larvae of Yellow Perch (Brandt et al. 1987). Similar results have been observed with the consumption of Lake Trout fry, and it is suspected that the Alewife actively select for larvae and fry as they are larger than their typical diet of zooplankton (Krueger et al. 1995, Brandt et al. 1987). Alewife have also become a major source of prey for adult Lake Trout within Lake Ontario, and this has also had negative consequences (Jones et al. 1993). Alewife contain high concentrations of an enzyme known as thiaminase, which breaks down thiamine, and can accumulate in Lake Trout when they consume Alewife (Fitzsimons 1995). Thiaminase-positive bacteria have been isolated from Alewife viscera, however, these bacteria are only considered to be one potential source of thiaminase in Alewives, while the other sources are still unknown (Honeyfield et al. 2002). Thiamine deficiency has been shown to be a cause of Early Mortality Syndrome (EMS) in Lake Trout, which has contributed to low levels of natural recruitment for this species in Lake Ontario (Fitzsimons et al. 1995). Evidence suggests that Alewives, through EMS, may have also contributed to the Atlantic Salmon extirpation (Madenjian et al. 2008).

By the mid-1900s, not only were the Alewife negatively impacting the ecosystem, they also began to have undesirable effects on humans. During the spawning season, Alewife would gather in such large numbers along the near-shore region that industrial and municipal water intake pipes would become clogged with fish (Scott and Crossman 1973). They also experienced massive die-off events throughout the Great Lakes where large amounts of dead Alewife would collect along shorelines and within harbours. Several factors have been suggested to account for the high mortality, such as spawning stress and low food availability, however, it seems their inability to quickly acclimate to changing temperature may be the most pertinent (Scott and Crossman 1973, Graham

1956). Lepak and Kraft (2008) found that cold weather led to osmoregulatory challenges and produced immunosuppression, which ultimately increases an Alewife's susceptibility to disease and mortality. To support this, years with severe winter temperatures are linked to major Alewife die-off events (O'Gorman and Schneider 1986). The die-off events resulted in millions of dollars being spent to remedy fouled tourist beaches and blocked water intakes for industrial and municipal facilities (Brown 1972). The negative impacts associated with large numbers of Alewife in Lake Ontario required methods to control and reduce the size of their populations.

Alewife on the Atlantic coast had been commercially harvested for both human consumption and for use in the preparation of pet food (Scott and Crossman 1973). Gillespie (1967) reported that the majority of commercially landed Alewife went towards pet food, however a small quantity of the 3.3 million kg that were caught annually were eaten fresh or smoked by humans. Landlocked Alewife were much smaller than those in the Atlantic and were therefore considered less desirable for human consumption. By the early 1960s, commercial fisheries were established in the Great Lakes to begin harvesting Alewife, which would be used in fertilizer and pet food production (Brown 1972). Bottom trawling was the preferred method for harvesting the fish, however, this method was not economically feasible as the cost of production was too high, market value of the products was too low, and the Alewife occasionally possessed levels of toxins that exceeded acceptable amounts (Emery 1985). It has been shown that DDT (dichloro-diphenyl-trichloroethane) would accumulate in the tissues of Alewife, particularly their body fat, as they fed on planktonic organisms that contained minute amounts of the chlorinated hydrocarbon (Scott and Crossman 1973). Since harvesting Alewife through commercial fisheries was not a feasible option, fisheries managers explored other methods of biological control. In 1968, an intensive salmonid stocking program was initiated with the objective of creating a self-sustaining population to fill the top predator void (Dettmers et al. 2012). If managed properly, this approach would reduce the numbers of Alewife through predation, thereby producing a healthier ecosystem and also minimizing the other unwanted impacts resulting from exceedingly high Alewife populations. In addition, the introduced salmonids could be targeted by anglers to create an offshore recreational fishery.

Salmonid Stocking

Since native predators in Lake Ontario had been largely extirpated, stocking programs were needed to re-establish their populations. At the time, it was also proposed that the introduction of some non-native species could be beneficial. Fish stocking had been occurring in Lake Ontario since 1866 for some species, including native Atlantic Salmon and non-native Rainbow Trout (*Oncorhynchus mykiss*). Historically, this was conducted in an effort to compensate for the decreasing commercial harvest rates in Lake Ontario at that time, however, the amount of fish being stocked was not very effective at establishing self-sustaining populations (Crawford 2001). It was not until 1968 that a much more intensive stocking program was developed in an effort to properly establish populations of both native and non-native piscivores in Lake Ontario. These populations were introduced with the intentions of controlling the Alewife population through predation (Jones et al. 1993). The major native species stocked was Lake Trout, while the non-native Pacific salmonids that were introduced were the Chinook Salmon (*Oncorhynchus tshawytscha*), Coho Salmon (*Oncorhynchus kisutch*) and Rainbow Trout, and also Brown Trout (*Salmo trutta*). While in the open-lake, these salmonids spend the majority of their time preying on Alewife. It has been reported that of all the predatory species in Lake Ontario, Chinook consume the most prey (Rand and Stewart 1998). Chinook have such high foraging rates that they reach reasonable sizes for recreational fishing within a couple of years. By the late 1970s, catch rates of Pacific salmon had reached high levels and large Chinook (15-20 kg) were being caught regularly by anglers. This enabled the fishery to provide a significant economic return through the establishment of a charter boat industry (Dettmers et al. 2012).

The salmonid introduction was deemed a success by many fisheries managers as there was a significant decline in the Alewife population, and the salmon fishery gained popularity with the general public (Emery 1985). It was such a success that managers were encouraged not only to continue stocking, but to increase the numbers of stocked salmon. By the mid-1980s stocking had peaked at around 8 million fish stocked annually, the majority of which were Chinook and Lake Trout (Jones et al 1993). This stocking rate stayed fairly constant until 1992 and the majority of the stocked fish came from American hatcheries (Jones et al. 1993). At this point, there was new concern about the stability of the Alewife population and the number of stocked salmonids was reduced to lower the predatory demand by 50% (Murry et al. 2010). It was theorized that natural reproduction of salmonids was now occurring in the lake and increasing predator demand. Murry et al. (2009) suggested that since 1992, wild reproduction was responsible for, on average, around 60% of the adult Chinook population in Lake Ontario. Other stocked species including Rainbow Trout, Coho Salmon, and Lake Trout were also reproducing naturally in Lake Ontario (Johnson and Ringler 1981, Marsden and Krueger 1991). Due to the complexities of stocking in conjunction with wild reproduction, the possibility of overstocking became a serious concern. The observed demand on prey populations risked exceeding the limits of what the forage base in Lake Ontario could support.

In 1987, a serious overstocking problem occurred in Lake Michigan that resulted in a dramatic decline in harvest rates, as well as massive mortalities of Chinook Salmon (Stewart and Ibarra 1991). The carrying capacity of the lake had been exceeded, which triggered an epidemic of bacterial kidney disease (Crawford 2001). The Alewife deficit in the system caused the Chinook to become severely stressed, which resulted in the expression of bacterial kidney disease (Nelson and Hnath 1990). Unanticipated reductions in Alewife populations have also been observed in Lake Ontario since 1990 (New York State Department of Environmental Conservation 2014). To date, however, there has not been a profound collapse of the fishery in Lake Ontario. Proper methods of population assessment, which include both stocked and natural reproduction, as well as understanding the current status of the forage base, are important tools that Lake Ontario managers are using to avoid the type of crash that occurred in Lake Michigan.

Current assessments of Lake Ontario salmonid populations include the Credit River Chinook Salmon Spawning Index, the Juvenile Chinook Assessment, the Duffins Creek Resistance Board Weir, the Fish Community Index Gill Netting, and angler creel reports (Ontario Ministry of Natural Resources and Forestry 2017). These assessments provide information used to build models to estimate open-lake abundances and distributions of the predators, as well as their interactions with prey such as Alewife (Jones et al. 1993, Murry et al. 2010, Rand and Stewart 1998, Rand et al. 1994). Alewife populations are currently estimated using traditional methods of assessment, such as trawling and gill netting. Since 1991, hydroacoustics have also been used in an attempt to gain lake-wide abundance estimates and to determine the distribution of prey species in Lake Ontario.

Hydroacoustics

Hydroacoustics is an assessment technique that uses transmitted sound to detect fish in water. Sound is transmitted as a pulse, also called a ping, from a device called the transducer, which converts an electrical signal into an acoustic pulse. This acoustic pulse travels through the water column until it reaches a target, such as a fish, or the bottom of the waterbody. When it reaches objects with a density that is different from that of the surrounding water, such as the air in the swim bladder of a fish, or the bottom substrate, the signal gets reflected back towards the surface of the water (Love 1971). This returning pulse, or echo, is received by the transducer which converts the acoustic pulse back into an electrical signal that can be sent to a computer for processing. The echo provides information on the target's size and location in the water column. Target strength is a measure of how strong the reflected pulse is, and is an indication of the size, or reflectivity of the object. The depth of the target can be determined by the time it takes for the signal to return because the speed of sound travelling through water has been well studied (Simmonds and MacLennan 2005). Volume backscattering is another measure of the signal that returns to the transducer. This measurement can provide information about the density of objects, such as the bottom of the lake. Measures of density can be used to classify the type of bottom, as different substrates have different amounts of reflectivity. In rivers and lakes, echosounders can be positioned either vertically or horizontally to record fish as they swim past. Echosounders may also be mounted or towed behind a watercraft to perform mobile surveys of a water body. This provides a mechanism to collect data along transects in a non-invasive and repeatable manner which allows for comparisons to be made between surveys (Taylor and Maxwell 2007).

Initial hydroacoustic survey technology which became popular in Canada during the early 1970s was somewhat limited (Pollom and Rose 2016). This resulted in difficulties discriminating between single targets and tightly clustered schools of fish, interference from surface noise, and the inability to confirm the species of fish recorded without accompanying biological sampling. Many of these limitations have been resolved in recent years with the introduction of new types of echosounders, which can also be towed further behind the watercraft with both upwards and down-facing transducers. Using biological information to coordinate surveys at times of the day when some of these problems can be avoided is another way that this form of assessment has been improved (Taylor and Maxwell 2007).

Fixed hydroacoustic systems have been utilized to monitor fish in freshwater rivers since the 1960s (Johnston and Steig 1995). It has not been until the last four decades that the use of mobile hydroacoustics surveys for assessing landlocked freshwater fish has also become popular (Thorne 1997, Burczynski and Johnson 1986, Parkinson et al. 1994). Surveys are typically conducted at night, as both the piscivores and the forage fish, which usually aggregate during the day, disperse in the water column at night to feed (Parkinson et al. 1994, Appenzeller and Leggett 1992). Single target counts provide more accurate abundance estimates, therefore observing targets that are dispersed at this time of day avoids some of the challenges associated with single target recognition. This vertical diel movement varies by season and can be influenced by factors such as temperature, oxygen concentration and the location of prey (Lucas et al. 2002). In order to confirm that the targets being recorded in the acoustic survey belong to a particular species of interest, some form of biological sampling gear is typically required. This can include midwater trawls, gill nets, electrofishing or angler surveys, all of which can also be used to confirm the size of the targets (Taylor and Maxwell 2007). Using the acoustic fish counts and lengths, in conjunction with weights collected from the biological sampling, it is possible to make biomass estimates for lake-wide populations. Ultimately, hydroacoustic technology allows for estimates to be calculated regarding absolute abundance, lake-wide biomass, as well as the distribution of the targets within the waterbody. These are all considered valuable parameters used to assess fish populations.

Target strength is measured through sound intensity, or decibels (dB), and relates to the reflective surface of a fish. The amount of reflective surface is proportional to fish length, which can be estimated using an equation with parameters that are species-specific and developed from previous tests (Love 1971). The relationship between the two measures is logarithmic, and as target strength increases, so does the predicted length of the fish. The orientation of the fish in the water can also influence its target strength because the perceived length will vary depending on whether the swim bladder is parallel to the transducer face, which is typically parallel to the surface of the water. When the swim bladder is parallel to the surface, it is presenting its maximum amount of reflective area. However, as fish change their orientation, which can occur as they dive away or swim towards the surface, this reflective area can become diminished. This can result in a fish with a certain true length to be recorded as a smaller fish in a hydroacoustic survey. Brooking and Rudstam (2009) used Alewife in net-cages to collect *ex situ* measurements of target strength for groups of fish whose mean length was known. They found that although the mean of the target strength distribution was significantly related to fish length, the distribution was left-skewed. It also had a range of up to 25 dB, thereby demonstrating the large degree of variability in observed target strength. These experiments provide a good measure of natural variations in Alewife target strength, however, they do not account for potential influences during a mobile survey, such as boat avoidance behaviour.

Similar work has been done to assess the distributions of target strengths observed for a single fish in horizontal hydroacoustic applications. As fish move through the lateral plane of the hydroacoustic beam, they can demonstrate varying target strengths as they swim towards or away from the transducer. These changes would be analogous to a fish in a vertical acoustic beam, moving towards or away from the transducer, exhibiting a vertical diving response. Rodríguez-Sánchez et al. (2016) used fish of a known size, placed in a stationary net-cage within a hydroacoustic beam, to test the influence of position and orientation on the change in target strength. They found that orientation played an important role, and that larger fish had a greater range of possible target strengths. The issue of quantifying how often fish are observed at their maximum target strength will be one of the topics addressed in this study.

Hydroacoustic surveys offer many benefits in the field of fisheries assessment. It is also apparent that many aspects of this technology continue to require study in order to fully understand its accuracy and limitations. This thesis will examine how the behaviour of Alewife in Lake Ontario affects their observed target strength in hydroacoustic surveys. Understanding this issue will help to improve the interpretation of data collected in these surveys and will therefore lead to more accurate population assessments using this approach.

Thesis Objectives

Avoidance of survey vessels has been well documented for many species of fish and is typically a result of underwater radiated noise produced by the survey vessel (De Robertis and Handegard 2013). The typical reactions include diving, horizontal movement and altered tilt angle distribution (Simmonds and MacLennan 2005). This thesis will examine the natural behaviours of Alewife in Lake Ontario and compare them to the behaviour of Alewife during a mobile hydroacoustic survey. It is hypothesized that the estimated lengths of Alewife from mobile hydroacoustic surveys are being underestimated because the amount of reflective surface for the hydroacoustic signal is reduced when they dive to avoid the survey vessel. This reduces their mean target strength and when the size threshold for identifying Alewife is applied to the targets, it may be excluding a significant number of fish from the survey which should be counted as Alewife.

A combination of stationary up-looking and mobile down-looking hydroacoustic transducers will be used to evaluate the potential importance of these movements in the survey results. Using hydroacoustic measures of Alewife behaviour, it may be possible to examine the differences between the mobile and stationary surveys to determine how the Alewife are reacting in the mobile survey. If the Alewife are spending a significant amount of time off-axis, then it may be appropriate to adjust the lower size threshold used to classify targets as Alewife in future annual lake-wide prey surveys. Reducing the lower threshold to include more off-axis fish in the survey as Alewife may help to reduce the differences in abundance estimates between hydroacoustics and other forms of assessment.

Aim 1: Target Selection

The first section of this study will examine the differences in the size distributions of fish observed in stationary and mobile surveys. Using the observed maximum target strengths of each track, it will be possible to compare the target strength distributions of the mobile and stationary targets to determine the proportion of targets that would be classified as Alewife using the current size thresholds. This process will determine which tracks should be classified as Alewife in the mobile and stationary surveys. Only the Alewife tracks will be used to compare the differences in tracks and their behaviours for the remainder of the analyses in this study.

Aim 2: Standardized Fish Tracks

Large variations in target strengths have been well documented for fish that demonstrate diving behaviours in response to noise radiating from a vessel (Ona et al. 2007). Vabø et al. (2002) used a stationary up-looking transducer to record Atlantic Herring (*Clupea harengus*) as a survey vessel passed above to demonstrate the effect the vessel had on the number of observed fish. The results indicated that there was a significant decrease in herring abundance as the vessel passed above as a result of fish being excluded from the view of the transducer. Although many studies demonstrate vessel avoidance for certain species, this reaction can vary with season. For example, another study found that spawning herring did not react to the survey vessel (Skaret et al. 2005). In the present study, the behaviour of Alewife is examined in Lake Ontario, during the same time period as the mobile survey.

Using fish tracking software, it will be possible to determine the various target strengths exhibited by a single fish that is not disturbed by the stationary survey. A collection of single Alewife distributions will be standardized to create an overall distribution of target strengths that would be expected by the average Alewife. This undisturbed behaviour will provide a baseline estimate of the range of target strengths observed for an Alewife when no boat avoidance is occurring. The same procedure will be used to create a distribution of target strengths exhibited by Alewife in the mobile survey. These two distributions will be compared to examine their median values and the shapes of these distributions. It is hypothesized that fish in the mobile survey will have a lower median target strength than fish in the stationary survey. More specifically, the distribution for the fish from the stationary survey will be more left-skewed than distribution for the fish from the mobile survey. The left-skew would indicate that fish from the stationary survey are spending more time on-axis than the fish from the mobile survey.

For the same tracks, the depths of targets within the tracks will be standardized for the fish from the stationary and mobile surveys. It is hypothesized that the median depth of the fish from the mobile survey will be deeper than the median depth of the fish from the stationary survey. An increase in depth would be indicative of a diving behaviour for the fish from the mobile survey in response to the approaching survey vessel.

Aim 3: Differences in Behaviour

From the fish tracks it will be possible to collect measures of behaviour which may be indicators of boat avoidance in fish during the mobile survey. The swimming speed, tortuosity (measure of linearity of the track), change in depth, and orientation of the track will be measured for each fish. It is hypothesized that fish in the mobile survey will be swimming faster and in a more linear path. These tracks are also hypothesized to increase in depth with a more negatively oriented direction relative to fish observed in the stationary survey. These behaviours will be used as indicators that the fish in the mobile survey are demonstrating a diving response, moving deeper and away from the survey vessel.

Aim 4: Predicting Changes in Target Strength

If differences in the change in depth and orientation are observed between the mobile and stationary surveys, then it may be possible to predict the change in target strength using these changes in behaviour. For two consecutive targets within a track, it will be possible to measure the change in target strength, the change in depth, and the tilt between the two targets. It is expected that there will be a negative linear relationship between changes in depth and target strength, as well as the orientation of the track and target strength. A fish that does not change depth or tilt would not be expected to demonstrate much change in target strength, since it would be expected that those fish are remaining parallel to the surface of the water and transducer.

Chapter 2: Methods

Study Site

Lake Ontario supports a wide diversity of both near-shore and pelagic fish, of ~130 different species (Crossman and van Meter 1979). This community is composed of both native and non-native species. The lake has a surface area of 18960 km^2, with an average depth of 86 m and a maximum depth of 244 m (Government of Canada and United States Environmental Protection Agency 1995). It is the last of the Great Lakes in terms of drainage, being supplied from the Niagara River and the upper Great Lakes, and draining through the St. Lawrence River to the Atlantic Ocean. The water clarity in the majority of the lake is typically high, and has increased since the introduction of dreissenid mussels (Holeck et al. 2008). Lake Ontario becomes thermally stratified during the summer, beginning with the nearshore, typically around mid-May to early July, followed by the deeper central zone later in the summer (Rodgers 1987). At the time of sampling for this study (late July), the lake had thermally stratified and the average depth of 10 ºC water was at ~20 m.

Hydroacoustic Sampling

In order to capture undisturbed movements and behaviours of Alewife using a hydroacoustic survey, a stationary sampling device was deployed in a location which would not be influenced by boat traffic. The hydroacoustic sampling device was anchored near the lake bottom, with the transducer facing towards the surface at three sites with varying depths (Table 1). The three locations were situated within transect corridors from the mobile survey in order to sample similar areas (Ontario Ministry of

Natural Resources and Forestry 2017). The stationary survey was conducted using a BioSonics DT-X SUB (BioSonics Inc. Washington, USA), autonomous submersible echosounder. Echosounder settings for the stationary survey are listed in Table 2. The echosounder was affixed to a floating sled which was anchored a few meters off bottom. An offset line to the surface with floating buoy was attached to the anchor for retrieval of the echosounder at the end of sampling. The line was offset at an adequate distance to ensure that it did not have an influence on the fish in the beam, nor was it recorded by the beam. Temperature profiles were conducted at each site.

The mobile survey data used in this study was collected as part of the 2017 OMNRF Lake-wide Hydroacoustic Assessment of Prey Fish, which began as a sampling program in 1991 and was standardized to an annual mid-summer survey in 1997 (Ontario Ministry of Natural Resources and Forestry 2017). The standard survey is comprised of five transects in the main lake and one in the Eastern Basin. The main lake transects run shore-to-shore in a north-south direction, while the Eastern Basin transect forms a U-shape. Three of the transects utilize an angled dogleg at the southern end to increase the amount of distance in a water depth of less than 100 m, as the southern shore has a steeper slope than that of the north. In 2005, a corridor approach was set up where transects were randomly selected each year within a predetermined corridor. This allowed the survey to incorporate a random aspect while still accommodating for logistical constraints such as suitable lengths of transects and available ports of departure. Three additional transects were conducted in 2017 to collect additional shallow water data (depth<100 m) and utilize higher ping rates. The mobile hydroacoustic data was collected using a BioSonics DT-X portable scientific echosounder (BioSonics Inc. Washington, USA), with a fixed-mount transducer attached to the side of the hull of the survey vessel, the Ontario Explorer. Echosounder settings for the mobile survey are listed in Table 2. Along each of the transect paths, multiple temperature profiles were conducted to facilitate the assignment of species to targets.

Both the stationary and mobile surveys occurred overnight, beginning approximately one hour after sunset, to account for the vertical diel movement of the fish in the upper part of the water column. This vertical dispersal allows for better single-target recognition and a more defined separation between the Alewife and Rainbow Smelt (*Osmerus mordax*) within the water column. Alewife occupy the region of the water column above the 10 ºC thermal boundary, while Rainbow Smelt occupy the region below (Ontario Ministry of Natural Resources and Forestry 2017).

Echogram Analysis

All echograms from the stationary and mobile surveys were processed using Echoview (version 8.0) analysis software, with the Fish Tracking module (Echoview 2018). For both surveys, only the tracks which were recorded between the depths of 2 m and 15 m were included in analysis. This section of the water column was used as it excluded noise from wave and boat action at the surface (depth<2 m) and was above the 10 ºC line (depth>15 m). The depth of 15 m was chosen as the lower limit, as the 10 ºC line was on average around 20 m, thus using a depth of 15 m added some buffer to ensure that the tracks being analyzed were only Alewife. Using the 10 ºC water line as a method of assigning species to hydroacoustic targets was used for this study as it is the standard practice used by the OMNRF for the Lake-wide Hydroacoustic Assessment of Prey Fish (Ontario Ministry of Natural Resources and Forestry 2017). Trawls in this section of the water column catch Alewife to such a degree that they are considered the only prey fish species at these depths (J. Holden, LOMU, personal communication). Only the sections of the mobile transects which occurred in areas of the lake with a bottom depth of 60 m or less were used to match the bottom depths of the stationary survey. In order to define a range of target strengths for classifying Alewife this study again used the standard practice from the Lake-wide Hydroacoustic Assessment of Prey Fish, which uses a size threshold defined for Alewife at the time of the sampling. The threshold is determined using biological samples captured in concurrent mid-water trawls, which sample fish from the same part of the water column, and at the same time, as the hydroacoustic survey. A length frequency distribution for the Alewife was determined using the trawl catches, and the target strength threshold was defined by the LOMU using the published relationship between fish length and target strength for Alewife in freshwater lakes (Ontario Ministry of Natural Resources and Forestry 2017, Warner et al. 2002). The upper threshold limit was set to -39 dB (170 mm), while the lower threshold limit was set to -50 dB (49 mm) (Ontario Ministry of Natural Resources and Forestry 2017).

Multiple detections of individual fish, termed tracks, were identified using the Fish Tracking module from the Echoview software which uses an algorithm based on work by Blackman (1986). For tracks to be identified as an Alewife, the individual targets had to be separated from each other by no more than three pings, and each track needed to contain a minimum of three single targets (Henderson et al. 2007). Targets that were separated by more than three pings were used to start a new track if they met the additional requirements. Maximum beam compensation was set to 4 dB and the single target compensation threshold was set to -70 dB. An example echogram from the stationary survey with hydroacoustic targets and tracks is provided in Appendix A.

The speed (m/s) and tortuosity of individual tracks were both calculated and exported by Echoview. Speed was calculated by dividing the overall 3-dimensional distance (m) travelled by the amount of time the track spent in the beam (s). Tortuosity refers to the 3-dimensional linearity of the track. It was calculated by summing the individual distances between targets, and dividing by the change in distance between the first and last target. A tortuosity value of one indicates a straight line, and the tortuosity value increases as the path becomes more curved.

Statistical Methods

All statistical analyses and data manipulation were conducted using R version 3.3.1 with the dplyr, ggplot2, and sfsmisc packages (R Core Team 2017, Wickham et al. 2017, Wickham 2009, Maechler 2018). Standardized track distributions were calculated using the mean and standard deviation of each track, for both target strength and target depth. Targets were identified as Alewife by only selecting the tracks which had a maximum target strength that fell within the -50 dB to -39 dB range. When analyzing the fish tracks, maximum target strength of the track was used because it provides the closest representation of the overall length of the fish. In contrast, the mean target strength of the track could be influenced by smaller values recorded within the track. To calculate the area under the probability density curves of the target strength and depth distributions, the `integrate.xy` function from the sfsmisc package was used.

The tilt of the fish's track between two consecutive targets was calculated using the same approach as Henderson et al. (2007).

$$\text{tilt} = \sin^{-1}\frac{\Delta z}{\sqrt{(\Delta x^2 + \Delta y^2 + \Delta z^2)}}$$

In this equation, Δz is the change in depth of the target, Δx is the distance along the minor axis of the beam (typically alongship), and Δy is the distance along the major axis of the beam (typically athwartship).

The linear models were analyzed using the base R statistical package. The absolute value of change in depth and tilt were used because a change in either direction would be expected to result in a reduction in target strength.

Table 1. Sampling sites used during the deployment of the up-looking echosounder for the stationary hydroacoustic surveys.

Year	Location	Date Deployed	Depth (m)
2013	43º 58.180’ N 076º 29.450’ W	2013-07-15	46
2017	43º 55.645’ N 076º 30.060’ W	2017-07-20	42
2017	43º 28.418’ N 076º 37.057’ W	2017-07-24	60

Table 2. Echosounder settings used for the collection of target strength measurements during the stationary and mobile surveys.

Setting	Stationary	Mobile
Echosounder	BioSonics DT-X SUB	BioSonics DT-X
Transmission frequency (kHz)	120	120
Beam Type	Split-beam	Split-beam
Pulse length (ms)	0.4	0.4
Ping rate (ping/s)	1-2	1-4

Chapter 3: Results

Target Selection

All split-beam target tracks from the stationary and mobile surveys were plotted as the maximum target strength observed for a given track (Figure 1). In order to make comparisons between the distributions for stationary (n=1398) and mobile (n=411) surveys without influence of sample size, probability densities were used rather than raw frequency. Both the stationary and mobile surveys exhibited a peak of targets within the range of the target strength threshold defined for Alewife. The number of targets with maximum target strengths within the Alewife threshold range for the stationary survey (n=766) represented 53% of all the stationary targets, whereas the mobile targets (n=155) in the threshold range represented 36% of all mobile targets observed (Figure 2a). Of these Alewife targets, only 56% of the stationary targets (n=429) and 31% of the mobile targets (n=48) would still be classified as Alewife when defined by the mean target strength of their respective tracks (Figure 2b).

Standardized Fish Tracks

The standardized distributions of target strength observed for Alewife in the stationary and mobile surveys were compared using a paired Wilcoxon Rank Sum test (Figure 3). This analysis compared the values of the probability density curves for the two distributions, which were determined to be significantly different ($W=6682$, $p<0.001$). The targets from the stationary survey exhibited a peak above their mean target strength, near their maximum target strength, with a left-skewed tail. In contrast, the targets from the mobile survey had a bimodal distribution around their mean target strength. The standardized distributions were shifted to their respective means which demonstrated that, on average, an Alewife in the stationary survey spent approximately 63% of the time at a target strength which would still define it as an Alewife, while an Alewife in the mobile survey only spent approximately 1% of the time in this range (Figure 4). The medians of these two distributions were compared using a one-sided Wilcoxon Rank Sum test (Figure 5). It was determined that the tracks from the mobile survey (median=-51.7 dB) were observed at significantly lower target strength values than the tracks from the stationary survey (median=-49.7 dB), exhibiting a difference of 2.03 dB ($W=522450$, $p<0.001$).

The standardized depth distributions for the tracks observed in the stationary and mobile surveys were compared using a paired Wilcoxon Rank Sum test (Figure 6). It was determined that the two distributions were significantly different from one another ($W=41879$, $p<0.001$). Alewife in the stationary survey occupied a median depth of 5.27 m, while Alewife in the mobile survey occupied a median depth of 10.6 m (Figure 7). The difference in depth between the two surveys was examined using a one-sided Wilcoxon Rank Sum test (Figure 8) and the fish from the mobile survey were determined to be significantly deeper (by 5.33 m) than the fish from the stationary survey ($W=6659200$, $p<0.001$).

The shapes of the distribution of standardized target strengths and standardized depths occupied by Alewife in the mobile survey were compared using a paired Wilcoxon Rank Sum test to compare the values along the probability density curves of the two distributions (Figure 9). The shapes of both distributions were bimodal and they were not significantly different ($W=68420$, $p=0.41$).

Differences in Behaviour

The fish in the mobile survey were determined to be swimming faster than the fish in the stationary survey using a one-sided Wilcoxon Rank Sum test (Figure 10). The median speed of the fish from the mobile survey (2.93 m/s) was significantly faster than the median speed of the fish from the stationary survey (0.46 m/s) by 2.53 m/s ($W=557960$, $p<0.001$). The tortuosity of the mobile and stationary tracks were compared to one another, and a value of 1, using one-sided Wilcoxon Rank Sum tests (Figure 11). The fish from the mobile survey had a significantly lower median tortuosity (1.06) than the fish from the stationary survey (2.28) ($W=32950$, $p<0.001$), and both were significantly greater than 1 (Mobile: $W=84666$, $p<0.001$) (Stationary: $W=977900$, $p<0.001$). A one-sided Wilcoxon Rank Sum test was used to compare the number of targets in a track between the mobile and stationary surveys (Figure 12). The mobile tracks had significantly fewer targets per track (median=3) than the stationary tracks (median=8) ($W=78702$, $p<0.001$).

The changes in depth between individual targets within a track were compared using a one-sided Welch Two-Sample t-test (Figure 13). The mobile targets had a mean change in depth (-0.021 m) which was significantly more than the mean change in depth for the stationary targets (0.007 m) ($t=-2.74$, $df=186.62$, $p=0.003$). The mean change in depth for the mobile targets was also significantly less than 0 (one sample t-test; $t=-2.19$, $df=154$, $p=0.015$). In contrast, a similar analysis showed that the stationary targets had a mean change in depth which was significantly greater than 0 (one sample t-test; $t=2.19$, $df=762$, $p=0.015$).

A one-sided Welch Two-Sample t-test was used to determine whether the tilt of a fish was significantly different when individual targets for the mobile and stationary surveys were compared (Figure 14). The mobile targets had a mean tilt (-2.07 º) which was significantly more downward than the mean tilt for the stationary targets (0.36 º) (t=-1.74, df=189.64, p=0.04). Neither the mobile targets, nor the stationary targets, had a mean tilt that was significantly different from 0 (one sample t-test; Mobile: t=-1.35, df=154, p=0.18; Stationary: t=1.46, df=762, p=0.14).

Predicting Changes in Target Strength

All of the predictor variables used in separate linear models were only able to explain a relatively small amount ($R^2 < 0.001$) of the variation in the changes in target strength (Table 3). Change in depth had a significant negative slope, such that targets which had a greater change in depth exhibited large negative changes in target strength (p=0.008). There was a significant difference for survey type between mobile and stationary targets, such that mobile targets had greater changes in target strength (p=0.026).

Figure 1. The probability densities of all split-beam targets from the stationary (in blue, n=1398) and mobile (in red, n=411) surveys, partitioned using the maximum recorded target strength from each track. The Alewife target strength thresholds are denoted by the black dashed lines.

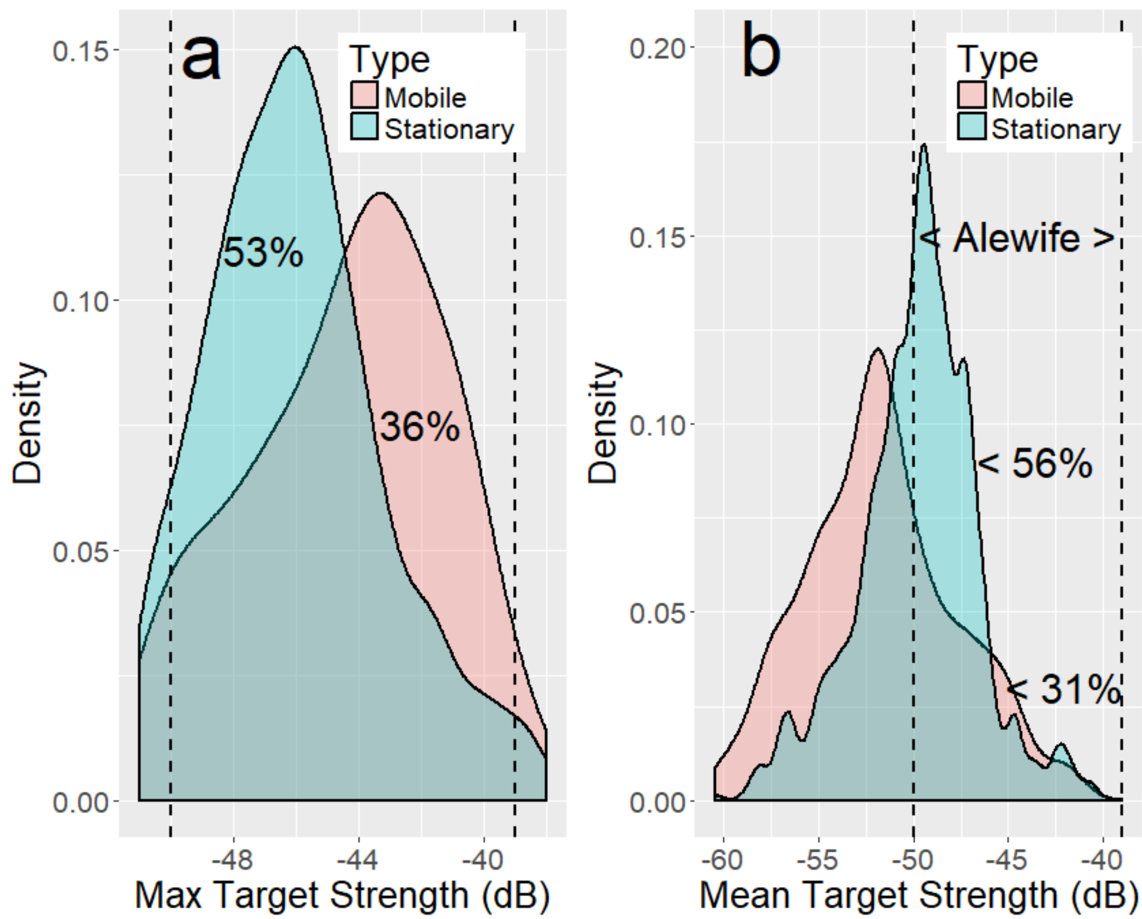


Figure 2. (**a**) The probability densities of targets within the size thresholds for Alewife using maximum target strength, for both the stationary (blue) and mobile (red) surveys. (**b**) The probability densities of the targets from **a** which would be defined as Alewife using their respective mean target strengths. The Alewife target strength thresholds are denoted by the black dashed lines.

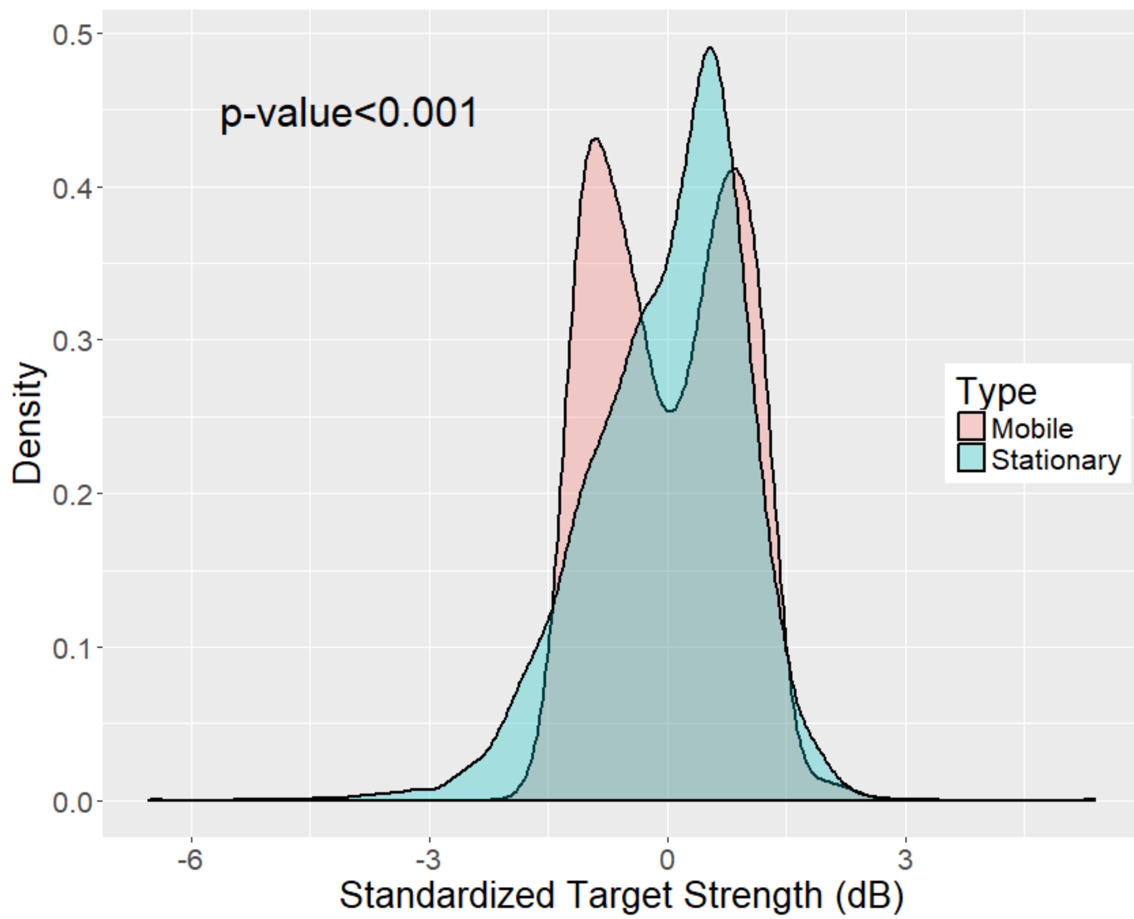


Figure 3. The probability densities of the standardized target strength distributions for Alewife tracks observed in the stationary (blue) and mobile (red) surveys, which were compared using a paired Wilcoxon Rank Sum test.

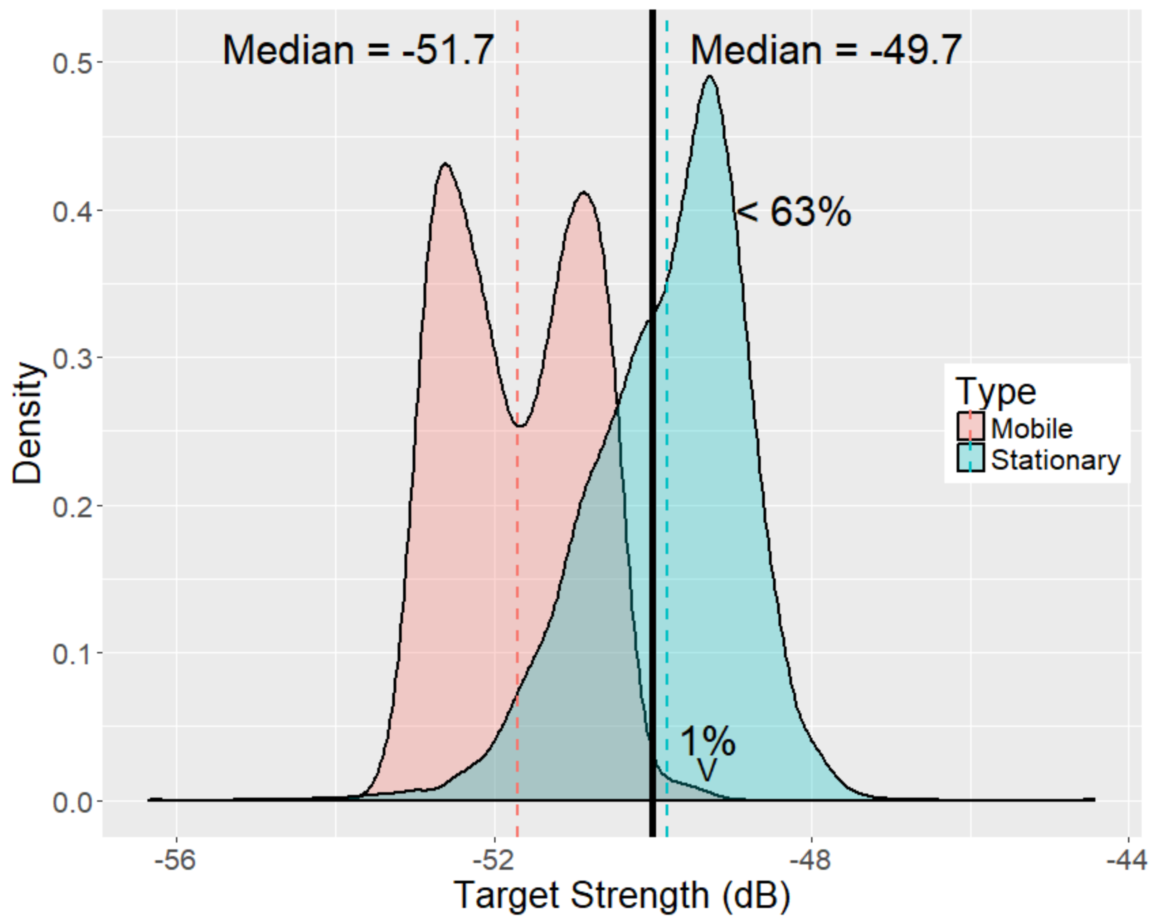


Figure 4. The probability densities of the standardized target strength distributions for Alewife tracks observed in the stationary (blue) and mobile (red) surveys, both shifted to their respective mean target strength. The lower targets strength threshold for Alewife set at -50 dB (black line) and the distributions' respective medians denoted by the dashed lines.

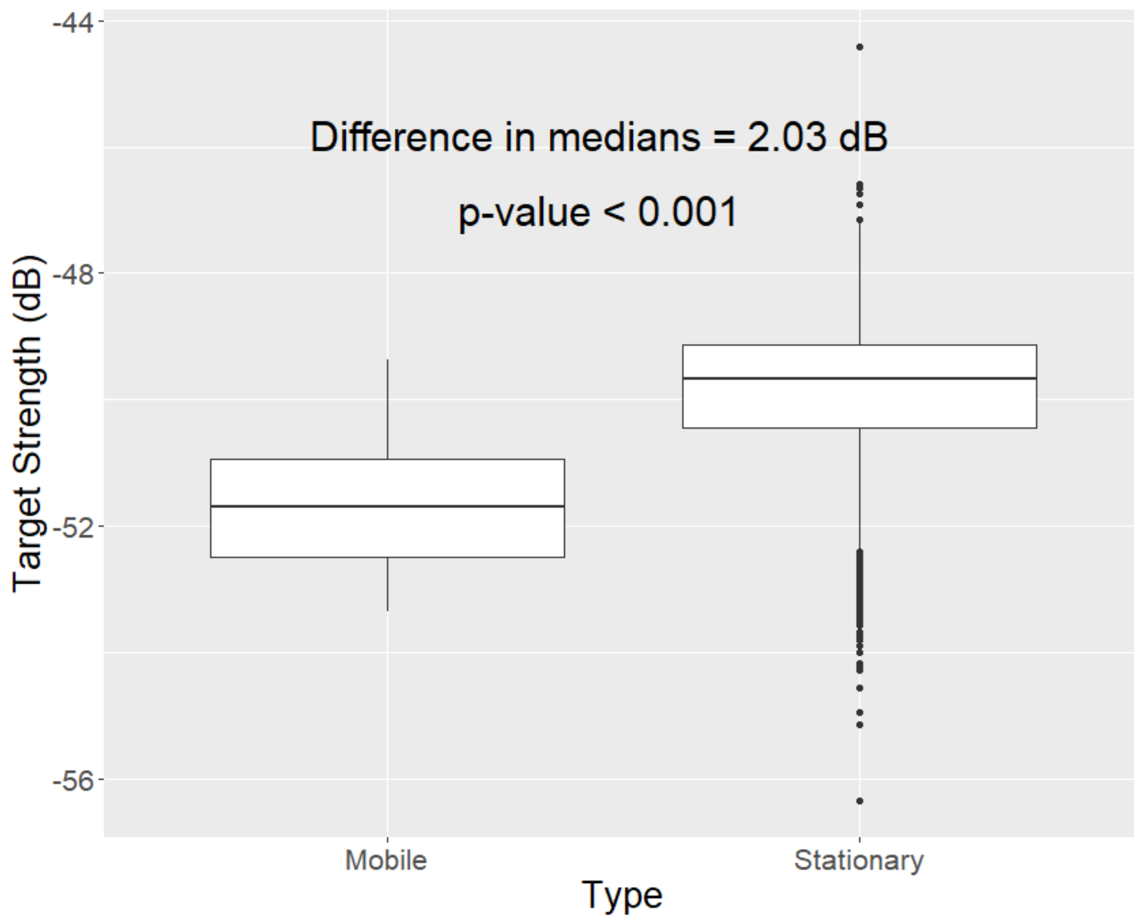


Figure 5. Standardized target strength distributions, both shifted to their respective means, for the Alewife tracks observed in the mobile and stationary surveys. Medians were compared using a one-sided Wilcoxon Rank Sum test.

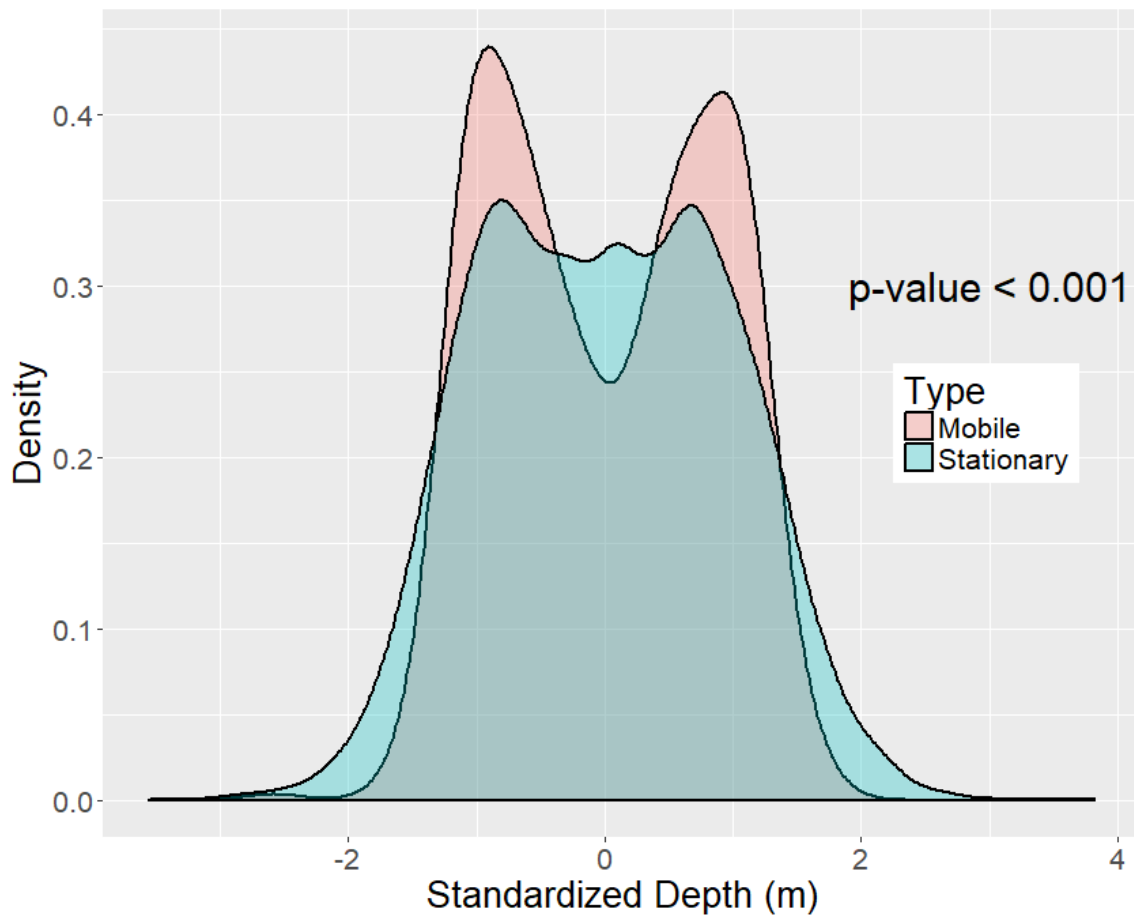


Figure 6. The probability densities of the standardized depth distributions for Alewife tracks observed in the stationary (blue) and mobile (red) surveys, which were compared using a paired Wilcoxon Rank Sum test.

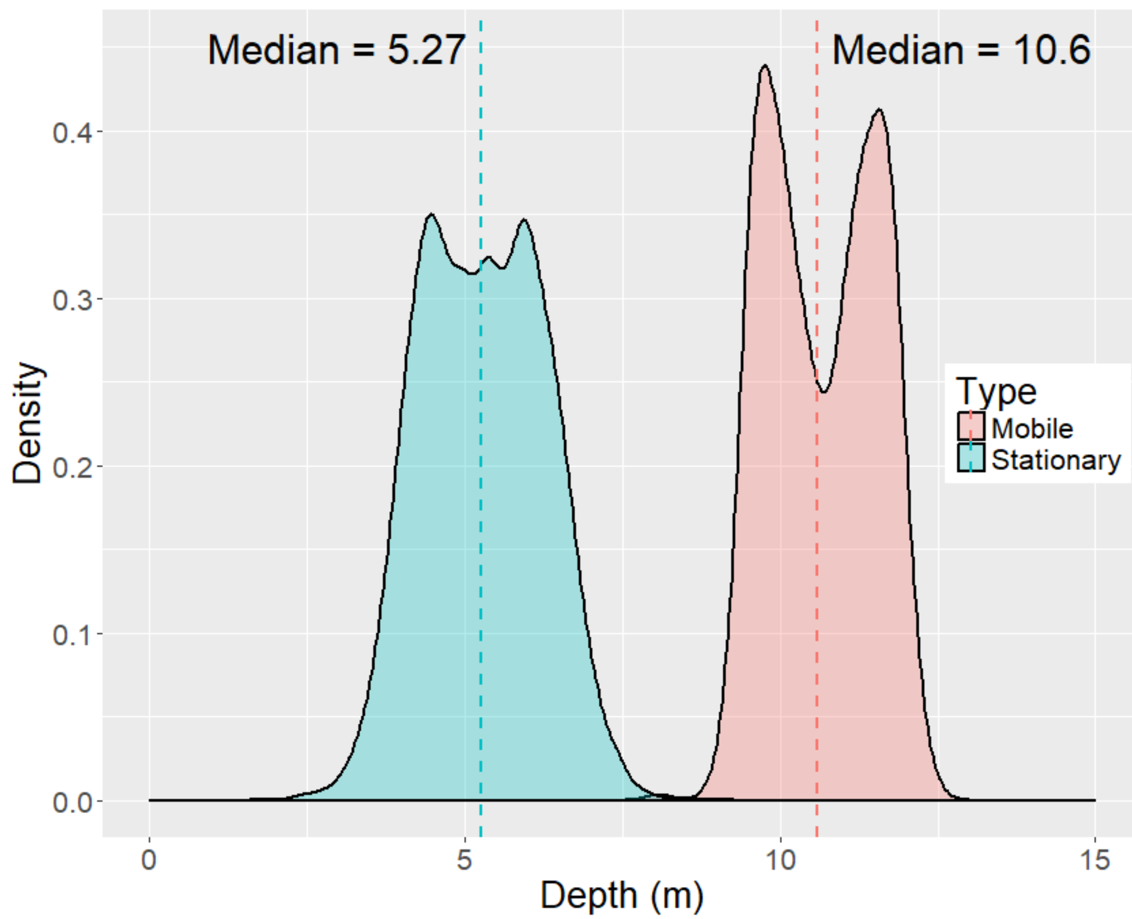


Figure 7. The probability densities of the standardized depth distributions for Alewife tracks observed in the stationary (blue) and mobile (red) surveys. Both distributions are shifted to their respective mean depth, and the distributions' respective medians are denoted by the dashed lines.

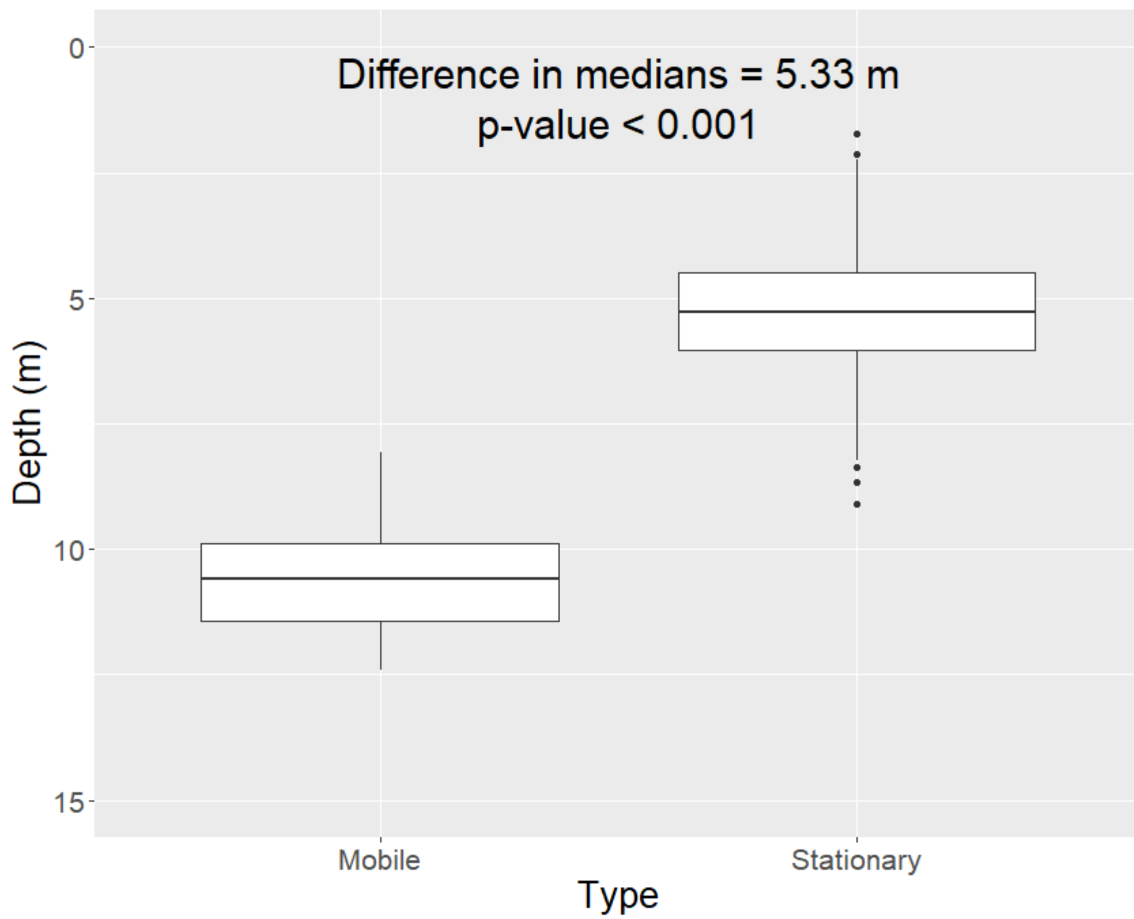


Figure 8. Standardized depth distributions, both shifted to their respective means, for the Alewife tracks observed in the mobile and stationary surveys, which were compared using a one-sided Wilcoxon Rank Sum test.

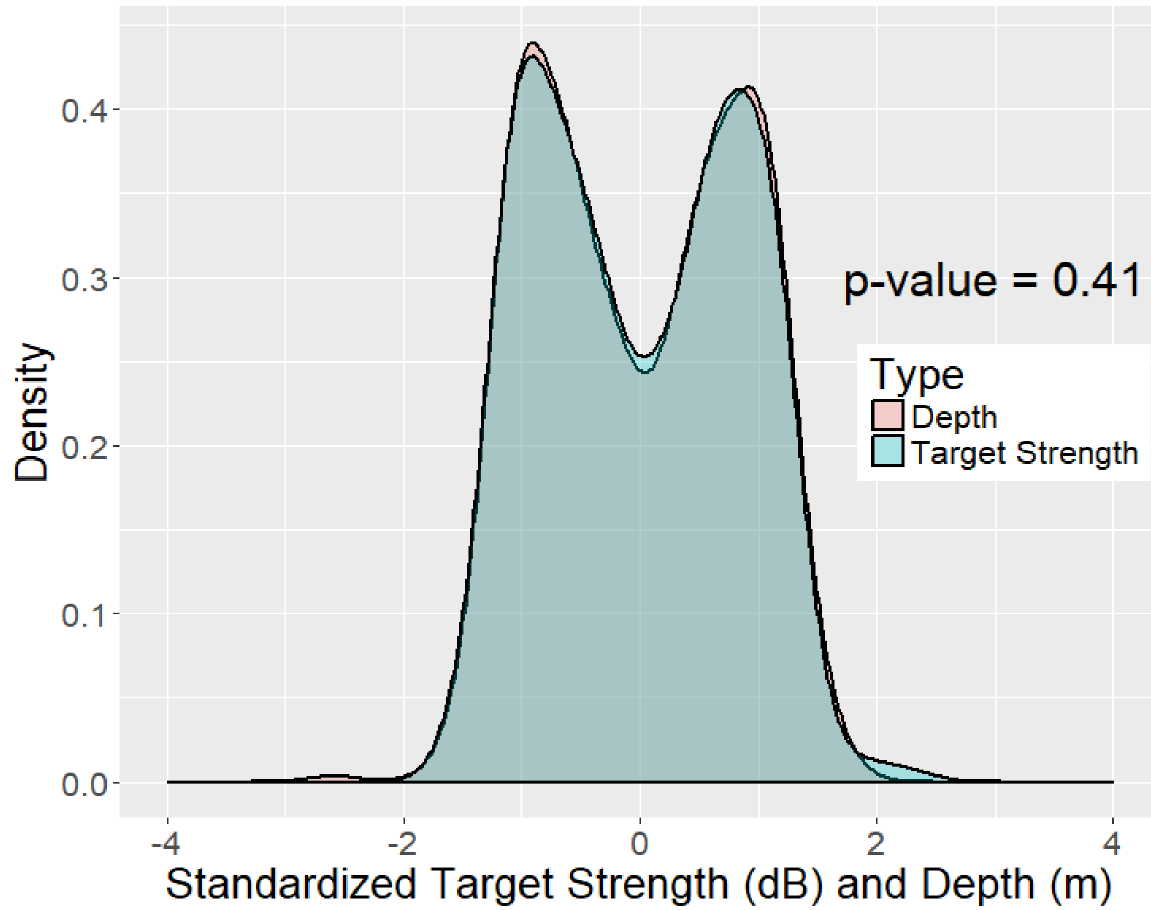


Figure 9. The standardized target strength (blue) and depth (red) distributions for Alewife tracks observed in the mobile survey, compared using a paired Wilcoxon Rank Sum test.

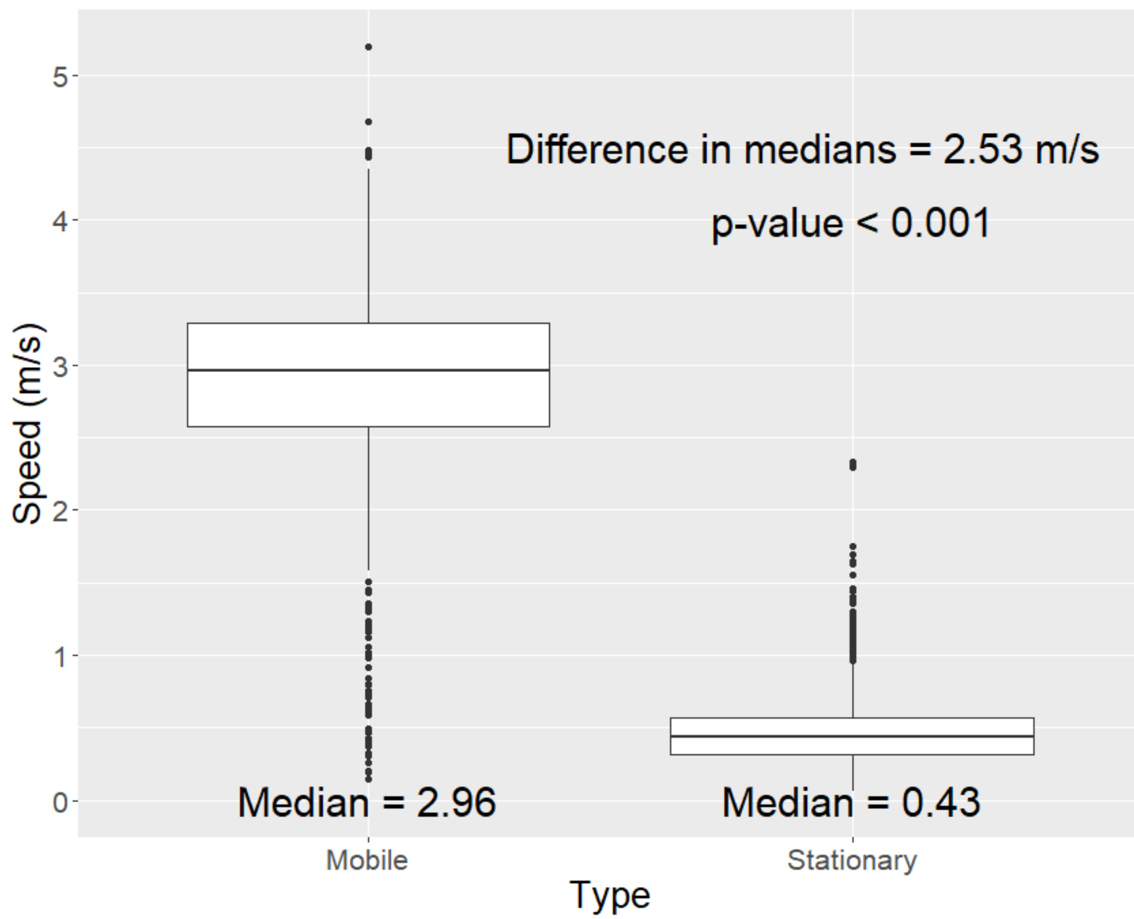


Figure 10. The speed of the Alewife travelling the length of their respective tracks through the water, for the mobile and stationary surveys, compared using a one-sided Wilcoxon Rank Sum test.

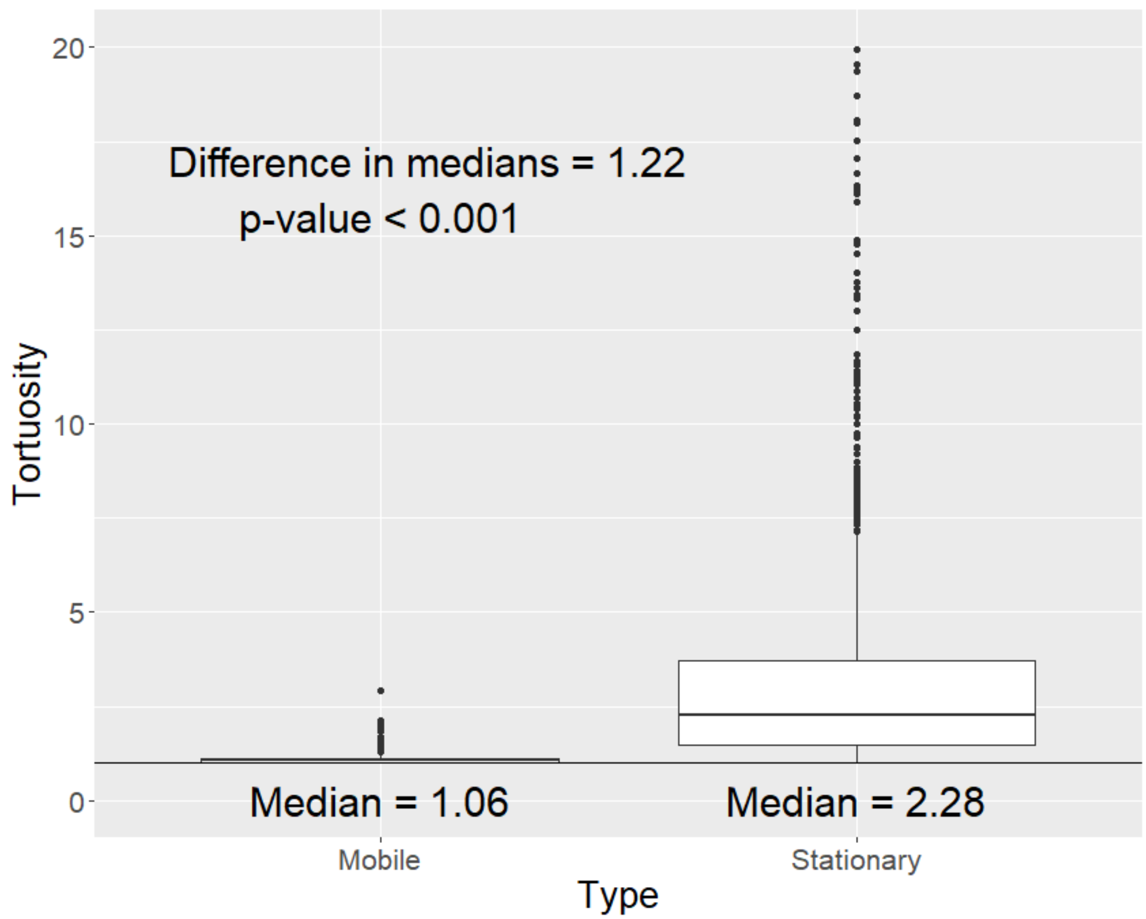


Figure 11. The tortuosity of the Alewife tracks from the mobile and stationary surveys, compared using a one-sided Wilcoxon Rank Sum test. The black horizontal line at a tortuosity value of 1 which represents travelling in a straight line.

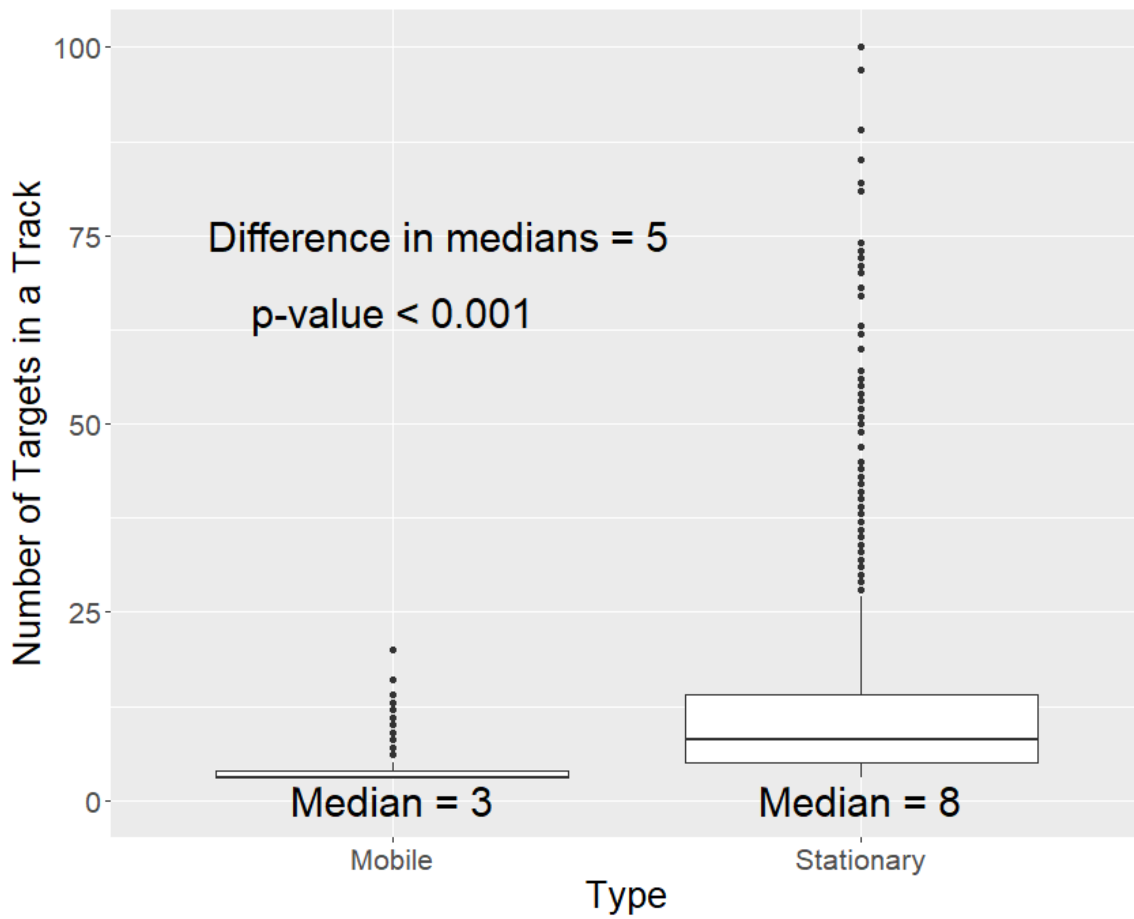


Figure 12. The number of recorded targets within an individual Alewife track (minimum number of targets possible is 3) for the mobile and stationary surveys, compared using a one-sided Wilcoxon Rank Sum test.

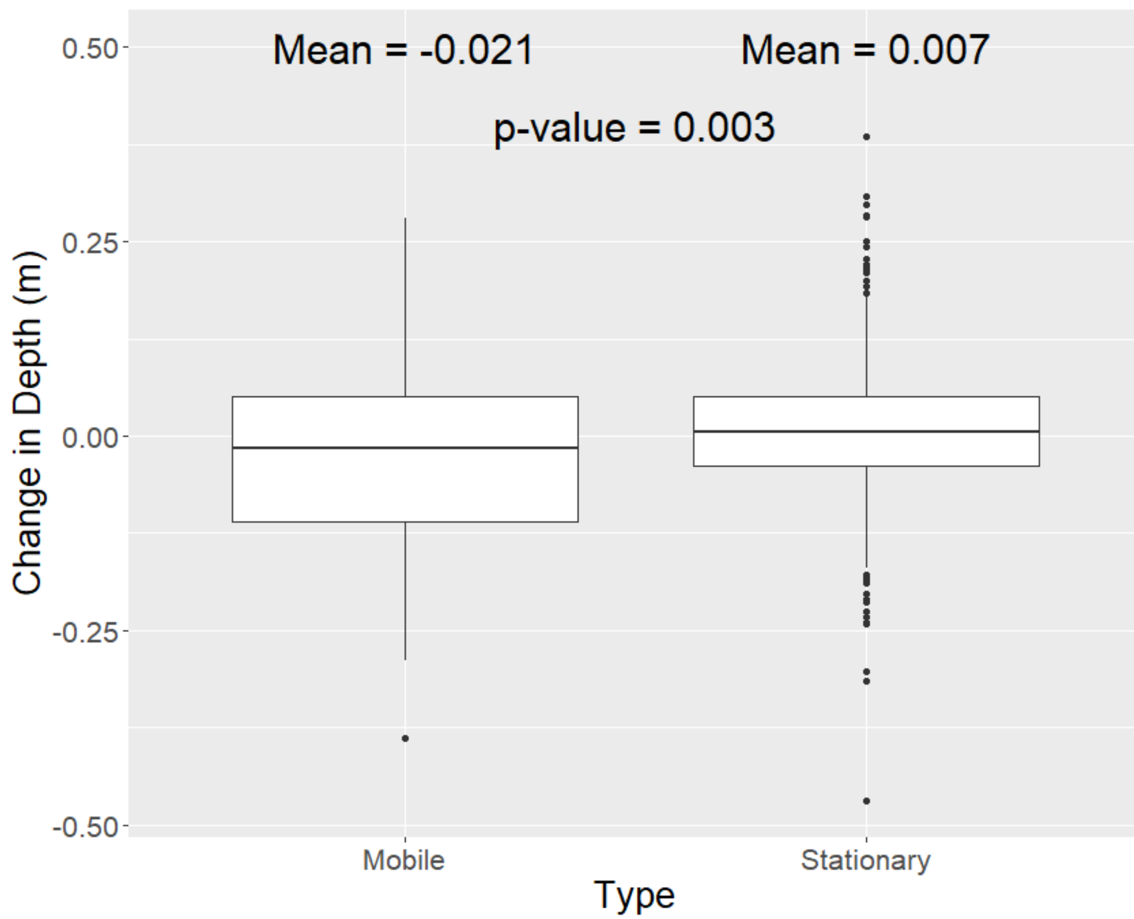


Figure 13. The change in depth between two consecutive targets within the Alewife tracks observed in the mobile and stationary surveys, compared using a one-sided Welch Two-Sample t-test.

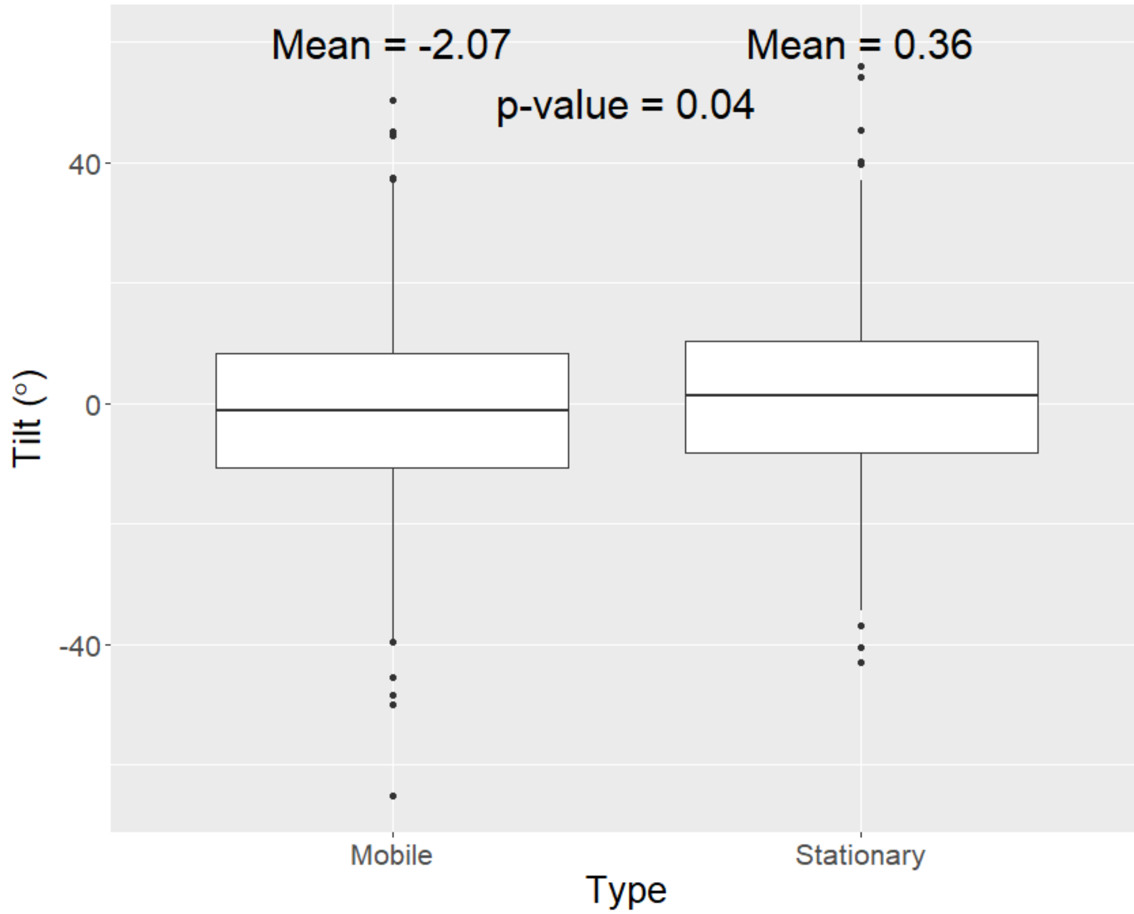


Figure 14. The tilt between two consecutive targets within the Alewife tracks observed in the mobile and stationary surveys, compared using a one-sided Welch Two-Sample t-test. A positive angle denotes the track travelling towards the lake surface and a negative angle denotes the track travelling towards the lake bottom.

Table 3. List of all Alewife track variables that were tested in separate linear models to predict the corresponding change in target strength (dB), using combined data from the mobile and stationary surveys.

Variable	Multiple R^2	F-Statistic	p-value
Change in Depth (m)	< 0.001	7.013	0.008
Tilt (º)	< 0.001	0.185	0.668
Survey Type	< 0.001	4.934	0.026

Chapter 4: Discussion

Target Selection

Plotting all targets observed in the stationary and mobile surveys by the maximum target strength recorded in a track resulted in notable differences in the surveyed samples. The probability density distributions for the two surveys were bimodal, with modes occurring at relatively similar values, however, the magnitude of each mode differed between surveys (Figure 1). A bimodal distribution may be indicative of two age classes of Alewife in the open-lake; the mode at lower target strengths representing yearlings and the mode at larger target strengths representing any Alewife older than a year. This is supported by results from Warner et al. (2002) who found that each mode within multimodal target strength distributions from hydroacoustic surveys of Alewives in Lake Ontario corresponded to different age classes of Alewives.

The differences observed between the mobile and stationary survey size distributions may be the first indication that the mobile survey is having an influence on the observations which it collects. If fish in the mobile survey were not being disturbed, it would be expected that the mobile and stationary (undisturbed fish) survey should produce similar probability density distributions for all targets. In contrast, the stationary survey observed more targets at the mode with the larger target strength value, while the mobile survey observed more targets at the mode with the smaller target strength value. Brooking and Rudstam (2009) also observed a greater than expected number of small target strength values in hydroacoustic assessments of Alewife than were predicted using data from gillnets. They suggested that the high number of small hydroacoustics targets could be accounted for by small fish and invertebrates which would not be caught in the gillnets. It is possible that the mobile survey from this study may be sampling more smaller targets, such as invertebrates and smaller fish, which could contribute to the higher mode of small targets. This is unlikely, however, since the two surveys were primarily sampling similar areas of the lake. Since they were covering similar areas, one would expect that the two surveys should be encountering the same types of targets. A more likely explanation for the differences observed in this study is that the mobile survey vessel is influencing the behaviour of the Alewife it is trying to assess. More specifically, the orientation of the Alewife is probably changing as they dive in response to the approaching survey vessel. This behaviour would cause them to reflect less of the acoustic signal back to the echosounder and they would appear as smaller targets.

Another important result in the present study was a shift in the right mode of the mobile survey, such that it peaked at a larger target strength value than the same mode of the stationary survey. If both surveys are sampling the same fish and the mobile survey is not influencing the behaviour of the fish, it would be expected that these modes should be occurring at the same target strength values in both the mobile and stationary surveys. The observed results are therefore another indication that some fish in the mobile survey are exhibiting a diving response. In some species, it has been reported that there can be a slight increase in a fish's target strength due to a behavioural change at the start of a dive (Foote 1985, Hazen and Horne 2004). More specifically, as the fish begins a dive, its head becomes tilted in a way that extends the reflective surface of the swim bladder. The increase in target strength associated with this type of behaviour may account for the observed shift in the right mode of the fish from the mobile survey. It is likely that this result represents fish that are beginning to dive and avoid the survey vessel. However, it is also important to note that the increase in target strength at the beginning of a dive is often so small that it can become concealed by the more influential decrease in target strength that follows as the rest of the body becomes oriented downwards (Hazen and Horne 2004).

When the size threshold is applied to select for only Alewife from all the recorded targets, the difference in the magnitudes of the modes between the two distributions becomes more apparent. In the stationary survey, approximately 53% of all targets were classified as Alewife when the size threshold was applied, whereas only 36% of the targets were classified as Alewife in the mobile survey (Figure 2a). This large reduction in fish classified as Alewife in the mobile survey may simply be a result of boat avoidance. In the mobile survey, fish may be appearing smaller as they dive vertically and are not meeting the target strength threshold required to be considered an Alewife. In addition, some fish may be moving laterally away from the hydroacoustic beam and may be completely undetected. Lateral boat avoidance is a common concern, which has been well studied for many species, however, the results vary and tend to be vessel and species specific (Handegard and Tjøstheim 2005, Misund et al. 1996, Pitcher et al. 1996, Xie et al. 2008). In one study, lateral boat avoidance reduced the amount of fish detected by a survey vessel's echosounder to just 41% of the total school (Soria et al. 1996). For species which occupy the top of the water column such as Alewife, it only takes a relatively small amount of movement to impact the detection probability within narrow acoustic beams (De Robertis and Handegard 2013).

In current hydroacoustic assessments, the targets are classified by their mean target strengths, but these mean values can be biased by diving behaviour. This bias was demonstrated by a greater shift towards smaller mean target strength values for Alewife tracks from the mobile survey (Figure 2b). Although both surveys had a shift to smaller target strength values, this was expected from the natural amount of variation in the orientation of fish swimming freely (Brooking and Rudstam 2009). For targets which were classified as Alewife (by maximum target strength), approximately 31% of those fish in the mobile survey would remain as Alewife when the mean target strength of their track was used. In contrast, approximately 56% of the fish from the stationary survey would still be considered Alewife. This provides evidence that Alewife which should be counted in the mobile assessments are being excluded when using their mean target strength value for species determination. A smaller mean value indicates that the track is spending a greater proportion of time off-axis, with less reflective surface area for the acoustic beam. These results are another indication that boat avoidance is biasing the estimates of abundance from the mobile surveys.

Standardized Fish Tracks

In order to understand how the behaviour of the average Alewife influences its target strength, individual fish distributions were standardized and combined. The standardized target strength distributions for fish tracks in the mobile and stationary surveys displayed differences that may be indicative of altered behaviours in the disturbed Alewife (Figure 3). When the fish were undisturbed (stationary survey), the tracks indicated that the fish typically remain on-axis. This is demonstrated by the median value being close to the maximum value of the distribution, with a left-skewed tail indicating some minor changes in orientation. The shape of the distribution for the undisturbed Alewife in this study is also similar to that of the undisturbed net-cage

Alewife studied by Brooking and Rudstam (2009), indicating this distribution is a good representation of target strengths exhibited by undisturbed Alewife. The primary difference between the distributions from this previous study and the current study is the range of values observed. The net-cage distributions include both larger and smaller target strength values, encompassing a range of ~25 dB, whereas the range of the distribution from the current study was ~12 dB. This is likely a result of the fish in the current study not being confined to remain within the acoustic beam, thus only recording the most common target orientations. If this is the case, it would exclude the more uncommon extreme values which would increase the range of observed values. The Alewife in Brooking and Rudstam's (2009) study were confined in a net-cage above the acoustic beam, meaning every possible orientation, and resulting target strength, would be recorded by the echosounder. The difference in target strength ranges might also be attributed to the fact that the net-cage distributions were the raw observed target strengths for a group of Alewife of known sizes. In contrast, the distributions for stationary surveys in this study were a collection of standardized distributions, corrected for fish of unknown true sizes. These results suggest that fish in the mobile survey are spending more time off-axis than the undisturbed fish in the stationary survey. This difference in orientation shows that Alewife in the mobile survey are exhibiting a behaviour which is reducing their observed mean target strength.

The shape of the standardized target strength distribution can also provide insights about the behaviour of the Alewife. The shape of the distribution for the fish from the mobile survey was bimodal, and significantly different than the stationary distribution (Figure 3). This distribution represents the target strengths observed during a single average Alewife track. Thus, it is unlikely that this bimodality would be a result of different age classes, as was proposed for the distributions of all targets from earlier in this study. The actual size of the fish should be irrelevant for this distribution as it represents the range of target strengths observed for an average Alewife. The bimodality is probably indicative of two different behaviours being recorded in the mobile survey. The first being that the fish are undisturbed, as indicated by the right side of the distribution which matches the shape of the stationary distribution. The second being the left side of the distribution where fish are being disturbed and demonstrating orientations that result in below average target strengths. The undisturbed behaviour in the fish from the mobile survey may be a result of some fish already being deep enough that boat avoidance is not a concern for the Alewife. Fish reactions to approaching survey vessels are often highly depth dependent, where a stronger response is often displayed by shallower fish (Vabø et al. 2002, De Robertis and Wilson 2010). When the magnitude of the two modes in the mobile distribution is examined, it appears that fish are observed at smaller target strengths for the majority of the time they spend in the hydroacoustic beam. These results provide support to the theory that Alewife in the mobile survey are diving at the time of the survey, and consequently reducing their mean target strength.

In addition to differences in the shapes of the standardized mobile and stationary target strength distributions, there were also differences in the means of these distributions. When these distributions were shifted to their respective means, the mobile standardized distribution encompassed smaller target strength values than the stationary distribution. Using these distributions as an indication of how often fish are observed at particular target strengths, the average fish in the stationary survey would be reported as an Alewife ~63% of the time (Figure 4). In contrast, an average Alewife in the mobile survey would be reported as an Alewife only ~1% of the time using the current threshold limits. This reduction in detection probability may have serious implications for abundance estimates being made using data collected by the mobile survey. The average Alewife track in the mobile survey produced target strength values which were significantly smaller than the Alewife tracks from the stationary survey (Figure 5, $p<0.001$). The two surveys sampled the same section of the water column, in similar locations, and at the same time of day and year. For these reasons, it would be expected that the mean target strength of these tracks should be the same for the two surveys. However, the Alewife from the mobile survey on average appear to be 2.03 dB smaller than the Alewife from the stationary survey. These results suggest that the mobile survey rarely records an Alewife at its true maximum target strength in a track, and the maximum used is only an observed maximum. Ona et al. (2007) reported that fish began to react to an approaching vessel by diving ~2 minutes before the vessel was overhead. At the time of mobile hydroacoustic detection, the average fish was already midway through its dive, thus even using target tracking, the true maximum target strength of the fish would not be observed. Early vessel avoidance such as this has been recorded at a distance of ~330 – 500 m for some species (Vabø et al. 2002, De Robertis and Wilson 2010). Bringing together the results of this study with observations made from similar studies, it appears that Alewife in the mobile survey are reducing their mean target strength through boat avoidance behaviour. This behaviour would ultimately reduce the number of Alewife counted in the annual survey by excluding them from the Alewife size thresholds.

The observed depths of fish in the water column can also be used as an indicator of behaviour, as a change from the preferred depth can be informative of reactions to stimuli. Depths of each target in an Alewife track were also standardized for this study, and these distributions were different between the mobile and stationary surveys (Figure 6). The standardized depth distributions for fish tracks in the mobile and stationary surveys displayed differences that further support the interpretation that a diving behaviour is being exhibited by the disturbed Alewife (Figure 7). The standardized depth of an Alewife in the mobile survey was significantly deeper (by 5.33 m) than an Alewife in the stationary survey (Figure 8, $p<0.001$). The fish from the mobile survey were almost twice as deep as the fish from the stationary survey. A similar difference in depth has been reported in disturbed and undisturbed herring (De Robertis and Handegard 2012). A change in depth from the surface to the 5-10 m depth layer was also reported by Gerlotto et al. (2004) as a moderate diving response for anchovy (*Engraulis ringens*) and common sardine (*Strangomera bentincki*). This change in depth for anchovies and sardines is very similar to that displayed by the Alewife in this study. This change in depth provides further evidence to support the interpretation that Alewife in the mobile survey are displaying boat avoidance behaviour. In order to better understand this behaviour, the relationship between the standardized depth distribution and the standardized target strength distribution was examined for the mobile survey.

The standardized target strength and depth distributions for Alewife in the mobile survey appeared to be related, as they exhibited nearly identical bimodal shapes. The standardized depth distribution was not significantly different from the distribution of standardized target strengths for the fish from the mobile survey (Figure 9, $p=0.41$).

These similarities suggest that there are two different behaviours being displayed by Alewife in the mobile survey. The first being that there are fish which are already deep at the time they are observed in the hydroacoustic beam. They could either have already exhibited avoidance behaviour before the boat was directly overhead, or were naturally deep enough that no reaction occurred (Vabø et al. 2002). This behaviour would result in only minimal changes in orientation, which may explain the larger target strength values observed when compared to the average Alewife track in the mobile survey. The second behaviour may be a result of Alewife which are mid-dive, similar to herring observed by Ona et al. (2007). These fish are still shallower than the average mobile track depth because they have not yet reached their maximum track depth. In this scenario they would be at an orientation which would reduce their reflective area, and as a result provide target strength values below the average mobile track target strength. These two behaviours have been reported in other studies examining similar species. Combining these two different boat avoidance behaviours explains the shape of the standardized distributions for the Alewife tracks from the mobile survey in this study. The first represents a behaviour which is heavily influenced by boat avoidance at the time the target is observed in the acoustic beam (mid-diving). The other, which is still a result of boat avoidance, involves a reaction that occurred before the target was observed in the acoustic beam, and so the result is less influential on the survey results. Through a combination of these two behaviours, these results suggest that changes in depth are related to the changes in target strength observed in Alewife from the mobile survey. In order to further support these findings, some direct measures of behaviours were examined between the Alewife in the mobile and stationary surveys.

Differences in Behaviour

There were several noticeable differences between the swimming behaviours of Alewife in the mobile and stationary surveys. The average swimming speed over the course of an Alewife track in the mobile survey was significantly faster than Alewife in the stationary survey (Figure 10, $p<0.001$). The Alewife in the mobile survey were swimming at a median value of 2.96 m/s, while the Alewife in the stationary survey were swimming significantly slower, at a median value of 0.43 m/s. Arrhenius et al. (2000) used split-beam echosounders to calculate average swimming speeds of various freshwater species, including Alewife. For Alewife of a similar size to those observed in this study the average undisturbed swimming speed was 0.42 m/s, which is only 0.1 m/s different than the speed of the Alewife in the stationary survey. These results support the idea that the stationary survey was observing fish which were undisturbed and behaving normally while in the hydroacoustic beam. Furthermore, Stringham (1924) reported the maximum swimming speed of Alewife to be 3.01 m/s, which is only slightly faster than the speed of the Alewife in the mobile survey. This indicates that fish in the mobile survey are swimming at nearly their maximum speed, and increased speed can be indicative of certain avoidance behaviours (Rakowitz et al. 2012). Fish attempting to avoid a survey vessel are likely exhibiting a flight reaction in response to the disturbance at the surface and swimming as fast as possible in order to escape.

This flight reaction may also be affecting the linearity of the track. Swimming in a straight line would be the most efficient manner to create the greatest distance between the fish and the disturbance at the surface. The measured tortuosity of the mobile and stationary tracks indicated the mobile tracks were significantly more linear than the stationary tracks (Figure 11, $p<0.001$). Both the stationary and mobile surveys' median tortuosity values were significantly greater than 1, indicating neither were a perfect linear path. Although not perfectly linear, the fish in the mobile survey had a median value of 1.06. This near-linear value was determined to be half as tortuous as the value observed for fish in the stationary survey. This also supports the idea that the fish in the mobile survey are actively swimming away from a disturbance at the surface. A change in tortuosity between undisturbed and disturbed fish was used as a measure of trawl avoidance in a study by Rokowitz et al. (2012). Although they saw more tortuosity in disturbed fish, this was likely a result of fish trying to avoid an underwater disturbance rather than one from the surface. Due to the fact that the disturbance in the mobile hydroacoustic survey is one at the surface, and Alewife may be diving to avoid it, a more linear path would be indicative of avoidance for the situation presented in this study. Although the path of Alewife in the stationary survey is less linear than those in the mobile survey, it is not indicative of erratic behaviour that would be associated with greater amounts of disturbance. The slight increases in tortuosity observed in fish from the stationary survey may simply be associated with natural behaviours such as feeding. Therefore, the observed difference in tortuosity provides support that fish in the mobile survey are diving linearly away from the surface, while fish in the stationary are moving around more naturally.

Another measure of boat avoidance would be the direction of vertical movement within the water column. To assess this trajectory of the tracks, a change in depth was used as an indication of an overall diving or surfacing behaviour displayed by the fish. The change in depth between two consecutive targets within tracks was used as an indication of directionality. Tracks in the mobile survey had significantly more negative changes in depth than tracks in the stationary survey (Figure 13, p=0.003). The average change in depth for fish from the mobile survey was -0.021 m, while fish in the stationary survey had an average change of +0.007 m. Both of these values were significantly different from zero. While the changes seem relatively small, this is expected as the change is only between consecutive targets within a track. More importantly, the magnitude of change is three times greater for fish from the mobile survey compared to fish from the stationary survey. The fish from the stationary survey demonstrated very little change, and even demonstrated a tendency to move slightly towards the surface. This may be a result of the natural feeding behaviours displayed by Alewife. Although they tend to encounter prey swimming horizontally, there can be a slight upward movement of the head when feeding (Janssen 1976). The tendency for fish in the mobile survey to swim deeper supports the results of the standardized depth distributions, and is consistent with other published studies on boat avoidance in pelagic fish species (Gelotto et al. 2004, Ona et al. 2007, Simmonds and MacLennan 2002, Vabø et al. 2002). This greater change in depth provides further evidence that the Alewife in the mobile survey are diving away from the surface, while Alewife in the stationary survey are again displaying more natural, undisturbed behaviours.

The tilt angle of the track was also examined as it is typically the orientation of the fish that can have profound effects on the observed target strength of a fish (Henderson et al. 2007, Rodríguez-Sánchez et al. 2016, Simmonds and MacLellaan 2005). Tilt of the track was determined in a similar manner as Henderson et al. (2009) who estimated the angle over the course of the entire track. In the present study, the individual angles between two consecutive targets within a track were used, similar to the method previously used for calculating change in depth. The results demonstrated that fish in the mobile survey were observed in a diving orientation a significantly greater proportion of time than the fish in the stationary survey (Figure 14, p=0.04). The average tilt angle of fish from the mobile survey was -2.07 º, while the fish from the stationary survey had an average tilt of 0.36 º. Neither of these angles were significantly different from 0 º. The average angle observed for fish from the mobile survey was almost six times greater in magnitude than the average angle for fish from the stationary survey, and in the opposite direction. This difference in track orientation indicates a strong difference in behaviour being demonstrated by the fish from the mobile survey as a result of boat avoidance. A negative orientation in these fish can be explained by a diving response that is also associated with a negative change in depth. This negative change in depth, and associated negative track orientation, is again consistent with other published studies on boat avoidance in pelagic fish species (Gelotto et al. 2004, Ona et al. 2007, Simmonds and MacLennan 2005, Vabø et al. 2002). The results of the Alewife behaviour examined in this study provides additional evidence that a substantial number of fish in the mobile survey are exhibiting diving behaviour.

Predicting Changes in Target Strength

Changes in fish depth and orientation often produce changes in the reflective surface for acoustic signals, which can reduce the target strength of a fish observed using an echosounder (Foote 1985, Hazen and Horne 2004, Henderson et al. 2009, Rodríguez-Sánchez et al. 2016, Simmonds and MacLellaan 2005). As demonstrated in other studies, it was predicted that a change in depth and track orientation would result in a change in target strength for Alewife in Lake Ontario. Using separate linear models to predict changes in target strength from changes in depth and track tilt between two consecutive targets, there was a large amount of unexplained variance in the data (Table 3). Both predictors had $R^2 < 0.001$ and while the slope of change in depth as a predictor was significant ($p=0.008$), the slope for tilt was not ($p=0.668$). The majority of the unexplained variation in the data was observed at values with little change in the predictor variables (Appendix B, Appendix C). These results indicate that it is possible to have large changes in target strength, while still having little change in the predictors tested. It is possible that there are some untested variables that would account for these large changes in observed target strength. One such variable would be the actual orientation of the Alewife.

In this study, tilt was measured using the angle between two consecutive targets as an estimation of fish orientation. However, this may not necessarily be indicative of the true orientation of the fish. It is possible that the orientation of the fish could change while maintaining a constant track angle. Alternatively, it may also be possible for the Alewife to rotate its body without large changes in depth. In the studies by Henderson and Horne (2007), and Rodríguez-Sánchez et al. (2016), where the same equation was used to calculate orientation of the fish, they found orientation to be a significant predictor of change in target strength. The main difference between the measures in those studies and measures used for this study were that they calculated changes between the beginning and end of the track, and not the changes between each target within a track. The overall change of the track could not be used in this study as there was variation in both the target strength and tortuosity within individual tracks which was not present in the other studies. Other studies selected only linear tracks, or in the case of Rodríguez-Sánchez et al. (2016), examined tracks using horizontal acoustic beams, and only examined tracks in the XY plane. Although tilt was not a significant predictor, change in depth was found to be significant. This may indicate that there could be a stronger relationship if the variation around zero was addressed. As change in depth got greater, there was much less variation in the data and the relationship appeared to become stronger. Including better estimates of the true fish orientation may reduce the variation at small changes in depth, resulting in a better fit for the model. Although it also had a lot of unexplained variance of the data, type of survey as a predictor also had a significant slope (Table 3). This model indicated that fish in the mobile survey were displaying more of a change in target strength than the fish from the stationary survey ($p=0.026$). These results add support to the argument that fish in the mobile survey are demonstrating greater changes in target strength in comparison to the undisturbed fish observed in the stationary survey.

Chapter 5: Conclusion

Overall, the results of this study provide strong support that boat avoidance behaviour is being exhibited by Alewife in Lake Ontario at the time of the LOMU's annual hydroacoustic assessment of prey species. The fish tracks from the mobile hydroacoustic survey suggest that the fish appear smaller than the fish in the stationary survey, despite being the same size in reality. Undisturbed fish in the stationary survey exhibited tracks that tend to remain at orientations which provide near-maximum reflective surface, with some variation towards smaller target strengths. The fish from the stationary survey also tend to have much shallower tracks than the fish from the mobile survey which were typically observed in deeper sections of the water column.

The behaviour of the fish in the mobile survey was indicative of boat avoidance. The majority of these fish swam faster, and in more linear paths. Their tracks tended to get deeper, with larger negative angles. The variables tested in linear models were not strong predictors of changes in target strength at relatively small values. The unexplained variance in target strength may be due to changes in other unexamined variables such as the true orientation of the fish.

The differences between the mobile and stationary surveys have important implications for population assessment. The size thresholds currently used to determine species and classify Alewife in the mobile survey assume that the Alewife are behaving similarly to fish in the stationary survey. This survey assumes that fish are typically remaining on-axis with a reflective surface that is representative of their true length. In contrast, the results of this study indicate that the majority of fish in the mobile survey do not behave in a similar manner to the undisturbed fish from the stationary survey. In fact, they typically appear much smaller than would be expected, and this may be excluding a large proportion of the Alewife sampled from being classified as Alewife. Another factor which may be influencing abundance estimates is lateral avoidance of the survey vessel. Lateral avoidance was not quantified in this study, however, it has been identified as a likely source of error in absolute abundance estimates for hydroacoustic surveys (De Robertis and Handegard 2013, Soria et al. 1996). It is important to note that the differences of behaviour observed in the mobile surveys do not necessarily bias estimates of relative abundance. This is true as long as the estimates of abundance are being used as an index of population size, tracking the trends in Alewife abundance from year to year, which is how hydroacoustic assessments are generally used (De Robertis and Handegard 2013, Dorn et al. 2008, Ontario Ministry of Natural Resources and Forestry 2017). The estimates should provide a reliable index of population trends through time, providing a measure of relative abundance of Alewife for fisheries managers. Larger variations will likely occur when comparing absolute abundance estimates produced from different types of assessment. Although the annual trends will likely be correlated, the estimates of absolute lake-wide abundance made from these assessments will likely vary.

The results of this study indicate that if the OMNRF and NYSDEC intend to use the annual lake-wide hydroacoustic prey survey as a means of estimating absolute abundance of Alewife in Lake Ontario, some adjustments should be made to the size thresholds currently in place. A conservative estimate would be to reduce the lower size threshold by 2 dB to account for the average diving Alewife, but as much as 4 dB to include the entire standardized distribution of possible diving target strengths (Figure 4). Reducing the lower threshold may also begin to introduce species which are not Alewife into the abundance estimates, biasing the estimates too high rather than too low. Future work may need to be conducted with the LOMU and the NYSDEC to determine an optimal decrease in the lower threshold within this 2-4 dB range which includes appropriate numbers of off-axis Alewife, while still excluding other smaller species. In order to avoid a crash in the Alewife population in Lake Ontario, such as that observed in Lake Michigan, more research should go into determining the optimal size thresholds for hydroacoustic estimates. There is a large focus on restoring native piscivores to Lake Ontario, while also maintaining rates of stocked Pacific salmon. These large predatory species will need a reliable forage base, and if Alewife are going to be a major component of their diet, understanding their population size is imperative.

Although these estimates appear to capture the average distribution of Alewife target strengths, future studies may be able to provide insights about the aspects that were difficult to address using data available for this study from the standard mobile survey. There was a significant difference in the number of targets in a track from the mobile and stationary surveys, where tracks in the mobile survey tended to be only as long as the minimum length required to be considered a track (Figure 12). A consequence of using data collected for the annual LOMU hydroacoustic survey is that the survey vessel tends to be travelling at a speed which is suitable for crossing the width of the Lake Ontario in a single night. This speed is typically too fast to capture long tracks of individual fish. The length of the tracks recorded are also decreased as a slower ping rate needs to be used when travelling over the deeper waters, thus there are not as many opportunities to get a returning echo off the fish. A series of slow transects, with a high ping rate, in shallow water would allow the survey vessel to collect longer tracks, which may be able to provide more information for the Alewife behaviour.

In order to address the issue of standardizing the tracks and not knowing the true target strength values for the Alewife being observed, a similar method to that of Brooking and Rudstam (2009) could be implemented. By having Alewife of a known size in a large net-cage with a stationary up-looking transducer below, boat avoidance of the Ontario Explorer could be truly quantified as it passed next-to, or above the net-cage. Tilt tags which detect the true orientation of the fish could also be implemented to correlate certain tilt angles with particular target strength values. Knowing the true sizes of the Alewife would allow for more accurate ranges of target strengths to be captured, with the full range of possible orientations being observed. This method could also be used to quantify lateral avoidance of the vessel. If the amount of boat avoidance is deemed too significant, other options for reducing the bias may be considered. Noise-reduced vessels have become more prevalent in assessment surveys and have been shown to reduce boat avoidance for some species (De Robertis and Handegard 2013, Mitson 1995). Although these vessels reduce the amount of underwater radiated noise, there can still be other stimuli detected by fish. This was true for some species which still altered their behaviour under noise reduced vessels (Ona et al. 2007). There continues to be a requirement to understand how the Alewife are responding to different types of survey vessels in Lake Ontario if assessment agencies such as the OMNRF and NYSDEC intend to use these surveys as a measure of absolute abundance in the future.

In conclusion, this study demonstrated that there are measurable differences between Alewife in the mobile and stationary hydroacoustic surveys. Currently, the annual hydroacoustic survey of Alewife in Lake Ontario assumes that fish are behaving naturally, however, this study found the fish to be highly disturbed at the time when they are observed. The differences in behaviour, which are biasing their observed target strength, have been identified and the reported differences can be used to compensate for these discrepancies. This study has also identified future directions which should be followed in order to completely address the issue of boat avoidance for the annual hydroacoustic prey survey. Taken together, the information obtained in this study can be used to help maintain the delicate balance between predator and prey abundance in Lake Ontario, and to conserve the valuable recreational fisheries in this body of water.

Literature Cited

Appenzeller, A. R., and W. C. Leggett. 1992. Bias in hydroacoustic estimates of fish abundance due to acoustic shadowing: evidence from day–night surveys of vertically migrating fish. Canadian Journal of Fisheries and Aquatic Sciences 49:2179–2189.

Arrhenius, F., B. Benneheij, L. Rudstam, and D. Boisclair. 2000. Can stationary bottom split-beam hydroacoustics be used to measure fish swimming speed in situ? Fisheries Research 45:31-41.

Bean, T. H. 1884. On the occurrence of the branch alewife in certain lakes of New York. The Fisheries and Fishery Industries of the United States. Sec 1:588-593.

Blackman, S.S. 1986. Multiple-target tracking with radar applications. Artech House, Norwood, Massachusetts.

Brandt, S. B., D. M. Mason, D. B. Macneill, T. Coates, and J. E. Gannon. 1987. Predation by alewives on larvae of yellow perch in Lake Ontario. Transactions of the American Fisheries Society 116:641–645.

Brooking, T. E., and L. G. Rudstam. 2009. Hydroacoustic target strength distributions of alewives in a net-cage compared with field surveys: deciphering target strength distributions and effect on density estimates. Transactions of the American Fisheries Society 138:471–486.

Brown Jr., E. H. 1972. Population biology of alewives, *Alosa pseudoharengus*, in Lake Michigan, 1949–70. Journal of the Fisheries Research Board of Canada 29:477–500.

Burczynski, J. J., and R. L. Johnson. 1986. Application of dual-beam acoustic survey techniques to limnetic populations of juvenile sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 43:1776–1788.

Crawford, S. 2001. Salmonine introductions to the Laurentain Great Lakes: an historical review and evaluation of ecological effects. Canadian Special Publication of Fisheries and Aquatic Sciences 132.

Crossman, E.J., and H.D. van Meter. 1979. Annotated list of the fishes of the Lake Ontario watershed. Technical Report No. 36. Great Lakes Fishery Commission. Ann Arbor, Michigan, United States.

De Robertis, A., and C. D. Wilson. 2010. Silent ships sometimes do encounter more fish. Part II: concurrent echosounder observations from a free-drifting buoy and vessels. ICES Journal of Marine Science 67:996–1003.

De Robertis, A., and N. O. Handegard. 2013. Fish avoidance of research vessels and the efficacy of noise-reduced vessels: a review. ICES Journal of Marine Science 70:34–45.

Dettmers, J. M., C. I. Goddard, and K. D. Smith. 2012. Management of alewife using Pacific salmon in the Great Lakes: whether to manage for economics or the ecosystem? Fisheries 37:495–501.

Dorn, M., K. Aydin, S. Barbeaux, M. A. Guttormsen, B. Megrey, K. Spalinger, and M. Wilkins. 2008. Gulf of Alaska walleye pollock. In Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Gulf of Alaska 53–167.

Echoview. 2018. Echoview software, version 8.0. Echoview Software Pty Ltd, Hobart, Australia.

Emery, L. 1985. Review of fish species introduced into the Great Lakes, 1819-1974. Great Lakes Fishery Commission 45:1–21.

Fitzsimons, J. D. 1995. The effect of B-vitamins on a swim-up syndrome in Lake Ontario lake trout. Journal of Great Lakes Research 21:286-289.

Fitzsimons, J. D., S. Huestis, and B. Williston. 1995. Occurrence of a swim-up syndrome in Lake Ontario lake trout in relation to contaminants and cultural practices. Journal of Great Lakes Research 21:277-285.

Foote, K. G. 1985. Rather-high-frequency sound scattering by swimbladdered fish. Journal of the Acoustical Society of America 78:688–700.

Gerlotto, F., J. Castillo, A. Saavedra, M. A. Barbieri, M. Espejo, and P. Cotel. 2004. Three-dimensional structure and avoidance behaviour of anchovy and common sardine schools in central southern Chile. ICES Journal of Marine Science 61:1120–1126.

Gillespie, G. C. 1967. Gaspereaux fishing in the Maritimes. Fisheries Canada 20:14-16.

Government of Canada and United States Environmental Protection Agency. 1995. The Great Lakes: an environmental atlas and resource book. 3rd ed. United States Environmental Protection Agency, Chicago, Illinois.

Graham, J. J. 1956. Observations on the alewife, *Pomolobus pseudoharengus* (Wilson), in fresh water. Publications of the Ontario Fisheries Research Laboratory No. 72.

Handegard, N. O., and D. Tjøstheim. 2005. When fish meet a trawling vessel: examining the behaviour of gadoids using a free-floating buoy and acoustic split-beam tracking. Canadian Journal of Fisheries and Aquatic Sciences 62:2409–2422.

Hazen, E. L., and J. K. Horne. 2004. Comparing the modelled and measured target strength variability of walleye pollock, *Theragra chalcogramma*. ICES Journal of Marine Science, 61:363–377.

Henderson, M.J., J.K. Horne, and R.H. Towler. 2007. The influence of beam position and swimming direction on fish target strength. Journal of Marine Science, 65:226-237.

Holeck, K.T., J.M. Watkins, E.L. Mills, O. Johannsson, S. Millard, V. Richardson, and K. Bowen. 2008. Spatial and long-term temporal assessment of Lake Ontario water clarity, nutrients, chlorophyll a, and zooplankton. Aquatic Ecosystem Health and Management, 11:377-391.

Honeyfield, D. C., J. P. Hinterkopf, and S. B. Brown. 2002. Isolation of thiaminase-positive bacteria from alewife. Transactions of the American Fisheries Society 131:171-175.

Janssen, J. 1976. Feeding modes and prey size selection in the alewife (*Alosa pseudoharengus*). Journal of the Fisheries Research Board of Canada 33:1972-1975.

Janssen, J., and S. I. Brandt. 1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 37:177-384.

Johnson, J., and N. Ringler. 1981. Natural reproduction and juvenile ecology of Pacific salmon and rainbow trout in tributaries of the Salmon River, New York. New York Fish and Game Journal 28:49–60.

Johnston, S. V., and T. W. Steig. 1995. Evolution of fixed-location hydroacoustic techniques for monitoring upstream migrating adult salmonids (*Oncorhynchus spp.*) in riverine environments. ICES Symposium of Fisheries and Plankton Acoustics, Aberdeen, Scotland.

Jones, M. L., J. F. Koonce, and R. O'Gorman. 1993. Sustainability of hatchery-dependent salmonine fisheries in Lake Ontario: the conflict between predator demand and prey supply. Transactions of the American Fisheries Society 122:1002–1018.

Krueger, C. C., D. L. Perkins, E. L. Mills, and J. E. Marsden. 1995. Predation by alewives on lake trout fry in Lake Ontario: role of an exotic species in preventing restoration of a native species. Journal of Great Lakes Research 21:458-469.

Lepak, J. M., and C. E. Kraft. 2008. Alewife mortality, condition, and immune response to prolonged cold temperatures. Journal of Great Lakes Research 34:134–142.

Love, R. 1971. Measurements of fish target strength: a review. Fishery Bulletin 69:703–715.

Lucas, M., L. Walker, T. Mercer, and J. Kubecka. 2002. A review of fish behaviours likely to influence acoustic fish stock assessment in shallow temperate rivers and lakes. R&D Technical Report, Environment Agency, Bristol, UK.

Madenjian, C. P., R. O'Gorman, D. B. Bunnell, R. L. Argyle, E. F. Roseman, D. M. Warner, J. D. Stockwell, and M. A. Stapanian. 2008. Adverse effects of alewives on Laurentian Great Lakes fish communities. North American Journal of Fisheries Management 28:263-282.

Maechler, M. 2018. sfsmisc: Utilities from 'Seminar fuer Statistik' ETH Zurich. R package version 1.1-2.

Mansueti, A. J., and J. D. Hardy, JR. 1967. Development of fishes of the Chesapeake Bay Region, Part 1. Natural Research Institute, University of Maryland, Baltimore, Maryland.

Marsden, E. J., and C. C. Krueger. 1991. Spawning by hatchery-origin lake trout (*Salvelinus namaycush*) in Lake Ontario: data from egg collections, substrate analysis, and diver observations. Canadian Journal of Fisheries and Aquatic Sciences 48:2377-2384.

Mills, E., J. Leach, J. Carlton, and C. Secor. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. Journal of Great Lakes Research 19:1-54.

Misund, O. A., J. T. Ovedal, and M. T. Hafsteinsson. 1996. Reactions of herring schools to the sound field of a survey vessel. Aquatic Living Resources 9:5–11.

Mitson, R. B. 1995. Underwater noise of research vessels: review and recommendations. ICES Cooperative Research Report 209.

Murry, B., M. Connerton, N. Ringler, and D. Stewart. 2009. Majority of age-3 chinook salmon (*Oncorhynchus tshawytscha*) in Lake Ontario were wild from 1992 to 2005, based on scale pattern analysis. Journal of Great Lakes Research 35:419–429.

Murry, B., M. Connerton, R. O'Gorman, D. Stewart, and N. Ringler. 2010. Lakewide estimates of alewife biomass and chinook salmon abundance and consumption in Lake Ontario, 1989–2005: implications for prey fish sustainability. Transactions of the American Fisheries Society 139:223–240.

Nelson, D., and J. Hnath. 1990. Lake Michigan chinook salmon mortality – 1989. Michigan Department of Natural Resources Fisheries Division Technical Report 90:4.

New York State Department of Environmental Conservation. 2014. 2013 Annual Report. Bureau of Fisheries Lake Ontario Unit and St. Lawrence River Unit to the Great Lakes Fishery Commission's Lake Ontario Committee, Albany, New York.

O'Gorman, R., and C. P. Schneider. 1986. Dynamics of alewives in Lake Ontario following a mass mortality. Transactions of the American Fisheries Society 115:1–14.

Odell, T. T. 1934. The life history and ecological relationships of the alewife (*Pomolobus pseudoharengus* (Wilson)), in Lake Seneca, New York. Transactions of the American Fisheries Society 64:118-126.

Ona, E., O. R. Godø, N. O. Handegard, V. Hjellvik, R. Patel, and G. Pedersen. 2007. Silent research vessels are not quiet. Journal of the Acoustical Society of America, 121:145–150.

Ontario Ministry of Natural Resources and Forestry. 2017. Lake Ontario fish communities and fisheries: 2016 annual report of the Lake Ontario Management Unit. Ontario Ministry of Natural Resources and Forestry, Picton, Ontario.

Parkinson, E. A., B. E. Rieman, and L. G. Rudstam. 1994. Comparison of acoustic and trawl methods for estimating density and age composition of kokanee. Transactions of the American Fisheries Society 123:841–854.

Pitcher, T. J., O. A. Misund, A. Ferno, B. Totland, and V. Melle. 1996. Adaptive behaviour of herring schools in the Norwegian Sea as revealed by high-resolution sonar. ICES Journal of Marine Science 53:449–452.

Pollom, R. A., and G. A. Rose. 2016. A global review of the spatial, taxonomic, and temporal scope of freshwater fisheries hydroacoustics research. Environmental Review 24:333-347.

Pritchard, A. L. 1929. The alewife (*Pomolobus pseudoharengus*) in Lake Ontario. Publications of the Ontario Fisheries Research Laboratory No. 38:37-54.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rakowitz, G., M. Tušer, M. Říha, T. Jůza, H. Balk, and J. Kubečka. 2012. Use of high-frequency imaging sonar (DIDSON) to observe fish behaviour towards a surface trawl. Fisheries Research 123-124:37-48.

Rand, P. S., B. F. Lantry, R. O’Gorman, R. W. Owens, and D. J. Stewart. 1994. Energy density and size of pelagic prey fishes in Lake Ontario, 1978–1990: implications for salmonine energetics. Transactions of the American Fisheries Society 123:519–534.

Rand, P., and D. Stewart. 1998. Dynamics of salmonine diets and foraging in Lake Ontario, 1983-1993: a test of a bioenergetic model prediction. Canadian Journal of Fisheries and Aquatic Sciences 55:307–317.

Rodgers, G. K. 1987. Time of onset of full thermal stratification in Lake Ontario in relation to lake temperatures in winter. Canadian Journal of Fisheries and Aquatic Sciences. 44:2225-2229.

Rodríguez-Sánchez, V., L. Encina-Encina, A. Rodríguez-Ruiz, and R. Sánchez-Carmona. 2016. Do close range measurements affect the target strength (TS) of fish in horizontal beaming hydroacoustics? Fisheries Research 173:4-10.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada. Bulletin No. 184, Ottawa, Ontario.

Simmonds, E., and D. MacLennan. 2005. Fisheries Acoustics, 2nd ed. Blackwell Science, Oxford, UK.

Skaret, G., B. Axelsen, L. Nøttestad, A. Fernö, and A. Johannessen. 2005. The behaviour of spawning herring in relation to a survey vessel. ICES Journal of Marine Science 62:1061-1064.

Smith, H. M. 1892. Report on an investigation of the fisheries of Lake Ontario. Bulletin of the United States Fish Commission. 10:177-215.

Smith, H. M. 1907. The fishes of North Carolina. North Carolina Geological and Economic Survey No. 2.

Smith, S. 1970. Species Interactions of the alewife in the Great Lakes. Transactions of the American Fisheries Society 99:754-765.

Soria, M., P. Preon, and F. Gerlotto. 1996. Analysis of vessel influence on spatial behaviour of fish schools using a multi-beam sonar and consequences for biomass estimates by echo-sounder. ICES Journal of Marine Science 53:453–458.

Stewart, D. J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978-88. Canadian Journal of Fisheries and Aquatic Sciences 48:909-922.

Stringham, E. 1924. The maximum speed of fresh-water fishes. The American Naturalist 58:156-161.

Taylor, J., and S. Maxwell. 2007. Hydroacoustics: lakes and reservoirs. Pages 153–172 *in* D. Johnson, B. Shrier, J. O'Neal, J. Knutzen, X. Augerot, T. O'Neil, and T. Pearsons, editors. Salmonid Field Protocols Handbook: Techniques for Assessing Status and Trends in Salmon and Trout Populations. American Fisheries Society, Bethesda, Maryland.

Thorne, R. E. 1979. Hydroacoustic estimates of adult sockeye salmon (*Oncorhynchus nerka*) in Lake Washington, 1972–75. Journal of the Fisheries Board of Canada 36:1145–1149.

Toner, G. C. 1934. Notes on the alewife. Canadian Field-Naturalist 48:51-52.

Tufts, B., J. Holden, and M. DeMille. 2015. Benefits arising from sustainable use of North America's fishery resources: economic and conservation impacts of recreational angling. International Journal of Environmental Studies 72:850-868.

Vabø, R., K. Olsen, I. and Huse. 2002. The effect of vessel avoidance of wintering Norwegian spring spawning herring. Fisheries Research 58:59–77.

Warner, D. M., L. G. Rudstam, and R. A. Klumb. 2002. In Situ Target Strength of Alewives in Freshwater. Transactions of the American Fisheries Society 131:212–223.

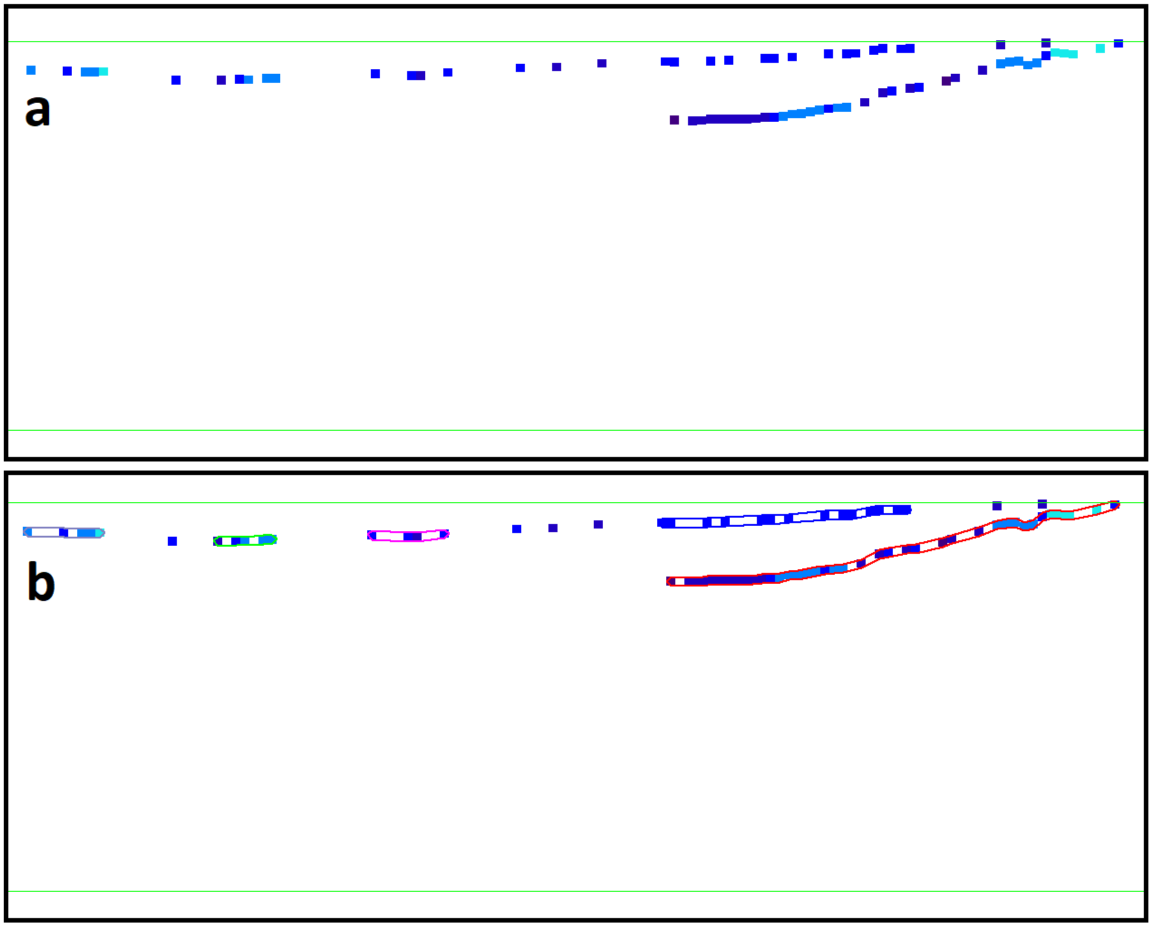
Wickham, H. 2009. ggplot2: Elegant graphics for data analysis. Springer-Verlag, New York.

Wickham, H., R. Francois, L. Henry, and K. Müller. 2017. dplyr: A grammar of data manipulation. R package version 0.7.4.

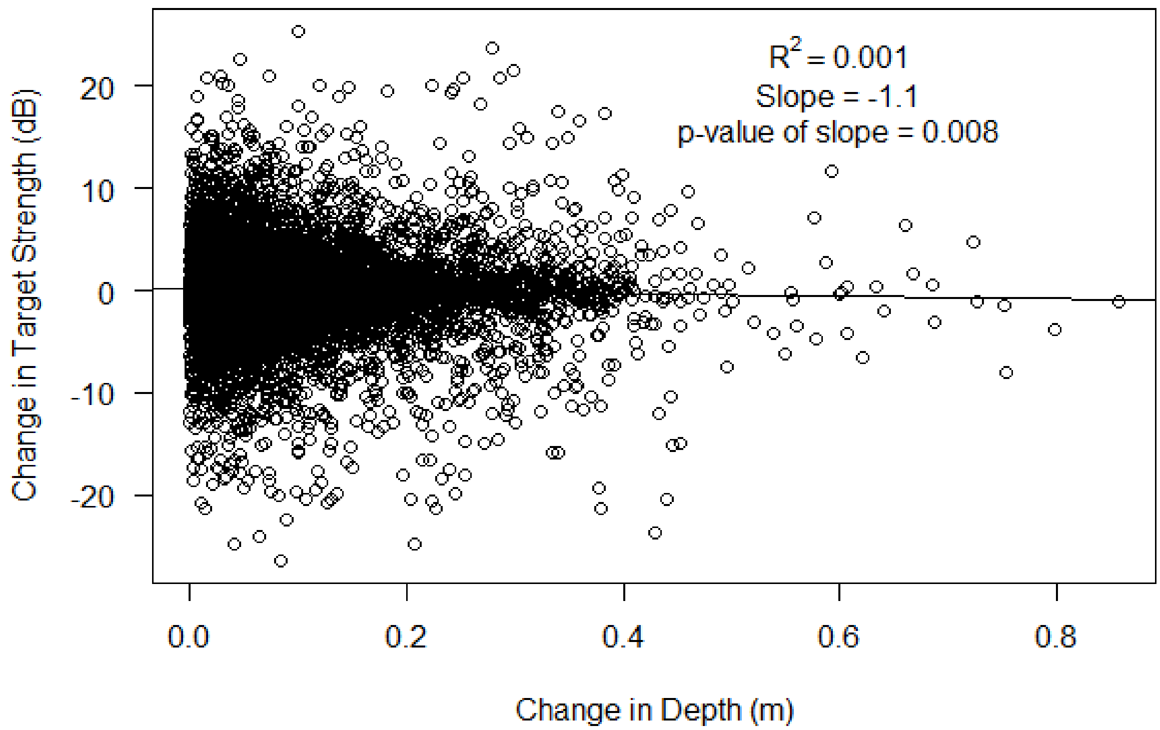
Xie, Y., C. G. J. Michielsens, A. P. Gray, F. J. Martens, and J. L. Boffey. 2008. Observations of avoidance reactions of migrating salmon to a mobile survey vessel in a riverine environment. Canadian Journal of Fisheries and Aquatic Sciences 65:2178–2190.

Appendices

Appendix A: Example echograms showing the 2 m surface exclude (top green line) and 15 m thermal barrier exclude (bottom green line), focussed in on the 13 m of water column used to identify Alewife targets. The top echogram depicts single targets and the varying colours represent changing target strength values (**a**). The bottom echogram demonstrates how single targets are grouped by the Fish Tracking module from the Echoview software to produce tracks for single Alewife (**b**).



Appendix B: Change in depth (m) as a predictor of change in target strength (dB) for a linear model with $R^2 = 0.001$, and a significant slope (p=0.008) of -1.1.



Appendix C: Tilt of the track (º) as a predictor of change in target strength (dB) for a linear model with $R^2 < 0.001$, and a slope of -0.001 which was not significantly different from 0 ($p=0.67$).