

# Strong Thermal Stratification Reduces Detection Efficiency and Range of Acoustic Telemetry in a Large Freshwater Lake

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## Research Article

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# Abstract

## Background

The successful use of acoustic telemetry to detect fish hinges on understanding the factors that control the acoustic range. The speed-of-sound in water is primarily a function of density, and in freshwater lakes density is primarily driven by temperature. The seasonal thermal stratification in the Great Lakes represent the strongest sound speed gradients in any aquatic system. Such speed-of-sound gradients can refract sound waves leading to greater divergence of acoustic signal, and hence more rapid attenuation. The changes in sound attenuation change the detection range of a telemetry array and hence influence the ability to monitor fish. We use three months of data from a sentinel array of V9 and V16 Vemco acoustic fish tags, and a record of temperature profiles to determine how changes in stratification influence acoustic range in eastern Lake Ontario.

## Result

We interpret data from an acoustic telemetry array in Lake Ontario to show that changes in acoustic detection efficiency and range correlate strongly with changes in sound speed gradients due to thermal stratification. The strongest sound speed gradients of  $10.38 \text{ ms}^{-1}/\text{m}$  crossing the thermocline occurred in late summer, which caused the sound speed difference between the top and bottom of the water column to be greater than 60 m/s. V9 tags transmitting across the thermocline could have their acoustic range reduced from >650 m to 350 m, while the more powerful V16 tags had their range reduced from >650 m to 450 m. In contrast we found that when the acoustic source and receiver were both transmitting below thermocline there was no change in range, even as the strength of sound speed gradient varied.

## Conclusion

Changes in thermal stratification occur routinely in the Great Lakes, on timescales between months and days. The acoustic range can be reduced by as much as 50% compared to unstratified conditions when fish move across the thermocline. We recommend that researchers consider the influences of thermal stratification to acoustic telemetry when configuring receiver position.

## Background

Acoustic telemetry is a widely used tool to monitor fish movement and behaviour (Cooke et al. 2004; Hussey et al. 2015) and understanding the performance of telemetry equipment is crucial for proper experimental design and interpretation of the data (e.g. Kessel et al. 2014). One variable which impacts acoustic detection performance, particularly in freshwater lakes, is thermal stratification. It is well known that many lakes have seasonal thermal stratification, with warm surface waters and cooler waters at depth. This thermal stratification strongly influences fish movement and behaviour (e.g. Roberts et al. 2009; Kraud et al. 2015). Furthermore, the associated sound speed gradients induced by temperature gradients also have implications to the detection efficiency of acoustic telemetry devices (which is

defined as the ratio of acoustic signals detected out of the total signals transmitted) and detection range (which is the range that detection efficiency drops to 50 % of acoustic telemetry systems) (Mathies et al. 2014). Detection efficiency can be influenced by thermal stratification because sound waves from an acoustic tag can refract and bend as they move from the epilimnion (warmer waters) to a receiver in the hypolimnion (cooler waters). Depending on how pronounced the sound speed gradients are, and the relative vertical locations of tagged fish and receivers, detection range may be significantly impacted in thermally stratified systems (Wells et al. 2021). There are many factors potentially affecting detection efficiency, and subsequently reduce detection range of acoustic telemetry. In previous studies, the effect of environmental noise, biological noise, and artificial noise has been shown to reduce detection efficiency (Kessel et al. 2014; Klinard et al. 2019; Loher et al. 2017). As well, thermal stratification can also influence the performance of acoustic telemetry gear (Wells et al. 2021). Recently, O'Brien and Secor (2021) reviewed the effects of thermal stratification on acoustic detection efficiency and range. Their findings suggest that in most cases, thermal stratification reduced efficiency and range, particularly when the acoustic signal traversed the thermocline. However, they also present new marine data from the mid-Atlantic Bight where detection range and efficiency increased for signal transmissions within the hypolimnion during strong thermal stratifications. Thus, understanding how thermal stratification influences the transmission of acoustic signals, particularly in freshwater lakes is important, especially as these are the focus of intense research activities.

The sound speed in shallow freshwater lakes is primarily a function of density, and in freshwater lakes, density is primarily a function of temperature. Such sound speed gradients can refract sound waves such as those produced by acoustic transmitters. In addition, the ambient noise produced by surface waves and wind at the surface of water bodies can also be refracted as it travels, potentially producing an hypolimnetic acoustic environment which is quite relative to the epilimnion (O'Brien and Secor 2021). When thermal stratification defocus sound waves, the refraction can lead to substantial decreases in acoustic signal intensity with distance (Figure 1). This increased loss is well known in marine systems (e.g. Shi et al. 2007) and has recently been identified as an important limit of detection range in strongly stratified lakes (Wells et al., 2021). A transmitted acoustic signal can be visualized as rays emanating from a source, with the distance between the rays being inversely proportional to the acoustic intensity. If there is no thermocline (Fig. 1a), then the main loss of signal strength is through three-dimensional spreading over distance (Wells et al. 2021). The detection efficiency thus decreases geometrically with distance, with power inversely decaying as the square of distance. However, once thermal stratification is formed, the refraction of acoustic signals intensifies this three-dimensional spreading loss, and further reduces detection efficiency, and thus reduces the detection range (Fig. 1b, c). In effect, refraction defocusses the sound, spreading out the sound waves even more and thus "dimming" the sound volume arriving at the receiver. Thus, the sound speed gradients lead to a refraction along the path of acoustic signals, which subsequently creates an acoustic shadow zone on the other side of the thermocline that can potentially reduce detection efficiency (Urick 1983).

In a typical year, the thermal stratification in dimictic Lake Ontario starts to form during May and disappears in October. During the hot summer months, stratification forms with warm surface water and

cold bottom water separated by thermocline, which is a zone that temperature drops rapidly with depths. Once the water temperature cools down in fall, the whole water column mixes due to a combination of winds and buoyancy forcing and becomes isothermal. Once the water cools below 4°C, a winter inverse stratification will form, with ice on top of warmer 4°C waters (Yang et al. 2017, 2020). When waters warm again in spring, there is another (shorter) isothermal period before summer stratification starts. The vertical temperatures difference during winter in Lake Ontario are at most 4 °C, which are significantly smaller than 10 to 20 °C differences possible during summer (Klinard et al. 2019). During stratified periods the depth of a summer thermocline is not static, as the depth of thermocline can change by as much as 10-20m on a daily basis. These changes are caused when wind blows across the lake surface, warm water in the surface layer is pushed away to the far end, and downwelling occurs. When wind blows from the opposite direction, upwelling of cold bottom waters will occur at the same end of the lake. When the wind stops, several cycles of internal movements can occur over periods of days. As a result, the depth of the thermocline in most large lakes is constantly changing (Chowdhury et al. 2016). Consequently, sound speed gradients can be potentially influenced by internal seiches, and hence change on short timescale.

A previous study on acoustic range in Lake Ontario by Klinard et al. (2019) focussed on the period between fall and spring, when the water column was nearly isothermal. During this time the detection range was between 700 m to 1700 m depending on the power outputs and the mooring depths of transmitters, and in extreme cases, signals could travel and be detected up to 9.3 km (Klinard et al. 2019). In this study the receivers were deployed in a ring with spacing of less than 1 km apart, as this was presumed to guarantee close to 100% detection efficiency of fish entering and leaving the array of over 60 receivers. However, the majority of the range testing described by Klinard et al. (2019) was during the isothermal period when the maximum top to bottom thermal differences throughout the study period were approximately 3 °C, while average differences were less than 0.5 °C. Hence the thermal stratification was likely a minor factor in this previous study. In contrast, during summer in Lake Ontario, top to bottom temperature differences are typically closer to 10-20°C (Huang et al. 2010). In Wells et al. (2021) observations in the Hamilton Harbour of Lake Ontario suggested the detection range of V13 tags could change between 300 and 500 m depending upon whether the water column was stratified or isothermal.

In this study, we extend the previous work of Klinard et al. (2019) by focusing on detection efficiency during the stratified summer, rather than focusing on the nearly isothermal winter conditions. In this paper, we examine the correlation between sound speed differences and detection efficiency over distances of 150-650 m in eastern Lake Ontario over a two-month period during late summer, when there is a transition from very strong thermal stratification to isothermal fall conditions. As well, we categorize sound speed differences into five different levels from low to high to observe the correlation between detection efficiency and distance. All the correlation tests are compared among transmitters deployed at different depths with different power outputs. Our hypothesis is that there is a correlation between sound speed difference and detection efficiency over a certain distance, and how much the detection efficiency is correlated to sound speed difference depends on transmitters and receivers' mooring positions and

transmitter power outputs. We then use a mathematical model with field observations as inputs to simulate transmission loss during the stratified period and isothermal period. The influence of thermal stratification based on analysis of field observations and results from mathematical model will then be discussed.

## Methods

### *Study Site*

In this study, the influence of thermal stratification upon detection efficiency was studied in a sentinel array located in the St. Lawrence Channel of eastern Lake Ontario (Fig. 2). Lake Ontario is a very large lake of area 18,960 km<sup>2</sup> with a maximum depth of 244 m and mean depth of 86 m. It is a dimictic lake, meaning that there is strong thermal stratification in summer with surface water temperatures above 20 °C while the deepest waters are close to 4 °C. There are two extended isothermal periods in fall and spring, and there is a weak inverse thermal stratification in winter when the deepest water is near 4°C and surface waters are near 0 °C (Rodgers, 1987; Huang et al., 2010). During summer the thermocline is typically at depths of 20 to 30 m (Huang et al., 2010). In addition to this seasonal variation in temperature, wind stress can tilt the thermocline and result in internal waves (Chowdhury et al. 2016). The eastern end of Lake Ontario typically accumulates ice for several months between January and March (Oveisy et al 2012). This sentinel array was part of a larger study to investigate the movement and fate of hatchery-reared Bloater (*Coregonus hoyi*) that were being reintroduced to Lake Ontario (Klinard et al., 2020). This specific region was chosen for the bloater release due to the presence of a relatively deep region at the lakebed in the St Lawrence channel.

In order to better understand acoustic range as part of the multiyear bloater study, four receivers (VR2W-69, Vemco Ltd., Bedford, NS, Canada) were deployed on four stationary moorings at approximately 52 m depth in the channel (43° 55.517' N, 76°31.354' W) with a distance of 150 m, 350 m, 450 m, and 650 m away from transmitter mooring (Station M5), respectively (Fig. 3). All four receivers were deployed at the same time period from August 31<sup>st</sup>, 2015 to May 25<sup>th</sup>, 2016. A subset of this data from October 22<sup>nd</sup>, 2015 to May 23<sup>rd</sup>, 2016 was previously analyzed in the overwinter study of Klinard et al. (2019) – they analyzed this later time-period as there were a total of 85 receivers deployed. In our study, the major findings are based on an earlier time frame from September 7<sup>th</sup> to October 27<sup>th</sup>, 2015 which covers the period of the strongest thermal stratification. At the source (Station M5), a chain of HOBO Pendant temperature loggers (accuracy of +/- 0.21 °C, Onset Computer Corp., Bourne, MA, USA) was deployed every 5 m from 10 m to 50 m depths. Temperature was recorded hourly. Two transmitters attached at 11 m depth, and another two attached at 50 m depth (Fig. 3). At both depths, a V9-6x-069k-3 and a V16-6x-069k-3 transmitter (Vemco Ltd., Bedford, NS, Canada) were deployed to generate sound signals every 30 minutes with power output of 146 to 151 dB re 1uPa at 1 m and of 152 to 162 dB re 1 uPa at 1 m, respectively (Vemco Ltd., Bedford, NS, Canada). Winds are taken from the Environment and Climate Change Canada buoy C45135 located at 43°46'48" N 76°52'12" W.

In this study, we analyzed both temperature and acoustic telemetry sentinel data from September 7<sup>th</sup> to October 27<sup>th</sup>, 2015 (DOY 250 to DOY 300 of 2015). The instruments sampled from August 31<sup>st</sup>, 2015 to May 25<sup>th</sup>, 2016; however, the data from first week were not completely recorded and the thermal stratification gradually completed transition to isothermal condition till late October around 27<sup>th</sup>. Thus, the analyzed data was a subset of the total field observations, which specifically focuses on the thermally stratified period and subsequent transition period. Daily averaged detection efficiencies and temperatures were calculated for correlating both variables and for subsequent analysis.

### *Calculation and Data analysis*

The sound speed difference, was calculated by comparing sound speed at the top water column (10 m) and bottom water column (50 m), and was calculated from the formula by Coppens (1981), as

$$(1) \quad v_0(T) = 1402.395 + 5.011T - 5.525 \times 10^{-2}T^2 + 2.3 \times 10^{-4}T^3$$

where  $v_0$  is the speed-of-sound in units  $\text{m s}^{-1}$ ,  $T$  is temperature in  $^{\circ}\text{C}$ , between 0 - 35  $^{\circ}\text{C}$ . During the sampling period, the water temperature varied from 4  $^{\circ}\text{C}$  to 24  $^{\circ}\text{C}$ , which means the speed-of-sound varied from 1421.6 to 1494.0  $\text{m s}^{-1}$

We estimate how the sound signals could travel under different thermal conditions by using an open-access modelling tool called Bellhop (Porter, 2011). Bellhop calculates the predicted path of sound waves and generates a visualization of acoustic power losses as the signal spreads away from the source (in this case, the reference fish tags) This publicly available model (<http://oalib.hlsresearch.com/AcousticsToolbox/>) can simulate acoustic transmission loss by inputting values of various characteristics, which includes date, depth, source depth, distance, temperature, and speed-of-sound conversion equations (Porter, 2011). In order to run the Bellhop model, it requires an input environment file which gives users the options to specify properties of upper and lower boundaries, transmitter frequency, number of sources and receivers as well as launching angles. The Bellhop model offers a number of output models, which the code name can also be specified within the environment file. In this study, we used a combination of incoherent acoustic pressure and Gaussian beam bundles to estimate acoustic transmission loss. One of the main conclusions of Wells et al. (2021) was that a drop of 65 dB in acoustic signal in the Bellhop model correlated with a detection efficiency of 50% for the V13 transmitters. This resulted in detection ranges reaching as low as 150 m during stratified conditions (where maximum temperature gradients were  $dT/dz > 1$   $^{\circ}\text{C}/\text{m}$ ) and reaching as high as 450 m isothermal conditions (where maximum temperature gradients were  $dT/dz < 0.1$   $^{\circ}\text{C}/\text{m}$ ). This threshold is specific to the V13 transmitter that have an output power between 147–153 dB re 1 $\mu\text{Pa}$  at 1 m. In contrast the V9 has 145–151 dB re 1 $\mu\text{Pa}$  at 1 m and V16 transmitter has 150–162 dB re 1 $\mu\text{Pa}$  at 1 m, so if all else is equal we might expect the detection range to be predicted by slightly different loss thresholds of 63 and 68 dB for the V9 and V16 units.

# Results

## *Observations*

The temperature profile shows the transition from summer stratification to fall non-stratified isothermal conditions (Fig. 4a). At the start of our record (DOY 250, Sept. 7<sup>th</sup>), the water column was strongly stratified in Lake Ontario, with surface temperatures of 24°C and bottom temperatures near 4 °C (the temperature at which water has its maximum density). A thermocline was typically found at depths of 10 m to 25 m where the maximum temperature gradients could reach 2.9 °C/m. The stratification was persistent, although the depth of thermocline changed as several upwelling and downwelling events occurred. The fall overturn began around DOY 285 after which the water column became isothermal. During the sampling period, changes in wind speeds and direction could be seen that were related to several upwelling and downwelling events through DOY 250 to DOY 285 (Fig. 4b). As sound speed is a function of water temperature, the sound speed gradient was also high at the start of record and reached 10.38 ms<sup>-1</sup>/m crossing thermocline. During the isothermal period the sound speed gradient was lower, and drops to near 0 ms<sup>-1</sup>/m in the whole water column. As an example, the sound speed difference could be over 60 m s<sup>-1</sup> when the water column was strongly stratified from DOY 250 to DOY 255, and reduced to nearly 0 m s<sup>-1</sup> when the lake became isothermal from DOY 290 to DOY 300 (Fig. 4c).

## *Correlations among detection efficiency, sound speed difference, and distance*

By correlating the daily average of the sound speed difference with the detection efficiency we can determine that sound speed gradients reduce detection efficiency (Figure 5). During the period studied from DOY 250 – 300, sound speed differences between the top and bottom of the water column varied from 0 to 65 m s<sup>-1</sup> (Figure 4c), the detection efficiency of the V9 transmitter located at 11 m depth decreased as a function of sound speed difference and distance from source (Figure 5a). There was a similar trend for the more powerful V16 transmitter located at 11 m depth (Figure 5c), but there was less reduction in detection efficiency with increasing sound speed differences. When the transmitter was located below the thermocline at 50 m depth, a positive relationship between sound speed difference and detection efficiency was found when the transmitter to receiver distance was 350 m and 450 m (Figure 5b). However for this case where source and receiver were both below the thermocline, there was virtually no dependence of the detection efficiency on the sound speed difference across the thermocline (Figure 5d). The average detection efficiencies were higher for the more powerful V16 transmitter (Figure 5a,c) than the V9 (Figure 5b,d) but the same general trends are seen.

To understand how the transmitter to receiver distance and sound speed difference affect detection efficiency, we categorized sound speed difference into five different groups, 0-15, 15-30, 30-45, 45-60 and >60 m s<sup>-1</sup> (Figure 6). Similar to the previous results when detection efficiency was a function of sound speed difference, increasing the distance between transmitter and receiver had a negative correlation with detection efficiency. For the V9 tags located at 11 m depth (i.e. above a thermocline), when sound speed difference was less than 30 m s<sup>-1</sup>, detection efficiency was over 50 % regardless of transmitter to receiver

distance (Figure 6a). As the sound speed difference increased to over  $30 \text{ m s}^{-1}$  detection efficiency declined rapidly with an average detection efficiency below 50 % when the transmitter to receiver distance reached 450 m. When the sound speed difference reached  $45 \text{ m s}^{-1}$  detection efficiency at the furthest sound signal receiving station (650 m) could decline to less than 20 %, which suggests most sound signals were lost on their path to the receivers over 650 m during summer stratification.

For the V16 transmitter, average detection efficiency at each distance with sound speed difference below  $30 \text{ m s}^{-1}$  maintained well above 80 % (Figure 6c). This means distances less than 650 m did not play an important role regarding attenuating sound signals in a stratified lake. As the sound speed difference increased above  $30 \text{ m s}^{-1}$  detection efficiency started declining with distance; however, comparing to observations of V9 transmitter, the higher power output V16 transmitter meant that attenuation induced by the combination of sound speed gradient and travel distance had less impact upon detection efficiency. When the V9 or V16 transmitter were located at 50 m depth (i.e. beneath the thermocline), the observed detection efficiencies were much higher (Figure 6b and 6d). For the V9 transmitter, there was a slight decrease with distance, but efficiency was still greater than 60 % at 650 m in all cases (Figure 6b). More strikingly for the V16 transmitter, the detection efficiency was close to 100 % in all cases (Figure 6d).

The use of the Bellhop model gave a prediction of how the sound signals travel in both stratified and isothermal conditions (Figure 7). In this case, we selected DOY 250, which is Sept. 7<sup>th</sup>, as a sample of a stratified condition (Figure 7a,b), and DOY 300, which is Oct. 27<sup>th</sup>, as a sample of an isothermal condition (Figure 7c,d). Since temperature loggers were only recording from 10 m to 50 m depths, temperature above 10 m depths were extrapolated the same as at 10 m depths. As well, parameter settings for Bellhop modeling were the same as in Wells et al. (2021). As mentioned earlier the threshold of  $65 \pm 5 \text{ dB}$  loss as a detection limit for the V13 tags would likely be 3 dB higher for the more powerful V16 tags and 3 dB lower for the weaker V9 tags. In these plots, the loss of signal was shown – the main feature was that the signal loss increased with distance from the source, reflecting the spherical spreading of acoustic sound. The details of the patterns of loss change with stratification. For the case where the transmitter was located at 11 m depth, there was greater attenuation of sound below the thermocline, so that a threshold of 63 dB and 68 dB loss of signal was reached at 50 m depth at 310 m and 367 m, respectively, from the source (Figure 7a). When the source is located at the 50 m depth, the threshold was reached at 50 m depth at 432 m and 594 m, respectively, from the source (Figure 7b). It is important to note that above the thermocline, there was also an acoustic “shadow zone” that mimicked that below the thermocline in Figure 7a. When isothermal conditions were used and the source was at 11 m or 50 m, the threshold of 63 dB and 68 dB loss of signal was reached at 50 m depth at 410 m and 510 m, respectively, away from the source for both case (Figure 7c,d). Such a tendency indicated that in the isothermal cases, there was much less variation with depth of the modelled acoustic loss, and that contours for the 63 dB and 68 dB loss occurred at larger distances than in the thermally stratified conditions (Figure 7 a,b).

## Discussion

The sound speed difference between top and bottom water column that exists in a large, deep freshwater lake has a strong influence on the detection efficiency of acoustic telemetry equipment. In general, there was a negative relationship between sound speed difference and detection efficiency (Figure 5 and 6), and the  $r$  square and adjusted  $r$  square values indicate how much they were corresponded (Table 1 and 2, see appendix). With tested  $P$ -values less than 0.05, the results from each set of comparison were significant. The sound speed difference was calculated as the difference in sound speed at 10 m and 50 m depth in the water column and thus indicated the presence of a strong gradient between these depths. Hence, the correlation between sound speed difference and detection efficiency we observed was expected when the transmitters sit at 11 m depth and receivers sit at 50 m depth, so that acoustic signals must cross the thermocline (Figure 5a, 5c). The strong relationship between sound speed difference and detection efficiency at 650 m in the linear regression indicated that more than half of the detection efficiency data at this distance can be explained by sound speed difference. As well as that, weak correlations could be observed at transmitter-to-receiver distances of 350 m and 450 m in the V9 transmitter data set (Figure 5a); however, that correlation of transmitter to receiver distance became lower in V16 transmitter data set (Figure 5c), which could mean the more powerful V16 transmitters have more resistance to these sound speed changes over the ranges up to 650 m considered here. The lack of correlation between sound speed difference and detection efficiency at transmitter-to-receiver distances of 150 m and depths of 11 m for both the V9 and V16 transmitters indicates sound speed difference would not cause attenuation of sound signals at short distances. When both transmitter and receiver were below the thermocline, the vertical sound speed difference was not important regarding sound signal attenuation. However, for the V9 transmitter data set, when transmitter to receiver distances were 350 m and 450 m, a weak positive relationship between sound speed difference and detection efficiency was observed, which is consistent with the findings of slight increases in range when source and receivers are both located under a thermal stratification (O'Brien and Secor 2021). Our Bellhop modelling also showed the increase of detection range when both source and receiver were located at 50 m depth in stratified conditions, as compared to isothermal condition (Figure 7b and 7d). While it was not a strong trend, it is interesting that same phenomenon induced by thermal stratification could be observed in Lake Ontario, as in the coastal ocean setting of O'Brien and Secor (2021). Although bottom increase of detection efficiency was observed in the field, we only saw a strong correlation at distance of 350 and 450 m, at smaller distances there was no trend as detection efficiency was always near 100%, while for greater distances of 650 m we found a lot of scatter data so could not fit a trend line (Figure 5b and 5d). The general trends in changes in detection range with stratification and speed of sound gradient that we observed in Lake Ontario are consistent with the modelling predictions (Figure 7). When a source is located above the thermocline, the detection range is reduced below the thermocline compared to non-stratified conditions. When the source is located below the thermocline, there is little difference in range measured at 50 m depth, although an acoustic shadowzone is visible in modelling above thermocline.

It is worth comparing the detection ranges found during these strongly stratified summer period, with the larger ranges found during the weakly stratified or isothermal time-period studied by Klinard et al. (2019). They found that over winter in the mainly unstratified conditions that detection range from the transmitter

at 11 m was 700 m for the V9 and 1300-1400 m for V16, and for the transmitter located at 50 m depth was 1100-1200 for the V9 and 1700 m for the V16 unit. During the period there was some weak inverse stratification, which might explain the larger ranges for the deeper transmitter. During the earlier period we analyzed at the same site, the furthest receiver was 650 m away from the transmitter, so our maximum range is by default 650 m. During the late summer, when there were very strongly stratified conditions, the range could be as low as 350 m. This shows the importance of summer stratification in changing the efficiency of the bloater array, where the receivers were spaced approximately 1 km apart based on the expected detection efficiency of 80 % at 600 m (Klinard et al. 2019).

Based upon our study we can make some recommendations for improving field deployments in thermally stratified systems. Firstly, it is important to measure temperature profiles, to be aware of possible thermal stratification influences. This should be done at start and end of deployments, and ideally as a continuous record with an in-situ chain of thermistors. We recommend the use of sentinel tags to know if there is a change in range associated with a variable thermocline. Also depending on where fish are expected to sit in water column, it would be advantageous to deploy receivers on both sides of the thermocline, so that shadow-zones are minimized.

Some species of fish in Lake Ontario occupy specific depth ranges at certain times of the year, so the influences of acoustic refraction upon detection can be estimated. For instance, in Klinard et al (2019) the target species was the benthic dwelling Bloater, so there would be no influence of the thermocline upon the detection range as there are no sound speed gradient between the tags and receivers. Other pelagic fishes, such as Walleye, American Eel, Smallmouth Bass and Muskellunge and Lake Trout, typically occupy species-specific temperature and dissolved oxygen ranges imposed by physiological requirements (Guzzo et al. 2017). Temperate freshwater fishes are often broadly classified into three thermal guilds based on the upper limit of their preferred thermal ranges (Hokanson 1977; Magnuson et al. 1979): warmwater (>25 °C), coolwater (19–25 °C), and coldwater (<19 °C) (Coker et al. 2001). In this study, the daily average temperature throughout the sampling period ranged from 4 °C to 22 °C at 10 m to 50 m. Based on Cherry et al. (1977) and Scott and Crossman (1973), this range of temperatures was not ideal for warmwater fish, for instance, Smallmouth Bass (*Micropterus dolomieu*) with temperature preference at 30.3 °C, and Muskellunge (*Esox masquinongy*) with temperature preference at 25.6 °C; however, the top 10 m of water column was not recorded. Given the widespread distribution of warmwater fishes such as Smallmouth Bass and Muskellunge and their robust populations we assume that epilimnion temperatures are suitable. For coolwater fish such as Walleye (*Sander vitreus*) and American Eel (*Anguilla rostrata*) with temperature preference at 22 °C and 19 °C, respectively (Wismer and Christie 1987; Minns et al. 1993), observed temperatures suggested the top 25 m of water column was ideal for them to grow. With occasional downwelling events during stratified period, the ideal temperature for coolwater fish could reach 30 m depth. Coldwater fish can survive with maximum temperature around 24 °C (Hasnain et al. 2010), which was the maximum daily temperature during sampling period from 10 m to 50 m; however, the ideal temperature for coldwater fish such as Lake Trout (*Salvelinus namaycush*) with temperature preference at 10 °C (Peterson et al. 1979) commonly occurred below 30 m depth at hypolimnion during summer stratification.

In most temperate lakes during the summer, thermal stratification physically partitions the lake into different zones suitable for different thermal guilds. Coldwater fishes that avoid warm waters typically reside in the cold hypolimnion, with the thermocline creating a sharp upper boundary, both in terms of temperature and depth. However, coldwater fish will make foraging trips into warmer waters and cross the thermocline. For example, Lake Trout in smaller lakes will move into the littoral zone to feed (Guzzo et al. 2017) and a subset of Lake Ontario Lake Trout have been shown to cross the thermocline to feed (Raby et al. 2019). Similarly, cool water fish would sit near the thermocline, and warm water fish at or above the thermocline. Here again, some warmwater species, such as Chinook Salmon (*Oncorhynchus tshawytscha*), will make trips below the thermocline, presumably to make digestion more efficient (Raby et al. 2019). As most receivers are located below the thermocline, it is likely that warm water fish would be most influenced by reduced detection range due to the sound speed gradients but cold or deepwater fish that cross the thermocline to feed would also be influenced during these movements. Fish might also be confined above the thermocline due to anoxia in the hypolimnion, as occurs routinely in the central basins on Lake Erie (Chamberlin et al. 2020), Green Bay in Lake Michigan (Klump et al., 2018) and Hamilton Harbour in Lake Ontario (Flood et al., 2021; Wells et al., 2021). In these locations, benthic receivers would have reduced range for fish above the thermocline.

The seasonal cycle of stratification is important to consider when interpreting fish telemetry data because tagged fish typically have specific thermal preferences and may use different parts of the lake during different seasons (Ivanova et al. 2020). For example, the bottom of many lakes lacks oxygen during the summer months, resulting in fish actively avoiding the deep waters (e.g. Roberts et al. 2009; Kraud et al. 2015). With the presence of a thermocline, this behaviour has implications for the interpretation of acoustic telemetry data because detection performance can vary depending on the depth of acoustic receivers relative to the thermal layer that the tagged fish chooses to occupy. Understanding the influence of thermal gradients on detection efficiency of telemetry equipment will facilitate more accurate analysis and interpretation of cross-seasonal telemetry data.

## Conclusion

During summer most large lakes in mid-latitudes are thermally stratified with a warm surface layer separated from a cold hypolimnion by a sharp thermocline. Such strong thermoclines produce rapid changes in sound speed, which refract and dim acoustic signals that cross the thermocline. Our study revealed that acoustic telemetry detection efficiency decreased significantly for signals crossing the thermocline when the thermal gradient was high, and there was temperature differences between top and bottom of water column up to 17 °C. In these summer conditions, we found that ranges could be limited to distances between 350 m and 550 m. By contrast, detection efficiency remained high when the thermal gradient was small, and when the top to bottom temperature differences was less than 4 °C, we observed a detection range up to 650 m. A similar reduction of detection efficiency was not observed for signals that did not cross the thermocline, so that when both the source and receiver were located at the lakebed the detection efficiencies were generally higher. In this study, the thermocline's depth was dynamic and varied at a timescale of days, therefore acoustic detection range could vary at similar timescales.

Refraction of sound mainly influences detection range and detection efficiency when acoustic signals cross the thermocline but not when the transmitter and receiver are on the same side of the thermocline. As most acoustic receivers are bottom-mounted (i.e. below most thermoclines in dimictic lakes), anticipating and measuring the tagged animals vertical position relative to the thermocline is an important consideration when designing acoustic telemetry studies and interpreting data.

## **Declarations**

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Not applicable.

### **Authors' contributions**

YK analyzed the data and led the writing of this paper; EAH, ATF and TBJ designed the methodology and collected the data; MGW conceptualized and supervised the study; EAH, ATF, TBJ, NVK, DW, SS contributed in writing and editing. All authors read and approved the final manuscript.

### **Availability of data and materials**

The datasets used and/or analyzed during this study are available from the corresponding author upon request.

### **Consent for publication**

Not applicable.

### **Competing interests**

The authors declare that they have no competing interests.

### **Ethics approval and consent to participate**

Not applicable.

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## **Declarations**

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## Figures

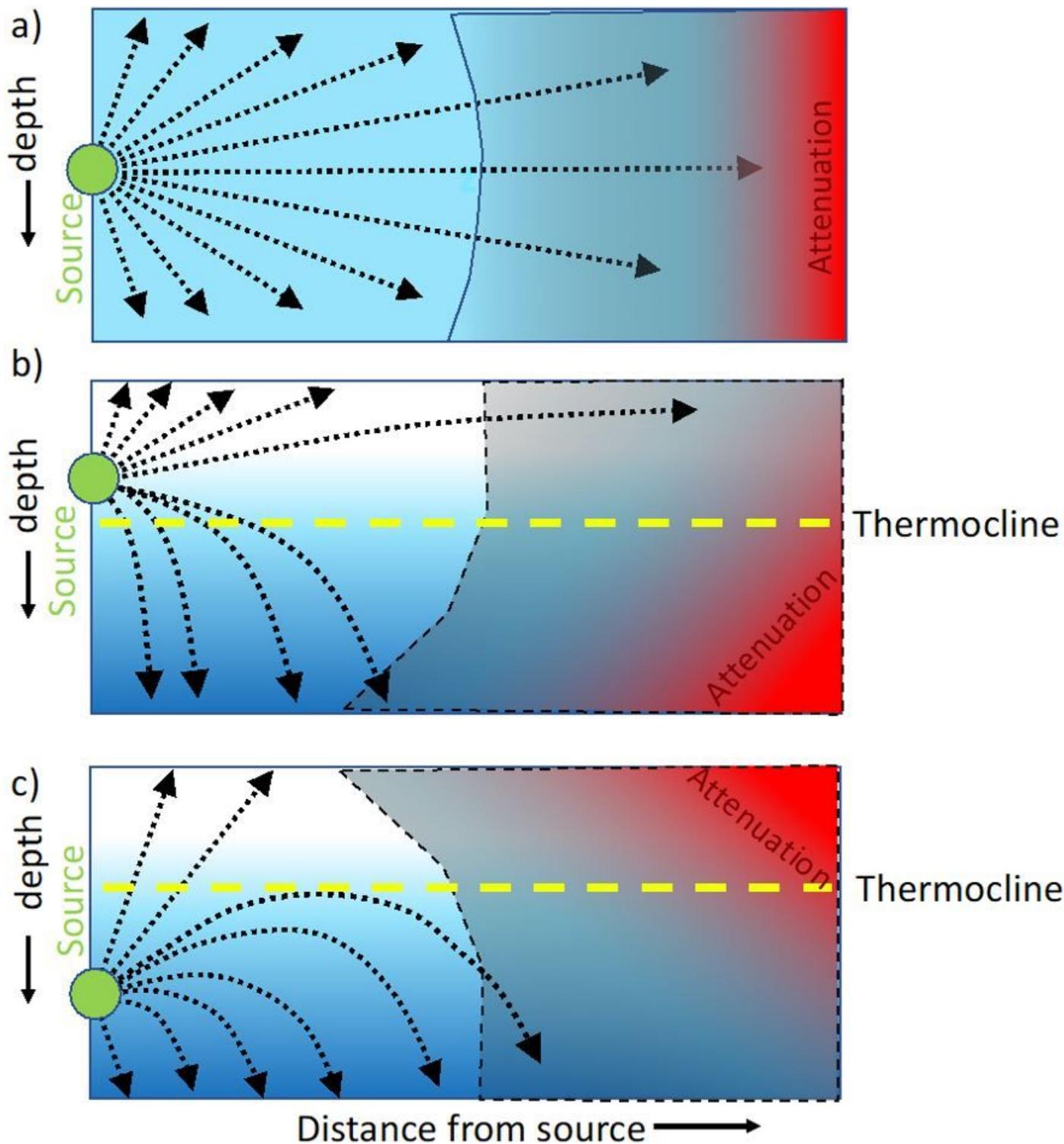


Figure 1

Illustration of how acoustic signals propagate in isothermal water with signal loss through three-dimensional spreading (a), and how acoustic signals propagate in thermally stratified water with signal loss through three-dimensional spreading that is amplified by refraction when the source is above the thermocline (b) and below thermocline in c). In a) the attenuation of acoustic signal is just a function of the distance from the source, whereas in b) an acoustic "shadow zone" of reduced sound intensity forms

below the thermocline, while in c) an acoustic “shadow zone” forms above the thermocline. The green circle represents the acoustic source, the gradients of blue shading represents speed-of-sound gradients, and red shading represent attenuation of sound intensity.

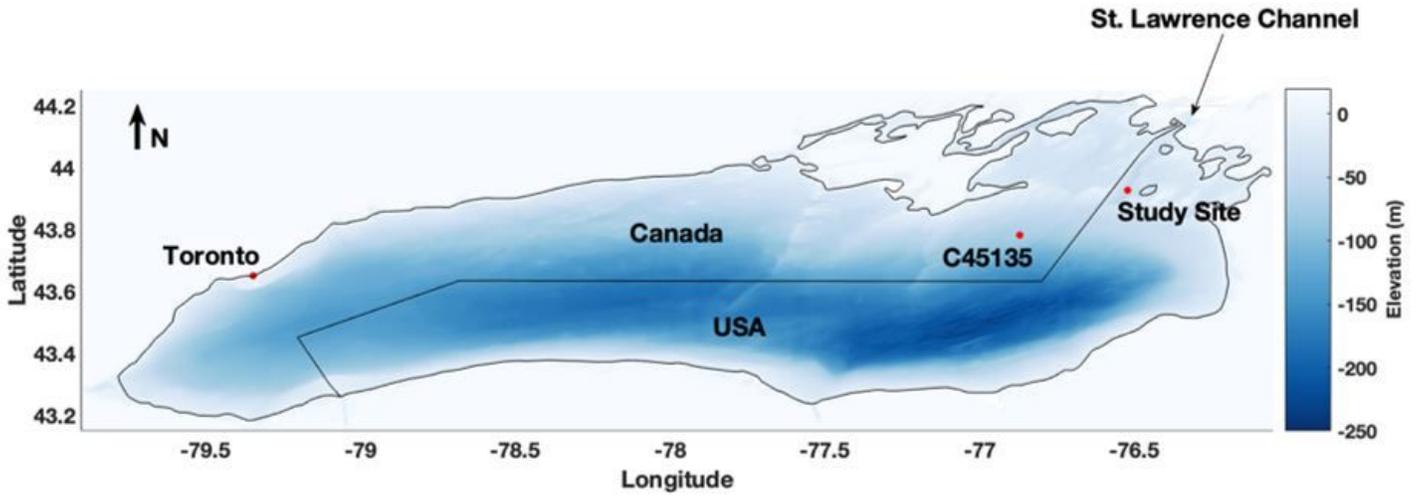


Figure 2

Bathymetry of Lake Ontario with the transmitter and receiver mooring site located in the St. Lawrence Channel of eastern Lake Ontario (study site), and with location of buoy station C45135 recording wind speed.

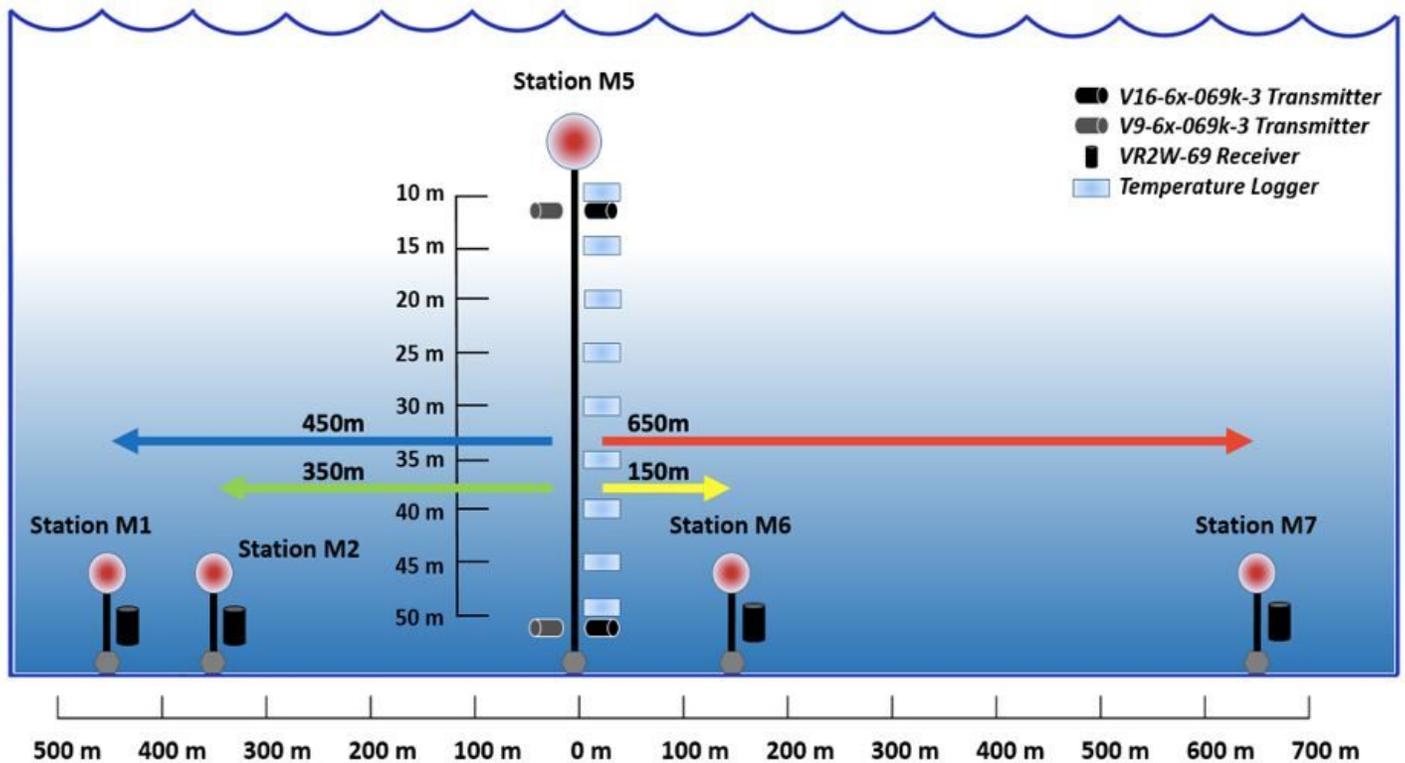


Figure 3

A detailed description of deployment site with V9 and V16 transmitters deployed along the string of temperature loggers. Four VR2W-69 receiver moorings were located at various distances.

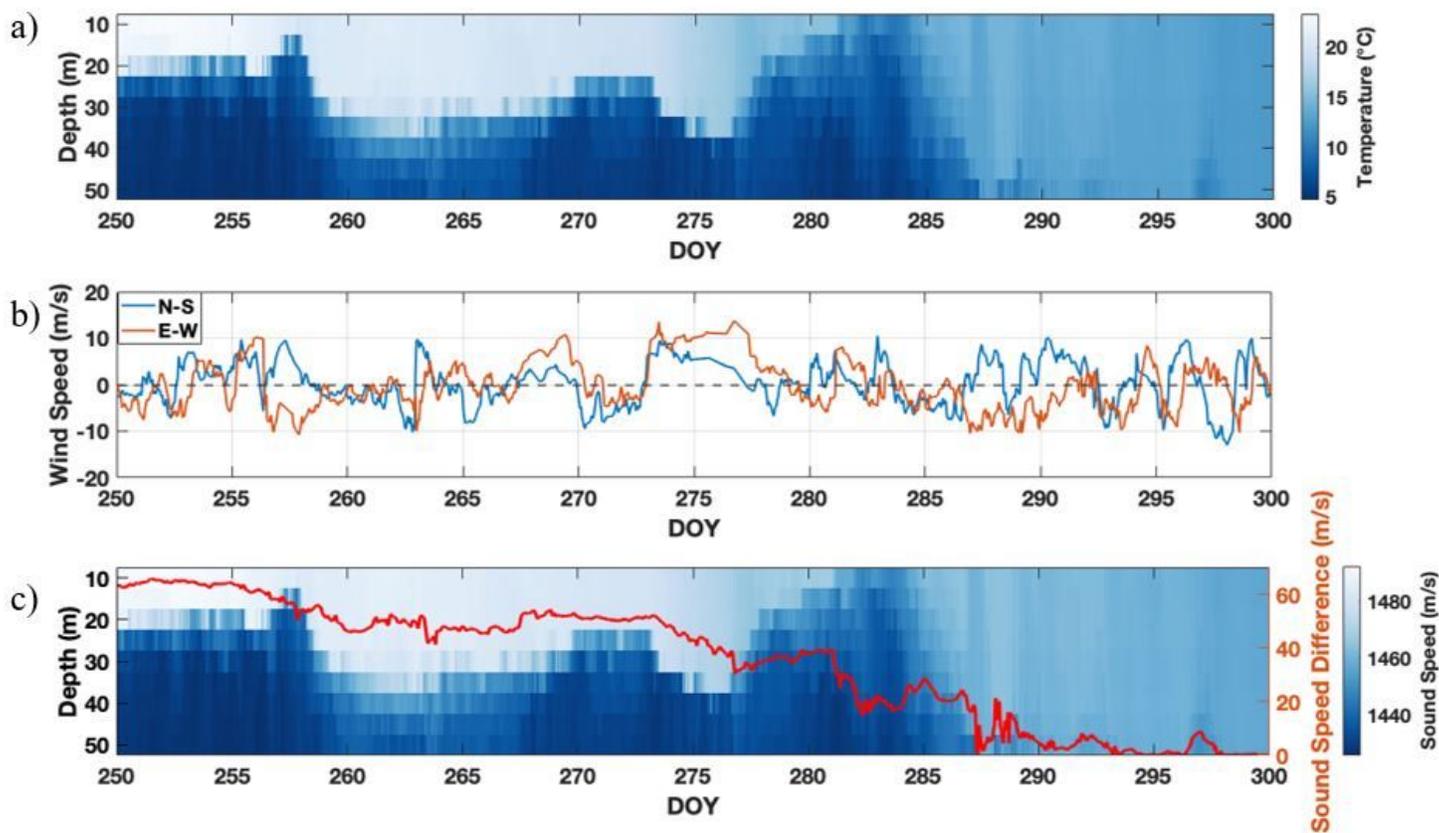


Figure 4

a) Temperature profile in St. Lawrence Channel of eastern Lake Ontario from DOY 250 to DOY 300. The profile indicates the existence of thermal stratification in late summer to early fall as well as the transition from stratification to isothermal condition starting from DOY 285 (mid-October). b) Wind speed vector from North to South (blue line) and from East to West (red line) above the lake surface near moorings. c) Calculated sound speed profile with sound speed difference (red line) between the sound speed at the top (10 m below the surface) and sound speed at the bottom (50 m below the surface).

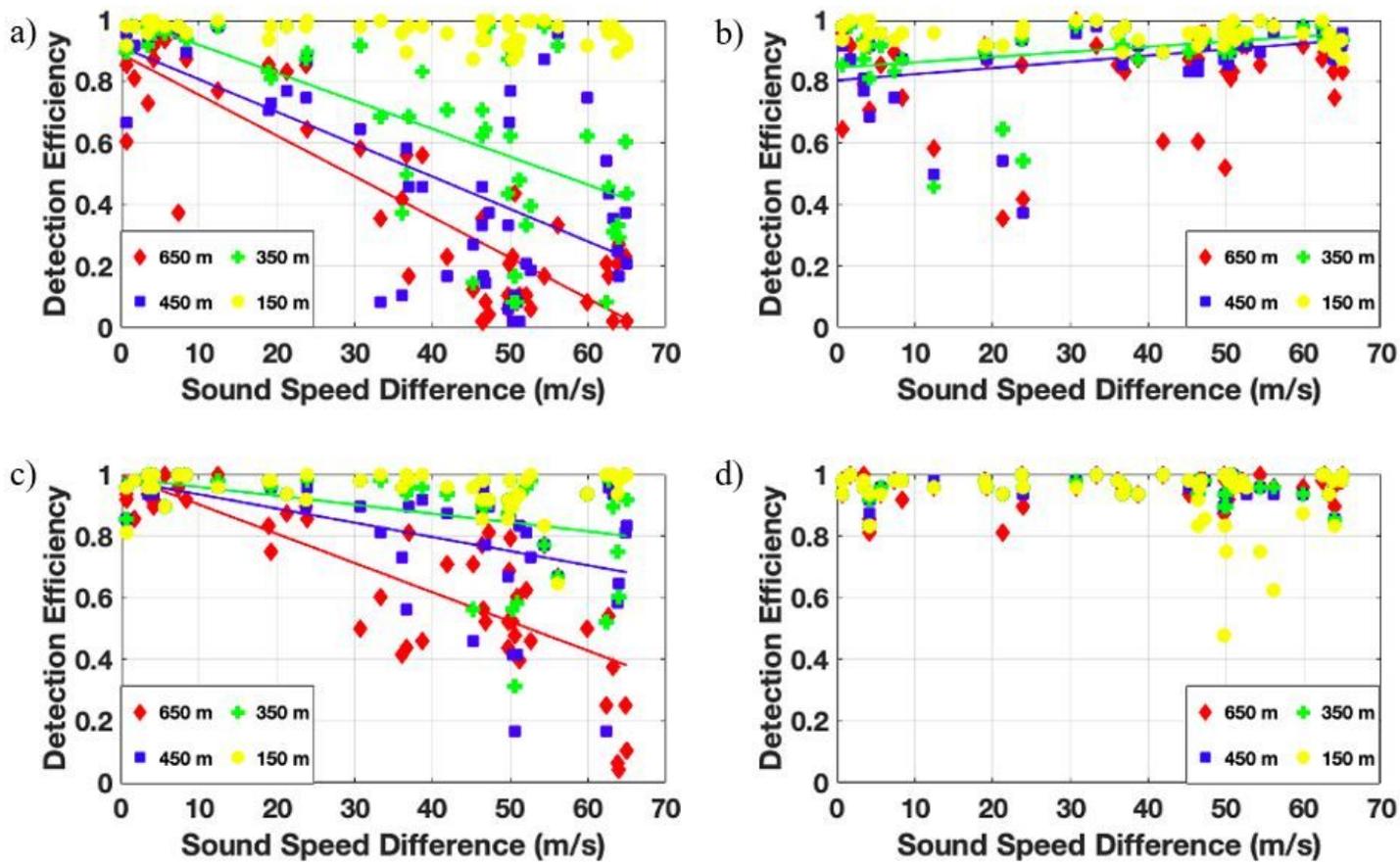


Figure 5

Comparison between sound speed difference and detection efficiency among four receiver moorings from DOY 250 to DOY 300 for a) V9 transmitter at 11 m depth, b) V9 transmitter at 50 m depth, c) V16 transmitter at 11 m depth, and d) V16 transmitter at 50 m depth. Data were fit with a linear regression model to indicate the relationship between sound speed difference and detection efficiency. Statistics of the model fit are included in Table 1 and 2.

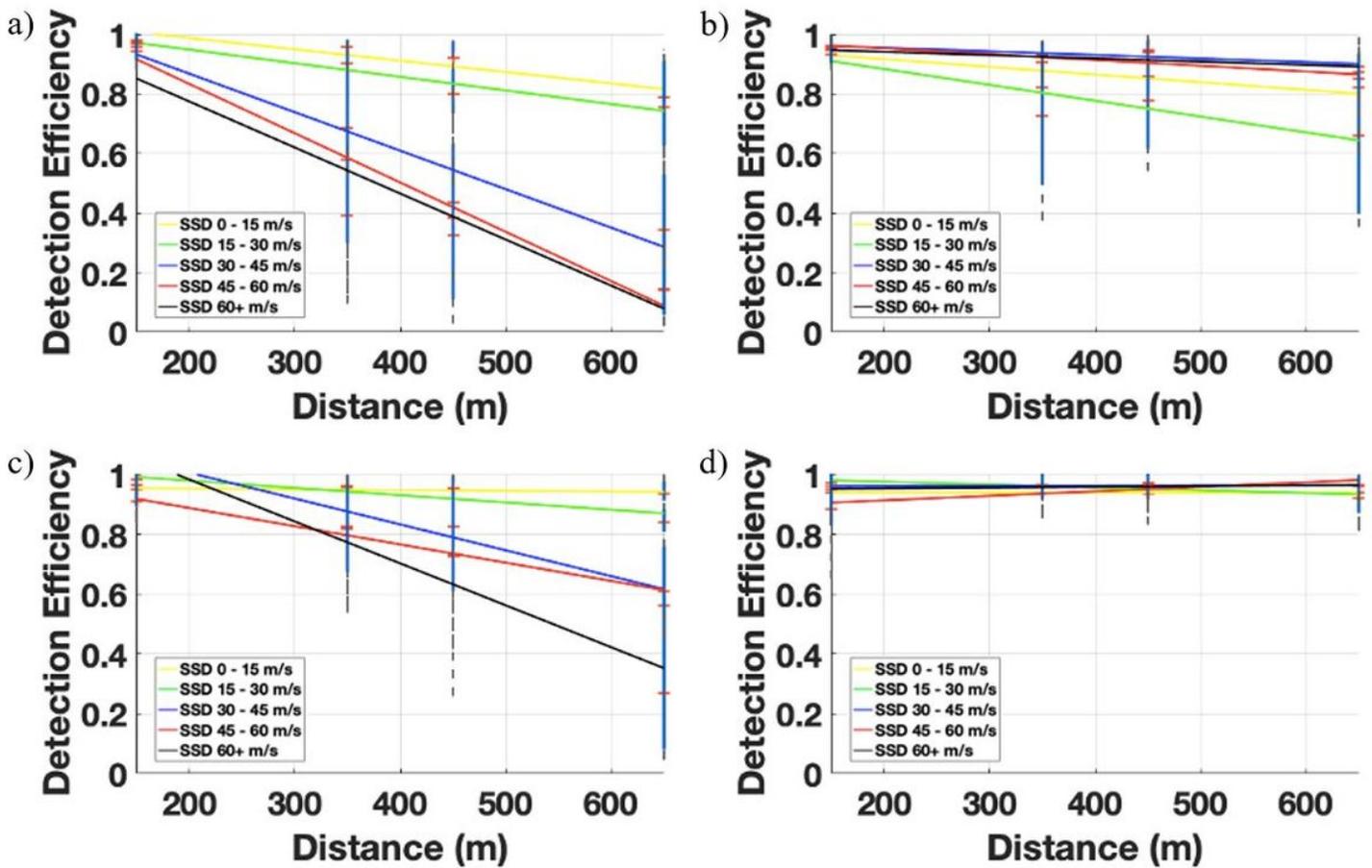
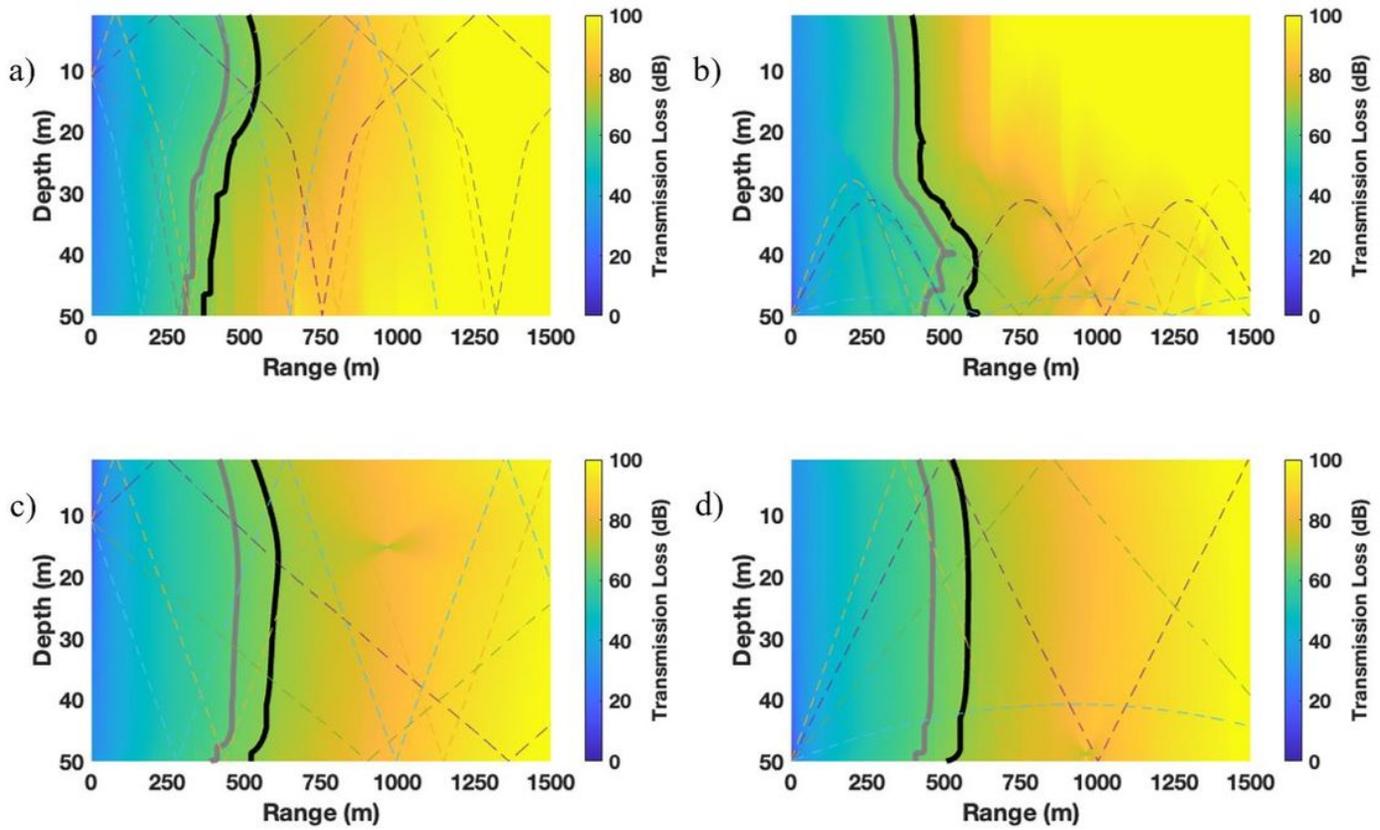


Figure 6

Range test of detection efficiency categorized by sound speed difference (SSD) indicating the effect of thermal stratification to a) V9 transmitter sitting at 11 m depth, b) V9 transmitter sitting at 50 m depth, c) V16 transmitter sitting at 11 m depth, and d) V16 transmitter sitting at 50 m depth.



**Figure 7**

Bellhop model predicts transmission loss and ray propagation on a) DOY 250 (summer stratified conditions) with transmitter sitting at 11 m, b) DOY 250 with transmitter sitting at 50 m, c) DOY 300 (fall isothermal conditions) with transmitter sitting at 11 m, and d) DOY 300 with transmitter sitting at 50 m. Two thresholds of transmission loss of 63 dB and 68 dB are indicated with grey line and black line, respectively. The faint dashed lines are representative acoustic rays used in the model.