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Integrating hydroacoustic and telemetric surveys to estimate fish abundance: a new approach to an old problem

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Abstract

Population abundance is a critical metric in fisheries and conservation, but it is very difficult to measure accurately. Existing estimation methods present significant challenges: mark–recapture methods are time- and labour-intensive, and hydroacoustic echo counting methods face issues with target identity and the habitat types where they can be effectively applied. We present a new methodology for abundance estimation that can improve the reliability of echo counting methods. Split beam hydroacoustic survey data are integrated with telemetry data from fish bearing acoustic transponder tags. These tags are counted by a spatially and temporally concurrent multibeam acoustic survey to produce mark–recapture abundance estimates. We assessed this approach on four wild lake trout populations, ranging in abundance from ∼200 to ∼3000 adults. Our abundance estimates were consistent with those derived from conventional Schnabel and Jolly–Seber mark–recapture studies. We show that the precision achievable with this method in 1 year of field work rivals that provided by long-term (>10 years) continuous mark–recapture studies. We also discuss other ecological questions that could be addressed with this approach.

Key words: estimating abundance, hydroacoustics, acoustic telemetry, mark–recapture, multibeam sonar

Introduction

> "Managing fisheries is hard: it's like managing a forest, in which the trees are invisible and keep moving around" —John Shepherd

Sustainable fisheries management requires the resource manager to ensure that some critical number of spawners (and/or amount of adult biomass) remains in the population after exploitation to ensure the relative stability of future population abundance. This demand has generated a vast amount of literature in fisheries science, much of it focused on how to estimate "sustainable" harvest as a fraction of existing population abundance, where knowledge of existing abundance is assumed. However, despite its importance in sustainable management efforts, estimating population abundance directly is challenging since fish populations are effectively invisible and hence difficult to count directly.

A common indirect approach for estimating abundance is based on the recapture of marked fish using passive sampling methods: the mark–recapture (MR) approach (see Schwartz and Arnason 1996; White and Burnham 1999; Amstrup et al. 2005 for details). Here, both capture and recapture sampling events typically rely on fish encountering sampling gear set at fixed locations. However, both methodological and logistical challenges can make this approach difficult to implement effectively. Some of the more critical methodological issues are as follows: (i) marked fish must mix completely with the overall population in the time interval between the marking sample and the recapture sample; (ii) the fraction of marked fish lost to either mortality or mark shedding over this interval must be known; (iii) on recapture, marked fish and unmarked fish must be equally catchable; and (iv) gear avoidance or gear attractance by marked fish must be accounted for. These methodological challenges are best addressed by (i) developing extensive background knowledge on the spatial behaviour of the population so that MR sampling can be focused at the times and places (typically spawning sites) where the adult population aggregates and hence mixing of marked fish with the rest of the adult population is naturally promoted; and (ii) maintaining an MR sampling program over several sampling periods so that advanced statistical models can be used to estimate both tag loss rates and the degree of recapture bias, thus permitting corrections for these potential biases to be included in the resultant time series of abundance estimates.

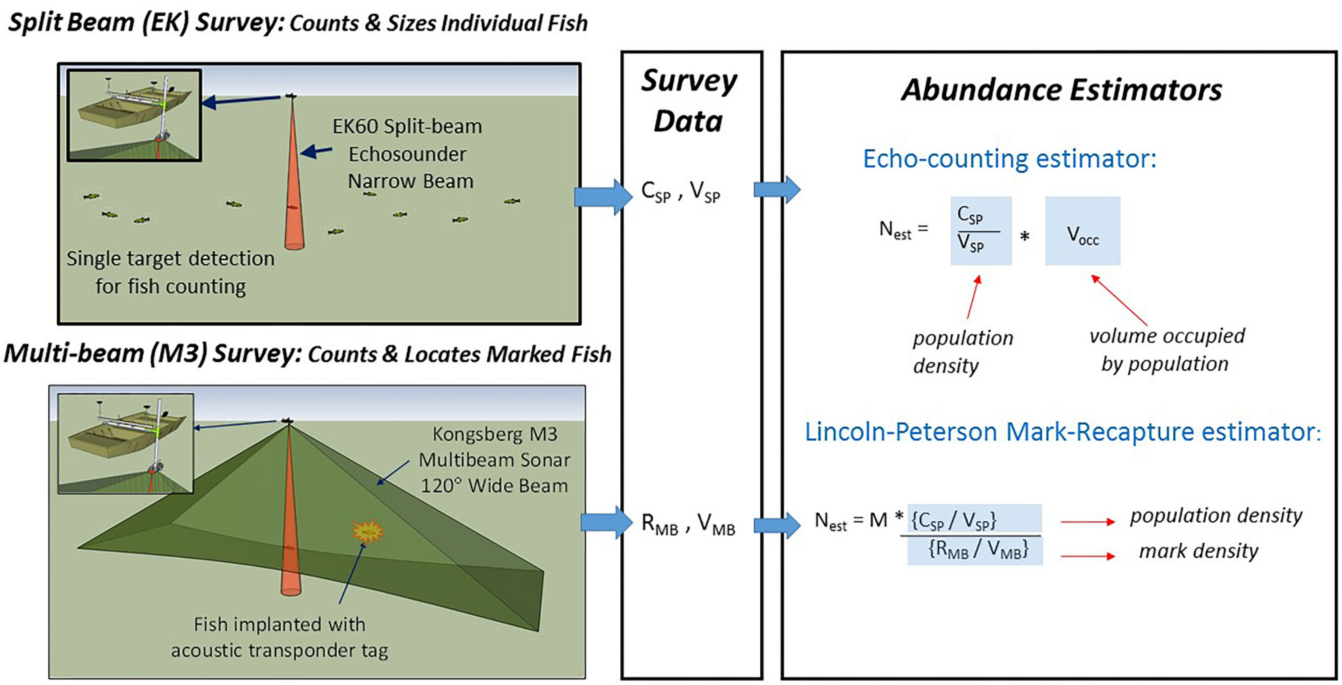
Some of the more critical logistical issues inherent in the MR approach include the following: (i) training and mobilizing a field crew of several individuals competent to handle the specialized gear used for safely and humanely capturing fish; (ii) training the crew in the specialized methods for handling marked fish to ensure marks are applied appropriately and that marked individuals will survive the handling procedure—additionally, these methods can require both government permitting for scientific collection and approval from animal care committees, each operating at different levels of institutional organization; (iii) historical sampling of significant duration is desirable to ensure reasonable levels of mixing between marked and unmarked individuals and to provide the direct estimates of tag loss rate and recapture bias that ensure reliability of current abundance estimates; and (iv) these methods can be difficult to apply accurately for large exploited populations where tag loss rates to the fishery may go unreported.

Since the 1950s, acoustic methods have been used to estimate population abundance directly using counts of fish from mobile transceivers (Simmons and MacLennan 2005; Rudstam et al. 2009; Gutierrez-Estrada et al. 2022). This method has significant advantages over MR methods from an animal welfare perspective as it does not require the direct handling of fish (nor the associated permitting required to do so). However, existing single frequency split-beam approaches are incapable of identifying targets beyond a simple size estimate based on echo strength (Simmonds and MacLennan 2005). As such, parallel direct collections of fish in the acoustic sample space (i.e., with net and/or trawl sampling) are typically required to determine species identity based on both the size and species distributions found in these "companion" samples. Further, with traditional acoustic methods (i.e., downlooking mobile surveys from vessels), the acoustic sample space excludes that part of the water column within ~2 m of the transducer face and within ~1 m of the lake bottom (Ona and Mitson 1996; Simmonds and MacLennan 2005). These limitations prevent its effective use in near-surface waters and in shallow waters generally. In addition, vessel avoidance can occur (e.g., Grow et al. 2020), leading to the underestimation of abundance. These shortcomings can limit the effectiveness of the method in some situations (Diner 2007; de Kerckhove et al. 2016; Wheeland and Rose 2016). In addition, the validity of the abundance estimator used in this approach depends on the validity of two critical assumptions: (i) that the population density in the acoustic sample is representative of the density throughout the unobserved portion of the population's habitat; and (ii) that the overall habitat volume occupied by the population at the time of the survey is known.

A significant advance in methods for abundance estimation can be achieved by combining conventional hydroacoustic echo counting with concurrent acoustic telemetry, where individuals from the population of interest are captured and implanted with transponder tags (Fig. 1). These tags are then "recaptured" during subsequent hydroacoustic surveys, where they are activated, identified, and counted by specialized hydroacoustic equipment. The MR estimator can then be applied directly to the survey data. Achieving this integration of technologies brings many advantages: (i) the validity of the resultant estimator no longer requires a priori knowledge of size of the habitat space occupied by the population, or direct estimation of that space; (ii) the validity of the estimator no longer requires that population density be similar both inside and outside the survey sample space; (iii) recapture sampling does not involve direct contact with marked or unmarked fish, thus minimizing the survey's impact on the population and eliminating concerns about mark avoidance of (or attractance to) the sampling gear; and (iv) the number of viable marks available immediately prior to each recapture sample can be estimated directly, eliminating the need to estimate tag loss rates. In addition, concurrent location telemetry from individuals belonging to the focal species and individuals of similar size belonging to other species can be used to (i) optimize the timing of acoustic sampling so that individuals of the focal species are plentiful in the sample volume; and (ii) information on the relative size and abundance of non-focal individuals in the sample space can be used to filter the total number of acoustic targets counted so that it includes only individuals belonging to the focal species. In principle, such a method minimizes the need for relatively extensive prior sampling of the population and offers the promise that levels of accuracy can be achieved in unstudied systems that approach those observed in well-studied systems where all the refinements provided to estimators based on fully parameterized advanced MR models (e.g., Jolly–Seber models) are in force.

In this paper, we describe and evaluate a new method that seeks to provide this integration of telemetric and hydroacoustic information, and thus overcome many of the limitations inherent in conventional methods of abundance estimation. This approach—the hydroacoustic transponder tag (HTT) approach—relies on integrating acoustic target count data from a "traditional" acoustic survey with concurrent information on the location and identity of acoustically tagged fish located in the survey search volume (Fig. 1). The method relies on the use of an acoustic transponder tag that (i) can be implanted in (or on) the body of the fish; (ii) broadcasts a unique, coded acoustic signal when activated by a ship-based acoustic activator; and (iii) can be identified and located in all three dimensions by a wide-swath multibeam echosounder system. The wide-swath, multibeam system is used to detect and count acoustically tagged fish in a known volume of water. A narrow, split-beam scientific echosounder is also used to count fish targets of similar size to those of the tagged fish, also in a known volume of water. We demonstrate that by collecting and integrating these two data streams in parallel (Fig. 1), we are able to generate an abundance estimate based on MR principles that can be easily compared with that obtained by echo counting. In this paper, we describe the method in detail and give results from extensive field trials of the method on four natural populations of lake trout (*Salvelinus namaycush*) with "known" abundance (as estimated using conventional MR methods) varying by over 1 order of magnitude (~200 to ~3000 individuals).

Fig. 1. Acoustic survey data and their application to estimating population abundance. The schematics illustrate how the split and multibeam sounders are mounted on the survey vessel and their respective roles in counting unmarked and marked population members during the survey. The "survey data" box identifies the survey data needed to estimate population abundance: C_{SP} and V_{SP} = the count of population members and the search volume, respectively, of the split beam sounder; R_{MB} and V_{MB} = the count of marked population members and the search volume, respectively, of the multibeam sounder. The "abundance estimators" box summarizes two methods for estimating the abundance of a population (N_{est}) from these survey data. The simpler echo counting method just relies on data from the split beam survey. In addition, it requires a priori knowledge of the total habitat volume (V_{occ}) occupied by the population. The mark–recapture estimator requires data from both surveys. Here, we adopt the familiar notation of Lincoln–Peterson, where M is the number of marked population members (i.e., the number carrying transponder tags) alive at the time of the recapture survey, the overall density of population members in the volume searched by the split beam component of the recapture survey is given by C_{SP}/V_{SP} and the overall density of marked members of the population in the volume searched by the multibeam component of the recapture survey is given by R_{MB}/V_{MB}. The Lincoln–Peterson estimator requires that the proportion of marked individuals in the survey volume be the same as that found throughout the population's habitat (i.e., V_{occ}). The accuracy of the echo counting estimator holds over a narrower range of situations than that of the Lincoln–Peterson estimator because it requires a priori knowledge of V_{occ} and it hinges on the more restrictive assumption that population density in the survey volume is the same as that found throughout V_{occ}.



Methods

Hydroacoustic studies

The development of the HTT system was a progressive process extending over 5 years of system testing and refinement. The final optimal design was completed in time for our 2017 field work and provides concurrent real-time data on (i) the identity and 3-D location of transponder tags in the survey search volume; (ii) the number of acoustic targets in the survey search volume; and (iii) the size distribution of those acoustic targets as reflected in the target strength frequency distribution. In surveys undertaken prior to 2017, the gaps in data resulting from our partially developed system were filled in as follows: (i) data on the spatial distribution of focal species was provided by concurrent and independent telemetry studies carried out in our IISD-ELA study lakes and (ii) reduced fish detection rates in 2013 and 2014 were amended using empirically determined correction factors. Details of the development process and specifics on how we dealt with data gaps in earlier surveys are provided in Supplement A.

1. Population estimators based on hydroacoustic surveys

General concepts

The absolute abundance of a population (N) can be estimated by counting the number (C) of population members in a sample space of known volume (V_{samp}) and then scaling that number up to include the whole population, using an estimate of the habitat volume occupied by the entire population (V_{occ}):

$$\widehat{N} = (C/V_{samp}) * (V_{occ}) \tag{1}$$

The accuracy of this estimate is dependent on (i) accurate knowledge of V_{occ} and (ii) validity of the assumption that the population density throughout the population's habitat is constant and identical to the density (C/V_{samp}) observed in the sample volume.

When scaling an abundance estimate beyond that observed in the sample volume, the MR approach to population estimation provides an estimate that holds over a wider range of biological situations than the counting approach. Given that marking does not affect the spatial behaviour of the individual, there should be no spatial variation in the fraction of the population that is marked, despite the likely spatial variation in local population density. Therefore, the following equation will hold:

$$[N/V_{occ}]/[M/V_{occ}] = \left[C/V_{samp}\right] / \left[R/V_{samp}\right]$$

where M is the number of marked individuals alive in the population at the time of sampling and R is the number of marked individuals counted in the sample space. V_{occ} cancels out, and rearrangement of the terms leads naturally to:

$$\text{(2)} \qquad \widehat{N} = \left[M * C/V_{samp}\right] / \left[R/V_{samp}\right]$$

which is essentially the simple Lincoln–Peterson population estimator (Amstrup et al. 2005). This estimator does not require knowledge of V_{occ} and it holds even if local population density ($\sim C/V_{samp}$) varies substantially across the habitat volume occupied by the population.

Translating these general MR equations into versions that match the specific characteristics of downlooking hydroacoustic surveys in limnetic environments requires that part of the focal population occupies that portion of the water column that is searchable by the hydroacoustic system in use. This searchable space typically starts ∼2 m below the surface and ends ∼1 m above the bottom (Ona and Mtson 1996; Simmonds and Maclennan 2005). If most of the population is located in this searchable space, then the real spatial distribution of the population comes close to matching the assumptions inherent in the counting estimator. In this situation, the reliability of an echo counting abundance estimate will approach that of the MR estimate. If a significant portion of the population is located outside the searchable space, then the MR estimate will be more reliable than the echo counting estimate.

The echo-counting abundance estimator

Count data from a split beam echosounder (the SP) are used to derive an abundance estimate for a focal population using a simple version (Fig. 1) of eq. 1:

$$\text{(3)} \qquad \widehat{N} = (C_{SP}/V_{SP})^{*}V_{occ}$$

where C_{SP} is the number of individuals belonging to the focal population counted in the split beam echosounder search volume, and V_{SP} is the search volume of the split beam echosounder. The overall count of fish in the V_{SP} is filtered to include just those individuals belonging to the focal population using (i) a priori information on the body size range of individuals belonging to the focal population; and (ii) direct information on the temperatures and depths occupied by marked individuals belonging to the focal population, ideally backed up by a priori information on preferences typical of the species.

The hydroacoustic transponder tag abundance estimator

A survey with the HTT system involves a simultaneous search (Fig. 1) of the survey space by (i) a split beam echosounder that counts all acoustic targets from the focal population in its relatively small sample volume; and (ii) a multibeam echosounder (the MB) that just counts the number of population members carrying transponder tags (i.e., the "marked" individuals) in its much larger sample volume. This leads to the following version of eq. 2 (Fig. 1):

$$\text{(4)} \qquad N = [M * C_{SP}/V_{SP}] / [R_{MB}/V_{MB}]$$

where R_{MB} is the number of focal individuals marked with transponder tags and counted in the multibeam search volume and V_{MB} is the search volume of the multibeam echosounder. Here, the larger search volume provided by the multibeam sounder compensates for the relatively small number of marked fish in the focal population. Ideally, this larger sample volume ensures the two density estimates have similar precision.

Normal statistics can then be applied to the output of multiple independent surveys carried out over a short time period to provide both an overall estimate of N and an estimate of inter-survey variability. This estimate of inter-survey variability then provides an estimate of the precision of the overall estimate of N. In conventional MR applications, the recapture count is a subset of the capture count, and hence R/V must be $<C/V$. In the HTT application, these two counts are independent of each other, and hence it is possible that R/V could exceed C/V. This is an unlikely occurrence, given that R is typically a small percentage of N; however, the possibility would be accommodated as just one more component in all the other sources of variation contributing to the observed between-survey variation in estimates of N.

In situations where individuals from non-focal populations are similar in size and share the same acoustic search space as individuals from the focal population, additional transponder tags could be applied to individuals from those non-focal populations, and their appearance in the shared search space could be used to inform the degree to which the total targets in the search space belong to the focal population. This mirrors the kind of information provided by companion netting in traditional acoustic surveys without the need to directly handle fish during the survey. Of course, some fish must be handled during the initial tagging phase of an HTT study, but no additional handling is required during the abundance estimation surveys that follow.

2. The hydroacoustic transponder tag abundance estimator

Acoustic transponder tags

The optimal tag design, as implemented in our 2017 surveys, was developed by Sonotronics Inc. (Tucson, AZ; model XP-500-91) and had the following specifications: length

55 mm; diameter 11.6 mm; weight in air 10 g; and weight in water 5 g. When activated, this tag would emit one identification signal and then return to "sleep" mode. The ID signal consisted of a 500 kHz unique pulse pattern, or pulse train; each unique pulse train included 3 or 4 pulses of 1 to 2.5 ms duration, with 0.5 to 5 ms spacing, for a total pulse train duration of 10, 13, or 15 ms. By generating a single ID pulse on activation, the receiving system could accurately estimate the time interval between the release of the activation signal and its receipt by the transponder tag. With this information in hand, the system could then estimate the position of the tag in the water column. The ID transmission pulse was broadcast after a fixed delay of 30–35 ms (with 10% variation) after activation. The tag then entered "sleep" mode for 120–150 ms before it was again open for activation. The ability of these acoustic transponder tags to remain quiet for long periods of time between activation events gives them the potential for a very long battery life (4+ years), allowing the user to monitor individual fish using this activation system over multiple years.

Transponder tag activator

The optimal activator design was embodied in the Kongsberg-Mesotech M3-Tag Activator Transducer Array (the M3-TATA). This device was designed to optimize power density by constraining acoustic directivity within a swath width of 30° to 140°. The high-power sonar system generated a measured source level (SL) of >200 dB referenced to 1 microPascal at 1 m at 200 kHz. The beam pattern of the M3-TATA hardware is similar to the ideal beam pattern of the tag detector system—the Kongsberg Mesotech M3-MBES. The M3-TATA and the M3-MBES were both fixed to the same support plate. The support plate was attached to the survey vessel via a vertically mounted pole. A spirit level was affixed to the top of the pole mount to ensure the transducer face remained parallel to the lake surface. A short length of aircraft cable attached to the foot of the transducer pole was extended to the bow to stabilize and reduce transducer movement when under survey. Figure 2 shows the relative positioning of these two components on their supporting plates and the orientation of the supporting plate during a survey.

Transponder tag detector system

Multibeam swath bathymetry and acoustic tag detection data were recorded using the Kongsberg Mesotech 500 kHz M3-MBES (see Supplement A for M3-MBES operational details). In addition, the tag activator (the M3-TATA) was synchronized to operate with the M3-MBES. This system has a nominal operating frequency of 500 kHz with a 100 kHz bandwidth. Acoustic pulses are generated on independent transmitters ("profiling" and "imaging" modes) and received on a 64-element array. The range (or depth) resolution is better than 2.0 cm. Ideal detection efficiency was achieved by using the profiling mode. In standard profiling mode, the associated signal processing software forms a 120° swath image (in azimuth) of the water column, formed by 256 receive beams, each with an apparent beamwidth of <1.6° × 3°. Real-time GPS data strings were provided to the M3-MBES system from a Hemisphere VS110 differential GPS system (with true heading). Raw beam-formed data were recorded in the Kongsberg *.mmb file format. In postprocessing, all raw *.mmb data were converted to the beam-formed *.imb file formats using the M3 sonar convertor software application (versions MUM 1.3, MUM 1.42 A3, MUM_V0162, and M3_V0201).

Overall search volume for a typical M3-MBES system survey was estimated (Fig. 3) by overlaying the potential search volume (as determined by the transect density and multibeam ping rate) onto a spatial model of the lake bathymetry and then removing from the potential search volume (i) the volume below the bottom of the lake and (ii) the volume outside the estimated occupancy space for the focal species (i.e., lake trout in our study systems).

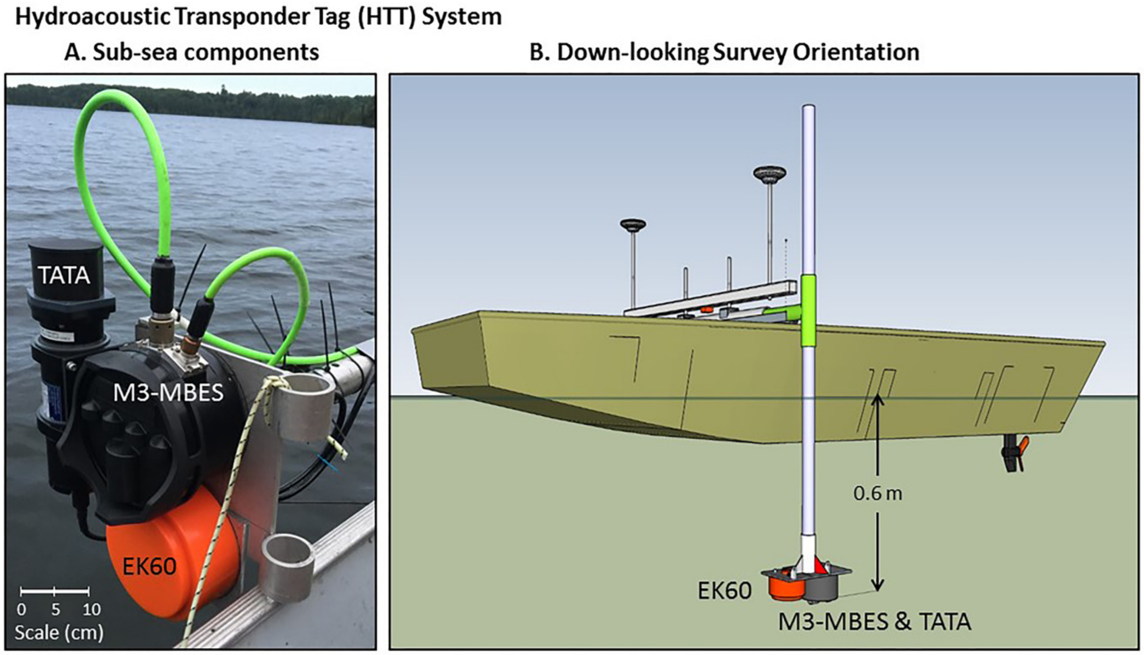
3. Split beam hydroacoustic system

Quantitative fisheries echosounder data were collected from 2013 through 2017 using a Simrad EK60 120 kHz split-beam echosounder system (see Supplement A for operational details). The EK60 transducer was mounted on the same supporting plate as the M3-TATA and the M3-MBES (see Fig. 2). The EK60 can accurately measure the acoustic backscatter (the target strength (TS)) of an individual fish (a single target (ST)) located in its detection beam. The TS is a measure of the beam-compensated echo strength from an ST and provides information about the size of the ensonified fish. Generally, larger fish have stronger echoes (Love 1971*a*, 1971*b*). We used the "fish track" (FT) detection function within Echoview to group STs that were likely detected from the same fish. An FT is a region defined by Echoview that clusters one or more single targets together into a single fish detection (see Supplement A).

The calibration of the Simrad EK60 120 kHz echo-sounder and ES120-7 C transducer was completed annually, immediately following the completion of the surveys for the year. Calibration was completed using a standard 23 mm copper calibration sphere. The Simrad EK60 transducer TS Gain applied within each year ranged between 25.91 and 26.24 dB and the S_a correction factor ranged between −0.61 and −0.54 dB. The calibrated circular 3 dB beam angle (major and minor axes) ranged between 6.35° and 6.44° and the calibrated angular offsets varied by 0.07°. In the first years of our study, manual data screening of FTs was undertaken to ensure that noise spikes from the M3-MBES were not mistaken for FTs. In the final year of our study, this step was not needed because the version of the HTT system implemented in that year had been redesigned to multiplex with the EK60, eliminating the possibility of cross-talk between the EK60 and the M3-MBES.

All hydroacoustic data were processed using Echoview (Echoview Software Pty. Ltd., versions 6.1.65.27984 to 8.0.97.32257) processing software. Raw ST detection data and measured TS (in dB) values were processed using the "Single Target Detect (Method 2) Operator" variable in Echoview. As noted earlier, we used the "FT" detection function within Echoview to group STs that were likely detected from the same fish. A fish density estimate was calculated by standardizing the total number of "FT" detections by the sample

Fig. 2. (A) Photograph of the HTT subsea acoustic components: the Kongsberg-Mesotech Ltd. 500 kHz M3 multibeam echosounder system (M3-MBES), the Kongsberg-Mesotech Ltd. M3-Tag Activator Transducer Array (TATA), and the Kongsberg Simrad EK60 120 kHz split-beam echosounder (EK60) on their aluminum support plate. (B) Illustration of how the support plate was attached and oriented to the small survey vessel during each survey.



volume of the acoustic beam. We calculated the total uncorrected volume (m^3) for each 1 m depth layer as follows:

$$\begin{aligned}\text{Volume}_u = &((\text{Tan}([\text{BeamWidth}]/2)^*([\text{Layer}]-[\text{OffSet}]))\\ &^*([\text{Layer}]-[\text{OffSet}])^*[\text{Dist}]) - ((\text{Tan}([\text{BeamWidth}]/2)\\ &^*([\text{Layer}]-1\text{m}-[\text{OffSet}]))^*([\text{Layer}]-1\text{m}-[\text{OffSet}])^*[\text{Dist}])\end{aligned}$$

where Layer is the maximum depth of a 1 m depth layer, BeamWidth is the angle (°) between the half-power points of the calibrated beam pattern, OffSet is a correction to account for the depth of the transducer (0.6 m), and Dist is the length of the elementary distance sampling unit (EDSU) in meters (~50 m).

The total beam area and volume at depth were estimated by summing all EDSUs along transects within the survey space. For those EDSU's that intercepted the lake bottom (or other "bad data" regions), we calculated the proportion of "valid" S_v samples (where S_v is the summation of the acoustic backscattering from all targets within a sampling volume scaled to 1 m^3 and expressed in dB units) from the observed number of S_v samples within the cell divided by the maximum possible number of S_v samples within a cell. We then calculated the corrected sampling volume (m^3) by multiplying the proportion of valid S_v samples observed within the cell by the overall volume of the cell. The total volume of lake trout habitat sampled by the EK60 for each lake and year was estimated by truncating the total EK60 sample volume for each survey to include just those depths defined by the minimum and maximum "FT" depth occupancy boundaries used to define lake trout habitat.

4. Survey design

Lake size (Table 1) was used as a rough guide to determine the number of transponder tags used in this study, with the largest lake receiving twice the number used in the smaller lakes (Table 2). We marked between 2% and 10% of the adults in each population based on conventional abundance estimates (Table 1). At the beginning of each annual survey cycle, the number of active tags in each lake was determined through a comprehensive lake-wide search with the M3-MBES and M3-TATA systems (Table 2).

For each lake, a set of linear transects was defined to provide systematic coverage of the pelagic zone. The distance between transects was set such that the search volume for the EK60 split-beam unit would cover a substantial portion of the total lake volume (0.4% to 1.6%; Table 3). Search volumes for the M3 multibeam sonar system were much greater (15% to 57% of total lake volume; Table 3). Each survey was carried out at mid-day (typically noon to 6 pm) during mid-summer. Each lake was surveyed several times in a single summer (Table 3). The same start and end points were used for each survey. An open-hulled 4.9 m aluminum vessel was used for all surveys. Ideally, operating noise should be minimized by using a low-noise electric motor for propulsion, with deep-cycle lithium batteries as a power source. Some of our 2017 surveys met this requirement using a 3 hp Torqeedo Travel 1003 C electric motor. In earlier years, a gas motor and gas generator were used and found to lead to significant vessel avoidance by our target species. Successive comparisons of measured fish density using gas vs electric power were used to quantify this

Fig. 3. Steps involved in estimating the volume of preferred habitat "searched" in a typical multibeam survey of Lake 224. (i) Generate the potential search volume for the survey: shown is the maximum sample wedge volume of the M3-MBES for 15 transects. Each transect is generated from overlapping contiguous "pings" (or receiver pulse volumes), where each ping volume is based on a swath of 120° × 30° and a vertical "height" = [maximum depth of the lake − depth of the transducer face]. The volumes for all individual pings are combined to generate a 3D solid model of the overall potential M3-MBES search volume. (ii) Generate a 3D model of the entire bathymetry of the surveyed lake. (iii) Overlay the bathymetry model on the potential search volume model and estimate the actual sonar search volume by clipping the 3D search volume with the 3D bathymetry model to exclude the volume below the lake bottom. (iv) Reduce the actual search volume to the search volume occupied by lake trout by further truncating the actual search volume model at both the observed minimum and maximum occupancy depths for lake trout. In the figure, the volume above the white horizontal surface represents depths shallower than the minimum occupancy depth and therefore has been removed from the estimate of the search volume occupied by lake trout. Similarly, the volume associated with depths greater than the maximum occupancy depth has also been removed.

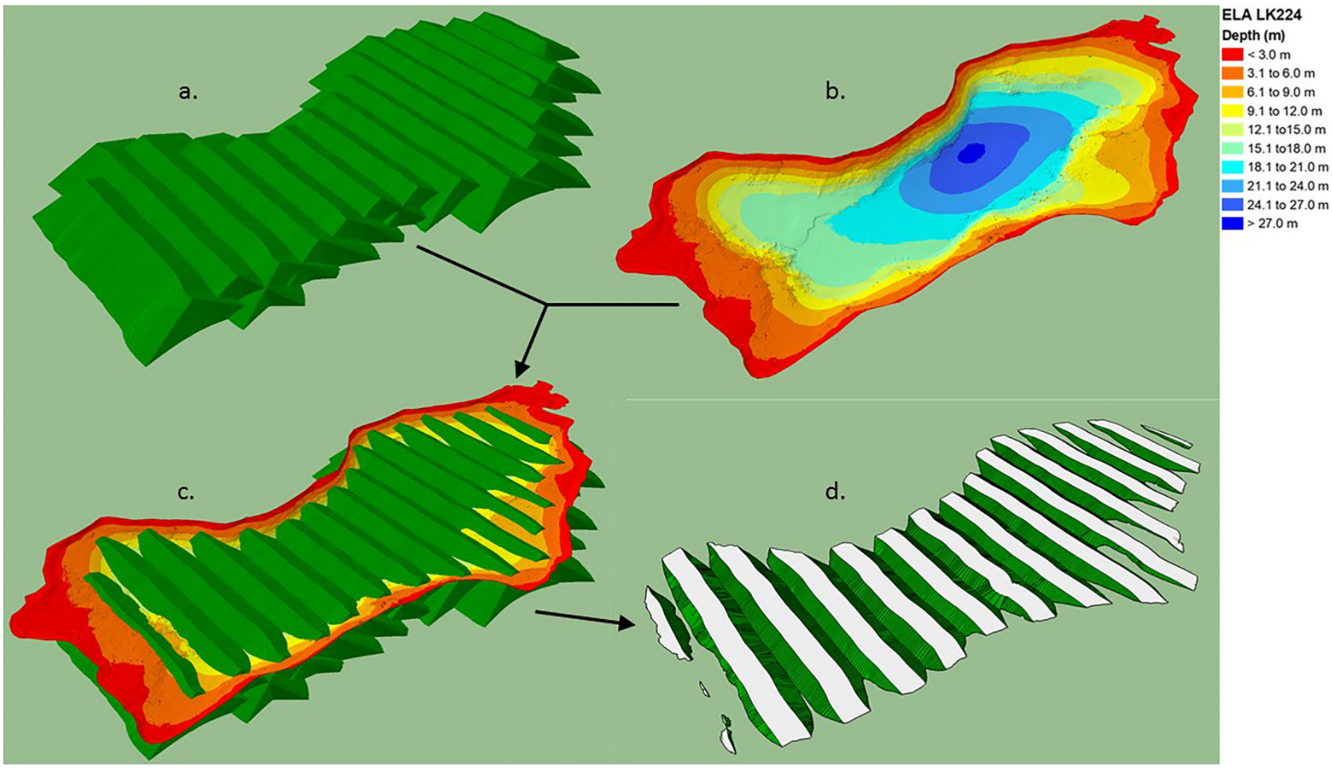


Table 1. Background information on study lakes and their lake trout populations.

Lake	Location (Lat, Long)	Lake area (km^2)	Lake mean depth (m)	Lake trout size at maturity (total length mm)	Lake trout instantaneous annual mortality rate		Lake trout abundance estimate with 95% confidence bounds (LB–estimate–UB)	
					Period	Mortality (std. error)	Period	Abundance
IISD-ELA 373	49° 44′; −93° 48’	0.27	10.7	437	2013–17	0.175	2013	247–286-330
						(0.011)	2014	228–262–300
							2015	244–287–339
IISD-ELA 626	49° 45′; −93° 48’	0.28	7.3	426	2013–17	0.147	2014	235–272–316
						(0.012)	2015	213–262–283
IISD-ELA 224	49° 41′; −93° 43′	0.26	12.7	407	2013–17	0.119	2016	261–289–320
						(0.009)	2005–2014	256–283–314
Squeers	48° 31′; −90° 33′	3.8	11.5	424	2005–14	0.476	2017	3669–4851–6034
						(0.019)	2017	1948–3630–7324

Note: Three of our study lakes are part of the IISD Experimental Lakes Area (IISD-ELA) located in northwestern Ontario Canada. The fourth lake is also located in Ontario, approximately 300 km east of the IISD-ELA lakes. See Supplement C for methods used to estimate mortality and abundance in all four lakes. IISD-ELA abundance estimates are derived by fitting a Jolly–Seber model to long-term (~20 years) mark–recapture data. The Squeers abundance estimate for 2017, our study year, is a Schnabel estimate based on a single year of mark recapture data. The abundance estimates for the historical period (2005–2014) are based on annual harvest data from an intensively monitored angling fishery (Supplement C).

Table 2. Size and number of new transponder tags implanted in lake trout in each lake and year.

Lake	Year	Number of tags implanted	Mean total length (mm) of newly implanted fish	Range for total length (mm)	Number of tags active at time of survey
373	2013	23*	456	411–495	22
	2014	9	462	416–501	12
	2015	0	–	–	4
626	2014	30	465	403–527	29
	2015	0	–	–	4
224	2016	30	440	389–486	28
	2017	0	–	–	12
Squeers	2017	63	517	385–935	62

*n = 15 XP-500-91 tags and n = 8 IBT-96-9-500 kHz tags.

Table 3. Daytime (∼10 am to ∼4 pm) acoustic surveys used for abundance estimation.

Lake	Year	Number of daily surveys	Total lake volume (m^3)	Total habitat volume (m^3)	% Lake volume sampled		% Habitat volume sampled	
					EK60	*M3*	*EK60*	*M3*
373	2013	5 (July 19–20)	2.437×10^6	1.488×10^6	1.4	56.6	2.2	92.8
	2014	4 (Aug 8–10)	2.437×10^6	1.739×10^6	1.6	47.3	2.2	66.3
	2015	6 (Aug 17–18)	2.437×10^6	1.027×10^6	0.9	34.9	2.1	82.8
626	2014	2 (Aug 6 -7)	1.428×10^6	0.617×10^6	0.7	23.4	1.6	54.1
	2015	6 (Aug 15–16)	1.428×10^6	0.642×10^6	0.7	24.1	1.6	53.6
224	2016	9 (Aug 8–9)	2.489×10^6	1.445×10^6	1.3	41.6	2.2	71.6
	2017	10 (Aug 3–5)	2.489×10^6	1.654×10^6	1.6	49.8	2.4	74.9
Squeers	2017	4 (July 26–27)	43.921×10^6	28.526×10^6	0.4	15.2	0.7	23.4

Note: The habitat volume is the volume of water lying between the minimum and maximum observed depths of lake trout targets in each year of the survey. The total search volumes of the EK60 and M3 sonar systems are given as the percentage of total lake volume searched and the percentage of total habitat volume searched.

avoidance effect and develop an empirical correction factors for it—See Supplement A for details.

5. Identifying the target population

We used a series of temporal, spatial, and biological criteria to focus our survey design, and filter our resultant data, so that lake trout FTs could be effectively isolated from all other FTs potentially detectable by the EK60 system. Known thermal and spatial habitat preferences for each of the large fish species found in our study lakes (Table 4) were used to select the season and time of day for our surveys. Size and depth filters were used to isolate lake trout FTs from all the FTs identified by the EK60 system in a particular survey. In 2017, we were able to confirm the validity of this procedure by comparing the depth distribution of lake trout carrying transponder tags with the depth distribution of FTs identified as lake trout by our size and depth filters.

Filtering by size

The relationship between lake trout length and TS has been independently determined (Middel 2005—Supplement B) and closely follows the general relationship given by Love (1971*a*, 1971*b*) and Hartman et al. (2000). For all four study lakes, conventional lake trout abundance estimates were focused on individuals with total lengths ≥300 mm. We used the TS value equivalent to this total length (−35.6 dB) as a size filter and removed all FTs with mean TS values less than this from our EK60 target density estimates.

Filtering by habitat preference

Lake trout typically spawn on shallow rocky substrates in the autumn and adults are expected to be concentrated in these habitats at this time (Scott and Crossman 1973). In contrast, during summer in stratified lakes, several field studies have shown that lake trout are typically concentrated in the pelagic zone, at depths below the thermocline, and typically at temperatures near their preferred temperature of ∼ 10–12 °C (Plumb and Blanchfield 2009; Hasnain et al. 2018; Cruz-Font et al. 2019). Of the larger fish species (i.e., white sucker, northern pike, and burbot) resident in our study lakes, only white sucker are known to be abundant. However, the preferred temperature for white sucker (∼24 °C—Hasnain et al. 2018) is much higher than that for lake trout, and hence it would be expected to avoid the depths preferred by lake trout in summer. A similar expectation holds for the much less abundant northern pike (preferred temperature: ∼21 °C—Hasnain et al. 2018). Burbot is the exception, with a preferred temperature (13 °C) that is just moderately higher than that of lake trout. However, burbot are nocturnal and typically inactive and benthically oriented during the day, and therefore should be spatially isolated from the metalimnetic habitat expected for lake trout in the daytime during the summer.

Table 4. Habitat preferences of lake trout in each study lake and of other species that are present and could exceed the hydroacoustic size threshold of 300 mm total length.

Species	Present in lakes	Preferred temperature	Known habitat preferences	Midwater pelagic occurrence
Lake trout	373, 626, 224, Squeers	11.8	*Spring:* littoral and pelagic areas; *summer:* pelagic areas; *fall:* inshore spawning sites	Concentrated: summer, day and night
Burbot (*Lota lota*)	Squeers	13.2	*All seasons:* benthic oriented and nocturnal; *winter:* season of greatest activity *summer:* restricted to deeper waters; inactive and benthic in the day, active in the water column at night	Occasional: summer, night
White sucker (*Catostomus commersonii*)	373, 626, 224, Squeers	23.4	*Spring through fall:* benthic oriented and diurnal	Rare: typically found in shallow warm waters in summer
Northern pike (*Esox lucius*)	Squeers	20.7	*Spring through fall:* shallow, littoral, and vegetated areas; large adults seek habitat structures that provide the cover necessary for sit-and-wait predation	Rare: typically found in shallow warm waters in summer

Note: All study lakes stratify in summer with epilimnetic temperatures that exceed 20 °C (e.g., Cruz-Font et al. 2019); hence, "expected midwater pelagic presence" is evaluated assuming that epilimnetic waters are avoided/selected by a species when epilimnetic temperatures are greater than/less than the preferred temperature of that species. The final column gives the period (season, time of day) when each species is expected to be concentrated in the portion of lake habitat (the midwater pelagic) that can be efficiently surveyed acoustically. Sources: preferred temperature—Hasnain et al. (2018); habitat preference: lake trout—Muir et al. (2021); burbot—Harrison et al. (2016); white sucker—Scott and Crossman (1973); northern pike—Pierce (2012).

Field studies

We tested our method on four natural populations of lake trout with known adult population sizes ranging from ∼200 to ∼4000 individuals (Table 1). We chose lake trout as the focal species for this study because extensive information exists on lake trout habitat preference (Table 4), typical adult sizes (Lester et al. 2021) and hydroacoustic target strength (Supplement B). Our study populations were chosen because extensive background knowledge was available for each population on (i) lake habitat; (ii) current abundance and mortality rate; (iii) individual sizes and habitat usage; and (iv) fish community composition (Tables 1 and 4, Supplement C). All four populations have been the subject of annual MR abundance surveys for over 20 years. For each population, local knowledge of spawning aggregation sites was used to establish mark and recapture survey areas that met the marked/unmarked mixing requirements of the MR method. In addition, the yearly data collection cycle in the 3 IISD-ELA lakes permitted the application of full Jolly–Seber models, where direct estimates of the annual mortality rate and tag loss rate were embodied in the resultant annual population abundance estimates.

1. Fish capture and application of acoustic tags

IISD-ELA lake trout and white sucker (*Catostomus commersoni*) were captured in the spring using a combination of trap netting and angling. Spring captures ensured that fish could be caught near the surface, typically while surface temperatures were below 11 °C (see Rennie et al. 2019 for more detail). Captured fish were returned to shore immediately and lightly anesthetized in a solution of tricaine methanesulfonate (TMS), buffered with sodium bicarbonate for approximately 2–3 min. Once anaesthetized, fish were measured for length in millimetres (mm), weighed in grams (g), and received a passive integrated transponder tag (Biomark, Inc.) in the dorsal musculature below the dorsal fin and above the lateral line. Fish were then placed dorsal-side down in a wet, padded trough with a maintenance concentration (45 mg·L^{-1}) of buffered TMS running through their gills. Each fish then underwent surgery to implant an acoustic transponder tag in its abdominal cavity, with the average surgery taking ∼6 min (including measuring and weighing—see Blanchfield et al. 2005; Blanchfield et al. 2009; Guzzo et al. 2017). The incision site was cleaned with povidone iodine prior to making the incision. For lake trout, the incision was made on the midline, ∼5 cm anterior to the beginning of the pelvic girdle. Implantation protocols were modified for white suckers to reduce the possibility of infection by moving the incision away from the midline of the body by 1–2 cm to minimize possible irritation caused by the typical bottom orientation of suckers. In all cases, tag weight was <2% of fish weight. All fish were collected and handled under the authority of Licenses to Collect Fish for Scientific Purposes issued by the Ontario Ministry of Natural Resources and Forestry, and under the approval of Animal Use Protocols issued by the Fisheries and Oceans Canada Animal Care Committee, the University of Manitoba, and Lakehead University.

Similar procedures for lake trout capture and tag implantation were followed in the spring of 2017 at Squeers Lake. For this segment of the study, relevant collection permits and animal use protocols were issued by the Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry.

2. Depth-use monitoring

Lake trout and white sucker depth-use data collected by acoustic telemetry were used to optimize the design of our hydroacoustic surveys by identifying when and where lake trout would be both (i) easily countable by our hydroacoustic gear and (ii) spatially isolated from white sucker of similar size. In 2013, acoustic telemetry data from lake trout implanted with VEMCO (now InnovaSea Systems, Inc., Boston, MA) depth-sensing transmitters (model V13P-1 L) in IISD-ELA

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Fig. 4. Seasonal changes in depth orientation of lake trout in two IISD-ELA study lakes in 2013. (A) Depth distributions of lake trout implanted with Vemco telemetry tags in lakes 626 and 373. The shift to shallower depths in the fall was observed in both lakes. (B) Horizontal orientation of lake trout implanted with transponder tags in lake 373. The shift to shallower inshore waters in the fall is evident.

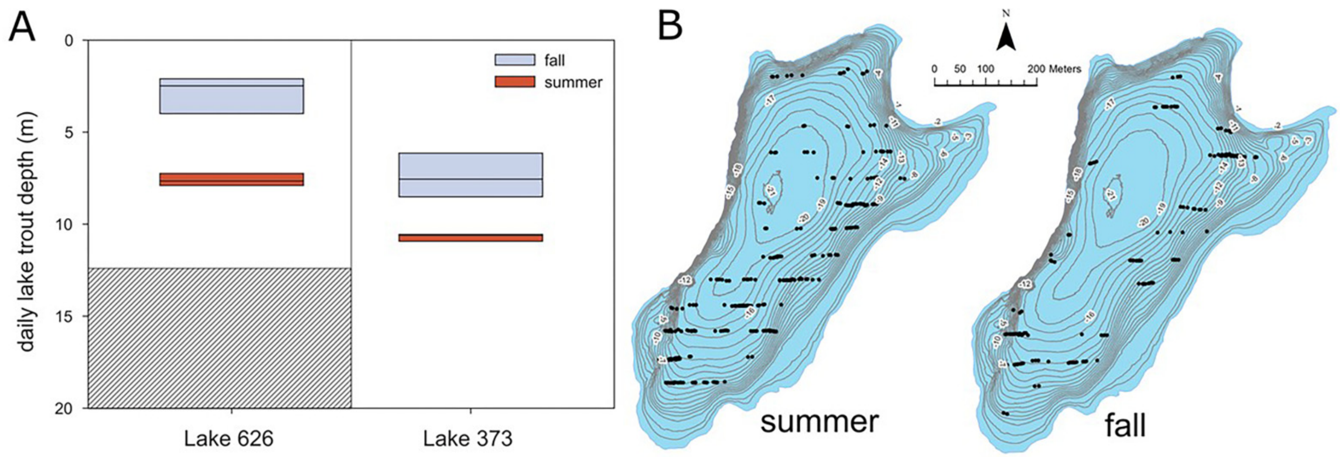
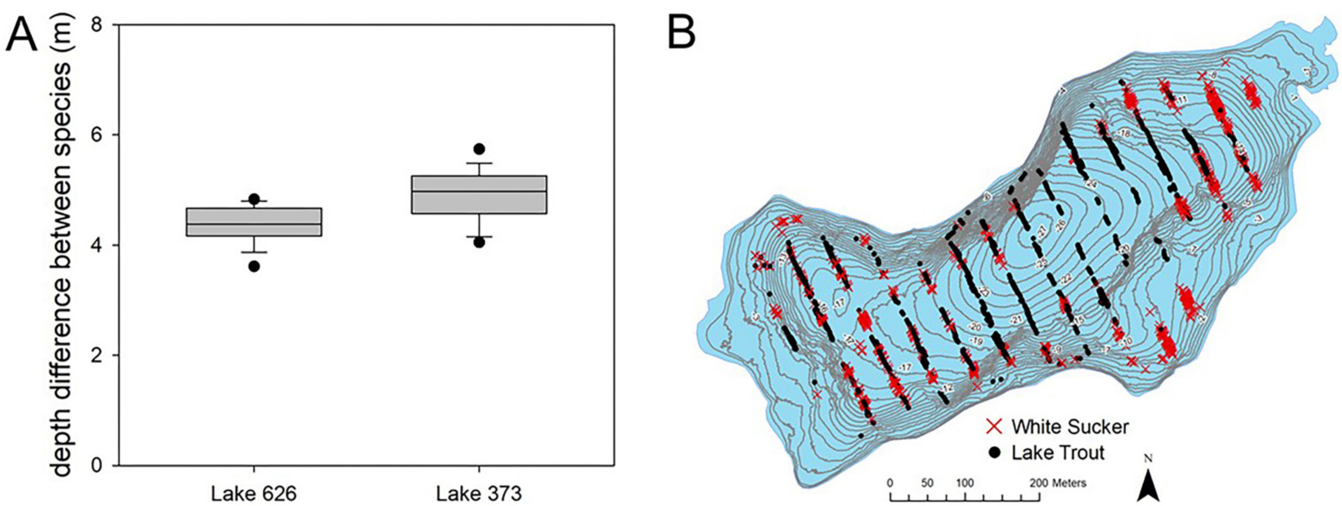


Fig. 5. Differences in the summer spatial orientation of lake trout and white sucker in three IISD-ELA study lakes. (A) Vertical orientation (lake trout depth-white sucker depth) of lake trout and white sucker implanted with Vemco telemetry tags in lakes 626 and 373 in 2015—lake trout were 4–5 m deeper than white sucker in both lakes. (B) Horizontal orientation of lake trout and white sucker implanted with transponder tags in lake 224 in 2016. The tendency for white sucker to frequent shallower, more littoral regions than lake trout is evident.



lakes 373 ($n = 7$) and 626 ($n = 6$) were used to assess daily and seasonal variation in lake trout depth use. That same year, HTT survey data from 23 lake trout in Lake 373 implanted with Sonotronics transponder tags were also used to compare seasonal habitat use. In 2015, acoustic telemetry data from lake trout and white sucker in IISD-ELA lakes 373 (seven lake trout and seven white sucker) and 626 (eight lake trout and six white sucker) were implanted with VEMCO depth-sensing transmitters (V13P-1 L) to assess the spatial separation of these two species in summer. To complement these data, HTT summer survey data from lake trout ($n = 30$) and white sucker ($n = 30$) implanted with Sonotronics transponder tags in Lake 224 in 2016 were used to assess the horizontal spatial separation of the two species.

Each of the VEMCO tags used in these studies randomly transmitted a coded signal every 16–64 s (V16) or every 120–300 s (V13). These depth data streams were monitored 24/7 through the summer and fall using four or five VEMCO omnidirectional hydrophone receivers (a mix of models VR2 and VR2W) with overlapping detection ranges distributed throughout the lake. Receiver coverage in these small lakes was essentially complete, with the interval between detections for a typical tag equal to 5–7 min.

3. Jolly–Seber and Schnabel abundance estimates

Conventional abundance values for all three IISD-ELA lakes were based on data collected from long-term (∼20

Fig. 6. Depth distribution of lake trout "targets" in all four study lakes. The depth distribution of single targets, grouped into "fish tracks", with an average estimated total length >300 mm (−35.6 dB) is shown for each survey lake in each survey year (labelled: split beam fish track detections). At the far right, the depth distribution of transponder-tagged lake trout is compared with the depth distribution of mean TS-filtered "fish tracks" in Squeers Lake in 2017.

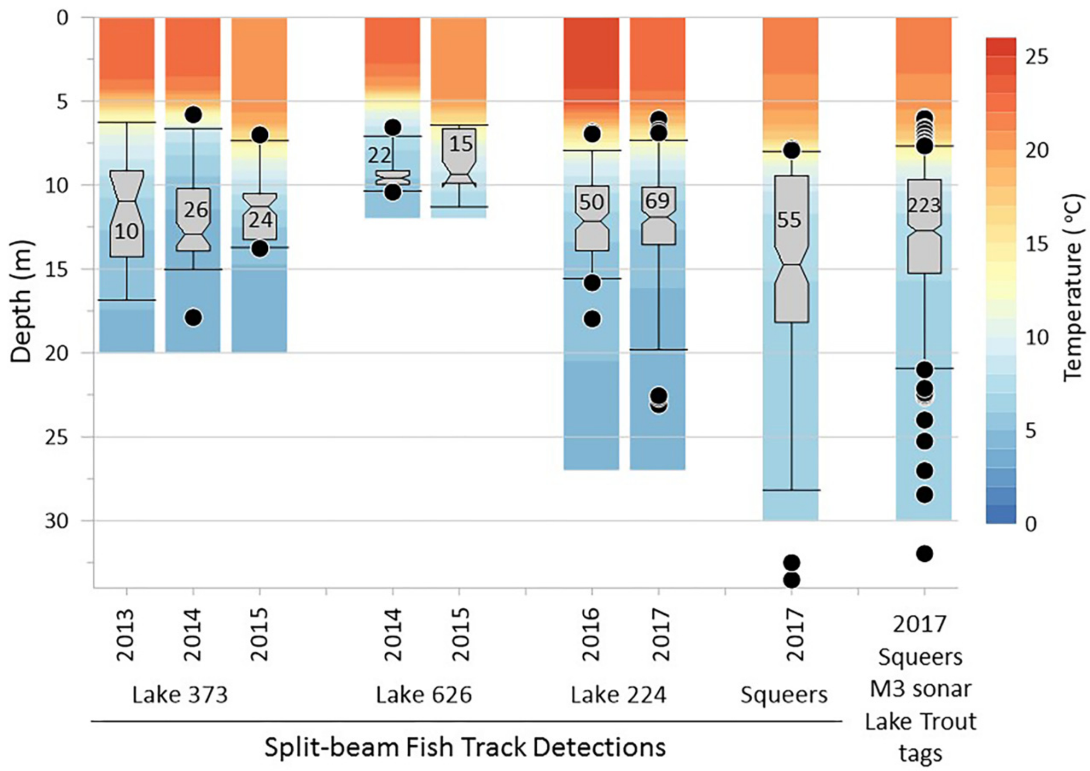


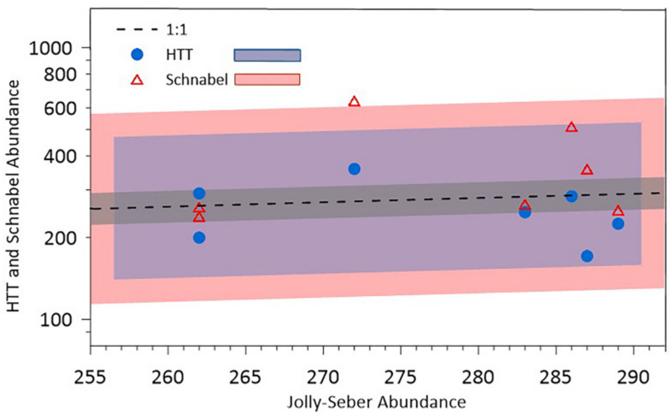
Table 5. Conventional abundance estimates and hydroacoustic transponder tag (HTT) abundance estimates for lakes 373, 626, 224, and Squeers.

Lake	Year	Conventional abundance estimates		HTT abundance estimate (number of surveys, precision)	Ratio: echocount abundance to HTT abundance
		Jolly–Seber (precision)	*Schnabel (precision)*		
373	2013	247–***286***–330 (1.34)	273–***512***–4148 (15.2)	90–***284***–480 (5, 5.33)	0.59–***0.67***–0.77
373	2014	*228–**262**–300* (1.32)	162–***239***–457 (2.82)	168–***291***–414 (4, 2.46)	0.57–***1.00***–1.44
373	2015	244–***287***–339 (1.39)	205–***357***–1379 (6.72)	83–***171***–259 (6, 3.12)	0.62–***0.91***–1.20
626	2014	*235–**272**–316* (1.34)	375–***636***–2072 (5.52)	***358*** (2, –)	***0.96***
626	2015	*213–**262**–283* (1.33)	184–***259***–439 (2.38)	74–***200***–326 (6, 4.41)	0.62–***0.87***–1.30
224	2016	261–***289***–320 (1.23)	185–***252***–392 (2.21)	144–***225***–305 (7, 2.11)	1.08–***1.15***–1.22
224	2017	256–***283***–314 (1.23)	216–***265***–342 (1.58)	167–***248***–330 (10, 1.98)	1.11–***1.18***–1.25
Squeers	2017	–	1948–***3629***–7324 (3.8)	1051–***2636***–4221 (4, 4.02)	0.52–***0.79***–1.06

Note: Each estimate is given in bold type and is flanked by its 95% confidence boundary values. For each lake and year, several independent HTT surveys were carried out from mid-July to mid-August—the bracketed number beside each HTT estimate is the number of surveys for that year. Each survey generated a simple Lincoln-Peterson abundance estimate; the reported estimate for each lake and year is the mean of those independent estimates; the confidence interval was calculated assuming a normal distribution for those estimates. Jolly Seber estimates are available for all ELA lakes and are based on up to 20 years of continuous annual tagging. Schnabel estimates are based on mark/recapture surveys carried out in the same year as the HTT surveys. Earlier abundance studies on Squeers Lake provided population estimates for 2013 and 2014 (3384–2266, respectively) that were consistent with annual estimates over the previous decade, as well as with the estimates obtained in 2017 (see Supplement C for details). Each estimate is accompanied by a measure of precision (upper 95% confidence bound/lower 95% confidence bound) that is unaffected by the fact that the confidence bounds from the conventional methods are asymmetric about each estimate, while the HTT bounds are symmetric about each estimate. The final column compares the echo counting estimate for each acoustic survey with the HTT abundance estimate, using a simple ratio; the value in bold type is the mean for the ratio and is flanked by its 95% confidence boundary values.

years) MR programs. They were derived using Jolly–Seber estimation models (Supplement C) and consequently produced estimates with good precision (see Table 1—[upper 95% confidence bound/lower 95% confidence bound] ~1.31). The conventional abundance value for Squeers Lake in 2017 was obtained using a Schnabel multiple recapture approach focused on a single year (2017). As expected, this estimate was less precise (upper 95% bound/lower 95% bound ~0.8) than the Jolly–Seber estimates. However, this value was well within the range expected from a time series (2005–2014) of estimates based on both harvest statistics and simple annual Lincoln-Peterson MR estimates (see Supplement C).

Fig. 7. Accuracy and precision of HTT abundance estimates for each year in each of the IISD-ELA lakes. The HTT and Schnabel abundance estimates are plotted against the Jolly–Seber abundance estimates. The dashed line is the 1:1 line and the vertical height of the grey-shaded region surrounding the 1:1 line illustrates the typical width of the 95% confidence intervals for the Jolly–Seber estimates. The vertical height of the blue-shaded region illustrates the typical width of the 95% confidence intervals for the HTT estimates. The vertical height of the pink-shaded region illustrates the typical width of the 95% confidence intervals for the Schnabel estimates. The values of precision used here are typical of the values found in our field studies—they are the means of the annual precision values given in Table 5: 1.31 for Jolly–Seber estimates, 3.34 for HTT estimates, and 5.01 for Schnabel estimates.



In addition to comparing the precision of our annual HTT estimates with Jolly–Seber estimates that are based on a sequence of MR samples over several years, we wished to compare the precision of our HTT estimates with the precision attainable from a conventional method based on multiple capture–recapture sampling within a year (Schnabel estimates). To this end, we generated annual Schnabel abundance estimates for each of the IISD-ELA lakes by extracting, from the long-term Jolly–Seber capture–recapture time series for that lake, just the capture–recapture data obtained within the fall sampling period (typically 2–3 weeks) for each year the lake was subjected to an HTT survey (Supplement C).

4. Hydroacoustic transponder tag abundance estimates

An HTT abundance estimate is based on several independent surveys carried out over a single time period. We assumed these independent samples were normally distributed around a mean value and applied normal statistical methods to the set of independent HTT survey values for each lake and year to arrive at an abundance estimate for the lake and year (the mean of the survey values) and a symmetric (about the mean) 95% confidence interval for that estimate based on the number of surveys and the standard deviation of the survey values. In principle, the precision of this estimate can be increased by increasing the number of independent surveys contributing to it.

5. Hydroacoustic transponder tag abundance estimates

We needed to compare the precision of our annual HTT estimates with the precision attainable with a conventional method requiring multiple capture-recapture sampling within a year (Schnabel method), as well as with a conventional method requiring a sequence of capture-recapture sampling over several years (Jolly–Seber method). The statistical models that underlie both the Schnabel and Jolly–Seber estimates generate confidence intervals that are asymmetric about the estimate, and the degree of asymmetry can be quite high. The confidence interval for each annual HTT estimate of abundance is symmetric about its abundance estimate. A simple index of precision that is unaffected by the presence/absence of symmetry in the position of the mean is the ratio of the confidence bounds. We used this index to compare precision across abundance estimation methods.

Results

1. Identifying the target population

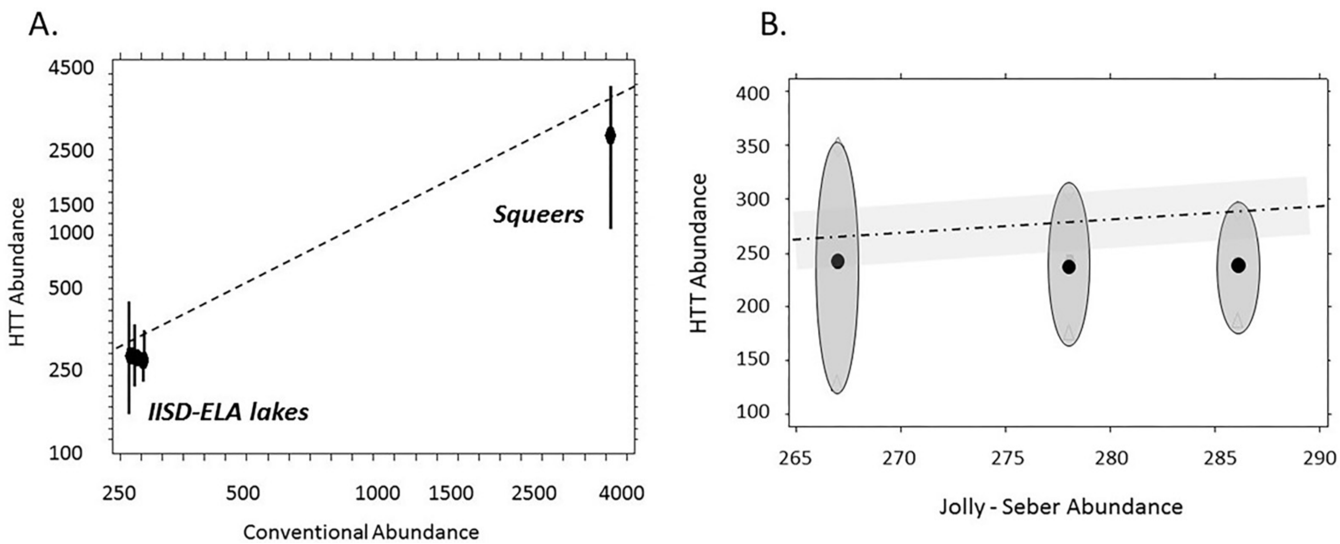
The expected seasonal difference (summer vs. fall) in habitat use by lake trout was confirmed empirically by both depth tag telemetry and multibeam transponder tag surveys (Fig. 4). The expected spatial separation of lake trout and white sucker in summer was also confirmed empirically by depth telemetry and multibeam surveys (Fig. 5). FT detections, with a mean TS that passed our size threshold, were all located at depths that offered temperatures less than or equal to the preferred temperature of lake trout. Further, from our 2017 surveys, the depth distribution of lake trout carrying transponder tags matched the depth distribution of our filtered FT detections (Fig. 6). Therefore, we felt justified in assuming that the density of size and depth-categorized FTs reflected the density of lake trout >300 mm, and these values were used in our HTT estimates of lake trout abundance.

2. Comparing abundance estimates

Transponder estimates of lake trout abundance (HTT_A) for each study lake were similar to the abundance estimates obtained with conventional methods (Conv_A):

(i) The eight annual HTT_A estimates with 95% confidence intervals (Table 5 and Fig. 7) all overlapped the 95% confidence intervals for the Conv_A estimates.
(ii) The four lake-specific HTT_A estimates all overlapped the 95% confidence intervals for the Conv_A estimates (Fig. 8).
(iii) Annual echo counting estimates of abundance (EC_A) varied around the HTT estimates: the ratio of the two (EC_A/HTT_A) ranged from 0.67 to 1.18, with the EC_A estimate for lake 373 in 2013 significantly below the HTT_A estimate and the EC_A estimate for lake 224 in 2017 significantly above the HTT_A estimate (Table 5).

Fig. 8. Accuracy and precision of HTT abundance estimates for each study lake compared with abundance estimates from conventional mark–recapture methods. For both HTT and conventional estimators, annual estimates for each lake were pooled across years to obtain a single, lake-specific estimate of abundance associated with each estimator. (A) Lake-specific HTT abundance (with 95% confidence interval) plotted against conventional mark–recapture abundance for all study lakes—the Jolly–Seber estimator is the conventional estimator used for the IISD-ELA lakes; the Schnabel estimator is the conventional estimator used for Squeers Lake. Lake-specific HTT abundance and precision values were derived by pooling individual HTT surveys across all study years for the lake. The dashed line is the 1:1 line. (B) Lake-specific HTT abundance (with 95% confidence interval) plotted against Jolly–Seber abundance (with 95% confidence interval) for IISD-ELA lakes only. The dashed line is the 1:1 line and the vertical height of the light-shaded region surrounding the 1:1 line illustrates the typical width of the 95% confidence intervals for the Jolly–Seber estimates. The dark-shaded ellipses illustrate the width of the 95% confidence interval surrounding each lake-specific HTT abundance estimate. Lake-specific HTT abundance estimates, 95% confidence intervals, and number of contributing surveys are as follows: lake 373 = 241 [175, 307], $n = 15$; lake 626 = 240 [132,348], $n = 8$; lake 224 = 239 [187,291], $n = 15$; and Squeers Lake = 2636 [1051,4221], $n = 4$.



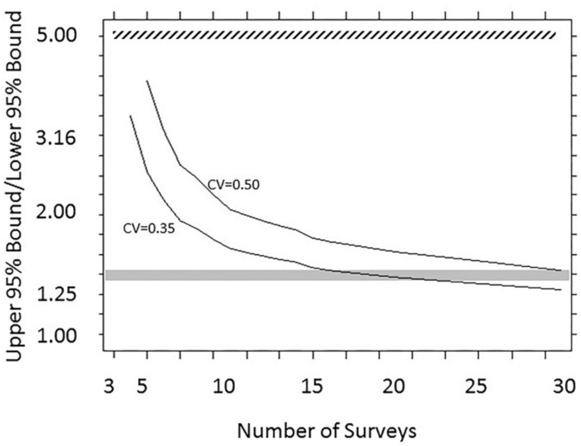
In addition, annual HTT_A estimates from our surveys were more precise than Schnabel estimates but less precise than Jolly–Seber abundance (JS_A) estimates: HTT confidence intervals were narrower than Schnabel estimates by a factor of 1.5, but wider than JS_A estimates by a factor of 2.5 (Fig. 7). When we simulated the increase in precision of HTT_A estimates expected from increasing the number of independent surveys conducted in a year (Fig. 9), levels of precision comparable to those obtained from JS_A estimates could be reached with ~15 independent surveys, assuming a value (~0.35) for the coefficient of variation typical of those observed in our field studies (Fig. 9).

Discussion

Our field trials have demonstrated that the HTT system can generate population estimates that match, in both accuracy and precision, estimates generated by conventional MR approaches operated under almost ideal conditions. The primary advantages of the HTT method are as follows: (i) freedom from the more restrictive assumptions that accompany conventional echo counting abundance estimates; (ii) elimination of some of the logistical concerns that can limit the effectiveness of conventional MR abundance estimates (e.g., the need to estimate rates of mark loss prior to recapture sampling and the need to handle fish directly during recapture sampling); (iii) the promise that levels of accuracy in abundance estimation can be achieved in unstudied systems that rival those achievable by the application of full Jolly–Seber models in well-studied systems; and (iv) the ability to tune management costs to management needs by adjusting sampling effort to match the level of precision required to make effective management decisions.

The disadvantages of the approach stem mainly from (i) high initial equipment costs; (ii) the time and expertise needed to capture and implant individual fish with transponder tags while minimizing handling stress; and (iii) the learning curve associated with effectively managing the acoustic equipment and resultant data streams. However, once the transponder tags are deployed in the field, survey labour costs are significantly reduced compared with those required to operate a vessel with acoustic equipment (i.e., one to two staff on a small lake), and individual survey times can be as low as 1 h, depending on the size of the lake. To achieve high levels of precision, the HTT system requires 10–15 surveys on a lake over the course of 3–4 days (excluding time for travel and setup/take-down), whereas the Jolly–Seber estimates available from 3 of our 4 study lakes required several (>3–5) consecutive years of intensive (2–3 weeks in duration) field sampling to achieve similar levels of precision. While the level of effort

Fig. 9. Precision of HTT abundance estimates as a function of the number of independent HTT surveys. Precision is quantified as the ratio of the upper to lower 95% confidence bounds. The marked regions designate "typical" levels of precision for the Schnabel (diagonal barred region) and Jolly–Seber (shaded region) estimators. The two curves simulate how the precision of the HTT estimator will increase assuming that individual survey estimates are normally distributed with (upper curve) a coefficient of variation of 0.5 or (lower curve) a coefficient of variation of 0.35. This range of values is typical of those observed in our field studies: the 8 CV values obtained from our 8 within-year studies had a mean value of 0.42, with a 95% confidence interval of [0.31, 0.53].



required to generate a Schnabel estimate is less than for the Jolly–Seber method, it still requires several weeks of intensive field work with no guarantee of obtaining sufficient recaptures to provide reasonable estimates. We do expect HTT time constraints to scale positively with lake size, such that more fish will need to be marked and a longer recapture period will be required for larger systems or even for sub-sectors of very large lakes (e.g., the Laurentian Great Lakes). However, conventional MR programs on large lakes often require the help of the public and commercial fisheries operators to report the catch or harvest of marked fish, and response rates can be low—especially if monetary incentives for recaptures are lacking. By contrast, the HTT approach offers a unique benefit to large systems since the effort aimed at marked fish detection is much more in control of the fisheries manager.

A simple protocol for organizing an HTT survey program is outlined in Table 6. Our experience with the method so far has highlighted the following important considerations when mounting such a program:

(i) The importance of testing for target avoidance by the survey vessel. We estimated and corrected for avoidance in our surveys, but we were still left with the tendency for our annual HTT_A estimates to lie just below the annual JS_A estimates (HTT_A estimates averaged ∼0.91 JS_A estimates), suggesting that we may not have fully eliminated avoidance bias from our estimates. A fully battery-powered vessel should deal effectively with the problem, but a careful empirical assessment of avoidance should be undertaken in each study system.

(ii) Thermal preference data for both the target species and other species in its environment are essential for assessing how best to isolate target population STs from the set of STs counted by the HTT system. Hasnain et al. (2018) currently provide the most comprehensive listing of thermal preference data for North American freshwater fish.

(iii) Basic life history information on the target species and knowledge of the set of species that are similar in size to the target species can provide valuable intelligence on when the target individuals are accessible to the acoustic gear and are spatially isolated from their "size" competitors. For example, (a) lake trout spawning season and habitat data identified summer as the season when lake trout were most accessible to the survey gear; (b) the contrast in temperature and food preference for lake trout and white sucker pointed to consistent summer spatial separation (pelagic for lake trout/littoral-benthic for white sucker) between these two species, and both of these expectations were tested and confirmed by our telemetry surveys (Figs. 4–6). Although we had to rely on independent telemetry studies for some of the data presented, the fully operational HTT system is capable of delivering species-specific depth distribution data at an operational cost that could be significantly lower than the costs associated with a fixed network of telemetry receivers.

(iv) The refined estimate of habitat volume achievable through the HTT system allowed us to set both our seasonal survey schedule and our survey-specific size and depth filters to ensure a "reasonable" estimate of V_{occ}. This permitted us to generate EC_A estimates that were close to both the HTT_A estimates and the JS_A estimates (Table 5). This illustrates how the HTT system could be used to develop a protocol for simple split beam surveys that would generate reliable EC_A values by ensuring that all surveys occur at the appropriate season, and employing size and depth filters to permit "reasonable" survey-specific estimates of V_{occ}.

Our focus in this paper has been on using the HTT system to estimate population abundance. However, other kinds of significant ecological knowledge can be acquired through the HTT system. Its promise lies in its potential to provide real-time, species-specific spatial data for both small and large individuals. These data may then be useful in assessing:

(i) seasonal patterns in the use of specific habitats by members of a particular species (e.g., Fig. 4);

(ii) the abundance of segments of a target population that are difficult to study with conventional methods; for example, the very precise Jolly–Seber estimates of mature IISD-ELA lake trout rely on known locations of autumn spawning site aggregations; immature lake trout do not aggregate in regular ways in areas that are suitable for capture with passive netting gear; this fact raises logistic

Table 6. Essential elements of an abundance survey using the hydroacoustic transponder tag (HTT) system.

Phase	Step
Preparation: implant transponder tags in a segment of the target population	Implant tags when target individuals are best able to recover from the implantation procedure. Allow for acclimation of individuals to tag implants—typically a period of several weeks
Hydroacoustic survey—Step 1: assess underlying assumptions	Assess diurnal and seasonal patterns of habitat use to determine when the spatial distribution of target individuals allows for the most accurate estimate of abundance
	Count the number of tagged fish that have survived and are active in the habitat occupied by the target population. This step requires a comprehensive survey of the relevant habitats using the HTT acoustic system
Hydroacoustic survey—Step 2: start surveys when and where underlying assumptions are best met	Conduct a formal stratified survey of the environment occupied by the target population using the EK60 and M3 sonar
	Replicate the survey as many times as feasible, ideally allowing for quantification of both within- and between-day variation
Population estimate	Generate a population estimate for each survey and then use normal sampling theory (or bootstrap methods if the number of surveys is sufficient) to establish a confidence interval for the estimate

problems for passive gear methods that might not apply to the HTT system.

(iii) the presence/absence of habitat sharing and hence the likelihood of competitive and/or predatory interactions among species, by tagging and surveying multiple species of interest.

In addition, current methods for providing real-time spatial data (e.g., acoustic receiver array systems—Brooks et al. 2019) demand long-term commitments of extensive receiver hardware to a dense set of fixed sites. This works well in situations where the locations of critical habitat regions are well known. The HTT system can provide spatial data of comparable accuracy on a coarser time scale without requiring a long-term commitment of detection hardware to fixed locations. Therefore, it could be used in new study areas to provide the spatial habitat information necessary for optimizing the location of a fixed-site receiver array.

Alternatively, in regions where telemetry arrays already exist and hydroacoustic surveys are conducted frequently, the HTT system could be deployed to augment the precision of abundance estimates to levels not possible with either telemetry or acoustic survey methods alone. Given the significant capital investment and running costs associated with both active telemetry arrays and acoustic surveys, adding the cost of HTT surveys to a system already supporting both conventional methods would represent a small additional investment in hardware (i.e., M3 infrastructure + responsive tags). The overall cost of the additional tagging effort required could be minimized by integrating it with the existing effort required to maintain a stock of active traditional telemetry tags. In our study, valuable ecological insights were gained by tagging only a small fraction of each population (e.g., 1.5% of the Squeers Lake population). Given this, the new knowledge gained by including HTT surveys in existing surveys of large systems could easily justify the additional cost. Candidate systems could include the Laurentian Great Lakes, where (i) extensive telemetry arrays exist (i.e., the Great Lakes Acoustic Telemetry Observation System; Kreuger et al. 2018); (ii) several hundred fish are tagged annually to support these systems; and (iii) ship-based acoustic surveys are common on all these lakes, primarily led by state, provincial, and federal agencies. The same is true of the many coastal regions globally that support both fixed telemetry arrays and hydroacoustic surveys.

Data collected over time with the HTT approach includes individual tag capture–recapture histories. Therefore, Jolly–Seber models could be applied to these data to generate more precise and more informative estimates of demographic parameters (e.g., in addition to abundance, rates of mortality, immigration, and emigration). Even if larger open systems require more effort (i.e., surveys conducted over larger areas over multiple years) than smaller closed systems, the effort may still be lower than that required by a conventional MR study. This approach might be particularly suited to situations where stock-specific abundance estimates are needed by management, where individual stocks are isolated during reproduction.

Although the use of acoustic telemetry and hydroacoustic surveys in fisheries management is well established, we believe this is the first time the technologies have been combined to answer significant ecological questions. The use of echo-sounding equipment to detect acoustically tagged fish and generate MR abundance estimates represents a new direction for this field and highlights the best features of each technology. Further development of the HTT system can improve its ability to provide useful new knowledge in fisheries studies. Areas of development that would be particularly helpful would involve (i) reducing the size of the transponder tags to facilitate tagging of a broader size range of fish, (ii) extending tag battery life, and (iii) improving the accuracy and narrowing the time scale of the real-time location information that the HTT system can provide.

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Data availability

The data underpinning this manuscript are available on request from the corresponding author.

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The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2022-0183.

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