

## In Situ Swimming Behavior of Lake Trout Observed Using Integrated Multibeam Acoustics and Biotelemetry

ERIN S. DUNLOP\*

*Ontario Ministry of Natural Resources, Aquatic Research and Development Section,  
2140 East Bank Drive, Peterborough, Ontario K9J 7B8, Canada*

SCOTT W. MILNE

*Milne Technologies, 91 Pinecrest Avenue, Post Office Box 237, Keene, Ontario K0L 2G0, Canada*

MARK S. RIDGWAY

*Harkness Laboratory of Fisheries Research, Ontario Ministry of Natural Resources,  
Aquatic Research and Development Section, 2140 East Bank Drive, Peterborough, Ontario K9J 7B8, Canada*

JEFF CONDIOTTY

*Kongsberg Simrad USA, 19210 33rd Avenue West, Suite A, Lynwood, Washington 98036, USA*

IAN HIGGINBOTTOM

*Myriax Software Pty Ltd, 2nd Floor, 110 Murray Street, Hobart, Tasmania 7000, Australia*

*Abstract.*—Multibeam echo sounder systems allow the in situ observation of swimming and foraging behavior and give insights into the ecology of fish at the individual level. In Lake Opeongo, Ontario, 16 adult lake trout *Salvelinus namaycush* were surgically implanted with ultrasonic tags, released, and studied by means of mobile fisheries acoustics. The transmitted pulses from the ultrasonic tags could be detected and displayed within the multibeam echogram in real time. Tagged lake trout were relocated on 131 occasions over 12 d, for a total of 11.7 h of echogram observations. From these events we observed and quantified the spatial relationships of individual lake trout to other fish targets, schools of cisco *Coregonus artedii*, and the surrounding habitat. We found that all but one tagged lake trout spent at least a portion of their time close to the lake's bottom, but interestingly, many made rapid vertical swimming movements into the water column. These burst vertical movements were sometimes targeted at schools of cisco, such attacks always occurring from below the schools. During such interactions, the lake trout showed distinct peaks in swimming speed when they were between 2.4 and 6.4 m from the schools; we interpret this as the range of their reactive distance in the field. Some of the lake trout were also found to travel alongside of or to actively swim toward other fish targets, whereas others were more solitary. This type of information, made possible by the integration of fisheries acoustics and biotelemetry technology, gives us a fuller understanding of the ecology of aquatic predators and their prey and provides the direct measurements needed to quantify the bioenergetics of lake trout in their natural environment.

Observations of individual fish movements, which are traditionally time-consuming and costly to obtain, provide important insights into the migratory patterns, habitat use, species interactions, and bioenergetics of fish populations. A reliable measure of movement is important for ecological considerations and ultimately for the effective management of exploited populations; examples of the latter include evaluating the efficacy of protected areas and refining bioenergetic models. Fisheries acoustics (Simmonds and MacLennan

2005), which allows the direct observation and quantification of individual fish movements, holds the most promise in this regard.

With fisheries acoustics (more generally referred to as hydroacoustics), known fish targets can be tracked over time in three-dimensional space and their location relative to other targets quantified. This technology has been used extensively in marine systems to understand the behavior of fish and invertebrates (e.g., Gerlotto and Paramo 2003; Klevjer and Kaartvedt 2003; Gerlotto et al. 2004; Onsrud et al. 2005) and has recently begun to be applied more extensively in freshwater systems (e.g., Gjelland et al. 2004; Milne et al. 2005; Mehner et al. 2007). As with other remote sensing techniques, one difficulty in using acoustics is

\* Corresponding author: erin.dunlop@ontario.ca

Received September 1, 2008; accepted October 10, 2009  
Published online January 14, 2010

resolving the identities of individual targets. In contrast, biotelemetry methods have been developed to follow the movements of ultrasonically tagged individuals of known identity. The integration of these techniques holds obvious promise, particularly in improving the movement components of bioenergetic models. Foraging-related activity costs have an important influence on bioenergetic model predictions, and their quantification can reduce model uncertainty (Rennie et al. 2005; Chipps and Wahl 2008). Furthermore, the use of multibeam echo sounder systems (MBES) to follow acoustically tagged individuals holds particular promise because it enables a greater portion of the aquatic environment to be characterized and monitored at any given time (Mayer et al. 2002). This is because the received pulses from the numerous independent transducer elements of an MBES can be digitally processed to display a wide swath of the water column (e.g., 120°, as opposed to the nominal beam widths of 6–11° typical of quantitative single-beam echo sounders), thus enabling a larger area to be sampled at any point in time. Despite the potential of MBES in this regard, to our knowledge the technology has yet to be used to quantify the in situ swimming behavior of tagged freshwater fish.

Analysis of the movements of lake trout *Salvelinus namaycush* based on biotelemetry point to individual niche variation as a key element of their ecology (for a general description of the importance of niche variation, see Bolnick et al. 2003). The individual movements of lake trout reveal habitat selection in the nearshore zone during spawning (Flavelle et al. 2002) and individual variation in foraging behavior, including potentially costly forays into warmer water in pursuit of prey (Morbey et al. 2006). Despite the advances in acoustic telemetry, it is not ideal for characterizing complex and rapid vertical movements or burst swimming events on smaller scales. It also does not provide information on the simultaneous locations of other organisms, including potential prey items, in the vicinity of the tagged individual or the social structure of predatory events. For this reason, little is known about the individual-level variation in vertical swimming speed and the interaction between individual lake trout, their prey, and other conspecifics.

In this study, we used an MBES to quantify the swimming speed, both vertical and horizontal, of acoustically tagged individual lake trout. We also characterized the spatial relationships between (1) individual lake trout and their pelagic fish prey and (2) individual lake trout and other fish targets. The integrated methodology introduced in this study could be a valuable tool for improving our understanding of freshwater fish bioenergetics.

## Methods

The study was conducted on Lake Opeongo, Ontario (45°42'N, 78°22'W), a large (58-km<sup>2</sup>), coolwater, oligotrophic lake, whose fish community has been extensively researched (e.g., Shuter et al. 1987; Dunlop et al. 2005; Morbey et al. 2007). The lake trout in Lake Opeongo feed primarily on ciscoes *Coregonus artedii* (also known as lake herring), a schooling species of pelagic fish that was introduced into the lake in 1948 (Matuszek and Shuter 1990). The population of lake trout reaches asymptotic lengths of 87.2 cm (Shuter et al. 1998), whereas the cisco population rarely reaches lengths beyond 18 cm (Milne et al. 2005). The ciscoes in Lake Opeongo feed on zooplankton and forage in schools during the daytime that break up at night; they are the dominant pelagic schooling fish in the lake, and their schools can be readily identified with fisheries acoustics (Milne et al. 2005). Other notable species of fish present in Lake Opeongo include lake whitefish *Coregonus clupeaformis*, burbot *Lota lota*, yellow perch *Perca flavescens*, smallmouth bass *Micropterus dolomieu*, and white sucker *Catostomus commersonii*.

*Lake trout tagging.*—The tagging of the lake trout took place between June 19 and 22, 2007. We used short-duration ( $87 \pm 7$  min [mean  $\pm$  SD]) gill-net sets at suspected lake trout locations within the South Arm of Lake Opeongo (Figure 1). Monofilament, mixed-mesh gill nets (consisting of 6 panels 2.2 m high with 3.8-cm and 5.1-cm stretch mesh) were set where bottom depths varied between 7 and 22 m (mean  $\pm$  SD =  $14.6 \pm 2.1$  m).

On retrieval of each net, lake trout of suitable size ( $>800$  g) were carefully removed from the meshes and placed into a large covered basin of water that was cooled to approximately 10°C with bottled ice. Before surgery, we anesthetized each fish in a bath of ethanol and clove oil (ratio, 9:1) and 20 L of freshwater. During the surgery, a mild clove oil and water solution was pumped over the gills to prevent tissue drying. Sixteen lake trout were successfully implanted with 200-kHz ultrasonic tags engineered and assembled by Lotek Wireless (Model MA11-18; 11 mm in diameter, 48 mm long, with weights in air and water of 8.9 and 4.2 g, respectively). Each tag was inserted into a small incision in the abdomen at the point of extension of the pectoral fins, and stainless steel surgical staples were used to close the wound. The tagged fish was then monitored in a recovery bath of coolwater and released over deep water near the netting site (Figure 1).

*Lake trout tracking.*—We used a Kongsberg Simrad Mesotech SM2000 multibeam echo sounder system to detect and track the tagged lake trout. The system includes a subsurface mono- or bistatic transducer array

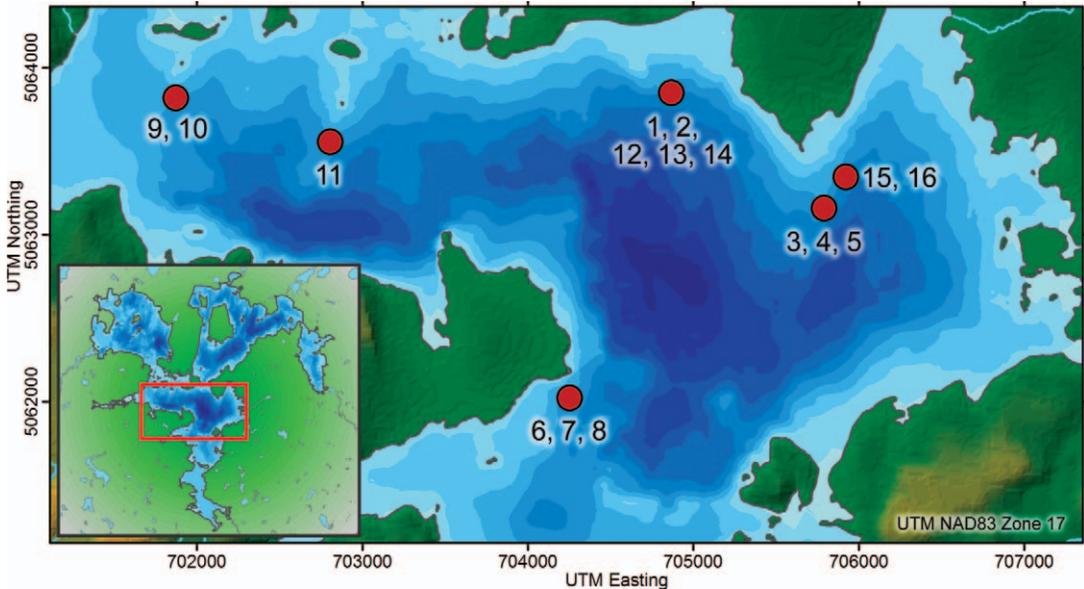


FIGURE 1.—Capture and release locations for lake trout tagged with ultrasonic tags and tracked with a mobile multibeam echo sounder system in Lake Opeongo. Tag numbers are shown. The red box in the inset delineates the South Arm of the lake, where the tagging and tracking took place.

and a ship-based CPU (Simrad SM20) for digital signal processing and data logging. The vertically oriented SM2000 imaging and profiling transducer arrays were affixed to an aluminum pole at the forward port side of the survey vessel. The operating frequency of the SM2000 MBES is 200 kHz, and the nominal maximum source level is 210 dB re 1  $\mu$ Pa at 1 m. The MBES was operated in either the sonar imaging or echo-sounding mode. In the sonar imaging mode, a single transducer array consisting of 80 independent elements both transmits and receives the signal pulses. The associated signal processing hardware forms a 120°-swath image (in the athwart-ship plane) of the water column formed by 128 receive beams, each with a beam width of 1.5°  $\times$  20°. The majority of the lake trout tracking was done in the echo-sounding mode. In this mode, the primary transducer array is only used to receive echoes. Signal transmission is provided by a narrow secondary array of 50 elements oriented perpendicularly to the primary signal reception array. As in the sonar imaging mode, the signal processing hardware forms 128 receive beams to display a 120° swath; however, in this mode the along-ship beam width is reduced from 20° to 1.5°. Although the positioning error of the target within the beam is reduced in the echo-sounding mode, we were able to detect tag transmission pulses through the full 20° along-ship beam width. The SM2000 echo sounder sampling rate (commonly referred to as the “ping rate”), pulse duration, and sampling interval varied

with sampling range. The data were logged using a maximum sampling range of either 30 or 50 m; the former range resulted in a sampling rate, pulse duration, and sampling interval of 5 Hz, 75  $\mu$ s, and 0.039 m, the latter in a sampling rate, pulse duration, and sampling interval of 3 Hz, 100  $\mu$ s, and 0.065 m.

In many applications, calibration of an echo sounder system is required to measure the system’s stability and correct for variations in the directivity and sensitivity of the beam-formed receive signal (Chu et al. 2001; Melvin et al. 2003; Foote and Chu 2005; Foote et al. 2005; Rudstam et al. 2009). Foote et al. (2005) suggest that calibration data are also important in imaging applications to quantify system performance in terms of measures such as the signal-to-noise ratio (SNR). However, calibration was not needed for this study for two reasons. First, we used the MBES only to enhance the visual display of the water column in order to track tagged fish and not, for example, to provide information on the area- or volume-backscattering strength of the acoustic targets. Second, although we did not directly measure the acoustic backscattering strength of an adult lake trout, our observations suggest that it was significantly greater than that of the relative reverberation background noise level when the range of the target was less than the primary bottom detection range (Hughes Clarke 2006). The SNR does drop significantly beyond the range of the primary bottom echo, and our ability to detect a target within this region is

limited. We therefore positioned the survey vessel as directly as possible above the target of interest to ensure that it remained within the high-SNR region of the echogram display, thus minimizing the need for calibration.

To provide more directional detection of ultrasonic tags and to prevent tag signals from being detected along the rear side of the hydrophone, we fitted a foam baffle around the hydrophone receiver (hydrophone Model MAP 600 RT-P1). The forward-facing hydrophone was submerged and mounted on the gunwale facing below the SM2000 transducer on the aft–port side. The face of the transducer was angled at an approximately 45° angle from the vertical to optimize tag detection below the transducer array and aid in searching in front of the vessel.

Lake trout tracking occurred during the day from July 4 to 17, 2007, in the South Arm of Lake Opeongo. The ultrasonic tags were designed to transmit at a frequency of 200 kHz with a pulse rate of 2.5 s. This is the same frequency as emitted by the MBES, making the acoustic pulses produced by the tags easily detected by the MBES array. The acoustic pulses appeared on the multibeam display in real time as a strong backscatter-like “flash” within one or more of the 128 virtual beams corresponding to the position of the target within the 120° swath (Figure 2). Detection of the tags by the MBES is enhanced when the signal detected from the one-way signal transmission of an active tag at 200 kHz is significantly greater than that of all other echoes received from the SM20 transmitted source. Typically, the survey crew would begin searching for tagged lake trout in a clockwise or counterclockwise direction around the basin following the 12–22-m contour until either a flash was observed on the SM2000 display or a strong tag pulse was recorded by the hydrophone receiver. When a tagged fish was detected, the crew steered the survey vessel in the direction that maximized the observed tag signal on the hydrophone software display while viewing the SM2000 multibeam display for tag flashes. The fish was then continuously tracked with the multibeam for up to about 2 h at a time.

On average, the survey crews completed 5.8 h of tracking per day over 12 d, for a total of more than 80 h of tracking (Table 1). Two of the 16 tagged fish (tags 5 and 11) were never located, and as they were not reported in the creel survey (Shuter et al. 1987), it is likely that they moved out of the South Arm survey area. One tagged fish (tag 7) was detected on the hydrophone but not tracked with the multibeam array. Another tagged fish (tag 12) was detected on the bottom with no movement and therefore either died or dropped the tag. All of the tags that were detected with

the hydrophone equipment were also detected by the SM2000 multibeam at least once over the survey period. Of the 80 h of multibeam data collection, over 10 h of the echogram segments included observations of tagged lake trout.

*Data analysis.*—Echoview software (version 4.30.48.9811, Myriax Pty Ltd, Tasmania, Australia) was used to analyze the logged magnitude beam-formed raw beam echograms. The echogram contains information on the depth of the fish as well as information to determine its positional  $x$ ,  $y$ , and  $z$  coordinates (see below and Figure 2); this information is extracted using the echo-processing software. Between observations or fixes (i.e., between subsequent acoustic pings), it was thus possible to measure the change in the positions of individual fish in three-dimensional space (Figure 2). The vertical depth of the target was estimated directly from the echogram data using the observed target range and beam angle. The easting and northing positions of targets were calculated from the vessel heading, vessel differential global positioning coordinate, and location of the target within the acoustic beam (Figure 2). The distances in each plane were used to calculate the three-dimensional (i.e., Euclidean) distance ( $d_E$ ) traveled by an individual lake trout between observations, that is,

$$d_E = \sqrt{(x_t - x_{t-1})^2 + (y_t - y_{t-1})^2 + (z_t - z_{t-1})^2},$$

where  $x$  is the distance traveled in the east direction,  $y$  is the distance traveled in the north direction,  $z$  is the distance traveled vertically, and  $t$  is the time of the latest observation. The velocity at which the fish traveled between observations was calculated as

$$s_E = d_E/\Delta t.$$

We characterized the spatial relationships between tagged lake trout and schools of ciscoes and between tagged lake trout and unknown fish targets. Detected schools of fish were assessed as ciscoes based on previous netting and acoustic research showing their characteristic depth distributions and backscattering properties (Milne et al. 2005). Unknown fish targets were not ciscoes in schools but other individual fish of unknown identity; they were probably lake trout but could also have been large lake whitefish. We identified tagged lake trout as having an association with a cisco school if the tagged individual was observed to directly swim toward or alongside the school. We similarly identified associations between tagged lake trout and unknown fish targets, between two or more unknown fish targets, and between unknown fish targets and cisco schools. The number and duration of these events and the three-dimensional locations and movements of the targets were analyzed.

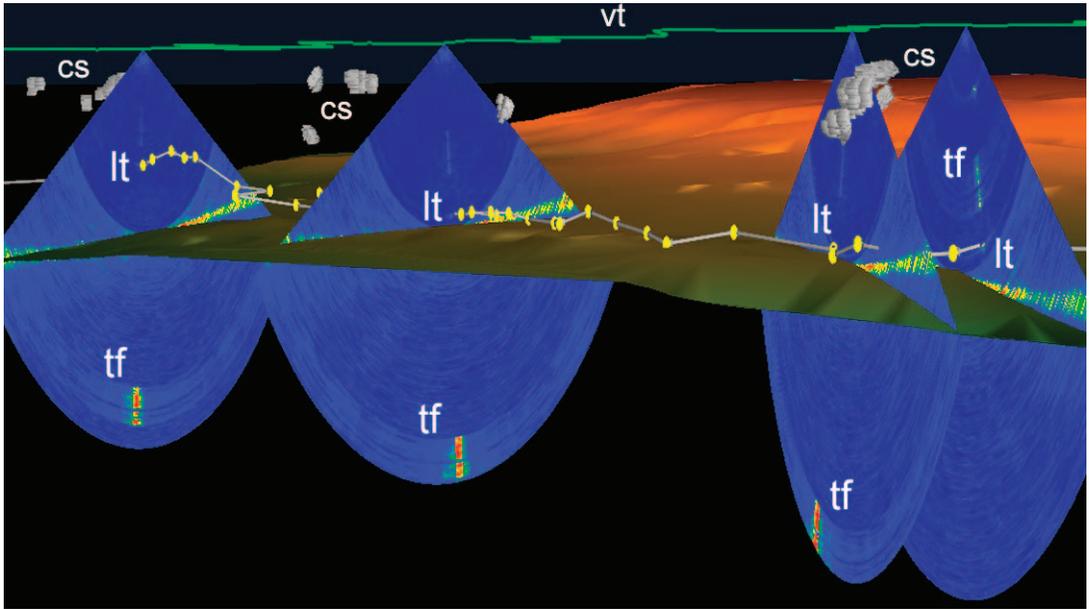


FIGURE 2.—Three-dimensional representation of the positional data collected by the multibeam echo sounder system (MBES) while the survey vessel was tracking a tagged lake trout. The vessel track at the lake's surface is indicated by the green line at the top of the figure (vt). Four MBES echogram segments of the water column are shown (two dimensional blue fan- or swath-like images). The transmitted pulse from the tagged lake trout appears as a flash (tf) that can be seen at the bottom or middle of each echogram. The gray three-dimensional polygons indicate schools of ciscoes (cs). The yellow spheres are lake trout (lt) positional fixes, and the gray lines are the estimated Euclidean distances traveled in the  $x$ ,  $y$ , and  $z$  directions between fixes. The brown surface is the lake bottom. The survey segment shown was approximately 200 m and was recorded from 1715 to 1726 hours on July 5, 2007.

*Sources of uncertainty.*—Vessel movement (heave, roll, and pitch), geographic positioning error, vessel heading calculations, and the unknown along-ship position of the target within the multibeam array could all introduce error into our measurements of an individual's spatial position. Studies using stationary

split-beam fisheries acoustics to measure the positions and swimming speeds of targets have applied smoothing functions to the data to reduce the influence of measurement error (Mulligan and Chen 2000; Klevjer and Kaartvedt 2003; Gjelland et al. 2004). The time series of individual positions that we obtained with the

TABLE 1.—Lake trout tagged with acoustic tags and tracked with a multibeam echo sounder system.

Tag	Fork length (cm)	Total length (cm)	Weight (g)	Time tracked (min)	Dates tracked (Jul 2007)
1	50.1	55.0	1,450	78.72	6, 11, 15, 16
2	69.9	75.6	3,760	39.55	7, 14, 17
3	48.3	53.4	1,400	54.50	4, 5, 16
4	54.2	59.6	2,100	33.40	16
5	48.6	53.7	1,400		
6	84.8	89.5	8,620	89.31	5, 7, 8, 16, 17
7	44.8	49.9	1,065		
8	48.4	53.6	1,475	102.06	11, 16
9	59.6	65.0	2,480	22.96	7, 15, 16
10	61.6	67.0	2,845	1.65	4
11	49.4	53.9	1,256		
12	46.2	50.4	1,140		
13	43.0	47.3	915	14.06	14
14	41.2	45.5	845	33.70	14, 15
15	53.8	58.8	1,860	47.68	15, 16
16	49.4	54.0	1,650	19.44	7

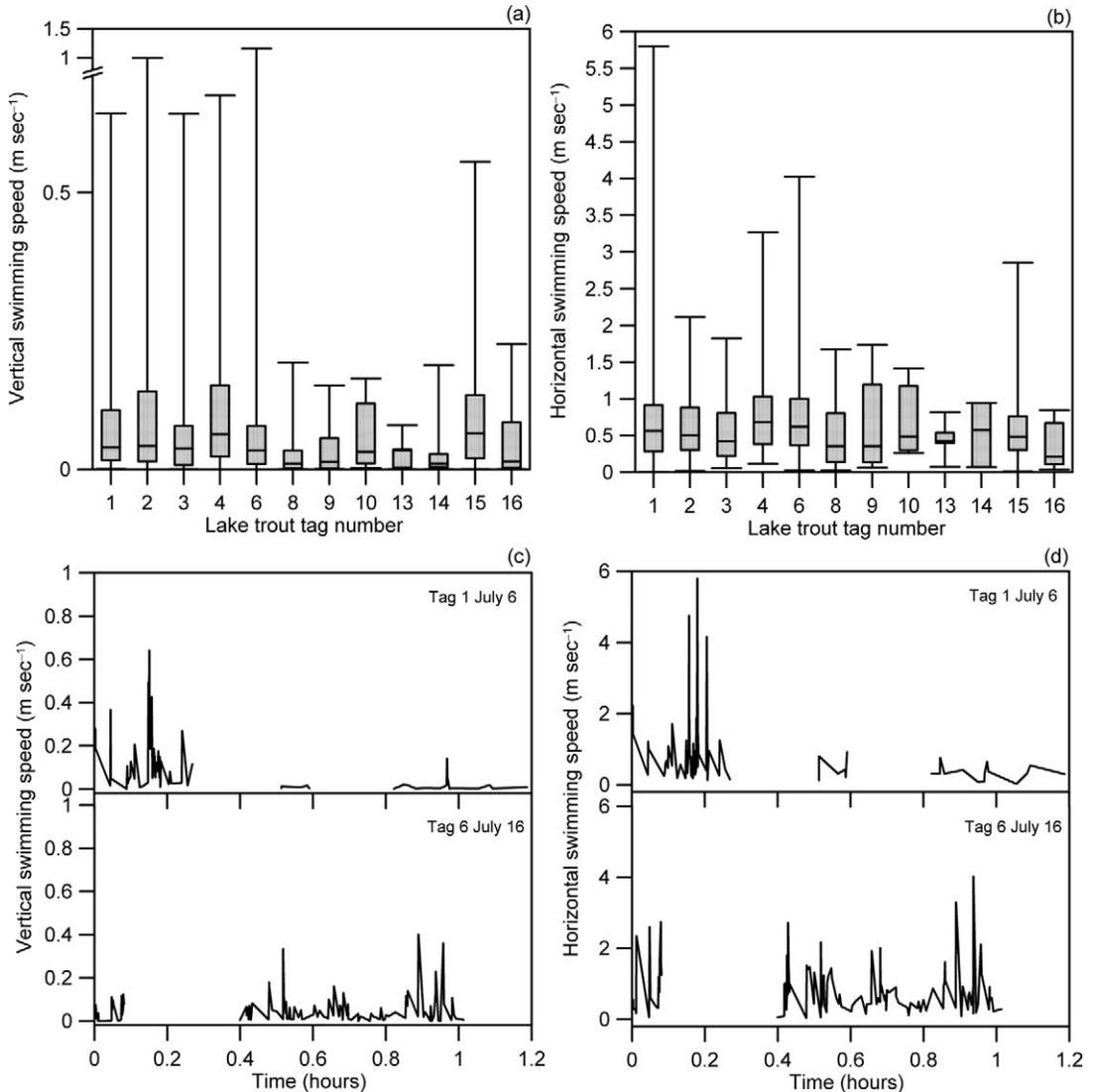


FIGURE 3.—Panels (a) and (b) show the vertical and horizontal swimming speeds for 12 tagged lake trout in Lake Opeongo, panels (c) and (d) the vertical and horizontal swimming speeds for lake trout 1 (July 6) and 6 (July 16) over approximately 1 h of tracking. The horizontal bars inside the boxes represent the medians, the lower and upper boundaries of the boxes the 25th and 75th percentiles, and the vertical bars the ranges in the vertical and horizontal swimming speeds.

mobile MBES are different from those in previous studies—the spatial and temporal scales were larger, the time over which a fish was followed was longer, and the observations were not made at fixed intervals. Applying smoothers in this case could further reduce the accuracy of the measurements and obscure the burst swimming movements of tagged individuals interacting with schools of ciscoes. We therefore did not apply smoothers to the data, and therefore our position estimates do contain errors.

The lake trout in this study were tracked for up to 12

d. Although they were not tracked for at least 12 d (and as much as 25 d) after tag implantation, there could still be an acclimation period that we did not account for in our study. However, we found no relationship ( $R^2 = 0.01$ ) between the Euclidean swimming speed of tagged lake trout and the duration of time since implantation, which suggests that we allowed sufficient postsurgery time before tracking and that tag acclimation did not have a large effect on our estimates of swimming speed.

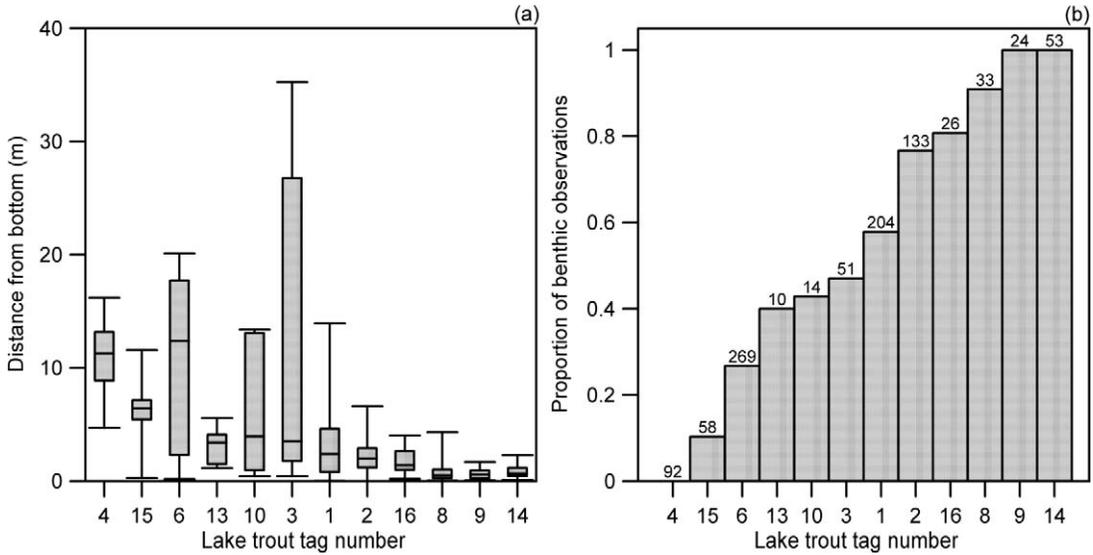


FIGURE 4.—Panel (a) shows the vertical distribution of 12 tagged lake trout in Lake Opeongo (see Figure 3 for an explanation of the box plots). Panel (b) shows the proportion of observations in which tagged individuals were 3 m or less from the bottom (“benthic”). The numbers over the bars are the numbers of observations.

**Results**

The swimming speeds of tagged lake trout were greater in the horizontal direction (mean, 0.69 m/s) than in the vertical direction (0.074 m/s; Figure 3). The median swimming speed was similar among individuals; however, there was a high degree of variation in maximum swimming speed between individuals (Figure 3a, b). Examining individual swimming patterns

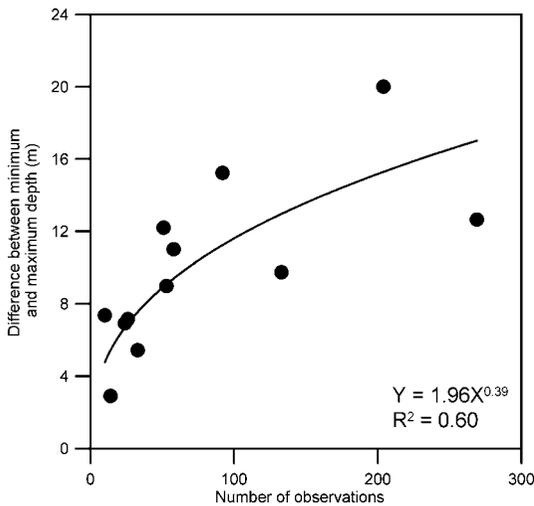


FIGURE 5.—Estimated relationship between the range of the vertical distribution and the number of observations for individual tagged lake trout.

makes it clear that some individuals exhibited frequent burst swimming activity in both the horizontal and vertical direction (Figure 3c, d).

With one exception (tag 4), all tagged lake trout spent at least a portion of their time close to the lake bottom (Figure 4). However, there was a high degree of variation among individuals in the proportion of time spent near the bottom, half of the fish spending less than 50% of their time near the bottom and the other half spending more than 50%. A few individuals spent all of their time on the bottom, whereas others spent almost all of their time further up in the water column. At least part of the variation can be explained by the lengths of time that the different fish were observed: the range of depths over which individuals were observed was positively related to the number of acoustic observations (Figure 5). There was also a slight tendency for fish that spent more time in the water column to show a greater range of depths (depth range [m] =  $-5.5 \times$  proportion of benthic observations + 13.0;  $R^2 = 0.16$ ).

We detected spatial associations between tagged lake trout and unknown fish targets (e.g., other lake trout) and between tagged lake trout and cisco schools (Figure 6; Tables 2, 3). In addition to the tagged individuals, unknown fish targets were observed associating with other unknown fish targets and with cisco schools (Table 3). On a few occasions, two or more tagged fish were observed simultaneously within the multibeam array; however, the close proximity of the tagged fish

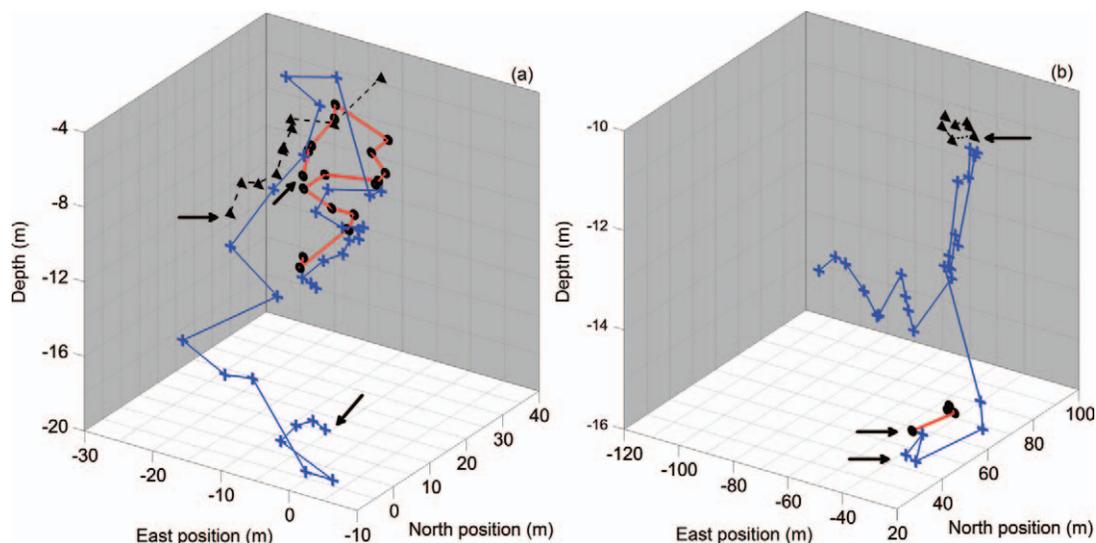


FIGURE 6.—Examples of the associations between tagged lake trout (plus signs) and cisco schools (triangles) and unknown fish targets (circles). The arrows indicate the first observation for each time series shown; distances are relative to that observation. Panel (a) shows lake trout tag number 1, tracked on July 6, 2007; panel (b) shows lake trout tag number 4, tracked on July 16, 2007.

made tag identification via the hydrophone difficult, so these events were excluded from our analysis and from the data in Tables 2 and 3. Interactions between known lake trout and unknown fish targets often extended over several minutes (Table 2).

Tagged lake trout made vertical movements toward cisco schools situated closer to the surface (Figure 6). The lake trout were always located underneath (at greater depths than) those schools (Figure 7b). In the case of other fish targets, tagged lake trout were observed either closely above or closely below those targets (Figure 7a). Most of the pairings were within 2 m of each other and not distributed uniformly across all possible distance categories.

When one examines the relationship between the distance to a school and the swimming speed of tagged individuals, a pattern emerges: all but one individual (tag 4) showed a distinct peak in swimming speed between 2.4 and 6.4 m from the school (Figure 8). In other words, the swimming speeds of individuals tended to be lower when they were very close to a school (when they could actually have been inside it) and when they were at least 6.4 m from the school.

### Discussion

Combining acoustic tracking of sonically tagged lake trout with multibeam fisheries acoustics enabled us to determine the vertical and horizontal swimming

TABLE 2.—Number and duration of events in which tagged lake trout were spatially associated with schools of ciscoes or unknown fish targets. Unknown fish targets (FT) are unresolved individual fish targets that are acoustically similar to tagged lake trout but could be other species (e.g., large lake whitefish).

Tag	Number of events		Duration of events (min)	
	Tagged-school	Tagged-FT	Tagged-school	Tagged-FT
1	1	5	2.33	11.22
2	3	7	7.65	9.94
3	0	0	0	0
4	2	0	4.51	0
6	4	7	8.19	25.31
8	0	6	0	8.32
9	0	2	0	2.02
10	0	0	0	0
13	0	0	0	0
14	0	2	0	0.47
15	2	2	2.68	2.68
16	0	0	0	0

TABLE 3.—Summary of observed events in which unknown fish targets (FT) were spatially associated with schools of ciscoes or other, unknown fish targets.

Event type	Number of events	Number of events involving tagged fish	Total event duration (min)
FT-school	16	7	17.73
FT-FT	31	25	49.92
FT-FT-school	8	6	14.85
Total FT-FT	39	31	64.77
Total FT-school	24	13	32.58

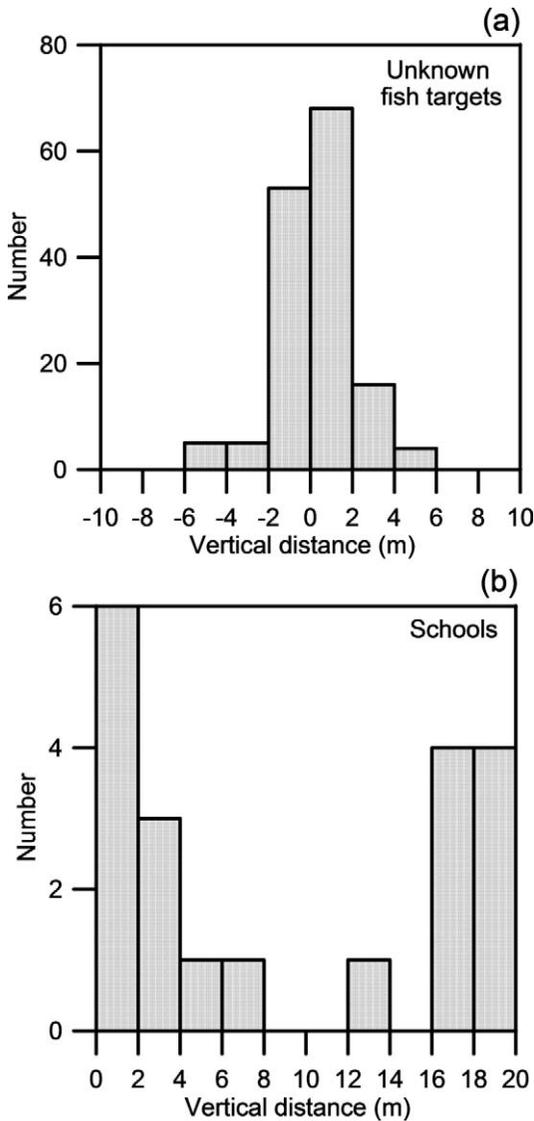


FIGURE 7.—Vertical distributions of tagged lake trout relative to (a) unknown fish targets and (b) cisco schools.

speeds of lake trout of known size and location. The free-ranging movements of known individuals, in both directions, would be extremely difficult to quantify otherwise. In a bioenergetics model of Lake Michigan lake trout, tracking data of ultrasonically tagged fish were used to provide an approximate in situ estimate of swimming speed (Stewart et al. 1983). In that study, the estimated swimming speed was 0.36 m/s; however, the tracking was conducted during the spawning season and the authors arbitrarily reduced the estimate to 0.27 m/s to compensate for possible bias due to spawning activity. The estimated swimming speeds provided by tracking ultrasonic tags represent those for horizontal movements. The horizontal swimming speeds of the lake trout in our study were higher than those of Stewart et al. (1983), the mean individual speeds ranging from 0.33 to 0.77 m/s. This is not surprising, as the use of an MBES enabled us to correct for the positions of individual lake trout within the acoustic beam.

Bioenergetics models rely on assumptions of activity patterns to derive estimates of consumption and growth (Hansen et al. 1993; Hartman and Kitchell 2008). The poor agreement between bioenergetics model predictions and field-based measurements of consumption can in part be explained by the lack of adequate data (Chipps and Wahl 2008). The lake trout bioenergetics model parameters of Stewart et al. (1983) have been used in other studies (Jensen et al. 2006; Morbey et al. 2006), but they do not incorporate vertical movements such as those we observed when lake trout are foraging. By not accounting for vertical movements, bioenergetics models underestimate the food requirements of lake trout. The temperatures experienced by lake trout when making vertical migrations (Morbey et al. 2006) and the energy expended when changing direction and speed (Krohn and Boisclair 1994) would further alter estimates of metabolism, consumption, and excretion. The estimates of swimming speeds in three dimensions (vertical and horizontal) that can be derived from integrating multibeam acoustics and telemetry as

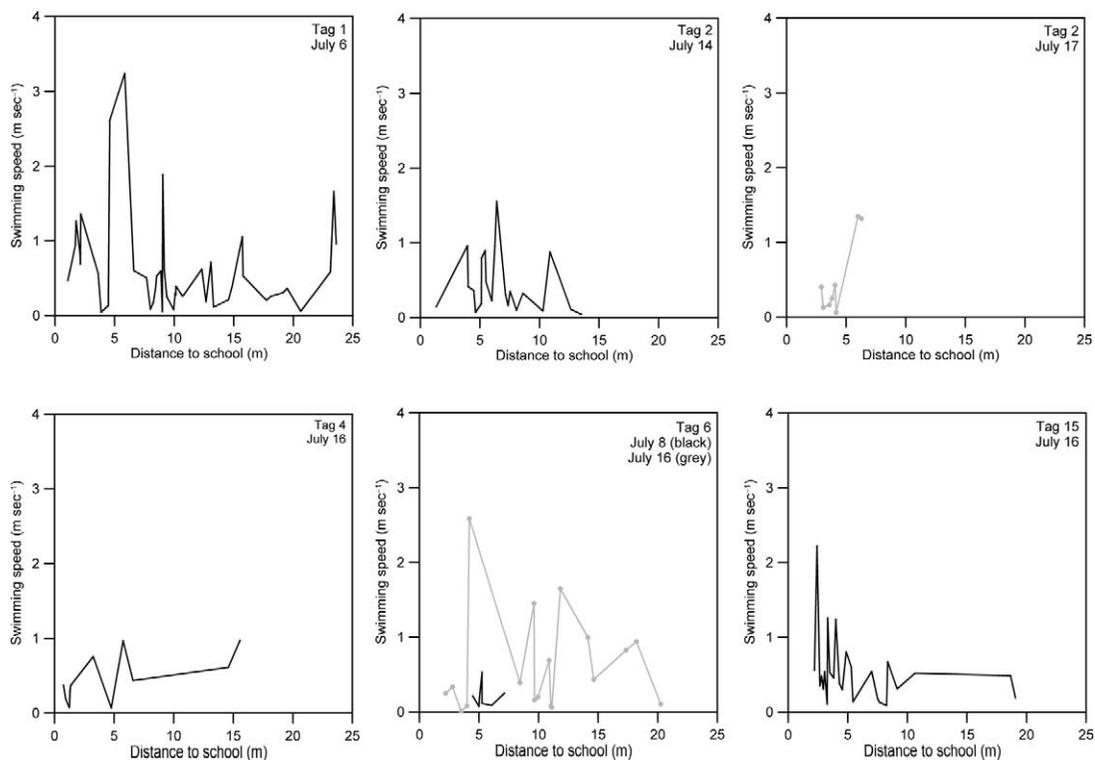


FIGURE 8.—Swimming speed of tagged lake trout as a function of the Euclidean distance to a cisco school for individuals showing an association with a school. Only lake trout with more than three subsequent observations and for which the distance to the school was less than 25 m are shown.

we have done can be used to improve the predictions of bioenergetics models.

In this study, lake trout were often observed to display burst swimming activity in both the horizontal and vertical directions. At least some of this activity is associated with foraging behavior, as the lake trout showed evidence of rapid directed movements and increases in speed when in the vicinity of cisco schools, their known prey (Matuszek and Shuter 1990). The study of foraging behavior using the integrated technique we introduce will have many potential applications. For example, a previous study of Lake Superior pelagic fish used trawl data and fisheries acoustics to suggest that siscowets (a deepwater morph of lake trout) were tracking the vertical migrations of their cisco prey (Hrabik et al. 2006). However, because the species of the individual targets in that study could not be determined precisely, it is not possible to rule out bias associated with target coincidence. These problems could be avoided by integrating technologies as we did because the targets would then be of known identity.

A previous study in the South Pacific revealed that

bigeye tuna *Thunnus obesus* make unexpected vertical forays (Dagorn et al. 2000), a finding similar to that of our study despite obvious differences between the systems. However, the tracking of individuals in the tuna study was done by means of biotelemetry, which provided less resolved, more large-scale information on movements (finer-scale factors, such as the distance between the fish and the hydrophone, could not be determined). While the tuna were being tracked, a split-beam acoustic unit was used to collect information on water depth and habitat. Our study was different because we did the actual tracking with a MBES that was then used to provide fine-scale depth and three-dimensional movement information with broader coverage of the water column. The integrated approach we present could be applied in marine systems to study the detailed swimming behavior of species such as tuna and obtain information about the influence of behavior on target strength.

A distinctive peak in swimming speed (i.e., a peak “attack” speed) occurred when tagged individuals were just below or just above 5 m from a school. We interpret these bursts as closing velocities on prey. In

the laboratory, lake trout have been observed to have average burst attack speeds of 2.8–3.1 m/s (Feldman and Savitz 1999), which is within the range of peak attack swimming speeds (0.46–3.2 m/s) that we observed for Lake Opeongo lake trout. Also in the laboratory, the reactive distance of lake trout has been observed to lie within 0.25 and 1 m, depending on water turbidity and the size of the prey (Vogel and Beauchamp 1999). Our study suggests that lake trout in the wild attack prey from greater distances, which is perhaps not surprising because the prey in this case is a school of fish and therefore much larger than an individual cisco. The interesting slowing down of swimming speeds that occurs at lesser distances could occur when the lake trout are actually eating the prey (perhaps representing handling time) and no longer in pursuit.

Another notable finding is that tagged lake trout were always observed to approach or interact with cisco schools from underneath the schools. One reason for this could be that individual lake trout are taking advantage of backlighting that makes the prey more visible against the sky. Prey falling within the so-called “Snell’s window” (Horvath and Varju 1995) would be more visible to lake trout and also less likely to see the ones that are outside the window, which might make it adaptive for lake trout to forage from underneath a school. Evidence for this phenomenon has been found for marine planktivorous fish (Janssen 1981; Onsrud et al. 2005).

Although we found among-individual consistency in many aspects of the foraging process (e.g., closing velocities and attack orientation), our results also confirm the clear presence of individual-niche variation that has been detected in other large-scale movement studies of lake trout (e.g., Morbey et al. 2006) and studies of lake trout trophic position (Rasmussen et al. 1990; Cabana and Rasmussen 1994; vander Zanden and Rasmussen 1996; vander Zanden et al. 2000). Most notably, the individual lake trout in our study differed greatly in the proportion of time they spent in proximity to the bottom as well as in their depth above the bottom. However, the results reported here also point to the possibility that coordinated attacks among individual lake trout occurred on cisco schools. In Figure 6a, it does appear that the pursuit path represented a coordinated movement between two lake trout (although the identity of one is unresolved). Although the reasons for the associations in this study are unclear, the social facilitation of foraging behavior (Brown and Laland 2003) may have contributed to the sizeable reaction distance we recorded.

Combining a MBES with biotelemetry enabled us to reveal interesting behavior in acoustically tagged lake

trout. Without the integration of these technologies, it would not have been possible to track the fine-scale movements of individuals of known size and to quantify their individual associations with schools of ciscoes and other fish targets. The methodology introduced in this paper has the potential to be usefully applied in future studies of lake trout and other species. Based on this initial experience, we can surmise that the integration of a MBES and biotelemetry will reveal many fascinating and previously unknown aspects of the spatial ecology, foraging behavior, and bioenergetics of freshwater fish at the individual level.

### Acknowledgments

We gratefully acknowledge the funding provided by Brian Shuter of the Ontario Ministry of Natural Resources. We also thank Doug Brown, Gary Ridout, and Trevor Middel of Harkness Laboratory for invaluable assistance in the field. We thank two anonymous reviewers, the associate editor, and editor for comments that helped improve the paper.

### References

- Bolnick, D. I., R. Svanback, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. A. Forrester. 2003. Comparative approaches to intrapopulation niche variation. *Integrative and Comparative Biology* 43:1078–1078.
- Brown, C., and K. N. Laland. 2003. Social learning in fishes: a review. *Fish and Fisheries* 4:280–288.
- Cabana, G., and J. B. Rasmussen. 1994. Modeling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature (London)* 372:255–257.
- Chipps, S. R., and D. H. Wahl. 2008. Bioenergetics modeling in the 21st century: reviewing new insights and revisiting old constraints. *Transactions of the American Fisheries Society* 137:298–313.
- Chu, D., K. C. Baldwin, K. G. Foote, Y. Li, L. A. Mayer, and G. D. Melvin. 2001. Multibeam sonar calibration: target localization in azimuth. Pages 2506–2510 in *Oceans 2001: proceedings of the MTS/IEEE Conference and Exhibition*. DOI: 10.1109/OCEANS.2001.968395.
- Dagorn, L., P. Bach, and E. Josse. 2000. Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. *Marine Biology* 136:361–371.
- Dunlop, E. S., J. A. Orendorff, B. J. Shuter, F. H. Rodd, and M. S. Ridgway. 2005. Diet and divergence of introduced smallmouth bass, *Micropterus dolomieu*, populations. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1720–1732.
- Feldman, A. C., and J. Savitz. 1999. Influence of prey behavior on selective predation by lake trout (*Salvelinus namaycush*) under laboratory conditions. *Journal of Freshwater Ecology* 14:399–406.
- Flavelle, L. S., M. S. Ridgway, T. A. Middel, and R. S. McKinley. 2002. Integration of acoustic telemetry and

- GIS to identify potential spawning areas for lake trout (*Salvelinus namaycush*). *Hydrobiologia* 483:137–146.
- Foote, K. G., and D. Chu. 2005. Calibrating multibeam sonar by the standard-target method: extending limited measurements. Pages 1–4 in *Oceans 2005: proceedings of the MTS/IEEE Conference and Exhibition*. DOI: 10.1109/OCEANS.2005.1639951.
- Foote, K. G., D. Z. Chu, T. R. Hammar, K. C. Baldwin, L. A. Mayer, L. C. Hufnagle, and J. M. Jech. 2005. Protocols for calibrating multibeam sonar. *Journal of the Acoustical Society of America* 117:2013–2027.
- Gerlotto, F., J. Castillo, A. Saavedra, M. A. Barbieri, M. Espejo, and P. Cotel. 2004. Three-dimensional structure and avoidance behaviour of anchovy and common sardine schools in central southern Chile. *ICES Journal of Marine Science* 61:1120–1126.
- Gerlotto, F., and J. Paramo. 2003. The three-dimensional morphology and internal structure of clupeid schools as observed using vertical scanning multibeam sonar. *Aquatic Living Resources* 16:113–122.
- Gjelland, K. O., T. Bohn, F. R. Knudsen, and P. A. Amundsen. 2004. Influence of light on the swimming speed of coregonids in subarctic lakes. *Annales Zoologici Fennici* 41:137–146.
- Hansen, M. J., D. Boisclair, S. B. Brandt, S. W. Hewett, J. F. Kitchell, M. C. Lucas, and J. J. Ney. 1993. Applications of bioenergetics models to fish ecology and management. Where do we go from here? *Transactions of the American Fisheries Society* 122:1019–1030.
- Hartman, K. J., and J. F. Kitchell. 2008. Bioenergetics modeling: progress since the 1992 symposium. *Transactions of the American Fisheries Society* 137:216–223.
- Horvath, G., and D. Varju. 1995. Underwater refraction polarization patterns of skylight perceived by aquatic animals through Snell's Window of the flat water surface. *Vision Research* 35:1651–1666.
- Hrabik, T. R., O. P. Jensen, S. J. D. Martell, C. J. Walters, and J. F. Kitchell. 2006. Diel vertical migration in the Lake Superior pelagic community, I. Changes in vertical migration of coregonids in response to varying predation risk. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2286–2295.
- Hughes Clarke, J. E. 2006. Applications of multibeam water column imaging for hydrographic survey. *Hydrographic Journal (April)*:1–33.
- Janssen, J. 1981. Searching for zooplankton just outside Snell's Window. *Limnology and Oceanography* 26:1168–1171.
- Jensen, O. P., T. R. Hrabik, S. J. D. Martell, C. J. Walters, and J. F. Kitchell. 2006. Diel vertical migration in the Lake Superior pelagic community, II. Modeling trade-offs at an intermediate trophic level. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2296–2307.
- Klevjer, T. A., and S. Kaartvedt. 2003. Split-beam target tracking can be used to study the swimming behaviour of deep-living plankton in situ. *Aquatic Living Resources* 16:293–298.
- Krohn, M. M., and D. Boisclair. 1994. Use of a stereo-video system to estimate the energy expenditure of free-swimming fish. *Canadian Journal of Fisheries and Aquatic Sciences* 51:1119–1127.
- Matuszek, J. E., and B. J. Shuter. 1990. Changes in lake trout growth and abundance after introduction of cisco into Lake Opeongo, Ontario. *Transactions of the American Fisheries Society* 119:718–729.
- Mayer, L., Y. C. Li, and G. Melvin. 2002. 3D visualization for pelagic fisheries research and assessment. *ICES Journal of Marine Science* 59:216–225.
- Mehner, T., P. Kasprzak, and F. Holker. 2007. Exploring ultimate hypotheses to predict diel vertical migrations in coregonid fish. *Canadian Journal of Fisheries and Aquatic Sciences* 64:874–886.
- Melvin, G. D., N. A. Cochrane, and Y. Li. 2003. Extraction and comparison of acoustic backscatter from a calibrated multi- and single-beam sonar. *ICES Journal of Marine Science* 60:669–677.
- Milne, S. W., B. J. Shuter, and W. G. Sprules. 2005. The schooling and foraging ecology of lake herring (*Coregonus artedii*) in Lake Opeongo, Ontario, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1210–1218.
- Morbey, Y. E., P. Addison, B. J. Shuter, and K. Vascotto. 2006. Within-population heterogeneity of habitat use by lake trout *Salvelinus namaycush*. *Journal of Fish Biology* 69:1675–1696.
- Morbey, Y. E., K. Vascotto, and B. J. Shuter. 2007. Dynamics of piscivory by lake trout following a smallmouth bass invasion: a historical reconstruction. *Transactions of the American Fisheries Society* 136:477–483.
- Mulligan, T. J., and D. G. Chen. 2000. Can stationary bottom split-beam hydroacoustics be used to measure fish swimming speed in situ? *Fisheries Research* 49:93–96.
- Onsrud, M. S. R., S. Kaartvedt, and M. T. Breien. 2005. In situ swimming speed and swimming behaviour of fish feeding on the krill *Meganyctiphanes norvegica*. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1822–1832.
- Rasmussen, J. B., D. J. Rowan, D. R. S. Lean, and J. H. Carey. 1990. Food chain structure in Ontario lakes determines PCB levels in lake trout (*Salvelinus namaycush*) and other pelagic fish. *Canadian Journal of Fisheries and Aquatic Sciences* 47:2030–2038.
- Rennie, M. D., N. C. Collins, B. J. Shuter, J. W. Rajotte, and P. Couture. 2005. A comparison of methods for estimating activity costs of wild fish populations: more active fish observed to grow slower. *Canadian Journal of Fisheries and Aquatic Sciences* 62:767–780.
- Rudstam, L. G., S. L. Parker-Stetter, P. J. Sullivan, and D. M. Warner. 2009. Towards a standard operating procedure for fishery acoustic surveys in the Laurentian Great Lakes, North America. *ICES Journal of Marine Science* 66:1391–1397.
- Shuter, B. J., M. L. Jones, R. M. Korver, and N. P. Lester. 1998. A general life-history-based model for regional management of fish stocks: the inland lake trout (*Salvelinus namaycush*) fisheries of Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2161–2177.
- Shuter, B. J., J. E. Matuszek, and H. A. Reiger. 1987. Optimal use of creel survey data in assessing population behaviour: Lake Opeongo lake trout (*Salvelinus namaycush*) and smallmouth bass (*Micropterus dolomieu*), 1936–83. *Canadian Journal of Fisheries and Aquatic Sciences* 44(Supplement 2):229–238.
- Simmonds, E. J., and D. MacLennan. 2005. *Fisheries acoustics: theory and practice*, 2nd edition. Blackwell Scientific Publications, Oxford, UK.

- Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. *Canadian Journal of Fisheries and Aquatic Sciences* 40:681–698.
- vander Zanden, M. J., and J. B. Rasmussen. 1996. A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. *Ecological Monographs* 66:451–477.
- vander Zanden, M. J., B. J. Shuter, N. P. Lester, and J. B. Rasmussen. 2000. Within- and among-population variation in the trophic position of a pelagic predator, lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries and Aquatic Sciences* 57:725–731.
- Vogel, J. L., and D. A. Beauchamp. 1999. Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. *Canadian Journal of Fisheries and Aquatic Sciences* 56:1293–1297.