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# Application of *in situ* target-strength estimations in lakes: examples from rainbow-smelt surveys in Lakes Erie and Champlain

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Acoustic abundance of fish depends directly on the target strength (TS) of the fish surveyed. We analyzed 70 and 120 kHz acoustic data from two lakes with abundant rainbow-smelt (*Osmerus mordax*) populations. Using repeated surveys through the summer growing season, we derived a relationship between TS (dB) and fish length L (cm) at 120 kHz ($TS = 19.9 \log_{10} L - 67.8$). Values for 70 kHz were similar. *In situ* TS increased with fish density, indicating a bias from accepting multiple targets at high fish densities. Correcting for this bias increased estimates of smelt abundance by up to 18% in Lake Erie and up to 100% in Lake Champlain. Multiple modes in the TS distributions observed for older fish do not reflect different size groups, as the same modes can be observed from measurements from a single fish. Smelt released gas bubbles during the evening ascent, and these bubbles had TS (−60 to −58 dB) within the range of TS observed from the fish. Gas-bubble release occurred mostly during the migration. Conducting surveys after the ascent is completed will decrease bias associated with counting bubbles as fish.



Keywords: bubble production, fish density, hydroacoustics, smelt, target strength.

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## Introduction

Smelts are abundant in the open waters of both North American lakes (rainbow smelt, *Osmerus mordax*) and European lakes (smelt, *Osmerus eperlanus*) (Nellbring, 1989). Therefore, hydroacoustics is ideal for estimating the abundance of these species (Lindem and Sandlund, 1984; Burczynski *et al.*, 1987; Brandt *et al.*, 1991; Appenzeller and Leggett, 1992; Argyle, 1992; Peltonen *et al.*, 1999). The results of these studies are difficult to compare, however, because abundance estimates rely on different assumptions about the relationships between target strength (TS) and fish length or weight. Predictions of TS for a 15-cm smelt differ by 10 dB when calculated from the different equations that have been previously applied to smelt (Table 1).

TS is not only a function of fish size, but it also depends on behavior, condition, maturity state, and changes in vertical position and orientation (e.g. Ona, 1990). These properties can change both seasonally and daily. *In situ* TS measurements collected simultaneously with echo-integration data are therefore preferable to standard equations for scaling volume backscattering to absolute fish abundance, as this approach will account for such variability in TS. Partly for this reason, *in situ* TS measurements are often used directly by investigators working in lakes (e.g. Brandt *et al.*, 1991; Rudstam *et al.*, 1993). This approach requires that surveys

Table 1. TS-to-length (L) relationships that have been applied to smelt in the literature. TS is in dB and L in cm.

| Equation | Frequency (kHz) | TS of smelt (dB) | | | Species mix | Source |
|---|---|---|---|---|---|---|
| | | 5 cm | 10 cm | 15 cm | | |
| *Empirical relationships* | | | | | | |
| $TS = 19.9 \log_{10} L - 67.8$ | 120 | −53.9 | −47.9 | −44.4 | Smelt | This study |
| $TS = 18.2 \log_{10} L - 67.5$ | 120 | −54.8 | −49.3 | −46.1 | Smelt | Argyle (1992) |
| $TS = 20 \log_{10} L - 72$[a] | 70 | −58.0 | −52.0 | −48.5 | Smelt | Horppila *et al.* (1996) |
| $TS = 52.6 \log_{10} L - 100$[a] | 120 | −63.4 | −47.6 | −38.3 | Alewife, Smelt | Fleischer *et al.* (1997) |
| $TS = 20 \log_{10} L - 68$ | 70 | −54.0 | −48.0 | −44.5 | Smelt, coregonids | Lindem and Sandlund (1984) |
| *Derived from Love (1971, 1977)* | | | | | | |
| $TS = 19.1 \log_{10} L - 63.85$[b] | 120 | −50.5 | −44.8 | −41.4 | Alewife, smelt, bloater | Brandt *et al.* (1991) |
| $TS = 18.4 \log_{10} L - 64.9$[c] | 120 | −52.0 | −46.5 | −43.3 | Smelt | Appenzeller and Leggett (1992) |
| *Other species* | | | | | | |
| $TS = 23.3 \log_{10} L - 77.1$ | 38 | −60.8 | −53.8 | −49.7 | Capelin | O'Driscoll and Rose (2001) |
| $TS = 20.5 \log_{10} L - 64.2$ | 70 | −49.9 | −43.8 | −40.1 | Alewife | Warner *et al.* (2002) |

[a]Derived from equation describing log(L) as a function of TS.
[b]Derived from Love (1971).
[c]Derived from Love (1977).

take place during the night, when the fish are dispersed and yield a large number of single fish targets. *In situ* TS may be biased high, though, if multiple echoes are accepted as single targets (Sawada *et al.*, 1993; Barange *et al.*, 1996; Gauthier and Rose, 2001), and applications of *in situ* TS to echo-integration values may lead to abundance estimates that are biased low. Fish densities may be reported without consideration of this bias because available commercial software produces density estimates using the *in situ* TS values in areas where multiple echoes may be a problem.

*In situ* TS distributions can also be useful for separating the contribution from different fish species or size groups or both these attributes (Rudstam *et al.*, 1993; Barange *et al.*, 1994; Warner *et al.*, 2002). To do this, we need an accurate TS-to-length relationship for the species in question. We also need to know the shape of the TS distribution expected from a given fish size. Multi-modal distributions from a single fish size have been observed (Williamson and Traynor, 1984; Ona *et al.*, 2001). Thus, caution is necessary when assigning a mode in a TS distribution to a particular fish size.

In Eastern Lake Erie (New York, Ontario) and Lake Champlain (New York, Vermont, Quebec), rainbow smelt dominate the pelagic fish community, often comprising 99% of the trawl catches (Einhouse *et al.*, 1997; Pientka and Parrish, 2002). In addition, young-of-year (YOY) and yearling-and-older (YAO) smelt are separated vertically in the water column during summer thermal stratification, with YOY fish residing in the epilimnion and YAO in the metalimnion and hypolimnion (Einhouse *et al.*, 1997; Pientka and Parrish, 2002). These lakes are therefore ideal for measuring the acoustic properties of smelt. In this paper, we use the change in TS of YOY and YAO smelt as they grow through the summer to derive a TS–L equation for rainbow smelt. The change in TS with fish density (measured as Sawada *et al.*'s, (1993) $N_v$ index) is used to filter the data to decrease the possibility of including multiple targets in the measurements. The potential bias associated with accepting multiple echoes as single fish is presented for several surveys. In addition, we analyze data from stationary measurements in June and early August in Lake Erie showing the range of TS to be expected from single fish as well as the incidence of bubble release from smelt during vertical migration.

## Materials and methods

Biological samples and acoustic data were collected over three seasons in both lakes: Lake Erie in 1998: 3–11 June, 7–14 July, and 27–28 October; Lake Erie in 1999: 5–10 June, 20–23 July, and 27–28 October; and Lake Champlain in 2001: 17–21 June, 22–26 July, and 16–20 September. All surveys were conducted at night, beginning at least 1 h after sunset and ending at least 1 h before sunrise.

Acoustic data were collected with SIMRAD EY500 split-beam echosounders (120 kHz, 6.6° half-power beam width, 0.3 ms pulse length in Eastern Lake Erie, and 70 kHz, 11.1° half-power beam width, 0.2 ms pulse length in Lake Champlain). The echosounders were calibrated with standard copper spheres during or within a few weeks of each survey. Deviations between calibrations were minor: less than 1 dB.

Acoustic data were analyzed using the EY500/EP500 analysis software (version 5.5, SIMRAD, 1998). This program separately calculates volume-backscattering strength and the TS of single targets by simultaneously applying a 20 and a 40 log R TVG function. The lower threshold for volume backscattering was set at −80 dB; the lower threshold for TS distributions was set at −70 dB in Lake Erie and −76 dB in Lake Champlain. The maximum depth for data included in the analysis was about 45 m. The noise levels at

45 m were less than −90 dB and, consequently, there should be no range bias against small echoes close to the threshold.

Each transect was divided into 500–1000 ping segments and analyzed in 2–5 m depth layers. For each segment, we calculated the $N_v$ index of Sawada *et al.* (1993) using the *in situ* TS measured in low-density areas at similar depth. This index is a measure of the average number of fish within the sampling volume and is therefore dependent on fish density, pulse length, beam width, and range. Each depth layer was classified as epilimnetic or meta/hypolimnetic based on the temperature profiles taken during the surveys. Average TS was calculated from backscattering cross-sections and plotted against the $N_v$ index for epilimnetic and meta/hypolimnetic waters. A positive relationship between TS and $N_v$ indicates a bias from the inclusion of multiple echoes in the *in situ* TS distributions (Sawada *et al.*, 1993; Gauthier and Rose, 2001).

Fish were sampled with midwater trawls in both lakes. In Lake Erie, we used a trawl with a 6-mm square-mesh codend and average fishing dimensions of 6 × 6 m. A sample of larval fish was also collected on 11 June 1998 using a 500-μm mesh larval net. In Lake Champlain, we used two trawls, a midwater trawl with a 6-mm square-mesh codend and fishing dimensions of 5 × 5 m, and a 2 × 2-m Tucker trawl with 1-mm mesh throughout. The Tucker trawl was used for sampling larval smelt. Fish were measured in the field. In Lake Champlain, YOY smelt larvae were frozen or preserved in ethanol in the field and measured in the laboratory. Measurements of larval fish preserved in ethanol were corrected for shrinkage (13%; Kruse and Dalley, 1990).

Net samples were correlated with acoustic data collected at the same depth and transect. Net samples were collected concurrently with acoustic data in Lake Champlain but were sometimes collected a few days after the acoustic sampling in Lake Erie. Temperature measurements ensured that the thermal structure was similar during trawl and acoustic sampling. The growth of smelt is minimal over periods of days and the separation of YOY and YAO fish by temperature is stable over time (Einhouse *et al.*, 1997). Therefore, this time delay should not affect our comparisons.

On two occasions in Lake Erie (5 June and 3 August 1998), we collected data around sunset while stationary at anchor. Single fish were identified from the echograms and the TS distribution was obtained with the EP500 software. The TS distribution from single fish was compared with that obtained from the ensemble of fish collected at similar depths. The timing of the production of bubbles by migrating smelt was also noted and the TS of these bubbles was measured.

## Results and discussion

### Field observations

The two age groups of rainbow smelt in Lake Erie (YOY and YAO) were separated by a strong thermocline in the July surveys. Almost no YAO smelt were caught in the epilimnion and no YOY smelt were caught in the hypolimnion (Figure 1). In 1998, temperatures in the epilimnion ranged from 21 to 23°C in July. Older smelt avoid these temperatures (Ferguson, 1965). The division was less pronounced in June, when epilimnetic temperatures were between 12 and 15°C and YAO smelt were found throughout the water column. In June 1998, larval smelt were caught in the epilimnion with a plankton net, but they were too small to be retained by our midwater trawl (average length 16.4 mm, range 13.6–20.3 mm). In October, YAO smelt were restricted to meta- and hypolimnion waters (below 30 m) even though the epilimnetic temperature was similar to that in June (14–15°C). However, the thermocline was sharper in October than in June. YOY smelt were caught in both deep and shallow trawls in October.

TS distributions reflected these changes in depth distributions over the season (Figure 1). In June, TS distributions reflected the presence of YAO smelt in both the shallow and deep waters of Lake Erie. In addition, small targets most probably representing larval smelt were present, but the −70 dB threshold used for TS analysis truncated this distribution (Figure 1). The TS distribution for targets larger than −64 dB was similar between shallow and deep waters and comprised two modes (at approximately −54 and −46 dB). In July, the TS distributions were dramatically different between the shallow and deep waters, reflecting the separation of the two size groups of smelt at that time. In shallow waters (epilimnion), the TS distribution was uni-modal, with a mode at approximately −60 dB. In deep waters, the TS distribution was again bi-modal and similar to the June distribution (Figure 1). Very few small targets were present below the thermocline. In October, the TS distribution in deep waters was almost uni-modal, with a mode at −47 dB. The TS distribution in shallow waters was broader with a tendency towards two modes at −61 and −52 dB.

The seasonal change in TS distribution in shallow waters was dramatic and reflects the growth of YOY smelt from 15 mm in June to around 60 mm in October in Lake Erie (Figure 1). YAO fish in deep waters grew about 20 mm from July to October. However, this increase was not reflected in an increase in average TS. Rather, the average TS in deep waters in October was slightly lower than in June and July, and the TS distribution was more peaked. The distributions of both fish and TS in 1999 were similar to observations in 1998.

In Lake Champlain, temperatures in the epilimnion were between 18 and 22°C on all three survey occasions, with temperatures dropping to below 15°C somewhere between 10- and 20-m depth. The thermocline depth is variable in this lake due to internal seiches. Very few YAO smelt were caught in the epilimnion on any occasion, and the TS distribution in June and October showed a dominance of small targets representing YOY smelt, increasing from a mode around −68 dB in June (average length 19 mm, range

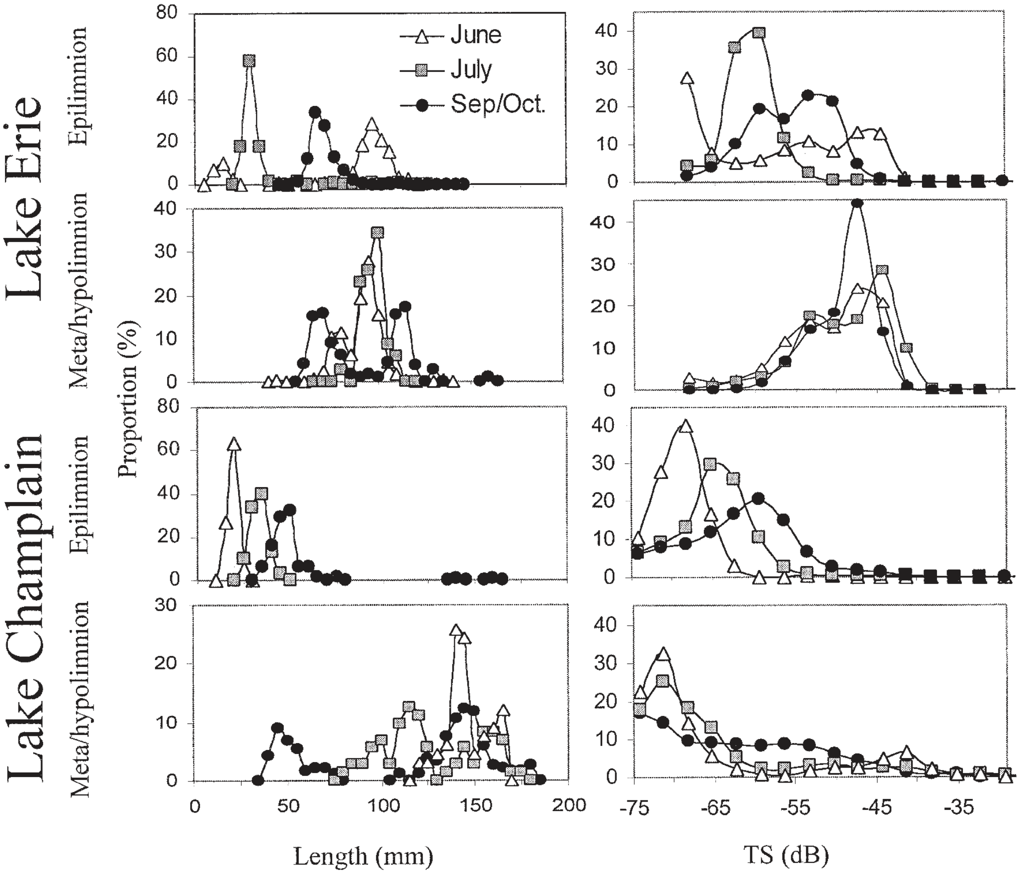


Figure 1. Seasonal changes in TS distribution and fish length from trawl samples at depths dominated by YOY smelt (epilimnion) and YAO smelt (meta- and hypolimnion). Depths included in each graph vary between seasons due to differences in thermal gradients over time. Data from Lake Champlain were collected in the Main Lake in 2001 and data from Lake Erie were collected in the eastern basin in 1998.

17–25 mm) to a mode around −59 dB in September (Figure 1, average length 44.8 mm, range 35–56 mm). The July TS distribution was more spread out in most areas of the lake, possibly as a result of the dense fish aggregation in this depth layer at the time. In the area with the lowest fish density in July (south Main Lake), the epilimnetic TS distribution was intermediate between that of June and September (Figure 1).

In the hypolimnion, YAO smelt dominated catches in June and July although we also caught some cisco (*Coregonus artedi*). Deep Tucker trawls caught opossum shrimp (*Mysis relicta*) but no YOY smelt in the Main Lake. As in Lake Erie, some YOY were caught in deepwater trawls in September, and the broader TS distribution in deep waters in September suggests the presence of YOY smelt. Unfortunately, we do not know the proportion of YOY in deep waters because these fish were also caught during the passage of the net through the dense YOY layer in the epilimnion. In contrast to Lake Erie, there are smaller targets (−66 to −76 dB) in deep waters (Figure 1). *M. relicta*, a 10–20 mm crustacean, is common in Lake Champlain but virtually absent from Lake Erie. This species will give rise to small acoustic targets also at 70 kHz (L. G. Rudstam, personal observation) and have TS around −75 dB (15-mm animal) at 420 kHz (Gal *et al.*, 1999).

## TS-to-L relationship

We compared "average TS" with "average fish length" (L) caught in the trawls by selecting acoustics data from the same transects and depth layers as the trawl samples and using only acoustic data from segments with an $N_v$ index <0.1. In Lake Erie, in June, we had to exclude targets smaller than −64 dB to remove contributions from larval fish that were not sampled with our trawl. We also removed targets larger than −49 dB from the July shallow waters in Lake Erie and June and July shallow waters in Lake Champlain. Occasional larger targets from predators such as walleye may inflate the TS estimate for YOY smelt. For consistency with June data, we used all targets greater than −64 dB from deep waters in July and October in Lake Erie. A −70 dB cut-off for those sampling periods and depths would only decrease the average TS by approximately

0.2 dB. In Lake Champlain, we limited the targets included in the deep waters to targets greater than −61 dB to avoid contributions from mysids. Only comparisons with trawl samples with narrow, fish-size distributions—excluding trawls with mixed YAO and YOY fish—were included in this analysis.

The resulting TS-to-L equation for Lake Erie (at 120 kHz) is highly significant (Figure 2). Here, we present both the equation for predicting TS from L and the equation for predicting L from TS (least-square fit, $n = 22$, $r^2 = 0.90$, 1 s.e. in parentheses):

$$TS = 19.9(1.5)\ \log_{10}(L) - 67.8(1.3).$$

$$\mathrm{Log}_{10}(L) = 0.045(0.003)TS + 3.14(0.17).$$

These equations yield TS in the mid-range of those previously found for smelt. The equations predicting larger targets for a given fish size were primarily obtained from mixed species including alewife or were derived from Love's (1971, 1977) equations (Table 1). Our results in Lake Champlain at 70 kHz were similar for fish larger than 25 mm (Figure 2) and were not significantly different from the Lake Erie regression (ANCOVA with log (L) as a covariate, $p = 0.864$, $L > 25$ mm). Rudstam *et al.* (1999) also found similar TS for smelt at 70 and 120 kHz. YOY smelt in June have lower TS at 70 kHz than expected from the regression (Figure 2). A TS lower than that predicted from standard equations for small fish has been observed elsewhere (Rudstam *et al.*, 2002) and is expected because these fish are small enough to scatter outside the geometric scattering region (MacLennan and Simmonds, 1992). This effect should be larger at 70 kHz than at 120 kHz.

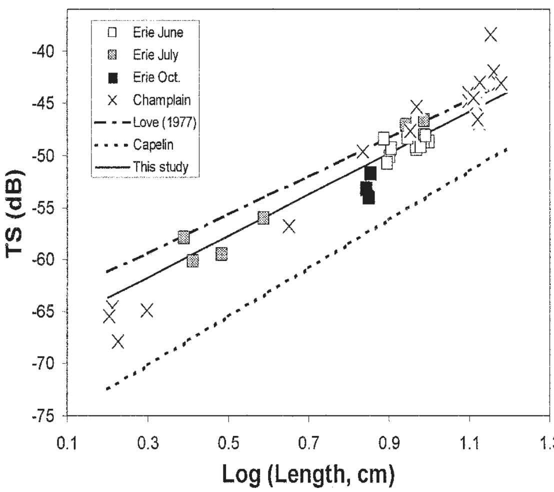


Figure 2. TS (dB) as a function of fish length (L, cm) for rainbow smelt in Lake Erie (120 kHz, both 1998 and 1999 data) and Lake Champlain (70 kHz, from 2001). The regression line represents the least-square fit to the data from Lake Erie. Two other relationships are included for comparison: Love's (1977) equation evaluated for 120 kHz, and O'Driscoll and Rose's (2001) equation for capelin at 38 kHz.

Rainbow smelt have a TS that is 5–7 dB higher than that of capelin (*Mallotus villosus*), a common marine osmerid (Table 1, Figure 2). Warner *et al.* (2002) found similar differences between the TS of freshwater and marine clupeids and suggested that the lower buoyancy of freshwater may necessitate a larger swimbladder, resulting in the higher TS. However, it is also possible that these differences are species-specific, since, in addition to swimbladder size, many factors affect TS (Ona, 1990). Moreover, the TS of marine clupeids may be higher than previously estimated (Ona *et al.*, 2001). Other comparisons between similar marine and freshwater species are needed before we can generalize about the effect of saltwater on swimbladder size and TS.

## *In situ* TS and fish density

"Average TS" was compared with the $N_v$ index of Sawada *et al.* (1993) calculated using the *in situ* TS derived from areas with low fish density. The average *in situ* TS increased with the $N_v$ index (Figure 3), and this increase was significant at the $p < 0.05$ level in most cases in both lakes. However, the degree of variance explained was rather low: $r^2$ ranging from 0.02 to 0.55 in Lake Erie and between 0.14 and 0.71 in Lake Champlain. Elsewhere, we have used $N_v = 0.1$ as the upper limit—the cut-off—for acceptable TS values in lakes (Rudstam *et al.*, 1999; Warner *et al.*, 2002). We used the 0.1 cut-off in the TS–L analysis for Lakes Erie and Champlain, as there was less than 1 dB increase in average TS between $N_v$ values of 0.01 and 0.1 (Figure 3). Sawada *et al.* (1993) suggested 0.04 as the cut-off. There is a need for further analysis of the

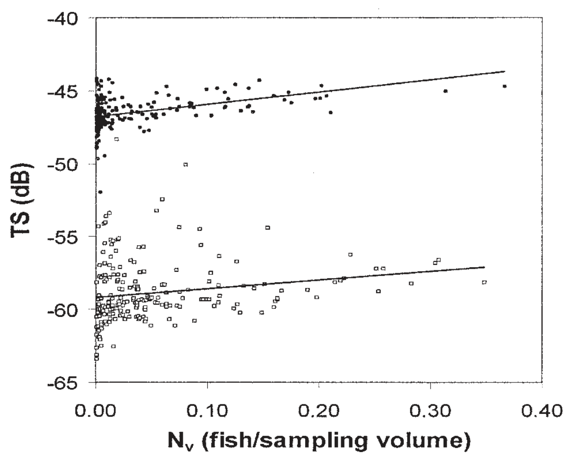


Figure 3. Example of TS as a function of the $N_v$ index of Sawada *et al.* (1993) from July 1998 in Lake Erie. The graph shows data from two depth layers, and both relationships are significant at the $p < 0.05$ level. Results from the other month and Lake Champlain were similar.

advantages and disadvantages of using different $N_v$ cut-offs in surveys (Ona and Barange, 1999).

Investigators working in lakes often apply concurrent *in situ* TS estimates to obtain absolute fish densities from the volume backscattering (e.g. Brandt *et al.*, 1991; Rudstam *et al.*, 1993). Although this has the advantage of accounting for behavioral and diel changes in TS, it can result in abundance estimates that are biased low if the *in situ* TS are biased high in high-density areas. Correcting for this bias by applying *in situ* TS obtained in low-density areas to high-density areas resulted in increased estimates of smelt abundance in Lake Erie in October by an average 5% (range 0–11%) in shallow waters and by 11% (range 5–18%) in deeper waters. The biases in June and July were smaller. However, for the denser smelt population present in Lake Champlain in 2001, the correction led to a doubling of the YOY smelt abundance estimates in the epilimnion in July and September. This bias can be avoided by replacing the *in situ* TS values in high-density areas with those obtained at the same depth in low-density areas. We suggest doing this if the calculated $N_v$ indices are higher than 0.1. Of course, this requires the assumption that fish in



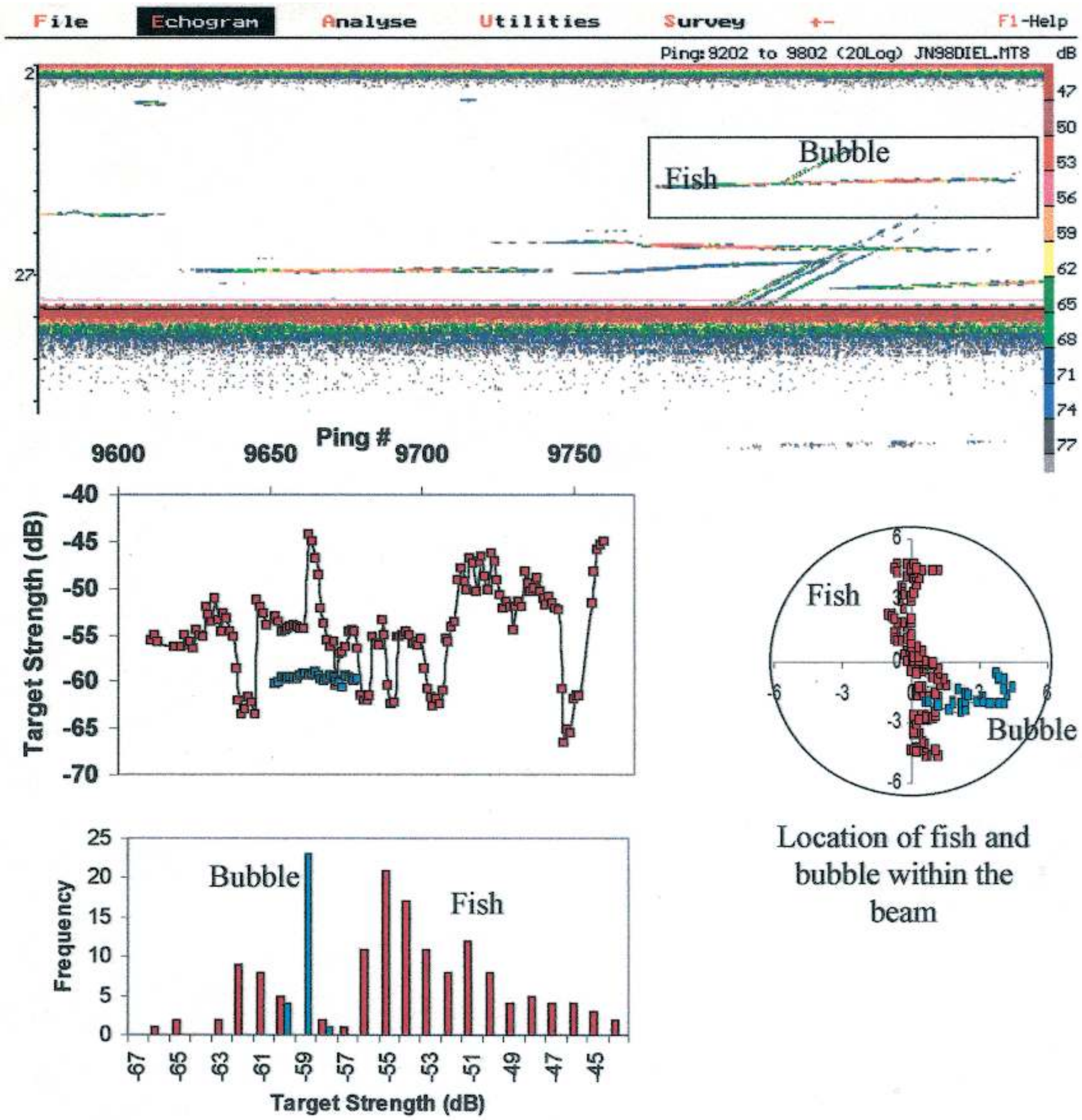


Figure 4. Example of results from a single fish collected on 5 June 1998 in Eastern Lake Erie. The fish is observed for over 150 consecutive pings as it moves slowly through the beam. A bubble is released by the fish at ping 9650 and ascends to the surface in a spiral motion (see location graph). The measured TS of the bubble (−60 to −58 dB) is within the broad range of TS measured for the fish (−67 to −44 dB). The distribution of TS from this fish has several modes. The autocorrelation of TS between successive pings suggests that these modes are the result of behavioral changes in the fish that are maintained for some time, likely a change in orientation.

denser aggregations are the same size and species as fish that are more dispersed. The alternative is to use a standard equation for TS given the species and size structure of the population, as is often done in marine surveys (MacLennan and Simmonds, 1992).

### Identification of modes in TS distributions

To investigate the identity of the modes in the TS distributions for YAO smelt observed in June and July, we analyzed data collected while anchored in Lake Erie. On these occasions, we were able to collect data from more than 20 fish that were observed for at least 30 consecutive pings. An example of the resulting distribution from one fish is presented in Figure 4. This TS distribution shows that a single smelt can give rise to a wide range of TS with multiple modes. The same pattern was observed on 3 August 1998. Multi-modal distributions from the ensemble of fish were similar to our observations from single fish at the same depth. Thus, we interpret the broad multi-modal TS distribution of smelt from our June and July surveys in Lake Erie as being caused by variability in TS from single fish rather than representing different age or size classes. In addition, age 2 and older smelt were scarce in both 1998 and 1999. Modes in the TS distribution of YAO smelt may represent two preferred orientations, possibly associated with different foraging behaviors (swimming and sit-and-wait). Orientation can dramatically affect TS by changing the aspect of the swimbladder relative to the sound beam (e.g., Horne *et al.*, 2000).

### Bubble production

On occasion, smelt released bubbles during the evening ascent (Figure 4). This is probably a response to decreasing pressure, as described elsewhere for herring (*Clupea* ssp., Thorne and Thomas, 1990; Nøttestad, 1998). The bubbles were readily detected as they rose to the surface during the stationary observation periods. The TS of these gas bubbles is between −60 and −58 dB, which is within the range observed from the fish itself. During a mobile survey, it would not be possible to separate these bubbles from fish and they will cause abundance estimates to be biased high. This phenomenon warrants further study, especially since it does not occur on all nights and at all locations. In the absence of additional information it is prudent to wait until the end of the evening ascent before surveying smelt populations.

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## References

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

Argyle, R. L. 1992. Acoustics as a tool for the assessment of Great Lakes forage fishes. Fisheries Research, 14: 179–196.

Barange, M., Hampton, I., Pillar, S. C., and Soule, M. A. 1994. Determination of composition and vertical structure of fish communities using *in situ* measurements of acoustic target strength. Canadian Journal of Fisheries and Aquatic Sciences, 51: 99–109.

Barange, M., Hampton, I., and Soule, M. A. 1996. Empirical determination of *in situ* target strengths of three loosely aggregated pelagic fish species. ICES Journal of Marine Science, 53: 225–232.

Brandt, S. B., Mason, D. M., Patrick, E. V., Argyle, R. L., Wells, L., Unger, P. A., and Stewart, D. J. 1991. Acoustic measures of the abundance and size of pelagic planktivores in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences, 48: 894–908.

Burczynski, J. J., Michaletz, P. H., and Marrone, G. M. 1987. Hydroacoustic assessment of the abundance and distribution of rainbow smelt in Lake Oahe. North American Journal of Fisheries Management, 7: 106–117.

Einhouse, D., Tyson, J., Bur, M., Deller, J., Haas, R., Murray, C., Nepszy, S., Sztramko, L., Thomas, M., Trometer, E., Rudstam, L., and Witzel, L. 1997. Report of the Forage Task Group to the Lake Erie Committee and the Great Lakes Fishery Commission, Ann Arbor, MI, USA.

Ferguson, R. G. 1965. Bathymetric distribution of American smelt (*Osmerus mordax*) in Lake Erie. Great Lakes Research Division University of Michigan Publication, 13: 46–60.

Fleischer, G. W., Argyle, R. L., and Curtis, G. L. 1997. *In situ* relations of target strength to fish size for Great Lakes pelagic planktivores. Transactions of the American Fisheries Society, 126: 786–794.

Gal, G., Rudstam, L. G., and Greene, C. H. 1999. Acoustic characterization of *Mysis relicta*. Limnology and Oceanography, 44: 371–381.

Gauthier, S., and Rose, G. A. 2001. Diagnostic tools for unbiased *in situ* target strength estimation. Canadian Journal of Fisheries and Aquatic Sciences, 58: 2149–2155.

Horne, J. K., Walline, P. D., and Jech, J. M. 2000. Comparing acoustic model predictions to *in situ* backscatter measurements of fish with dual-chambered swimbladders. Journal of Fish Biology, 57: 1105–1121.

Horppila, J., Malinen, T., and Peltonen, H. 1996. Density and habitat shifts of a roach (*Rutilus rutilus*) stock assessed within one season with cohort analysis, depletion methods and echo-sounding. Fisheries Research, 28: 151–161.

Kruse, G. H., and Dalley, E. L. 1990. Length changes in capelin, *Mallotus villosus* (Muller), larvae due to preservation in formalin and anhydrous alcohol. Journal of Fish Biology, 36: 619–621.

Lindem, T., and Sandlund, O. T. 1984. New methods in assessment of pelagic fish stocks—coordinated use of echo-sounder, pelagic trawl and pelagic nets. Fauna, 37: 105–111.

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

Love, R. H. 1977. Target strength of an individual fish at any aspect. Journal of the Acoustical Society of America, 62: 1397–1403.

MacLennan, D. M., and Simmonds, E. J. 1992. Fisheries Acoustics. Chapman and Hall, London. 325 pp.

Nellbring, S. 1989. The ecology of smelts (Genus *Osmerus*): a literature review. Nordic Journal of Freshwater Research, 65: 116–145.

Nøttestad, L. 1998. Extensive gas bubble release in Norwegian spring-spawning herring (*Clupea harengus*) during predator avoidance. ICES Journal of Marine Science, 55: 1133–1140.

O'Driscoll, R. L., and Rose, G. A. 2001. *In situ* acoustic target strength of juvenile capelin. ICES Journal of Marine Science, 58: 342–345.

Ona, E. 1990. Physiological factors causing natural variations in acoustic target strength of fish. Journal of the Marine Biology Association of the United Kingdom, 70: 107–127.

Ona, E., and Barange, M. 1999. Single target recognition. *In* Methodology for Target Strength Measurements, pp. 28–43. Ed. by E. Ona. ICES Cooperative Research Report, No. 235.

Ona, E., Zhao, X., Svellingen, I., and Fosseidengen, J. E. 2001. Seasonal variation in herring target strength. *In* Herring: expectations for a New Millennium, pp. 461–487. Alaska Sea Grant College Program.

Peltonen, H., Ruuhijarvi, J., Malinen, T., and Horppila, J. 1999. Estimation of roach (*Rutilus rutilus* (L.)) and smelt (*Osmerus eperlanus* (L.)) stocks with virtual population analysis, hydroacoustics and gillnet CPUE. Fisheries Research, 44: 25–36.

Pientka, B., and Parrish, D. L. 2002. Habitat selection of predator and prey: Atlantic salmon and rainbow smelt overlap based on temperature and dissolved oxygen. Transactions of the American Fisheries Society 131: 1180–1193.

Rudstam, L. G., Hansson, S., Lindem, T., and Einhouse, D. W. 1999. Comparison of target strength distributions and fish densities obtained with split and single beam echo sounders. Fisheries Research, 42: 207–214.

Rudstam, L. G., Lathrop, R. C., and Carpenter, S. R. 1993. The rise and fall of a dominant planktivore: effects on zooplankton species composition and seasonal dynamics. Ecology, 74: 303–319.

Rudstam, L. G., VanDeValk, A. J., and Scheuerell, M. D. 2002. Comparison of acoustic and Miller high-speed sampler estimates of larval fish abundance in Oneida Lake, New York. Fisheries Research, 57: 145–154.

Sawada, K., Furusawa, M., and Williamson, N. J. 1993. Conditions for the precise measurement of fish target strength *in situ*. Journal of the Marine Acoustic Society of Japan, 20: 73–79.

Thorne, R. E., and Thomas, G. L. 1990. Acoustic observations of gas bubble release by Pacific herring (*Clupea harengus pallasi*). Canadian Journal of Fisheries and Aquatic Sciences, 47: 1920–1928.

Warner, D. M., Rudstam, L. G., and Klumb, R. A. 2002. *In situ* target strength of alewives in freshwater. Transactions of the American Fisheries Society, 131: 212–223.

Williamson, N. J., and Traynor, J. J. 1984. *In situ* target-strength estimation of Pacific whiting (*Merluccius productus*) using a dual-beam transducer. Journal du Conseil International pour l'Exploration de la Mer, 41: 285–292.