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A method for evaluating the effects of biological factors on fish target strength

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Understanding the relationship between fish biology and target strength potentially improves the accuracy of acoustic assessments. The effects of individual biological factors (e.g., length, tilt, and depth) on backscatter amplitude have been examined, but the relative contribution of each factor has not been quantified. Dimensionless ratios, which facilitate comparison of disparate quantities, were used to evaluate the effects of individual biological factors on echo intensities. Ratios from 25 adult walleye pollock (*Theragra chalcogramma*) were calculated using a Kirchhoff-ray-mode, backscatter model parameterized for each fish. This comparative approach can be used to identify the influence of biological factors on backscatter intensity and is potentially a tool for improving accuracy when converting acoustic size to fish length.

Keywords: acoustics, backscatter, Boyle's law, fish behavior, swimbladder, target strength, tilt angle.

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Introduction

Accurate target-strength (TS) measurements are needed to convert integrated echo measurements to abundance estimates (MacLennan, 1990; MacLennan and Simmonds, 1992). The variability in TS measurements potentially reduces the accuracy of abundance estimates (Midttun, 1984; Foote, 1991; Misund, 1997). Analyses of acoustic-survey data incorporate TS regression equations that typically include only length (e.g. Foote and Traynor, 1988) as an independent variable. These equations assume equal positive and negative biases for other factors (Foote, 1980a). Biological factors such as tilt (Love, 1971; Nakken and Olsen, 1977; Blaxter and Batty, 1990), physiology (Ona, 1990), depth (Mukai and Iida, 1996), and physical factors such as frequency (Foote, 1985; Holliday and Pieper, 1995; Horne and Jech, 1998) are known to influence TS but are rarely compared with other factors (but see Vabø, 1999) or included in regression equations. Identifying and comparing the relative importance of factors that influence TS is a necessary first step towards improving the accuracy of acoustic assessments (Midttun, 1984).

Biological variation in backscatter is dependent on behavioral, morphological, ontogenetic, and physiological factors (Foote, 1980a; Ona, 1990; MacLennan and Simmonds, 1992). An air-filled swimbladder can contribute up to 90% of backscattered sound (Foote, 1980b). Length (Nakken and Olsen, 1977), tilt (Love, 1971; Foote, 1980b; Blaxter and Batty, 1990), and depth (Ona, 1990; Mukai and Iida, 1996; Gauthier and Rose, 2002) influence the shape or orientation of the swimbladder and have a major influence on TS (Ona, 1990). Frequency (Foote, 1985; Holliday and Pieper, 1995) also influences the amount of sound reflected by a fish. Reviewing the literature published on the influence of biological factors on TS, length, and tilt appear to be the more important factors followed by the influence of depth (Table 1). These factors differ in units ranging from meters to kilohertz (kHz), which prevents the direct comparison of each factor's per unit change influence on TS. A method that compares the effects of each quantity on echo intensities from individual fish would provide a useful analytic tool.

One approach that allows the direct comparison of factors with different dimensions and units (e.g., length (mm), tilt (degrees), depth (m), frequency (kHz)) is the use of non-dimensional metrics. A dimensionless ratio can compare disparate quantities because factors are converted to a unitless "common currency". Dimensionless ratios have been used to compare rates (e.g. respiration rate/pulse rate) or efficiencies (e.g. mouse heart compared with whale

Table 1. The maximum reported change in TS values.

Factor	Reported Δ in TS	Change in factor	Source
Swimbladder	>90%	Presence or absence	Foote (1980b)
Length	25 dB	500 mm	Nakken and Olsen (1977)
Tilt	30 dB	45°	Foote (1980b) (from graphs)
Depth	5 dB	35 m	Mukai and Iida (1996)
Gonads	5 dB	61% of swimbladder volume	Ona (1990) (from graphs)
Feeding	5 dB	50% of swimbladder volume	Ona (1990) (from graphs)

heart) of disparate quantities (Stahl, 1962). This approach can be adapted to quantify and rank the influence of biological and physical factors on fish TSs. As an example, the metric ($\%\Delta RSL/\%\Delta F_i$) can be used to characterize deviance in reduced-scattering length (RSL), a non-dimensional measure of backscatter intensity per percentage change in any biological factor F_i.

There are many methods used to measure TS, but examining factors in isolation is difficult. The effects of one factor, such as tilt, cannot be separated from the influence of other factors, such as length or swimbladder shape. TS can be measured *in situ* (Ehrenberg, 1983), experimentally (Nakken and Olsen, 1977), calculated from an equation (Love, 1971), or modeled based on fish anatomy (Foote, 1985; Foote and Traynor, 1988; Clay and Horne, 1994). Backscatter modeling allows manipulations of individual factors. A Kirchhoff-ray-mode (KRM), backscatter model (Clay, 1991, 1992; Clay and Horne, 1994) was used in this study because it has been validated for length and tilt (Jech *et al.*, 1995; Horne *et al.*, 2000) and because modeling depth effects on backscatter could be implemented. We combine modeled backscatter from walleye pollock (*Theragra chalcogramma*) with dimensionless ratios to quantify and compare each factor's relative influence on acoustic backscatter.

Methods

Backscatter data

Twenty-five, adult walleye pollock were imaged at the Hatfield Marine Science Center in Newport, OR. Standard lengths ranged from 350 to 600 mm. Individual fish were anesthetized in a 50-ppm bath of clove oil to suppress movement while imaging. Fish were radiographed dorsally and laterally at 60 kVp for 0.17 s using a portable XTEC Laseray 90P veterinary, X-ray unit on cassettes containing rare-earth film (Figure 1). For each image, the body and swimbladder were traced on acetate sheets, scanned, and then digitized at 1-mm resolution. To represent a fish body and swimbladder in three dimensions, dorsal and lateral points were elliptically interpolated into 1-mm thick cylinders.

The KRM-model output provides echo intensity data over specified ranges for each factor. All backscatter was calculated in the linear domain and then logarithmically converted to TS in dB. Maximum and minimum values for each factor were chosen from the literature: length 350–600 mm (Hughes and Hirschorn, 1979; Akira *et al.*, 2001), tilt 45–135° (Huse and Ona, 1996; McClatchie *et al.*, 1996), depth 100–300 m (Hughes and Hirschorn, 1979), and frequency 12–200 kHz (Foote, 1985; Horne and Clay, 1998; Horne and Jech, 1999). Backscatter was predicted for each of the 25 pollock over the range of each factor using a frequency of 120 kHz. To enable model calculations at each length within the specified range, fish bodies and swimbladders were scaled proportionately. For tilt- and depth-backscatter calculations, all pollock were scaled to 450 mm. The tilt angle of the fish was rotated from horizontal (90°) in 1° increments. Backscatter intensity was calculated while incrementing frequency in 1-kHz steps from 12 kHz to 200 kHz.

To simulate the effect of pressure on swimbladder shape and resulting echo intensity, the swimbladder volume was scaled according to Boyle's law prior to the backscatter calculation (cf. Mukai and Iida, 1996). Swimbladder compression at depth was assumed isotropic. Mean TSs from the 25 fish at depth were then converted to fish length using the current TS–length regression for walleye pollock (Foote and Traynor, 1988):

$$TS = 20 \log(\text{Length}) - 66 \tag{1}$$

where fish length is in centimeters. Predicted backscatter values were used to compare the effects and relative influ-

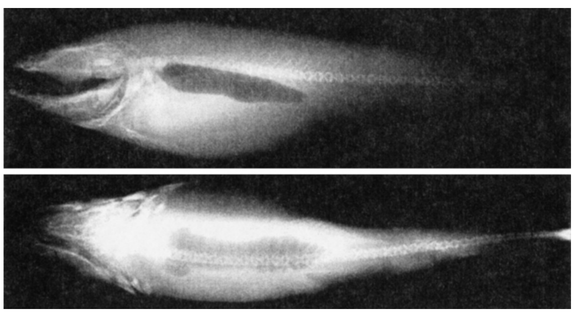

Figure 1. Walleye pollock (*T. chalcogramma*): lateral (top) and dorsal (bottom) radiographs. The swimbladder is the dark structure in the center of the body and is tilted at approximately 8° posterior.

ence of each factor on TS. When calculating dimensionless-ratio values, backscatter was calculated for each fish and then averaged across all fish at each point within a factor's range.

Dimensionless ratios

The absolute change in backscatter $|\Delta RSL|$ and absolute unit change of a factor $|\Delta F_i|$ were converted to absolute percent change $|\%\Delta|$. Percent change is calculated by dividing the absolute difference between two values, such as length by the maximum of the two ($|$length 1 − length 2$|$/max length). The greater value of F_i is used as the denominator to ensure that the ratio is independent of direction (i.e. the order of the two values). For example, the percent change between a 75 and 125 mm fish would be the same as the percent change between a 125 and 75 mm fish. The next step is to calculate a ratio of percent changes by division (e.g. %ΔRSL/%Δlength). Unitless ratios can be directly compared over equivalent interval sizes (e.g. 75 and 125 mm would result in an interval size of 50 mm). A comparison ratio can then be calculated to compare two factors by dividing the ratio for factor A by the ratio for factor B$[(\%\Delta RSL/\%\Delta F_A)/(\%\Delta RSL/\%\Delta F_B)]$. The resulting unitless ratio has three possible interpretations: if it is greater than 1, then the factor in the numerator is expected to have a greater influence on backscatter than the denominator; if it is less than 1, then the factor in the denominator has a greater influence; when the comparison ratio is equal to 1, the factors are expected to have equal influence.

Ratio applications

To compare the potential maximum effect of each factor on TS, the absolute change in each factor and corresponding RSL value were calculated and converted to a percent change. We create a dimensionless ratio $(\%\Delta RSL/\%\Delta F_i)$ by dividing the resultant percent change in RSL (%ΔRSL) by the percent change in a factor i ($\%\Delta F_i$) to quantify the maximum influence of length, tilt, depth, and frequency on echo intensity. The maximum-to-minimum range of RSL values for each factor is used to calculate the maximum-intensity change as a proxy for the maximum influence of any factor. The resulting values can then be ranked to determine the relative maximum influence of each factor on TS.

Contour plots allow comparison of ratio values at multiple intervals and visually contrast each factor's relative influence on backscatter. Each ratio is calculated from the smallest to the largest value within a factor's range at an interval size of 1. The resulting ratios with an interval size of 1 are averaged and stored in a matrix of contour values for factor i. This process is repeated, incrementing the interval by 1 until the increment size equals the entire range of the factor. Percent change in RSL of factor i at a starting value of j with an interval size of k is:

$$\%\Delta RSL_{i,k} = \frac{|RSL_{i,j} - RSL_{i,j+k}|}{RSL_{max}}. \tag{2}$$

Using a tilt range of 70–110° as an example, with $j = 0$ and $k = 1$, the ratio would first be calculated at 71° and 70°. An index of $j = 1$ ($k = 1$) would correspond to 72° and 71°. An index of $k = 2$ ($j = 1$) would correspond to 73° and 71°. The ratios are then averaged at each interval size until an average is determined for the entire range (i.e. $k = 1$ through 30). The interval size for any two factors $(i = 0, 1)$ is plotted on the graph with contour values equal to the comparison ratio $(M_{0,k}/M_{1,k})$, where $M_{0,k}$ represents the interval average for the factor on the y-axis and $M_{1,k}$ represents the x-axis factor. Contour lines are then drawn at the appropriate point between nodes using a triangular interpolation scheme, where triangles are created by connecting the points in the plane using straight-line segments. A least-squares-error fit of the data to a bivariate polynomial is used for smoothing. Interpolation along the edges of the triangles is used to create the contours. A reference line is plotted to show the average comparison ratio along equal interval sizes.

Results

Before ratio values can be determined, the effect of pressure on swimbladder shape and resulting backscatter intensity must be estimated. As swimbladder size decreases due to pressure, the TS of the fish also decreases (Figure 2). An initial TS was calculated for 25 fish, all scaled to a length of 400 mm. As pressure increased with depth from 0 to 300 m, the average estimated fish length from Foote and Traynor's

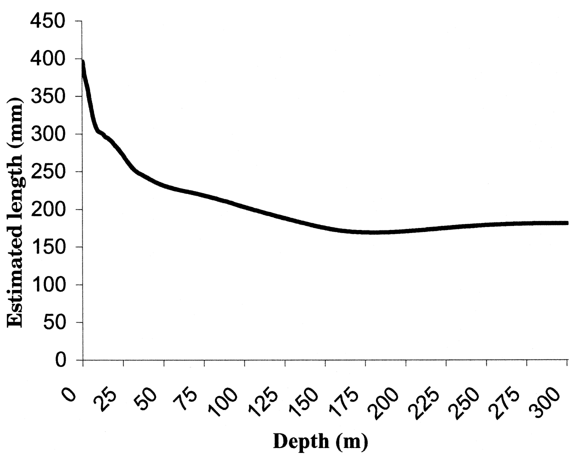

Figure 2. The estimated average length of 25 walleye pollock (*T. chalcogramma*) calculated from modeled TS at 120 kHz and the TS = 20 log(L) − 66 (Foote and Traynor, 1988) equation.

Table 2. A comparison of maximum echo-intensity changes in length, tilt, and depth. F_i is the range of each factor. ΔF_i is the corresponding change in RSL value calculated at 120 kHz. ΔRSL is the absolute change in RSL divided by the maximum of the range. $\%\Delta F_i$ is the absolute change in RSL divided by the corresponding maximum RSL value. The maximum-influence ratio is %Δ RSL/$\%\Delta F_i$.

F_i	ΔF_i	Δ RSL	$\%\Delta F_i$	%Δ RSL	Maximum-influence ratio
Tilt (degrees)	35	0.07	0.44	0.91	2.08
Length (mm)	148	0.01	0.26	0.13	0.49
Depth (m)	80	$\ll$0.01	0.80	0.17	0.21

(1988) equation decreased from 400 to 180 mm, a reduction of 55%. The largest rate of decrease in estimated length occurred within the first 50 m. Estimated fish length decreased only 50 mm through a depth change from 50 to 300 m.

Ratios of each factor pair were used to compare each factor's relative maximum influence on echo intensity. Fish tilt has a greater maximum influence on acoustic backscatter than length or depth. The maximum-influence ratios were approximately 2 for tilt, 0.5 for length, and 0.2 for depth (Table 2). Over a tilt range of 35°, the RSL value changed 0.07 units compared with an RSL change of 0.01 over a 148 mm length range. Depth had an absolute change in RSL value of less than 0.001 over an 80-m depth change.

Comparison ratios and corresponding contour plots were used to evaluate each factor's effect on acoustic backscatter. Tilt has a larger effect on backscatter than length (Figure 3). Comparison-ratio values ranged from 5 to 2 along the 1 : 1 reference line (i.e. equal interval sizes such as 50 mm and 50°). The ratio of rates approaches 1 at small and large ranges of tilt (<2° or >70°) and large length intervals (>200 mm). The contour plot of length versus depth (Figure 4) agrees with the results of the numeric, relative maximum influences (Table 2). The comparison ratio (i.e. the change in echo intensity due to swimbladder compression over the change in echo intensity due to length) is less than 1, indicating that length has a greater influence on TS than depth. The exception is at extremely large- and small-length intervals where the ratio of rates approaches 1.

The relative influence of frequency on TS has not been compared with that of biological factors. Using a similar approach, comparison ratios were calculated and each biological factor was contoured against frequency on the x-axis (Figure 5). Tilt had a greater influence on TS than frequency except at extreme tilt angles. Both length and depth had a smaller ratio of percent changes (i.e. a comparison ratio <1) throughout most of the plots than frequency (Figure 5b, c). Both factors influence echo intensity less than frequency, except at frequency intervals close to 1 kHz, where factors have equal influence. The resulting hierarchy of importance (tilt > frequency > length > depth) agrees with the maximum intensity comparison of tilt, length, and depth at the same frequency (Table 2).

Discussion

We used a group of 25 adult walleye pollock to examine the influence of biological factors and frequency on changes in TS. The results of this study should be applicable in the case of other walleye pollock life-history stages. Contour plots of juvenile pollock ratios, not shown, differed in pattern from those observed for the adults, but the relative

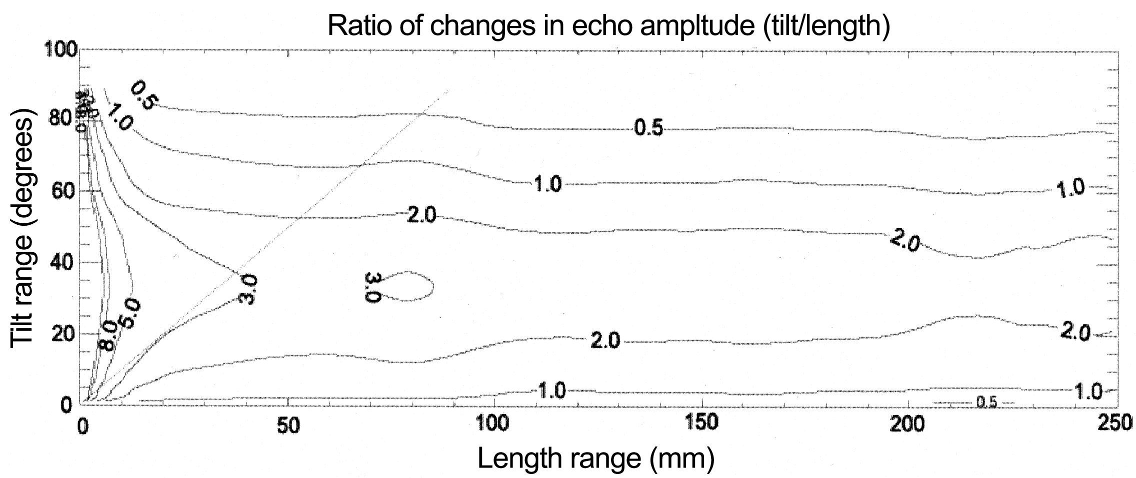

Figure 3. Comparison ratios $[(\%\Delta RSL/\%\Delta tilt)/(\%\Delta RSL/\%\Delta length)]$ for tilt (F_A) plotted against length (F_B) from 45° to 135° degrees and 350–600 mm on echo intensity at 120 kHz. The x- and y-axes are the interval sizes for each factor. The diagonal line identifies equal interval sizes.

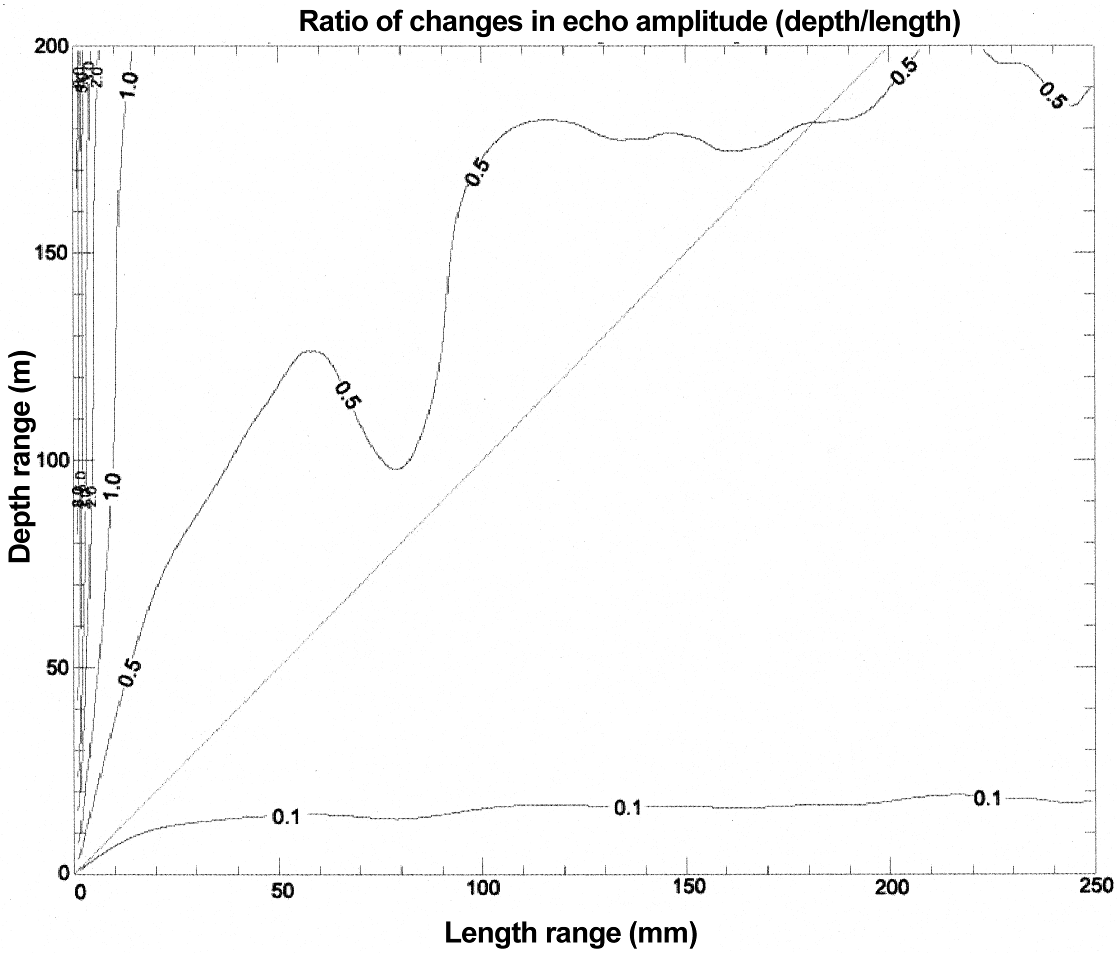

Figure 4. Comparison ratios [(%ΔRSL/%Δdepth)/(%ΔRSL/%Δlength)] for depth (F_A) plotted against length (F_B) through ranges of 100–300 m depth and 350–600 mm length at 120 kHz. The x- and y-axes are the interval sizes for each factor. The diagonal line identifies equal interval sizes.

rankings of the biological factors and frequency remained the same. Backscatter modeling generated data that included simultaneous and continuous ranges of fish tilt, length, and the effects of pressure on the swimbladder. Forming dimensionless-ratio values from backscatter predictions created a common currency that facilitated continuous graphical representation and comparison among factors.

While length is often the main factor in TS regressions, the influence of tilt and frequency on TS is greater than that of length per-unit-change:

Tilt > Frequency > Length > Depth

Tilt has been shown to have a major influence on TS (Foote, 1980c; Blaxter and Batty, 1990; Horne and Jech, 1999). This ranking corroborates Foote's (1980c) assertion that tilt needs to be incorporated in TS regressions. During an acoustic survey, large sample sizes will contain TS measures from a variety of fish orientations. Non-unique TS values for multiple tilt angles (i.e. ascending and descending limbs of a TS–tilt curve) potentially decrease the effect of tilt relative to other factors and may reduce the average TS of the population (Foote, 1980a). If a consistent behavioral bias exists, such as head-up swimming at night (Huse and Ona, 1996) or fish diving to avoid a vessel (Mitson, 1993), averaged TSs may degrade the accuracy of the abundance estimates.

Acoustic sampling should be designed to minimize changes in fish tilt by surveying when tilt angles average to horizontal or are least variable. Foote (1980c) used normal distributions of tilt angles to represent tilt functions quantitatively in TS regressions. Acoustic-survey analyses that include individual target tracking (e.g., Ehrenberg and Torkelson, 1996; Huse and Ona, 1996) potentially provide tilt-angle distributions that can be used in TS regressions (Foote, 1980b). Fish tilt angles are variable (e.g. 12° to −5.6°; McClatchie *et al.*, 1996), depending on the activity of the fish (Torgersen and Kaartvedt, 2001). Frequency

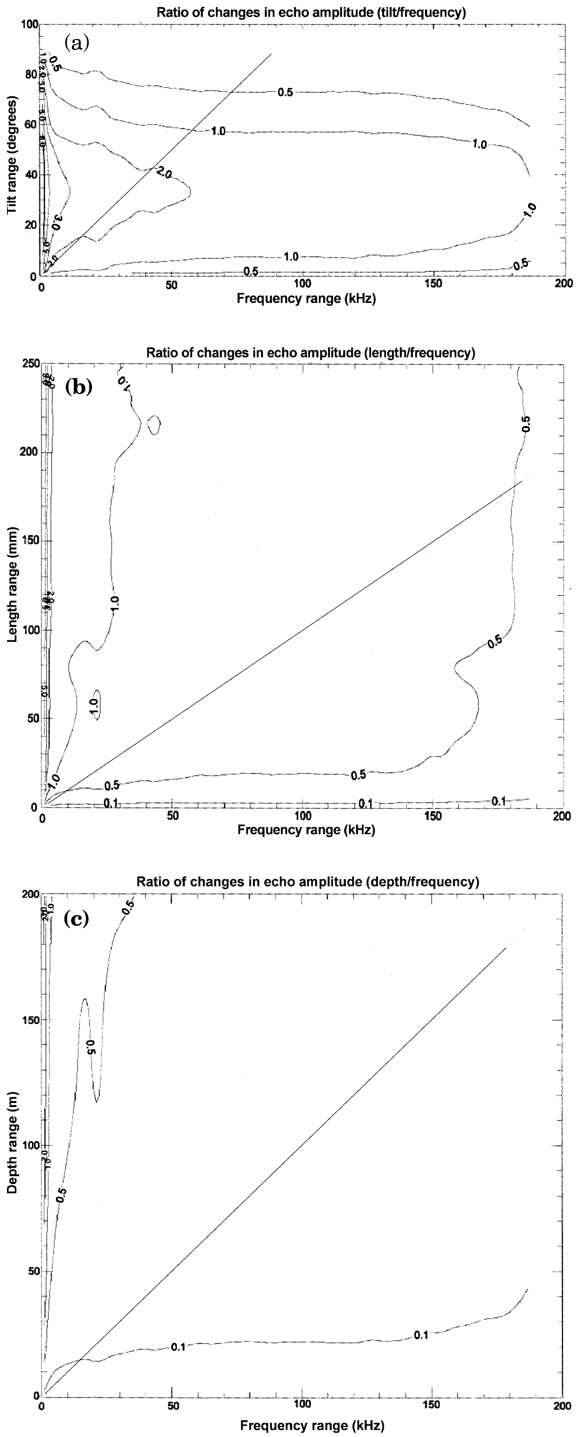

Figure 5. Comparison ratios for F_A plotted against F_B; (a) tilt against frequency, (b) length against frequency, and (c) depth against frequency. The x- and y-axes are the interval sizes for each factor. The diagonal line identifies equal interval sizes.

influences TS. Our analyses support Foote's (1985) and Horne and Clay's (1998) statements that it is important to choose an appropriate carrier frequency based on the size of the organisms being ensonified. As the effect of frequency is related to fish length (Foote, 1985; Horne and Clay, 1998; Horne and Jech, 1999), the ratio of L/λ should be used when choosing frequency instead of frequency in isolation. As L/λ increases, the influence of tilt angle on TS generally increases (Horne and Clay, 1998).

Depth did not have as great an effect on TS as length or tilt. We assumed the isometric contraction of the swimbladder with pressure because we do not know how the shape of walleye pollock swimbladder changes with pressure; but see Figure 7 of Blaxter and Batty (1990). We do know that the volume of gas in the swimbladder must follow Boyle's law and have adjusted the shape to conform to volume changes. The most dramatic change in apparent fish length due to changes in TS occurred in the top 50 m of water. Since adult pollock are often found below 100 m (Hughes and Hirschorn, 1979), the effect of depth per-unit-change is reduced compared with that in shallow waters.

The effect of depth on walleye pollock TS should be common among other physoclist species. Physoclists regulate gas through secretion and absorption (Blaxter and Tytler, 1978; Blaxter and Batty, 1990; Ona, 1990). Any sudden change in depth will cause the gas volume in the swimbladder to conform to Boyle's law (Mukai and Iida, 1996). Gas-volume change may not directly affect TS. Gauthier and Rose (2002) found that the TS of redfish (*Sebastes* spp.) did not decrease with depth, as Mukai and Iida (1996) suggested. Additional measures of swimbladder shape and volume under pressure are needed to verify swimbladder compression and the subsequent effects on TS. Fish with wax-filled swimbladders (cf. Kloser *et al.*, 1997), physostomous species (cf. Thorne and Thomas, 1990; Nøttestad, 1998), or species lacking swimbladders (cf. McClatchie *et al.*, 1999) could have different rankings of factors.

Comparing the relative influence of biological factors on changes in TS allows managers to assess which factors need to be considered when converting acoustic size to fish size. There are many ways to compare the effects of each factor on TS. The absolute change in linear backscatter measures the intensity difference between the maximum and minimum value but is independent of the rate of change. A percent ratio averages all rate values at an interval size of 1. A maximum-influence ratio is calculated from the maximum and minimum RSL values within a factor's range. The maximum-influence ratio incorporates intensity and rate into the calculation. Table 3 compares metrics from the three different methods used to examine the relative influence of biological factors. The absolute change in the RSL metric ranks length and depth above tilt. Both the percent ratio and maximum-possible-influence ratio metrics rank tilt above length and depth. Depth has a greater possible intensity change than tilt, but when the

Table 3. Comparison of the three techniques used to compare a factor's influence on the TS of walleye pollock varying 45–135° (tilt), 350–600 mm (length), and 100–300 m (depth). |Δ RSL| is the absolute change in RSL calculated at 120 kHz from the minimum and maximum of the factor's range. Percent ratio is (%Δ RSL/%Δ F_i) calculated as a percent change (i.e. an interval size of 1). The maximum influence ratio (%Δ RSL/%Δ F_i) is calculated using maximum RSL values within the range.

Factor	|Δ RSL|	Percent ratio	Maximum-influence ratio
Tilt (degrees)	0.00017	5.62	2.08
Length (mm)	0.0037	1.62	0.49
Depth (m)	0.0024	0.199	0.21

rate of change is considered, tilt has the greatest relative importance. The comparison ratio used in all contour plots is the most powerful tool for comparison because it incorporates intensity and rate of change at any interval size.

Earlier TS studies (Love, 1971) suggest that variability in TS measurements is not very important. Our study shows that additional factors contribute to echo intensity and variability other than those traditionally used in TS–length regressions. Behavioral factors contribute to variability, but at different rates. Sampling rates need to correspond to the rates of change of interest. Identifying and quantifying the sources of TS variability will continue to increase the accuracy of acoustic-based length and abundance estimates.

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