

Target strength of the lanternfish, *Stenobranchius leucopsarus* (family Myctophidae), a fish without an airbladder, measured in the Bering Sea

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This paper reports theoretical values of target strength (TS) for the lanternfish *Stenobranchius leucopsarus*, a fish without an airbladder, which dominates the Subarctic marine mesopelagic fish community. Two models for liquid-like slender bodies, the general prolate-spheroid model (PSM) and the deformed-cylinder model (DCM), were used to compute the TS of the fish relative to its orientation. The relative mass density g and the sound speed h in seawater were measured and used in both models. To confirm the appropriateness of the models, tethered experimental measurements were carried out at 38 kHz for five specimens. The value of g measured by the density-bottle method was very low (1.002–1.009) compared with that of marine fish in general. The value of h measured by the time-average approach was 1.032–1.039 at the water temperature at which *S. leucopsarus* is found. TS-fluctuation patterns against fish orientation (the TS pattern) estimated from the DCM and PSM were in good agreement in the area of their main lobes. Both models reproduced the main lobes of the measured TS patterns in near-horizontal orientation ($< \pm 20^\circ$), and they were considered to be effective in measuring the TS of *S. leucopsarus* in a horizontal (swimming) position. After these comparative experiments, we computed the TS of 57 fish (27.8–106.9 mm) at 38, 70, 120, and 200 kHz, using the DCM. A plot of body length (in log scale) against TS showed a non-linear relationship at all frequencies. *S. leucopsarus* had a very low TS (< -85 dB, TS_{cm}), suggesting that acoustic assessment would be highly sensitive, especially when the proportion of small fish is high (e.g. $L/\lambda < 2$), and an appropriate frequency should be considered that takes into account both the length composition and the depth of occurrence.

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Introduction

Stenobranchius leucopsarus is one of the most abundant members of the mesopelagic fish community of the Subarctic Pacific (including the Bering Sea and Sea of Okhotsk), and is an important prey for larger fish, seabirds, and marine mammals, and an important predator of zooplankton (Beamish *et al.*, 1999). For a better understanding of the Subarctic marine ecosystems reliable biomass data of the species in the region are needed, but just not available. This is because conventional methods of biomass estimation using many types of net gear have highly inherent

bias associated with net avoidance (Holliday and Pieper, 1995; Medwin and Clay, 1998).

Acoustic methods are considered to be a more reliable approach to the estimation of the biomass of mesopelagic fish, including *S. leucopsarus* (Koslow *et al.*, 1997; Benoit-Bird and Au, 2001). Acoustic surveys measure the amount of scattered sound in the water column, so we must know the target strength (TS) of individual fish to convert the measured backscattered energy into estimates of fish biomass. TS has been measured directly with split- or dual-beam echosounders (*in situ* measurement) for many fish species (Ehrenberg, 1983; Foote, 1991). *S. leucopsarus*,

however, is difficult to detect as a single target in the field, because it occurs in deep water (200–400 m) and does not have a gas-filled swimbladder that can provide high acoustic reflection (Taylor, 1968; Yasuma, 2004); *in situ* TS measurements are therefore not available. On the other hand, TS can also be computed from theoretical sound-scattering models for *S. leucopsarus*. The purpose of this study was to obtain reliable estimates of TS and its frequency characteristics using theoretical-model computations.

Theoretical models approximate the target organism as a geometric configuration, and many useful approximate methods have been developed to date (Ye, 1997). The use of theoretical models for estimating TS has several merits; they can estimate, for example, both the frequency characteristics of backscatter, and the backscatter pattern related to fish orientation, and can reduce the number of experimental measurements. However, there is no single theoretical model that applies to all fish. The approximate shape and applicable condition vary with each model, so we must confirm the appropriateness of a given model for each target fish species by comparison with experimental TS measurements. Additionally, if the target species does not contain any gas in its body, like *S. leucopsarus*, the use of a theoretical model requires estimates of the parameters g , the mass density of the body relative to that of the surrounding water, and h , the relative sound speed of the body. In this study, we first measured the values of g and h for *S. leucopsarus* for use in two theoretical models: the prolate-spheroid model (PSM; Furusawa, 1988) and the deformed-cylinder model (DCM; Ye et al., 1997). Then, tethered experimental (*ex situ*) measurements at 38 kHz were made to compare the estimated results of both models. Finally, we estimated the theoretical TS of *S. leucopsarus* at the frequencies commonly used in scientific echosounders, namely 38, 70, 120, and 200 kHz.

Material and methods

Fish samples

All fish samples were obtained in the winter of 2002 as part of a Bering Sea pollock survey conducted by the Hokkaido National Fisheries Research Institute of Japan. They were collected in the deep-scattering layer (280–400 m deep) around Unalaska Island, Alaska (51°30′–54°30′N, 165°00′–179°30′W), in seven tows of a large midwater trawl approximately 200 m long with a net opening of 50–60 m and a codend of 12 mm mesh. Hauling speeds were slow (about 0.6 m s⁻¹) to reduce damage to the fish. Live individuals were selected from the catches and kept for several hours in a tank on board, after which they were placed in plastic specimen bottles containing seawater and frozen at -40°C.

Measurement of body-mass density and sound speed

In the laboratory, the specimen bottles were thawed slowly in cold water. A subsample of 94 individuals (31.0–104.0 mm

standard length, SL) was used to measure the body-mass density, ρ , via a density-bottle method (Greenlaw, 1977; Mikami et al., 2000). In this method, fish mass density was determined by evaluating the buoyancy of each sample via a series of 1000 ml beakers containing seawater–glycerol solution of different density, ranging from 1.026 (seawater) to 1.100 g cm⁻³ at 0.002 g cm⁻³ steps. We defined the value of the bottle in which the fish was neutrally buoyant as fish mass density. If the specimen was not neutral in any solution, an average between the last sinking bottle and the first floating bottle was taken. The relative mass density g was obtained by dividing ρ by the density of seawater (1.026 g cm⁻³). We used water sampled 300 m deep to determine the value of seawater density. The density of each bottle was confirmed using a glass areometer (standard 15°C), and the solution in each bottle was kept at 15°C. The speed of sound through the fish body was estimated by a time-average approach. The underlying principle is based on the measurement of the time-of-flight of acoustic pulses through a uniform mixture of water and marine organisms, where the volume of water and animals is estimated (Greenlaw, 1977; Foote, 1990).

We used an acrylic ‘T-tube’ (Foote, 1990; Mikami et al., 2000) for the measurement (Figure 1). A continuous, sinusoidal-wave pulse of 400 kHz, 5 μ s was radiated from one side of the tube to the other, and the time it took the pulse to pass through the tube containing seawater and fish was measured with a digital oscilloscope.

In the time-average approach, an empirical equation is used to relate passing time T_{total} through the mixture to the proportion of the volume filled by animals V as

$$T_{\text{total}} = (1 - V)T_{\text{sw}} + VT_{\text{fish}}, \quad (1)$$

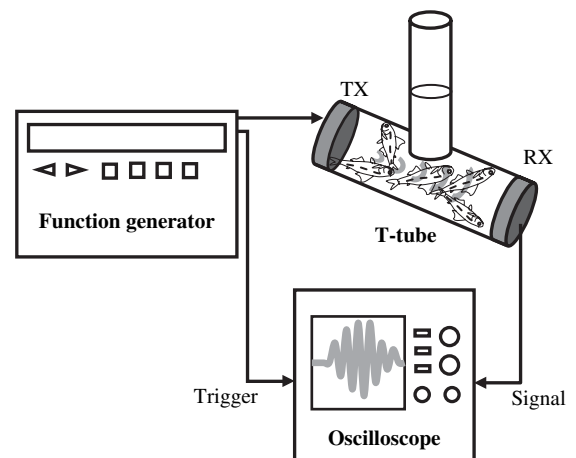


Figure 1. Instrumentation for sound-speed measurement of *S. leucopsarus*. PZT-transducers are mounted on each side of the T-tube. The bore of the tube is 40 mm and the measurement distance 200 mm.

where T_{sw} and T_{fish} are the “passing time” of sound through the seawater and through the fish body, respectively. The sound speed ratio h is given by

$$h = \frac{T_{sw}}{T_{fish}} = \frac{C_{fish}}{C_{sw}}, \quad (2)$$

where C_{sw} and C_{fish} are the speed of sound through seawater and fish body, respectively. As C_{sw} is known from T_{sw} , the measurement distance (20 mm), C_{fish} can be deduced. The fish proportion, V in Equation (1), was estimated by submerging a fish specimen in a graduated cylinder after the measurement. In all, 13 adult fish of about 100 mm SL were used, and V was 0.55. The optimum range of V is 50–60% for the T-tube measurements of sound speed through the fish body (Yasuma, 2004). The T-tube was sunk in a temperature-controlled tank and measured between 2°C and 23°C at 1°C steps.

Models of sound scattering by fish

As *S. leucopsarus* has no gas in its body, it was modelled as a liquid-filled, slender scatterer, following Ye and Farmer (1997) and Sawada *et al.* (1999). We selected the liquid, prolate-spheroid model (PSM) and the liquid, deformed-cylinder model (DCM) to compute the backscatter from a liquid-like, slender body related to its orientation. In both models, the body was approximated as a given geometric shape based on the outlines of its dorsal and lateral aspects, obtained by tracing digital photo images of each. The mass density and speed of sound through the body are the most important physical parameters in both models.

The PSM approximates the body shape as a spheroid, using its major and minor axes. We defined fish SL as the major axis, and the average value of body height and body width as the minor axis, measuring outlines of the dorsal and lateral aspects. Although the PSM is generally unable to account for the detailed body shape, because it is exact in general solutions, it can provide guidance for other models. Also, from its general properties, it can provide general trends of scattering by fish. Details of the model are described in Furusawa (1988) and Furusawa *et al.* (1994).

The DCM describes a fish body shape as a series of adjacent, disc-like, cylindrical elements. We divided each outline into 20 equal parts, with 19 lines drawn perpendicular to the major axis, following Sawada *et al.* (1999). Although the DCM describes the body shape more precisely than the PSM, there are theoretical limitations. A peculiar limitation of this model is that the aspect ratio has to be large (approximately >5) and the fish-tilt angle not be too large (approximately <50°; Sawada *et al.*, 1999). Our calculations are within these limitations. Details of this model are described in Ye (1997) and Ye *et al.* (1997). The DCM can produce results in reasonable agreement with the exact PSM (Ye *et al.*, 1997).

Experimental measurement

To confirm the appropriateness of the two theoretical models, tethered experimental measurements were carried out at the National Research Institute of Fisheries Engineering (NRIFE), Japan. An indoor tank measuring 10 m × 10 m × 15 m was used with a 38-kHz echosounder for measuring TS. The tank was filled with freshwater. Although marine fish are better measured in seawater, it was not possible to use it in this case. Theoretical models, however, can estimate the TS when the surrounding physical parameters change, and we calculated the theoretical TS assuming that each fish was in freshwater. This point is discussed later.

The fish suspension and rotating system followed that of Sawada (2002), with some modifications (Figure 2). A 38-kHz transducer mounted on the bottom of the tank transmitted pulses (pulse width 0.6 ms; beam width 6.2°; repetition period 213 ms) to the water surface, and received the echoes from the on-axis fish. Each fish was stitched with nylon lines through snout and tail to keep it upside-down (Figure 2), then located between vertical suspension lines. These vertical lines were connected to two sides of a rotating bar mounted on the axis of a stepping motor. The vertical lines were kept taut using a weight-and-pulley system. The distance between the transducer and the fish was about 5.5 m, sufficient to satisfy a far-field condition (Sawada, 2002). A 38-mm standard sphere (tungsten carbide) was suspended at about the same depth as the fish before the calibration. Additionally, the temperature and the sound speed through the surrounding water were measured just before the TS measurement.

Five fish (59.2–101.1 mm SL) were used for the measurements. Each specimen was thawed and placed in the water tank without being exposed to the air. We revolved the stepping motor from –50° to +50° (head-down to head-up aspect) in 1° steps, and recorded five pings at each angle. Additional details of the experimental set-up and data-recording process are given in Sawada (2002).

For both model estimation and experimental measurement, we defined the maximum TS as the peak value in the plot of TS against fish-tilt angle. The tilt-angle distribution is required to calculate the average TS, according to Foote (1980a). In this study, we applied a distribution within a mean of 0° (horizontal direction) and a standard deviation of 15°. It is often convenient to normalize the TS by length-squared. This is termed the reduced TS (dB) and shown as TS_{cm} when fish length is in centimetres.

Results

Mass density and speed of sound through the fish body

The body-mass density, ρ , ranged from 1.027 to 1.044 g cm⁻³ ($g = 1.002–1.019$) and averaged 1.033 g cm⁻³. There was no significant relationship between mass density

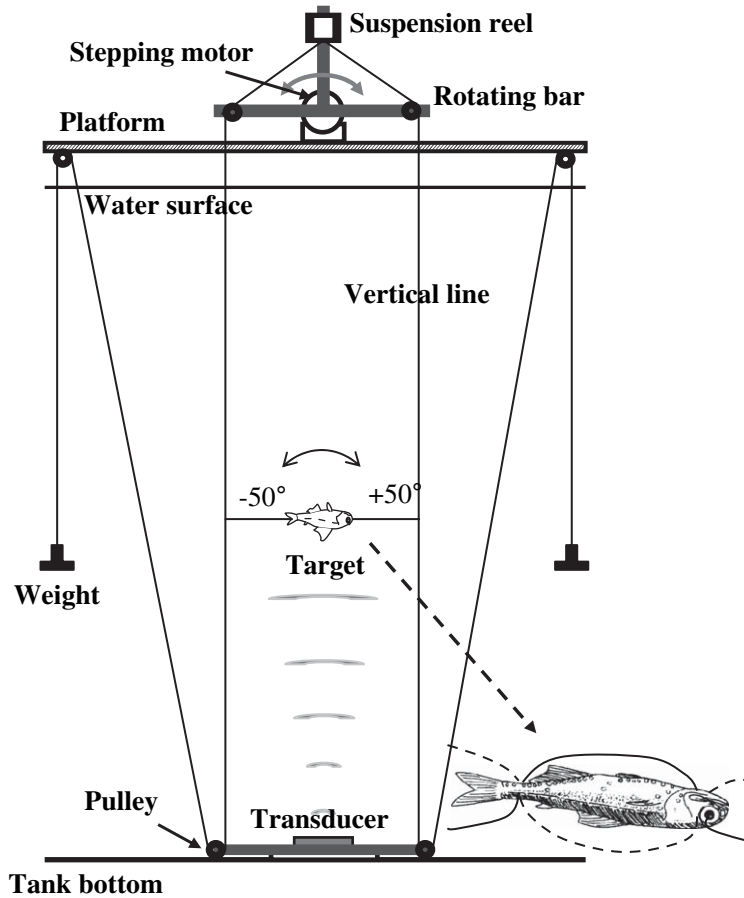


Figure 2. The suspension and rotating system for TS measurement. A 38-kHz transducer is mounted on the bottom of the tank. The fish was kept upside-down with two nylon lines pinching the body. The distance between the bottom and the water surface is about 9 m, and that between the transducer and the fish specimen is about 5 m.

and standard length (Figure 3). The sound speed through seawater, C_{sw} , the sound speed through the fish, C_{fish} , and the relative sound speed through the fish body, h , are listed in Table 1. Sound speeds through both seawater and fish increased with temperature. The sound speed was higher in the body of the fish than in seawater within the temperature range examined (Table 1). The relative sound speed, h , was high (about 1.035) below 6°C, decreased between 7°C and 15°C, and was very low (about 1.010) above 20°C. This means that given its habitat temperature, the h of *S. leucopsarus* is between 1.032 and 1.039 (Table 1).

Comparison of experimental and model results

The experimental and model-based TS are plotted against the tilt angles (TS patterns) in Figure 4, and the values of maximum and average TS are given in Table 2. In the theoretical-model computations, we used parameters according to tank water temperature (10°C), and our

measurements of body-mass density and sound speed: the sound speeds in freshwater and the fish were 1451 and 1531 m s^{-1} ($h = 1.055$), respectively; and the densities of freshwater and fish were 1.000 and 1.035 g cm^{-3} ($g = 1.035$), respectively.

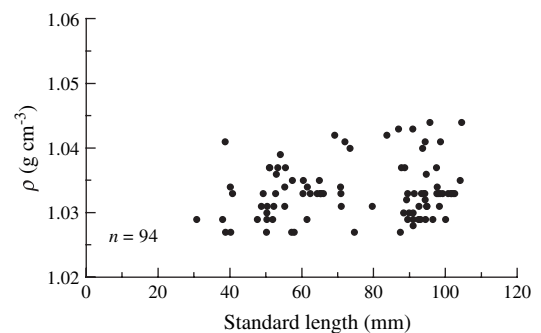


Figure 3. The relationship between mass density ρ and standard length of *S. leucopsarus* measured by the density-bottle method.

Table 1. The speed of sound through seawater, C_{sw} , and through the fish body, C_{fish} , and the relative sound speed through the body, h , by temperature. Proportion of sample volume to the volume of T-tube, V , and sample number and mean length \pm s.d. put in the T-tube are given. Emboldened values are the temperatures at which *S. leucopsarus* are found in the wild (Watanabe *et al.*, 1999; Moku, 2000).

$V = 55\%, 12(93.9 \text{ mm} \pm 6.5)$			
Temperature ($^{\circ}\text{C}$)	C_{sw}	C_{fish}	h
2	1448	1505	1.039
3	1452	1508	1.038
4	1457	1510	1.037
5	1461	1514	1.037
6	1465	1519	1.037
7	1469	1521	1.036
8	1472	1520	1.032
9	1476	1519	1.029
10	1480	1518	1.026
11	1483	1519	1.024
12	1487	1520	1.022
13	1490	1520	1.020
14	1494	1524	1.020
15	1497	1522	1.017
16	1500	1526	1.017
17	1503	1529	1.017
18	1506	1528	1.015
19	1509	1530	1.014
20	1512	1529	1.011
21	1514	1532	1.012
22	1517	1532	1.010
23	1520	1535	1.010

In the experimental measurements, the TS of all five fish peaked when the head was positioned slightly downwards (-5° to -8°). These peaks were quite narrow and pronounced, suggesting that changes in fish orientation would have a major effect on TS variance (Figure 4). The values of measured maximum TS were very low (-56 to -67 dB), and there was a 5–6 dB difference between the maximum and the average TS (Table 2).

The estimated TS patterns of the DCM and the PSM were in good agreement, especially in the area of the main lobe (Figure 4). The respective values of the maximum and average TS are also close (Figure 4, Table 2). The main lobes of the measured TS pattern are accurately described by both models, although there were differences between measured and modelled patterns at steep angles ($> \pm 20^{\circ}$), especially for larger fish (Figure 4). The measured maximum and averaged TS were about 2–3 dB lower than model estimations for two fish (numbers 3 and 4; Figure 4, Table 2). However, in those fish, the experimental and the model results agreed more closely than in earlier comparative studies (e.g. Sawada *et al.*, 1999), and other fish also showed very good agreement. Therefore, we

considered both models to be suitable for estimating the TS pattern of *S. leucopsarus*.

TS estimation using a theoretical model

As there was good agreement between the measurements and the models, practical TS patterns were calculated from a wider range of frequencies using the DCM. In total, 57 juveniles and adults (27.8–106.9 mm SL) were studied at 38, 70, 120, and 200 kHz, the frequencies widely used in studies with scientific echosounders. In these computations we used the following parameters in reference to CTD data at the capture site (water temperature 4°C ; salinity 33.8 psu): the sound speeds in seawater and in the fish body were 1466 and 1510 m s^{-1} , respectively; and the densities of freshwater and fish body were 1.025 and 1.035 g cm^{-3} . The sound speed through seawater was calculated using Mackenzie's equation (Mackenzie, 1981).

The reduced average values of TS are shown in Figure 5 as a function of the standard length divided by the wavelength (L/λ). They vary about the asymptotic values (-85 to -89 dB) for $L/\lambda > 2$. For $L/\lambda < 1$, the Rayleigh scattering regime, they are very low, and increase as L/λ approaches about 2.

Figure 6 shows the relationship between average TS and the logarithmic scale of fish standard length (cm), at the four frequencies. Within the limits of body length used for model calculation, non-linear fitting was better at all frequencies. Results of the non-linear regressions are listed in Table 3.

Discussion

Mass density and sound speed of fish body

For a 10 cm liquid-spheroid, Yasuma (2004) reported that a 3% shift of relative mass density and sound speed caused a 3–5 dB difference in the maximum TS estimated from the PSM and the DCM. As a slight variation in body-mass density and sound speed would lead to a major change in the TS of a fish without a swimbladder, it is important to know the values of these parameters for target species before applying theoretical models.

Relative sound speeds, h , decreased as temperature increased (Table 1). The difference between the maximum (1.039) and the minimum (1.010) values of this parameter in our measurements was about 3%. Although there is little information on the sound speeds of aquatic organisms in relation to water temperature, *Euphausia pacifica* occupies a similar temperature range as *S. leucopsarus* (Mikami *et al.*, 2000). *S. leucopsarus* is widely distributed in Subarctic oceans and undergoes extensive vertical migrations (Beamish *et al.*, 1999), suggesting that it will be found over a wide range of temperature. Therefore, it is critical that the value of h selected that takes account of the

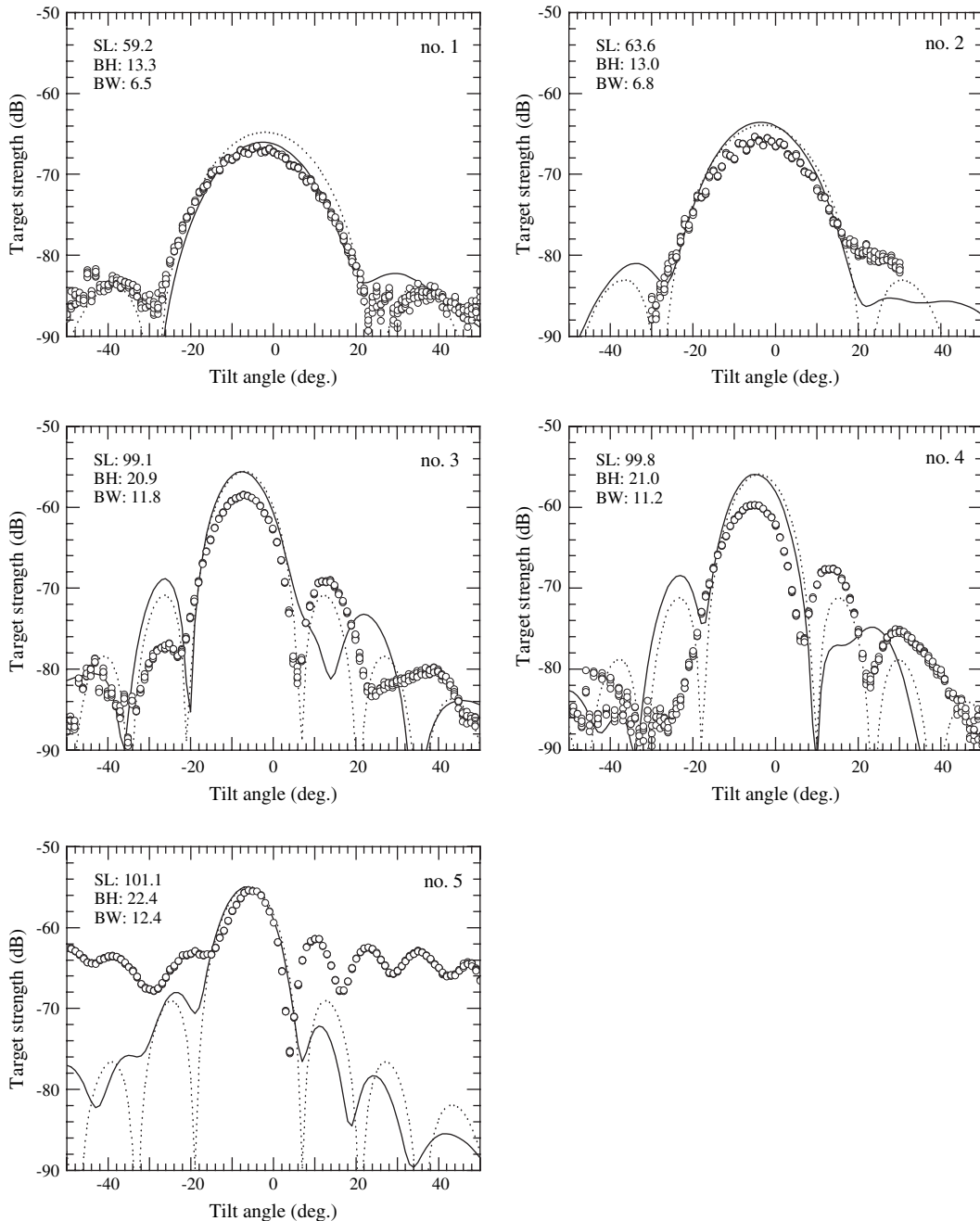


Figure 4. Theoretical and experimental TS as functions of tilt angle. Experimental measurements are shown by open circles. Results from the PSM and the DCM are shown by the dashed line and the continuous line, respectively. Fish number, standard length (SL), body height (BH), and body width (BW) are noted for each.

temperature of the different habitats in which the species is found.

Body-mass density, on the other hand, was measured at a constant temperature. However, the mass densities of seawater and of lipid, a major component of myctophid bodies, change less than 0.03% between 4°C and 30°C; such

a change is negligible (Butler and Pearcy, 1972; Neighbors and Nafpaktitis, 1982). Salinity variation may also influence the value of g . Although we used local seawater (33.8 psu) to determine the value of g , salinity will change with area and depth. However, a total of 25 CTD casts from surface to 500 m deep conducted in the survey area revealed that

Table 2. The value of maximum TS (TS_{\max}) and average TS (TS_{ave}) from experimental measurement, PSM, and DCM in freshwater.

Fish number	TS_{\max} (dB)			TS_{ave} (dB)		
	Measurement	PSM	DCM	Measurement	PSM	DCM
1	-66.7	-64.8	-66.1	-69.8	-67.7	-69.2
2	-65.4	-64.0	-63.6	-69.0	-67.0	-66.9
3	-58.5	-55.6	-55.6	-63.4	-60.7	-60.7
4	-59.8	-56.0	-55.9	-64.7	-61.0	-61.1
5	-55.6	-55.0	-55.0	-60.4	-60.2	-60.2

salinity was within the narrow range 32.9–34.0 psu. Such a range would result in $<0.0004 \text{ g cm}^{-3}$ difference in seawater density (UNESCO, 1981) and minimal variation ($<0.1 \text{ dB}$) in the modelled estimate of TS.

In most fish species, g ranges from 0.98 to 1.07 and h from 1.01 to 1.05 (Shibata, 1970; Butler and Percy, 1972; Chu *et al.*, 2003). Furusawa (1988) analysed published data and determined that the most common values of g and h are 1.04 and 1.02, respectively, and these values are used in many model studies (Sawada *et al.*, 1999; Yasuma *et al.*, 2003). Taking into account the temperature where *S. leucopsarus* is found, the values of h are 1.1–1.7% higher than those generally found (Table 1). The values of g , on the other hand, are much lower (about 3.7% lower) than the norm and close to the value for many fish larvae (Shibata, 1970; Chu *et al.*, 2003) or zooplankton and medusae ($g = 1.003$; Shibata, 1970).

These characteristics of g and h are due to the unique character of the flesh of myctophid fish, which contains a large proportion of lipids (e.g. wax esters and triglycerides). The proportion and composition of lipids may vary with area or season as well as with fish species (Butler and Percy, 1972; Kayama and Nevenzel, 1974), and this may cause variation in the TS. Future studies need to

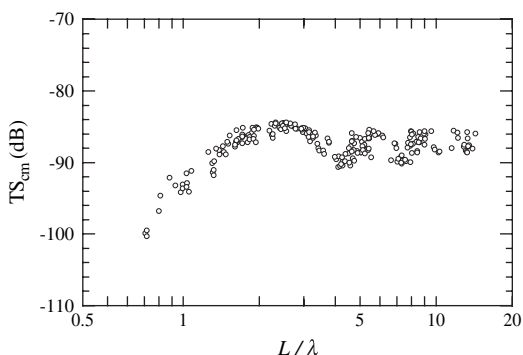


Figure 5. The reduced average target strength TS_{cm} from DCM as a function of the wavelength normalized standard length, L/λ . The normalization is done by squared standard length in centimetres.

investigate the variations in body-mass density and sound speed and their possible links with changes in chemical composition, using samples from different areas or seasons.

Appropriateness of the PSM and the DCM, and the theoretical TS of *S. leucopsarus*

Although the theoretical model estimates were used for this marine fish species, we conducted the comparative experiments in a freshwater tank to confirm the appropriateness of the PSM and the DCM. Figure 7 compares the theoretical TS patterns for fish number 5 (of those shown in Figure 4), using different parameters. The continuous lines in Figure 7 assume that the fish is in 10°C freshwater ($g = 1.035$, $h = 1.055$), and the dashed line assumes it is in seawater of the same temperature ($g = 1.007$, $h = 1.026$). Although the estimated TS patterns differ with the values of physical parameters, each curve shifts synchronously with fish orientation (Figure 7). All five specimens used for the TS measurement showed the same trend. This means that the theoretical TS pattern in freshwater can be assumed to be the same in seawater and confirms the appropriateness of TS models for *S. leucopsarus*.

The theoretical TS patterns tended to be similar, especially in the vicinity of the main lobe. There, the theoretical patterns agreed closely with the measured TS patterns (Figure 4). In contrast, the patterns were very different where the angle of tilt was steep ($>\pm 20^\circ$). In the tilt angles of this study, the differences in mean TS would be negligible, but there would be a huge difference in the estimates of TS if the fish is very tilted in the water column. There is little information about the swimming behaviour (orientation) of myctophid fish. Barham (1957) observed some myctophids with an underwater camera and reported that many orientate almost vertically at night and that most orientate virtually horizontally by day. Nevertheless, the tilt-angle distributions of myctophids are virtually unknown, and direct visual observations, with a video camera for example, are required to estimate the TS more exactly.

According to Sawada *et al.* (1999), the PSM provides only general trends because it uses few parameters. Further, Yasuma *et al.* (2003) computed the average TS of the larger myctophids *Notoscoptes japonicus* and *Symbolophorus californiensis*, neither of which has swimbladders, to be 38 kHz, and reported that TS values from the PSM were 3–4 dB higher than those from the DCM. In this study, however, the difference between the theoretical TS (from the PSM and the DCM) and the measured TS was $<3 \text{ dB}$ (Table 2), suggesting that both models would provide relatively accurate TS values for *S. leucopsarus*. *S. leucopsarus* is relatively small (maximum size $<110 \text{ mm}$), and the influence of body shape on the calculations might be less than in larger species. At higher frequencies, though, the differences may be greater, so comparative experiments using multiple frequencies in future may be revealing.

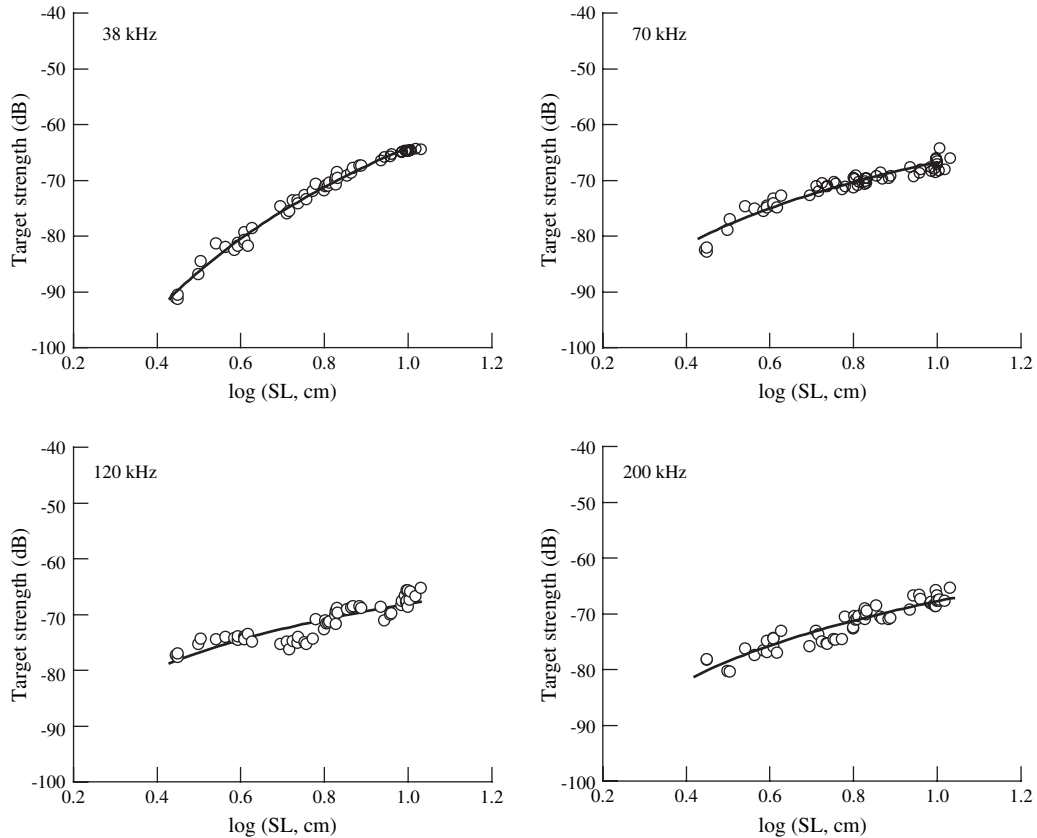


Figure 6. Plots of mean TS against log SL from the DCM at four frequencies ($n = 57$). Regression equations are given in Table 3.

According to the results from the DCM here, TS_{cm} varies asymptotically in the region $L/\lambda > 2$, a spread of -85 to -89 dB (Figure 5). These values are very low for fish sound scattering. TS data for myctophids are currently very limited (Saenger, 1989; Koslow *et al.*, 1997; Benoit-Bird and Au, 2001; Yasuma *et al.*, 2003). The TS_{cm} values calculated by those authors (-60 to -70 dB) are much higher than those calculated here, but they were of species with developed or atrophic swimbladders, so that there could well have been some gas in the bodies of the fish. Although there is little information about the TS of fish without swimbladders (Foote, 1980b; McClatchie *et al.*, 2000),

Foote (1980b) reported that the TS_{cm} of such a pelagic fish ranged from -90 to -80 dB, similar to the range calculated here.

Our plots of TS against log SL (Figure 6, Table 3) are non-linear, but it is known that backscattering is proportional to length-squared and that the TS vs. log length relationship is linear with a regression coefficient close to 20. In this case for *S. leucopsarus*, the use of a 20 log length relationship (Foote, 1979; MacLennan and Simmonds, 1992) should be reasonable within the limited length range ($L/\lambda > 2$). However, our analysis covering juvenile to adult stages of the species indicates that the use of a 20 log length relationship is not appropriate. This result supports some recent reports that exclude the use of a 20 log length relationship (McClatchie *et al.*, 2003; Yasuma *et al.*, 2003).

Here, we have modelled TS values for *S. leucopsarus* at different frequencies, and to the best of our knowledge this is the first time the TS of a lanternfish without a swimbladder has been reported. We believe that the method used here would be applicable to studies on other fish species with the same characteristic. The equations given in Table 3 are suggested for use at each of the four frequencies, and they should be of value to those making acoustic observations.

Table 3. Results of non-linear regressions shown in Figure 6. $x = \log(SL)$. The \ln denotes natural logarithm.

Frequency (kHz)	Approximate expression	r^2
38	$TS = 32.1 \ln(x) - 64.1$	0.99
70	$TS = 16.2 \ln(x) - 66.7$	0.92
120	$TS = 12.6 \ln(x) - 68.1$	0.76
200	$TS = 15.5 \ln(x) - 67.8$	0.86

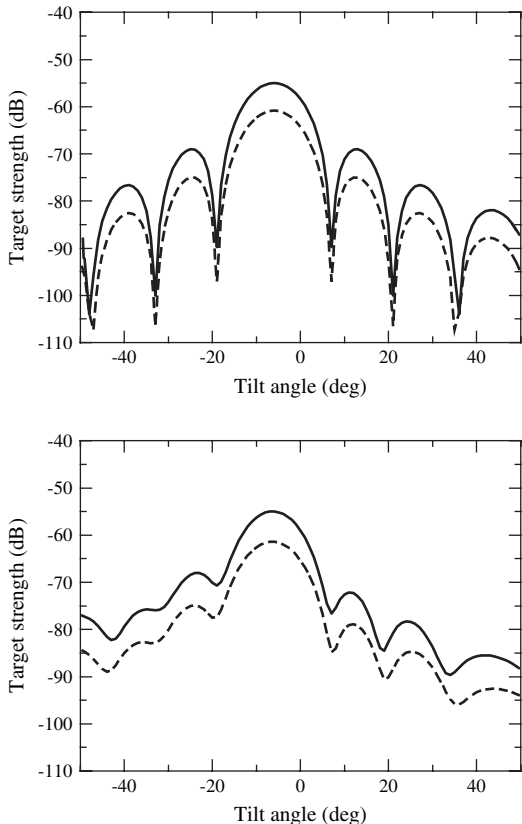


Figure 7. Comparison of the theoretical TS patterns using different values of g and h . Continuous lines assume that the fish is in freshwater ($g = 1.035$, $h = 1.055$), dashed lines in seawater ($g = 1.007$, $h = 1.026$). The estimated TS patterns for fish number 5 (see Figure 4) are shown. The upper panel is computed by the PSM and the lower panel by the DCM.

Because of the unavailability of other echosounders, the measurements were made at 38 kHz only. Higher frequencies should be used in the field if the target school has a high proportion of small fish (e.g. < 7.8 cm, $L/\lambda < 2$, at 38 kHz) in which TS variation would not be so sensitive. Additional experimental measurements and comparative studies at higher frequencies may provide better data. On the other hand, schools of *S. leucopsarus* in the Bering Sea comprise mainly adults (Gjøsaeter and Kawaguchi, 1980). In our sample, for example, $> 90\%$ were large adults (> 90 mm; Yasuma, 2004). Consequently, the use of 38 kHz is considered to be the most reasonable in this area because *S. leucopsarus* aggregates in deep water.

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