Comparison of in situ, ex situ, and backscatter model estimates of Pacific hake (*Merluccius productus*) target strength

Mark J. Henderson and John K. Horne

Abstract: To convert acoustic energy into estimates of fish density, the target strength (TS) of a representative fish must be known. TS is a measure of the acoustic reflectivity of a fish, which is variable depending on the presence of a swimbladder, the size of the fish, its behavior, morphology, and physiology. The most common method used to estimate the TS of a fish is a TS-to-length empirical regression, with TS values increasing with fish length. This study uses in situ and ex situ TS measurements and a backscatter model to develop TS-to-length conversions for Pacific hake (*Merluccius productus*). Results from in situ and ex situ measurements had regression intercepts 4–6 dB lower than the previous Pacific hake TS-to-length regression. These differences suggest that an individual hake reflects 2.5–4 times less acoustic energy than was previously estimated.

Résumé : Pour pouvoir convertir l'énergie acoustique en estimations de la densité de poissons, il est nécessaire de connaître l'intensité de la cible (TS) constituée par un poisson représentatif. TS est une mesure de la réflectivité acoustique d'un poisson et elle varie en fonction de la présence d'une vessie natatoire, de la taille du poisson, de son comportement, de sa morphologie et de sa physiologie. La méthode la plus couramment utilisée pour estimer la TS d'un poisson se base sur une relation empirique entre TS et la longueur dans laquelle les valeurs de TS augmentent en fonction de la longueur du poisson. Notre étude utilise des mesures in situ et ex situ de TS et un modèle de rétrodiffusion pour mettre au point une méthode de conversion des TS en longueurs chez le merlu du Pacifique (*Merluccius productus*). Les résultats de nos mesures in situ et ex situ donnent, dans les régressions, des valeurs de l'ordonnée à l'origine de 4–6 dB inférieures à celles des régressions faites antérieurement reliant TS à la longueur chez le merlu du Pacifique. Ces différences laissent croire que la rétrodiffusion d'énergie acoustique faite par un merlu individuel est de 2,5–4 fois moins importante que dans les estimations antérieures.

[Traduit par la Rédaction]

Introduction

The target strength (TS) of a representative fish is an essential quantity for acoustic-based estimates of fish abundance. TS is a measure of the acoustic reflectivity of a fish, which is variable depending on the presence of a swimbladder, length, behavior, morphology, and physiology of the fish (Foote 1985; Ona 1990; MacLennan and Simmonds 1992). An acoustic survey, using a downward-looking transducer, converts acoustic energy (i.e., backscatter) into estimates of fish density by dividing the total reflected energy attributed to a species of interest by the representative TS. Erroneous TS estimates for the surveyed species will bias the abundance estimate (Midttun 1984; Foote 1991; Misund 1997).

In marine ecosystems, the most common method used to estimate TS values is a log-linear regression that estimates TS as a function of animal length (L):

$$\mathrm{TS} = m \log L + b + \varepsilon \tag{1}$$

where m and b are species-specific slopes and intercepts, respectively, and ε is the residual error term. In fisheries acoustics, one form of this regression sets $m = 20$ (Foote 1979) because backscattering is expected to be proportional to the cross-sectional area (L^2) of a target (Love 1971; MacLennan and Simmonds 1992), and a common slope facilitates comparison among species (Foote 1979). In some species, regression slope values deviating from 20 provide a better TS-to-length fit. McClatchie et al. (2003) advocate discontinuing setting the regression slope equal to 20 and

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Table 1. Transceiver settings used during National Marine Fisheries Service (NMFS) in situ target strength measurements and this study's ex situ experiments.

	38 kHz					120 kHz
	1992	1995	1998	2001	Ex situ	Ex situ
Transducer depth (m)	0	9.15	9.15	9.15	0	0
Sound velocity ($m \cdot s^{-1}$)	1471	1471	1471	1471	1488	1488
Absorption ($dB \cdot km^{-1}$)	10	10	10	10	9.3	36.7
Power (W)	2000	2000	2000	2000	500	500
Pulse length	1.024	1.024	1.024	1.024	0.512	0.512
Alongship angle sensitivity	21.9	21.9	21.9	21.9	12.5	21.0
Athwartship angle sensitivity	21.9	21.9	21.9	21.9	12.5	21.0
Two-way beam angle (dB)	–20.6	–20.6	–20.6	–20.7	–15.9	–20.5
Volume backscattering strength gain (dB)	27.5	27.1	27.1	25.5	NA	NA
Target strength gain (dB)	27.4	27.3	27.1	25.8	22.4	25.3
Alongship 3 dB beam width (dg)	7.2	7.2	6.7	6.9	12.3	7.2
Athwartship 3 dB beam width (dg)	7.2	7.2	6.7	6.8	12.1	7.2
Alongship offset (dg)	–0.1	–0.9	–0.9	–0.8	0	0
Athwartship offset (dg)	–0.2	–0.2	–0.2	–0.3	0	0

recommend fitting an empirical TS-to-length relationship for each species.

To estimate appropriate slopes and intercepts for TS-to-length regressions, three techniques are used: in situ (i.e., free-swimming) measurements, ex situ (i.e., controlled) measurements, and numeric or theoretical backscatter models based on fish anatomy. The major challenge of in situ measurements is obtaining representative trawl samples that correspond to TS measurements (MacLennan and Simmonds 1992). Ideally, in situ TS values are measured when animal density is approximately 1 target·pulse resolution volume^{-1} and no other species are in the area to contaminate measurements (Sawada et al. 1993; Ona and Barange 1999). Ex situ TS measurements are used to examine how variables such as species, length, and orientation influence individual fish TS values (e.g., Love 1971; Nakken and Olsen 1977; Gauthier and Rose 2001), although results from these measurements may be influenced by behavioral changes not representative of in situ behaviors (Edwards and Armstrong 1984; MacLennan and Simmonds 1992). Backscatter models facilitate the manipulation of variables over broader ranges than is feasible with ex situ experiments (Foote 1985; Stanton 1988; Clay and Horne 1994). Backscatter models have been used in conjunction with ex situ and in situ measurements and in many cases have shown fair to excellent agreement between model predictions and empirical measurements (e.g., Foote 1985; Clay and Horne 1994; Hazen and Horne 2004).

This study uses in situ single target detections, ex situ TS measurements, and backscatter modeling to develop TS-to-length regressions for Pacific hake (*Merluccius productus*). Pacific hake, also known as Pacific whiting, are one of the most ecologically and commercially important fish species off the west coast of North America. They are the most abundant groundfish species in the California Current ecosystem and compose an integral part of the ecosystem as both predator and prey (Francis 1983; Livingston and Bailey 1985). As a commercial resource, Pacific hake support a large fishery in the United States and Canada, composing approximately 90% of the total west coast groundfish catch (PFMC 2004). Biomass estimates of Pacific hake, which are used to determine fishing quotas, are calculated using measurements from joint USA and Canadian acoustic–trawl surveys extending from southern California to northern Vancouver Island. The TS-to-length regression currently used in Pacific hake assessments, developed by Traynor (1996), is based on seven in situ measurements on aggregations of adult hake larger than 40 cm. In his paper, Traynor (1996) stated that it would be beneficial to have in situ TS measurements from smaller hake, TS measurements of tethered fish, and to conduct "theoretical investigations" based on swimbladder morphology. Our goal was to address these research needs by increasing the number and the length range of data points used in the TS-to-length regression and to validate our in situ results using ex situ measurements and backscatter models.

Materials and methods

In situ TS measurements

Single target detections

In situ TS measurements were collected as part of National Marine Fisheries Service (NMFS) Pacific hake acoustic–trawl surveys in 1992, 1995, 1998, and 2001 aboard the NOAA vessel *Miller Freeman* using a SIMRAD 38 kHz and 120 kHz splitbeam EK500 echosounder (Wilson and Guttormsen 1997; Wilson et al. 2000; Guttormsen et al. 2003). Transceiver settings are listed in Table 1. In all years, the echosounder was calibrated using 60 mm (38 kHz) and 23 mm (120 kHz) copper spheres following Foote et al. (1987). To collect TS measurements, the vessel would drift over low-density aggregations during dark hours when Pacific hake are dispersed. The species composition was sampled prior to the drift using an Aleutian Wing midwater trawl net with a headrope and footrope measuring approximately 82 m and an average mouth opening of 25.63 m^2 (range: 21–37 m^2). Stretch mesh sizes tapered from 3.25 m in the forward section to 8.9 cm in the cod end. The net was also fitted with a 3.2 cm cod-end liner. If time allowed, a second trawl was conducted after TS measurements were completed to verify that species composition and length frequency distributions had not changed. Single targets used for TS analysis were restricted to the depth strata fished. To increase confidence that TS measurements were Pacific hake, trawl catches had to be a minimum of 85% hake by weight and by numbers to be included in this study. During the four surveys included in this study, 13 drift periods were considered appropriate for TS analysis (Fig. 1, Table 2). Of these, 10 drift periods had trawls conducted before and after each drift. The 1992 drift period analyzed in this study matches that analyzed by Traynor (1996) and was used to compare analytic techniques and results.

Single targets were initially identified and processed by the NMFS Alaska Fisheries Science Center using BI-500 software and subsequently analyzed using Sonardata's Echoview (version 3.25, SonarData Pty. Ltd., Hobart, Tasmania, Australia). An echo amplitude threshold of –62 dB re 1 μPa @ 1 m was used for all years except 1992 when the threshold was set to –60 dB re 1 μPa @ 1 m. The minimum and maximum echolength was 0.6 and 1.8 ms except for 1992 when they were set at 0.8 and 1.8 ms. The maximum TS compensation was set at 3 dB to restrict echoes to those within the main lobe of the acoustic beam and to minimize the bias against smaller targets at the edge of the beam (Traynor and Ehrenberg 1979).

To ensure that multiple fish occupying the same acoustic volume were not accepted as single targets, the number of fish·pulse resolution volume^{-1} (i.e., density) was estimated using eq. 6.7 from Ona and Barange (1999):

$$N = \frac{s_A (c\tau/2) r^2 \Omega_D}{4\pi 10^{(\mathrm{TS}/10)} \Delta z (1852)^2} \tag{2}$$

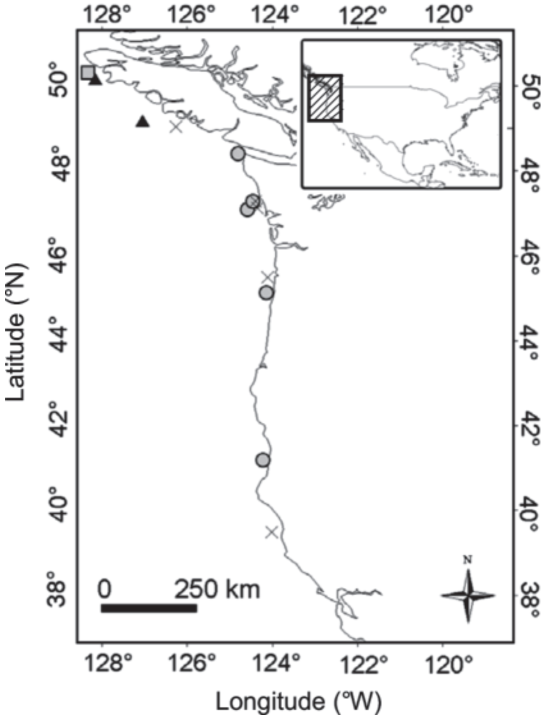
where N is the number of fish in the detection volume, s_A is the nautical area backscattering coefficient, c is the speed of sound in water, τ is the pulse length, r is range to target, Ω_D is the solid angle of the sampled volume, TS is the expected TS, and Δz is the depth interval. The expected TS for each drift was calculated using the average length from the trawls and the Traynor (1996) regression. If two trawls were associated with the drift, length measurements from both trawls were combined to calculate an average length and coefficient of variation (CV). These density values were plotted against TS to examine the relationship between TS and N. A large increase in average TS with small increases in N was attributed to multiple targets being accepted as single targets (Sawada et al. 1993). After preliminary examination, a density threshold of 0.07 fish·pulse resolution volume^{-1} was implemented to reduce the probability of multiple targets.

Ex situ TS measurements

Specimen collection

Fish were collected using hook-and-line in the Strait of Juan de Fuca outside of Neah Bay, Washington. All fish were caught at depths less than 20 m, with the majority of fish caught within 7 m of the surface. After capture, fish were kept in live wells with running seawater. No more than 15 fish were placed in the well to reduce stress due to high densities. Total time in live wells ranged from 1 to 5 h. Upon returning to shore, fish were transferred to a 1.3 m × 1.3 m × 1.3 m net pen beside the experimental location. Fish handling time during capture and transfer was minimized and was generally less than 1 min.

Fig. 1. Location of National Marine Fisheries Service (NMFS) Pacific hake (*Merluccius productus*) trawls conducted in association with 1992 (squares), 1995 (triangles), 1998 (circles), and 2001 (Xs) in situ target strength measurements.



TS measurements

Individual animals were tethered in a frame for TS measurements. Prior to TS measurements, fish were kept in the net pen for at least 3 h. Only fish that were swimming normally after 3–24 h of acclimation were used in experiments to reduce the possibility that barotraumatic stress (i.e., swimbladder rupture) associated with capture would influence TS measurements. Fish were removed from the net pen with a dip net and placed in a small tote filled with water to be transferred to a monofilament sock used to suspend the fish within the TS measurement tilt frame (see Hazen and Horne 2004 for description of tilt frame). Fish were anesthetized using MS-222 (tricaine methanesulfonate) to reduce stress during transfer and to minimize movement while TS measurements were recorded. After the fish was placed in the monofilament sock, the tilt frame was lowered using a stepper motor until the fish reached 4–6 m depth, depending on tidal state. This depth range ensured that fish were out of the transducer near fields (38 kHz, 1.09 m; 120 kHz, 1.47 m).

TS values were measured using a SIMRAD EK-60 split-beam echosounder operating at 38 and 120 kHz. Transmit power was set at 500 W, and pulse length was set at 0.512 ms for both frequencies. Calibrations, following Foote et al. (1987), were conducted using a 38.1 mm tungsten carbide calibration sphere prior to TS measurements. Conductivity–temperature–depth casts were conducted throughout the study period to measure water temperature and salinity. Speed of sound was calculated using Del Grosso and Mader (1972). Using a disengageable axle and

Table 2. Summary of trawls and drifts used for in situ target strength (TS) estimates.

					% hake				TS measurement					
Year	Haul	Haul back time	Head rope depth (m)	Bottom depth (m)	Weight	Numbers	Average length (cm)	Length CV	Start	End	TS drift distance (nm)	No. single targets	Average target depth (m)	Density
1992	56	0610	96	224	96.9	98.3	46.99	5.08	636	1108	15.91	26 958	114	0.09
	57	1203	100	224	96.3	98.7								
	56 (*N*)	0610	96	224	96.9	98.3	46.99	5.08	636	1108	5.14	8 502	111	0.05
	57 (*N*)	1203	100	224	96.3	98.7								
1995	80	0747	75	167	88.0	92.6	48.37	4.49	820	1110	3.06	3 778	82	0.02
	81	1206	76	162	94.7	96.6								
	84	0250	121	937	88.9	95.3	48.79	5.02	446	752	1.31	9 422	80	0.02
	85	0842	83	495	98.5	99.4								
1998	16	0724	70	130	97.0	99.6	30.9	20.77	814	1054	3.39	13 572	72	0.02
	47	0901	124	155	99.4	99.3	38.51	17.95	923	1227	3.84	4 963	88	0.03
	60	0823	99	192	97.7	99.0	40.52	12.11	858	1113	2.73	8 862	109	0.01
	61	1241	128	191	94.0	91.8								
	64	0808	77	114	96.3	93.1	41.65	12.82	921	1113	2.05	6 585	66	0.01
	65	1236	75	111	97.6	97.1								
	74	0917	76	140	99.9	99.8	41.23	8.05	1011	1120	1.22	4 070	57	0.01
2001	10	0442	110	152	99.9	99.6	33.9	10.84	630	755	1.42	1 937	87	0.03
	12	0849	118	153	92.9	98.6								
	37	0443	75	112	99.9	99.8	47.25	9.36	558	921	3.12	4 442	67	0.01
	38	1033	64	105	99.9	99.4								
	49	0644	41	70	97.5	92.1	48.81	5.98	741	929	1.89	2 856	40	0.01
	50	1039	35	67	96.6	88.4								
	52	0334	52	77	84.7	95.8	48.92	7.08	456	655	1.56	1 776	51	0.01
	53	0810	45	77	96.8	86.1								
	82	0901	75	136	94.8	86.9	50.34	6.61	943	1115	1.95	2 767	83	0.02
	83	1211	70	135	99.1	98.7								

Note: Haul back times as well as TS measurement start and end times are in GMT (PDT + 7 h). Hauls followed by (*N*) were filtered based on density.

computer-controlled stepper motor, the tilt frame and thus the fish were tilted in 5° increments from –45° through 45°. Positive tilt angles represent a fish with a head up orientation. Tilt was measured using an Applied Geomechanics 900-H biaxial clinometer placed within a waterproof housing mounted on the upper polyvinyl chloride (PVC) frame. Owing to placement of the transducers, depth constrictions, and horizontal shifting of the frame when tilt angles were incremented, accurate TS measurements were restricted to –45° through 25° for the 38 kHz transducer and from –15° through 45° for the 120 kHz transducer. After TS measurements were completed, each fish was removed from the monofilament sock and radiographed. The radiographs were used to model backscatter (see below) and to verify that the swimbladder of each fish had not ruptured during capture.

Analysis

Ex situ TS values were processed using Sonardata's Echoview software (version 3.25, SonarData Pty. Ltd.). Prior to analysis, a depth gate was created around the known depth range of the tethered fish to eliminate echoes from other animals that may have been swimming in the experimental area. A threshold of –70 dB re 1 μPa @ 1 m was used to filter ambient noise and to exclude other non-fish targets. Single target acceptance criteria included the following: minimum echolength = 0.4 ms, maximum echolength = 1.8 ms, maximum standard deviation of TS measurements for the major and minor axis = 7.0°, maximum compensation level = 10 dB for the 38 kHz transducer and 12 dB for the 120 kHz transducer (see Echoview 2007 for further description of single target detection algorithm). The maximum standard deviations and the maximum compensation values were necessary because a fish's position within the acoustic beam was not static because of tidal currents, wave action, and horizontal shifting of the frame when tilt angles were incremented. Maximum compensation values were determined for each transducer based on the deviation of calibration sphere TS values from the expected TS of the calibration sphere.

Each target accepted by Echoview was analyzed to ensure that backscatter originated from the tethered fish. To remove targets that swam through the analyzed depth layer, each target's three-dimensional beam position was plotted. Targets that were not within the expected volume were removed from analysis. Backscatter from the monofilament sock was subtracted from the TS measurement of the fish. At 120 kHz, the TS of the empty monofilament sock was –64.0 dB, which is equivalent to a backscattering cross-section (i.e., σ_{bs}) of 3.65×10^{-7} μPa. No backscatter was detected from the monofilament sock at 38 kHz. All TS measurements were binned in 5° tilt increments and averaged as backscattering cross-sections.

Backscatter modeling

Specimen collection

A total of 34 fish, ranging in fork length (FL) from 20 to 67 cm were used to model acoustic backscatter from Pacific hake. All fish were alive and acclimated to surface pressure prior to being radiographed for modeling purposes. Seven of the fish were collected for ex situ measurements in Neah Bay, six fish were collected from the mouth of the Columbia River, and 21 fish were collected off the California coast near Monterey. Specimens from the mouth of the Columbia River were collected in surface trawls conducted by the F/V *Sea Eagle* during June–July of 2003. The trawl was 100 m long with a mouth area approximately 30 m wide and 20 m deep. Ship speed was approximately 7.4 km·h^{-1} while trawling. Fish collected on the *Sea Eagle* were acclimated at the surface for 3–5 h prior to being imaged. Fish collected off the California coast in May 2004 were captured by the NOAA vessel *David Starr Jordan*. A modified Cobb midwater trawl with a 26 m headrope and a 1 cm cod-end liner was used to collect specimens at a depth of 30 m. Ship speed was approximately 3.7 km·h^{-1} while trawling. Immediately after trawling, fish in good condition were transferred to a cooler with a volume of approximately 110 L. A larger recovery tank was not available because of space constraints. Fish collected on the *David Starr Jordan* were acclimated to surface pressure for 3–15 h prior to being radiographed.

Table 3. Density (ρ) and speed of sound (*c*) estimates used in backscatter models.

	ρ (kg·m^{-3})	*c* (m·s^{-1})	$g = \rho_2/\rho_1$	$h = c_2/c_1$
Water	1026	1488	—	—
Fish body	1070	1570	1.04	1.06
Swimbladder	7.44	335	0.007	0.21

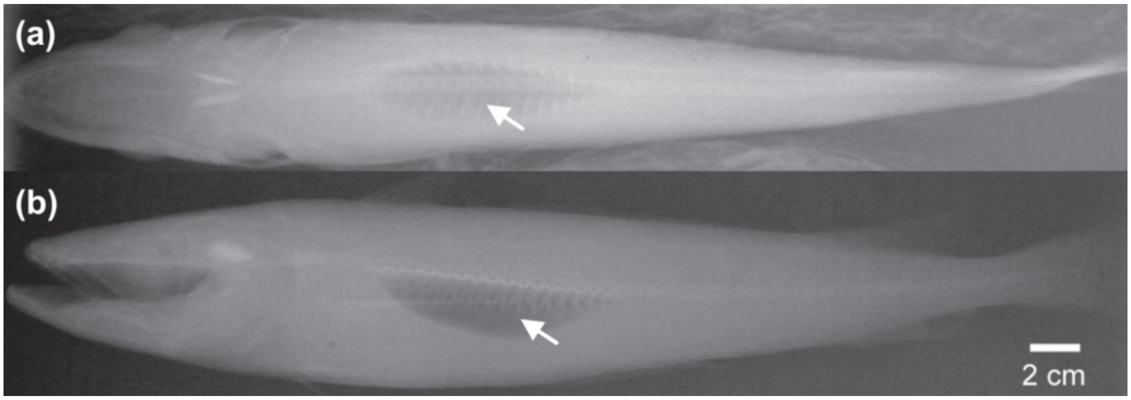
Note: The *g* and *h* values are the ratios between density (*g*) and speed of sound (*h*) of two mediums at an interface (i.e., water and fish body or fish body and swimbladder).

Kirchoff Ray-mode (KRM) backscatter model

The KRM backscatter model (Clay and Horne 1994) combines the breathing mode and Kirchoff approximation to estimate the intensity of reflected sound based on the sound speed and density contrasts among water, the fish body, and the swimbladder (Table 3). This model requires a three-dimensional image of the fish body and swimbladder. Dorsal and lateral images of the fish body and swimbladder were obtained using an X-tec Laserary 90P portable X-ray unit and rare earth film (Fig. 2). The pencil and measure tools in Adobe Photoshop (version 6.0, Adobe Systems Incorporated, San Jose, California) were used to trace and measure the fish body and swimbladder. Digital measurements were calibrated with the known standard length (SL) for each fish. Dorsal and lateral radiographs were elliptically interpolated to a three-dimensional digital representation of each fish. The digital representation of the fish was divided into 1 mm fluid (fish body) and gas (swimbladder) filled cylinders. Backscatter was estimated based on the size of the cylinder, the cylinder's orientation relative to the incident acoustic wave, and the acoustic carrier frequency. Backscatter from each cylinder was coherently summed to estimate fish TS. TS values were calculated as reduced scattering lengths (RSL), a nondimensional, linear measure. RSL is equivalent to the square root of the backscattering cross-section divided by the length of the fish in metres (Clay and Horne 1994). RSL is converted to TS and length (*L*) using

$$\text{TS} = 20\log(\text{RSL}) + 20\log(L) \tag{3}$$

Fig. 2. Dorsal (*a*) and lateral (*b*) radiograph of a 48 cm Pacific hake (*Merluccius productus*) collected for ex situ experiments in Neah Bay, Washington. The swimbladder in both radiographs is identified with a white arrow.



TS values for each fish were estimated at 38 and 120 kHz with the fish tilted from –45° (head down) to 45° (head up) in 1° increments. Mean TS estimates from the backscatter model were compared with ex situ mean TS measurements using a paired *t* test ($\alpha = 0.05$). All averaging and comparisons were calculated using backscattering cross-sections (σ_{bs}), which were then converted to TS values.

TS-to-length regressions

Prior to comparing in situ, ex situ, and backscatter model estimates of TS, we investigated methods used to estimate TS values of an individual fish. Ex situ TS values were estimated using three methods: maximum dorsal aspect TS, the average TS of a fish normal to the transducer (0° tilt), and the tilt-averaged TS. Each of these methods has previously been used to regress TS with fish length (Love 1971; Foote 1980*a*; McClatchie et al. 1996*a*). The average TS of a fish normal to the transducer was the average of all σ_{bs} values in the 0° tilt bin for an individual fish (number of observations per fish ranged from 130 to 543). Tilt-averaged TS values were calculated for each fish by randomly selecting 5000 σ_{bs} values from the 5° tilt bins based on the probability of occurrence in a truncated Gaussian tilt distribution. Two tilt distributions were used to determine how different distributions influence average TS. The first tilt distribution had a mean of 0° (i.e., horizontal) and a standard deviation of 15° (N[0, 15]) and has previously been used to average fish TS as a function of orientation (McClatchie et al. 1996*b*; Hazen and Horne 2004). The second tilt distribution, with a mean of –4.4° and a standard deviation of 16° (N[–4.4, 16]), was introduced by Foote (1980*a*) based on in situ observations of Atlantic cod (*Gadus morhua*) by Olsen (1971). For both tilt distributions, extracted σ_{bs} values from all bins were averaged and converted to TS values. Ex situ tilt-averaged backscattering cross-sections, maximum dorsal aspect backscattering cross-sections, and horizontal backscattering cross-sections values were compared using an analysis of variance (ANOVA) followed by Tukey's test for honestly significant differences.

For backscatter-modeled fish, weighted average TS values were calculated using the same Gaussian tilt distributions (N[0, 15] and N[–4.4, 16]) and the same 5° tilt bins (–40° through 20°) used to calculate average TS values from ex situ measurements. Average TS values were also calculated for backscatter modeled fish using tilt angles ranging from –45° through 45°. Combining the two different tilt distributions and tilt ranges resulted in four estimates of average σ_{bs} for each fish, which were compared using ANOVA. Average σ_{bs} values from the backscatter model were converted to TS and then regressed against the log-transformed FL of the fish. When needed, FL was converted to SL using a linear regression (FL = 1.07(SL) + 3.35, $r^2 = 0.99$) developed by Henderson (2005) based on 34 fish ranging in FL from 21 to 54 cm.

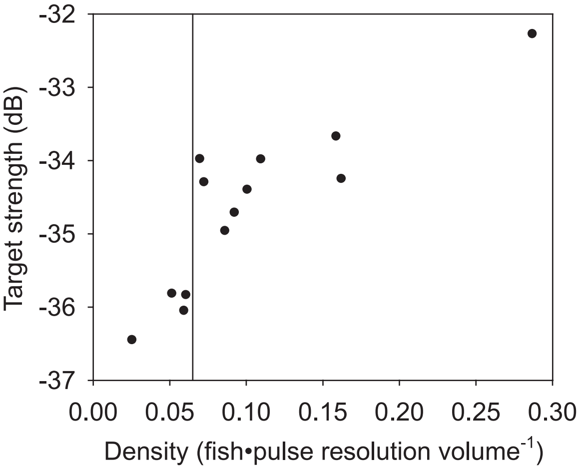
We used tilt-averaged TS estimates to compare in situ, ex situ, and backscatter model TS-to-length regressions to ensure that all data sets were comparable (i.e., included a tilt angle distribution). In situ backscatter measurements were averaged in the linear domain, converted to TS, and regressed against the average fish length from trawl catches corresponding to those measurements. The average TS values, calculated using a Gaussian tilt angle distribution with a mean of –4.4° and a standard deviation of 16°, were used for ex situ and backscatter model TS-to-length regressions. This distribution was selected because it is one of the few empirical estimates of an in situ tilt angle distribution (Foote 1980*a*; McClatchie et al. 1996*a*). Only the average TS values calculated using the full tilt range (–45° through 45°) were used to compare the backscatter model regression with the in situ and ex situ models. For each regression, the slope, intercept, and fit (r^2) were calculated with a fixed slope of 20 and as a best-fit line. A two-tailed *t* test ($\alpha = 0.05$) was used to test whether slopes of the best-fit regressions were significantly different from 20. An analysis of covariance (ANCOVA) followed by Tukey's test for honestly significant differences was used to compare all regressions, including the regression from Traynor (1996).

Results

In situ TS measurements

Fish densities were low during all in situ TS measurements except for those in 1992. Excluding the 1992 drift, the highest N was estimated to be 0.03 fish·pulse resolution volume^{-1}. Based on Ona and Barange (1999), an N of 0.03 corresponds to a 1% probability of multiple targets detected within the sample volume. The 1992 drift, which was also analyzed by Traynor (1996), had an N value three times larger than that of any other drift in this study (Table 2). The 1992 drift sample was split into thirteen 1 nautical mile (1 n.mi. = 1.852 km) sections to identify areas of low den-

Fig. 3. Target strength (dB) versus density (N, number of fish·pulse resolution volume^{-1}) for the drift associated with hauls 56 and 57 in 1992. The 1–2 dB increase in target strength at N values greater than or equal to 0.07 (vertical line) is attributed to multiple target detections.



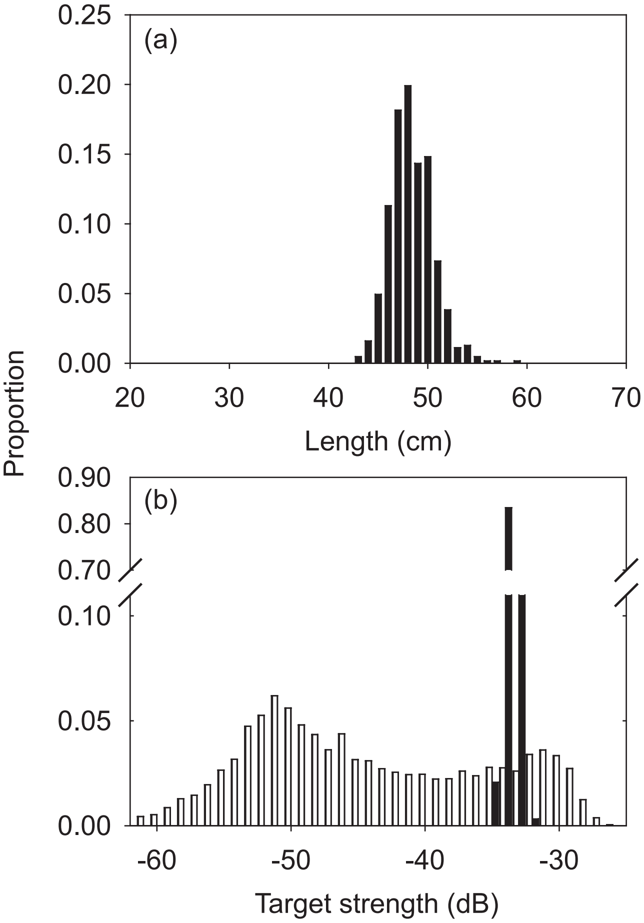
sity. N was calculated for each section and plotted against the average TS from that section (Fig. 3). When N values were ≥0.07, average TS increased 0.9–2.2 dB. This increase was attributed to multiple targets accepted as single targets, and any section with an N larger than 0.07 was excluded from the 1992 drift data analysis. When the filtered 1992 data set was used to calculate average TS, the value decreased from –34.5 dB in the original data set to –36.0 dB in the filtered data set. Without density filtering, the average TS for this drift was similar to the average TS values estimated by Traynor (1996) for the same measurement period (–33.2 and –35.5 dB depending on depth). Comparison of these average TS measurements verifies that under the same sampling and analytic conditions, the techniques and computer software used in this study produces comparable results with the techniques and software used by Traynor (1996).

The average FL of Pacific hake from the in situ drift periods selected for analysis ranged from 31 to 50 cm (Table 2). This extends the minimum size of in situ TS estimates by 16 cm for Pacific hake. Length distributions from each trawl or trawls associated with each drift had narrow ranges (Table 2). CV values ranged from 4.49% to 20.76%, with 8 of 13 drifts having CVs < 10%. The largest CV value (20.76%) was from haul 47 in 1998. The average length from this haul was 39 cm, but the catch also contained a group of 18–25 cm hake. Although trawl length distributions were generally unimodal, TS histograms from the drifts were multimodal (Fig. 4). TS modes were separated by approximately 20 dB in each frequency distribution. The location and size of the modes varied by TS measurement drift.

Ex situ TS measurements

Of the 24 fish collected for ex situ experiments, nine (44–53 cm FL) were deemed appropriate for TS measurements based on survival and swimming behavior. The mean number of TS estimates accepted in the 5° bins was 135 (range: 1–543). TS values were highly variable and dependent on tilt angle at both 38 and 120 kHz. Values ranged from –27.6 to –65.4 dB at 38 kHz and from –23.7 to –65.1 dB at 120 kHz. Maximum TS values in ex situ experiments were observed at a tilt angle of –5° at both 38 and 120 kHz. The average 38 kHz TS at this tilt was –33.1 dB (Fig. 5*a*) for fish with FLs ranging from 44.4 to 53.3 cm. Within 10° of horizontal, there was a 9–12 dB decline in TS. After the initial sharp decline, which was steeper for a fish assuming a head down orientation, the TS remained relatively stable as the tilt angle increased. At 120 kHz, the peak TS was –33.0 dB, which also occurred at a tilt angle of –5° (Fig. 5*b*). TS declined 5–10 dB as tilt angles deviated from –5°. Measurements at 120 kHz had a local maximum TS of –40.4 dB at a tilt of 20° that did not occur in the 38 kHz measurements.

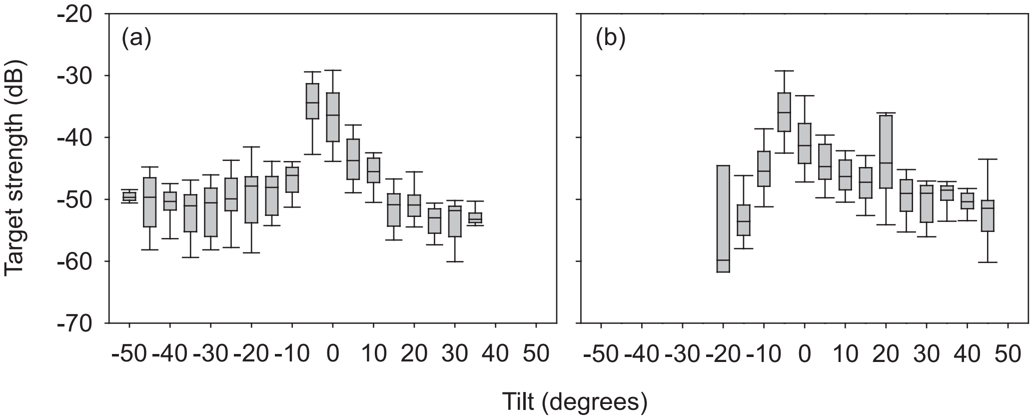
Fig. 4. (*a*) Pacific hake (*Merluccius productus*) trawl length frequency catch distribution from hauls 80–81 in 1995 and (*b*) the associated in situ target strength distribution (open bars). The 20 log(L) – 68 target-strength-to-length regression, developed by Traynor (1996), was used to convert length frequencies into target strength (solid bars in (*b*)) for comparative purposes.



Backscatter modeling

There were two distinct length modes of fish used to model Pacific hake backscatter. Among the 15 smaller fish (FL 20–24 cm) the average swimbladder length was 4.1 cm, the average swimbladder dorsal surface area was 5.88 cm^2, and average swimbladder volume was 3.13 cm^3. The larger fish (FL 42–66 cm) had an average swimbladder length of 10.8 cm, an average dorsal swimbladder area of 32.83 cm^2, and an average swimbladder volume of 36.21 cm^3 (Table 4).

Fig. 5. Box plots of target strength distributions for (*a*) 38 kHz and (*b*) 120 kHz ex situ single target detections. Upper and lower limits of the box indicate 25th and 75th percentile values, respectively. The horizontal line within the box is the median. The whiskers show the 5th and 95th percentile values, respectively, of target strength distributions.



The modeled TS values of the smaller fish ranged from –79.3 to –35.9 dB, while that of the modeled large fish ranged from –74.7 to –23.7 dB. The swimbladder contributed the majority of the backscatter in both small and large fish. Compared with the whole-fish backscatter, the predicted backscatter from the swimbladder averaged 106% in small fish and 98% in large fish. The backscatter from the fish body averaged 15% (small fish) and 16% (large fish) of the whole-fish backscatter. The percentages add up to more than 100% because of destructive interference of the acoustic waves when both the swimbladder and fish body were included in the model.

The backscatter model relationship between tilt angle and TS at 38 kHz was similar to the relationship observed during ex situ backscatter measurements. A paired *t* test comparing modeled σ_{bs} with measured σ_{bs} at each 5° tilt bin only found a significant difference ($p < 0.05$) for one out of seven fish (Table 5). When models and measures for each fish were averaged, a paired *t* test found that modeled values were not significantly different from the measured values ($p = 0.15$). The modeled average TS was consistently 3–5 dB higher than that of the measured TS from tilt angles of –15° through 30° (Fig. 6*a*). The largest difference was 12 dB at a tilt angle of –10°.

There was also reasonable agreement between the 120 kHz backscatter model predictions and ex situ measurements. A paired *t* test found no significant ($p < 0.05$) differences between the modeled σ_{bs} and the measured σ_{bs} for any individual fish (Table 5). Likewise, there was no significant difference when models and measurements from all fish were averaged ($p = 0.19$). For all measurements at angles less than 15° head up, model predictions were 1–5 dB higher than ex situ measurements. At angles larger than 15°, measurements were 1–9 dB higher than those of the model predictions (Fig. 6*b*).

TS-to-length regressions

The three methods (maximum dorsal, 0° tilt, and average TS) used to estimate TS for an individual fish resulted in large differences in the TS-to-length regressions (Fig. 7, Table 6). When the slope was fixed at 20, intercept values varied nearly 10 dB between the maximum dorsal aspect regression and the tilt-averaged regressions. A *t* test found that the slopes of the best-fit regressions were significantly different from 20 for the maximum dorsal aspect (51.68, $t_{[0.05(2),\ 7]} = 2.66$, $p = 0.03$), average TS ($N[0, 15]$) (81.50, $t_{[0.05(2),\ 7]} = 2.99$, $p = 0.02$), and average TS ($N[-4.4, 16]$) (83.12, $t_{[0.05(2),\ 7]} = 3.14$, $p = 0.02$). The best-fit regression calculated using TS values of a fish normal to the transducer (0° tilt) had a slope of 113.90 and was not significantly different from 20 ($t_{[0.05(2),\ 7]} = 2.08$, $p = 0.08$). The r^2 values for the best-fit regressions (range: 0.48–0.73) were larger than the r^2 values from the fixed slope regressions (range: 0.15–0.46). There were significant differences between the methods used to estimate backscattering cross-sections (ANOVA, $F_{[0.05(1),\ 3,\ 32]} = 33.28$, $p \ll 0.05$). Tukey's test for honestly significant differences (q critical $_{[0.05,\ 32,\ 4]} = 3.85$) found that the maximum dorsal backscattering cross-section (σ_{bs}) values were significantly different from values estimated using each of the other methods ($q_{\text{max dorsal vs. 0° tilt}} = 9.81$; $q_{\text{max dorsal vs. avg } (N[0,15])} = 12.05$; $q_{\text{max dorsal vs. avg } (N[-4.4,\ 16])} = 9.81$). None of the other methods used to estimate backscattering cross-section (σ_{bs}) values were significantly different from each other ($q_{\text{0° tilt vs. avg } (N[0,15])} = 2.24$; $q_{\text{0° tilt vs. avg } (N[-4.4,16])} = 2.34$; $q_{\text{avg } (N[0,15]) \text{ vs. avg } (N[-4.4,16])} = 0.10$).

A comparison of the tilt angle distributions ($N[0, 15]$ and $N[-4.4, 16]$) and the tilt ranges (–40° through 20° and –45° through 45°) used to calculate average TS for backscatter-modeled fish found no significant differences (ANOVA, $F_{[0.05(1),\ 3,\ 128]} = 0.42$, $p = 0.74$). As the tilt angle distributions had no significant influence on average TS estimates of the ex situ measurements or the backscatter model predictions, only the results from the tilt distribution with a mean of –4.4° and a standard deviation of 16° are reported in detail. For both the truncated (–40° through 20°) and full (–45° through 45°) tilt ranges, the slope of the best-fit lines were not significantly different from 20 (two-tailed *t* test, $p > 0.05$). When the slope of the backscatter model regression line was fixed at 20, the intercept was 0.5 dB higher with the truncated tilt range than with the full tilt range (Table 7). There was minimal variation in the fit of the backscatter model data to the regression lines regardless of what tilt range was used or whether the slope was fixed at 20 ($r^2 = 0.94–0.99$). This result is attributed to the similarity of hake

Table 4. Capture location, fork length (FL), and swimbladder (SWB) measurements for backscatter-modeled fish.

			SWB					
Fish	Location	FL (cm)	Length (cm)	Dorsal surface area (cm^2)	Volume (cm^3)	FL/SWB length	FL/λ (38 kHz)	FL/λ (120 kHz)
60	California	19.7	2.89	2.91	1.08	0.15	5.03	15.90
62	California	21.6	4.20	5.87	2.91	0.19	5.50	17.37
69	California	21.6	3.56	4.03	1.61	0.17	5.50	17.37
68	California	21.8	3.88	4.41	1.84	0.18	5.55	17.54
53	California	22.0	4.32	6.42	3.47	0.20	5.61	17.71
54	California	22.1	4.28	7.53	4.96	0.19	5.64	17.80
52	California	22.3	3.92	5.10	2.41	0.18	5.69	17.97
59	California	22.3	4.67	7.58	4.45	0.21	5.69	17.97
63	California	22.3	4.17	5.86	2.96	0.19	5.69	17.97
58	California	22.5	2.86	3.08	1.18	0.13	5.75	18.14
55	California	22.6	4.38	7.24	4.43	0.19	5.77	18.23
64	California	22.8	4.28	7.62	5.01	0.19	5.83	18.40
66	California	23.5	4.31	5.93	2.84	0.18	5.99	18.92
65	California	24.0	4.81	7.70	4.24	0.20	6.13	19.35
67	California	24.1	4.70	6.92	3.56	0.19	6.16	19.44
56	California	42.4	8.98	29.50	34.73	0.21	10.80	34.12
76	Neah Bay	44.4	8.49	18.15	14.08	0.19	11.32	35.76
61	California	44.7	8.85	16.67	10.23	0.20	11.41	36.02
78	Neah Bay	45.7	9.87	23.96	19.77	0.22	11.66	36.81
71	California	45.7	9.88	30.11	31.09	0.22	11.65	36.79
77	Neah Bay	46.5	10.29	27.60	26.87	0.22	11.86	37.45
73	Neah Bay	46.8	9.98	25.87	23.30	0.21	11.94	37.69
50	Astoria	47.7	9.96	27.49	26.49	0.21	12.17	38.43
51	Astoria	47.7	10.09	30.44	32.48	0.21	12.17	38.43
79	Neah Bay	48.4	10.23	25.96	22.78	0.21	12.34	38.98
74	Neah Bay	49.6	12.89	36.63	36.90	0.26	12.65	39.95
48	Astoria	49.7	10.90	31.46	32.63	0.22	12.66	39.99
46	Astoria	52.3	12.97	48.39	65.03	0.25	13.35	42.15
49	Astoria	52.3	10.27	28.88	26.62	0.20	13.35	42.15
75	Neah Bay	53.3	11.62	33.93	31.05	0.22	13.59	42.93
47	Astoria	53.9	12.46	41.38	48.09	0.23	13.76	43.44
70	California	60.3	12.94	53.89	74.58	0.21	15.37	48.54
72	California	66.5	13.76	60.74	95.09	0.21	16.96	53.54

Note: Swimbladder measurements were made digitally using radiographs of live fish acclimated to surface pressure.

Table 5. Results of paired *t* tests comparing ex situ backscattering cross-section (σ_{bs}) measurements with backscatter model predictions.

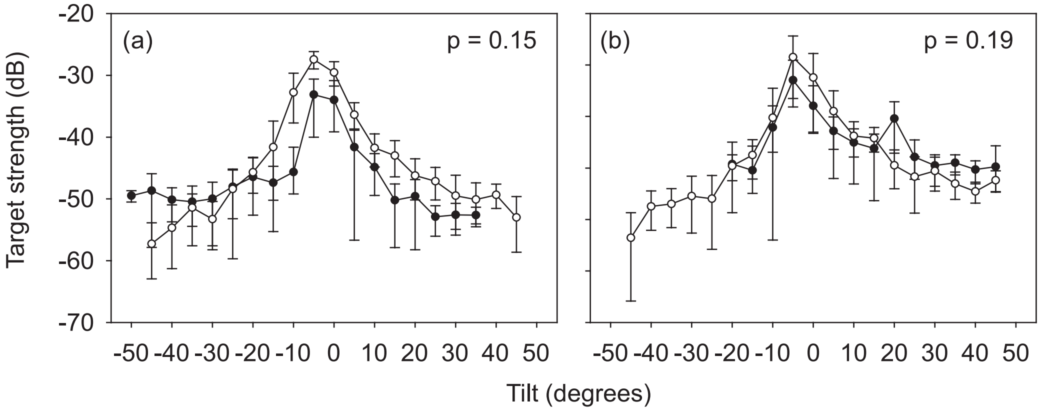
	38 kHz				120 kHz			
Fish	Tilt distribution	$t_{[0.05(2),\ \mathrm{df}]}$	df	*p*	Tilt distribution	$t_{[0.05(2),\ \mathrm{df}]}$	df	*p*
73	–40° – 30°	2.01	14	0.06	–15° – 45° [30°]	1.12	12	0.29
74	–45° – 25°	1.76	14	0.10	–15° – 25°	1.32	9	0.22
75	–45° – 20°	1.42	13	0.18	–15° – 25°	0.74	9	0.48
76	–45° – 30° [25°]	2.24	14	0.04	–15° – 25°	1.75	9	0.12
77	–45° – 30°	1.86	15	0.08	–20° – 45°	1.54	14	0.15
78	–45° – 25°	1.79	14	0.10	–15° – 30°	1.34	10	0.21
79	–45° – 25°	2.02	13	0.06	–15° – 20°	1.29	8	0.23
Average	–45° – 35°	1.50	16	0.15	–20° – 45°	1.38	14	0.19

Note: Values were compared for every tilt bin for which there was a valid ex situ measurement. Tilt distribution values in brackets are bins within the tilt distribution for which there were no valid measurements.

swimbladder morphologies (Table 4) and to the deterministic backscatter modeling technique.

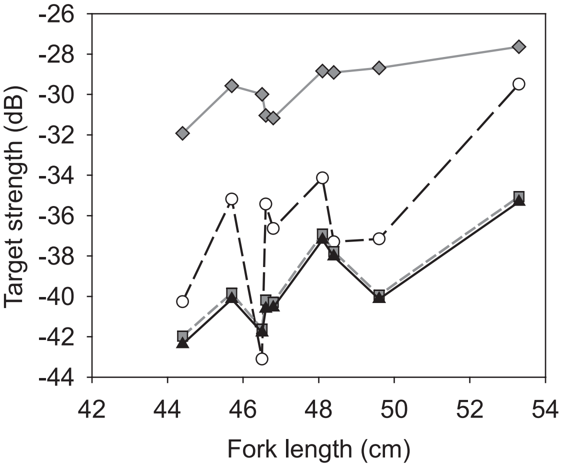
Differences were observed when we compared the tilt-averaged TS-to-length regressions developed using data from Traynor (1996) and our in situ measurements, ex situ measurements, and backscatter model calculations (Table 7, Fig. 8). A two-tailed *t* test found that the slopes of the best-fit regressions were not significantly different from 20 for

Fig. 6. Fish tilt angle versus target strength at (*a*) 38 kHz and (*b*) 120 kHz based on Kirchoff Ray-mode (KRM) model predictions (open circles) and ex situ measurements (solid circles) of seven fish. Student's *t* test *p* values are given in the upper right of each plot. For comparisons between KRM model predictions and ex situ measurements of individual fish, see Henderson (2005).



regressions developed using data from Traynor (1996) (16.63, $t_{[0.05(2),\ 3]} = 0.15$, $p = 0.89$), in situ measurements (24.15, $t_{[0.05(2),\ 11]} = 0.32$, $p = 0.75$), the backscatter model with the truncated tilt distribution (17.78, $t_{[0.05(2),\ 31]} = 1.00$, $p = 0.32$), and the backscatter model with the full tilt distribution (19.11, $t_{[0.05(2),\ 31]} = 1.03$, $p = 0.31$). The slope of the ex situ best-fit regression was much larger than the other slopes (83.12, $t_{[0.05(2),\ 7]} = 3.14$, $p = 0.02$), which was probably a result of the narrow length range (44–53 cm FL) used in ex situ measurements. With regression slopes fixed at 20, intercept values ranged from –68.2 (Traynor 1996) through –74.0 (in situ measurements). An ANCOVA found significant differences among intercepts of the regressions with a fixed slope of 20 ($F_{[0.05(1),\ 3,\ 54]} = 26.49$, $p << 0.05$). Pairwise comparisons using the Tukey method (q critical $_{[0.05,\ 52,\ 4]} = 3.79$) found significant differences between the Traynor regression and the in situ ($q = 8.15$) and ex situ ($q = 6.86$) regressions. There were also significant differences between the backscatter model regression and the in situ ($q = 12.54$) and ex situ ($q = 8.88$) regressions. The only regressions that were not significantly different from each other were the Traynor and backscatter model regressions ($q = 1.00$) and the ex situ and in situ regressions ($q = 1.51$) (Fig. 8).

Fig. 7. Target strength (TS) versus fish length based on ex situ target strength measurements. The three methods used to estimate TS were (*i*) maximum dorsal aspect TS (diamonds), (*ii*) average TS of fish with 0° tilt (circles), and (*iii*) an average TS calculated with σ_{bs} values randomly selected based on the probability of occurrence in a Gaussian tilt distribution with either a mean of 0° and a standard deviation of 15° (squares, broken line) or a mean of –4.4° and a standard deviation of 16° (triangles, solid line).



Discussion

Ex situ and in situ TS-to-length regressions developed in this study have intercepts 4–6 dB lower than the intercept of the regression developed by Traynor (1996), indicating that an individual Pacific hake would reflect 2.5–4 times less energy then was previously estimated. If our measurements are representative of Pacific hake backscattering characteristics, then use of the Traynor regression will result in an underestimate of Pacific hake density. Regressions based on independent in situ and ex situ measurements from this study were not significantly different from each other, providing support that these results are not an artifact of the measurement or analytic technique. In contrast, the regression based on the backscatter model was not significantly different from the Traynor regression. At this time we cannot identify a single factor that accounts for the observed differences among our measurements, previous measurements, and the backscatter model predictions.

Differences between in situ TS measurements in this study and those reported in previous work may be attributed to (*i*) animals reflecting sound as nonpoint source targets, (*ii*) acoustic detection of non-hake targets that were underrepresented in trawl catches, and (*iii*) differences in methods used to filter TS values. Limited evidence suggests that fish can act as complex reflectors rather than point source targets (e.g., Ehrenberg and Johnston 1996; Dawson et al. 2000). A current example demonstrated that fish orientation relative to the incident wave front and body curvature influenced the number of modes and the intensity of echo envelopes returned from Chinook salmon (*Oncorhynchus tshawytscha*) at side aspect (Burwen et al. 2007). If this occurs, an individual fish may be detected as more than one target, each of which would have a lower than expected TS. Other small targets that contribute to acoustic backscatter may also not be representatively captured by midwater trawls. As an example, si-

Table 6. Target strength (TS)-to-length regressions based on three methods of estimating target strength using ex situ data.

	Fixed slope			Best fit		
	Slope	Intercept	r^2	Slope	Intercept	r^2
Max. dorsal	20	–63.3	0.46	51.68*	–116.5	0.73
0° tilt	20	–70.1	0.15	113.90	–227.7	0.48
Average TS (*N*[0, 15])	20	–72.9	0.30	81.50*	–176.1	0.69
Average TS (*N*[–4.4, 16])	20	–73.1	0.30	83.12*	–179.1	0.71

Note: Regressions were calculated for the best-fit line as well as with a slope fixed at 20. The average TS values were calculated using two Gaussian tilt distributions: one with a mean of 0° and a standard deviation of 15° (*N*[0, 15]) and the other with a mean of –4.4° and a standard deviation of 16° (*N*[–4.4, 16]). See text for further description of averaging and σ_{bs} selection methods.

*Slope significantly different ($p < 0.05$) from 20 based on two-tailed *t* test.

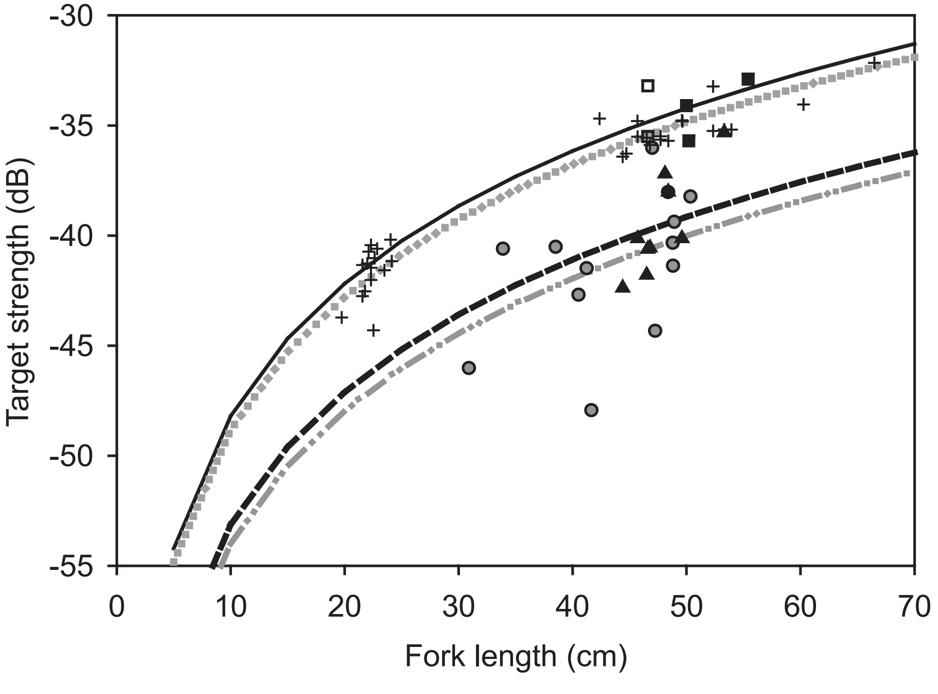
Table 7. Coefficients and fit for target strength-to-length regressions calculated using ex situ, in situ, and backscatter-modeled data.

	Fixed slope			Best fit		
	Slope	Intercept	r^2	Slope	Intercept	r^2
Traynor regression	20	–68.2	0.15	16.6	–62.5	0.16
In situ single targets	20	–74.0	0.23	24.2	–80.8	0.24
Ex situ (–40° through 20°)	20	–73.1	0.30	83.12*	–179.1	0.70
Model (–40° through 20°)	20	–68.3	0.99	17.78	–64.8	0.99
Model (–45° through 45°)	20	–68.8	0.94	19.11	–67.4	0.94

Note: Values in parentheses are tilt angle distributions used to calculate average target strengths. For simplicity, ex situ and model regression parameters are only shown for regressions calculated using the Gaussian tilt distribution with a mean of –4.4° and a standard deviation of 16°.

*Slope significantly different ($p < 0.05$) from 20 based on two-tailed *t* test.

Fig. 8. Target strength-to-length regressions with a fixed slope of 20 calculated using data from Williamson and Traynor (1984) (solid squares), Traynor (1996) (open squares, solid line), in situ (circles, dash-dotted line), ex situ (triangles, broken line), and the Kirchoff Ray-mode (KRM) model (cross-hairs, dotted line). Regression intercepts and fit are given in Table 7.



phonophores have large acoustic returns (e.g., –62.5 dB at 24 kHz (Warren et al. 2001); –68.3 dB at 38 kHz (Trevorrow et al. 2005)) relative to their size because of the presence of a gas inclusion called a pneumatophore (Stanton et al. 1998*a*, 1998*b*). These animals are easily destroyed by typical sampling equipment, and their abundance would not be accurately represented in trawl catches. Underrepresented small targets in trawls may partially explain multimodal TS distributions observed with unimodal trawl catches in multiple species (e.g., Hammond 1997; Cordue et al. 2001; Jørgensen and Olsen 2002), including Pacific hake (Williamson and Traynor 1984). To exclude small, presumably non-hake targets from in situ TS measurements, previous studies used an echo-amplitude threshold. The in situ TS measurements conducted by Williamson and Traynor (1984), which were incorporated in the regression developed by Traynor (1996), used a threshold between –50 and –55 dB. Ex situ TS measurements in this study suggest that Pacific hake TS values lower than –60 dB are possible for fish with FLs of 44 to 53 cm. A threshold as high as –50 dB will exclude TS measurements from Pacific hake and will artificially increase average TS estimates. To reduce this potential bias in the NOAA data, the echo-amplitude threshold was reduced to –62 dB for all in situ measurement periods except 1992, when the threshold was set at –60 dB. This study is also the first to remove regions of high hake density from average TS calculations. Density calculations, using eq. 2, indicated that the 1992 TS data used by Traynor (1996) had a 5% probability of multiple targets being accepted as single targets. Excluding the 1992 data, in situ TS data used in this study only had approximately a 1% chance of accepting multiple targets as a single target. Implementing a density threshold to limit the probability of multiple detections as single fish targets reduced the average TS of the 1992 data by 1.5 dB. Without a density threshold filter, average TS values in this study agreed with Traynor's (1996) average TS estimates.

This study also differed from previous studies in the quality of the samples used for ex situ TS measurements and backscatter modeling. The only other study attempting ex situ measurements and backscatter modeling of Pacific hake used dead, frozen fish that had been trawl-caught at 90 m depth and not acclimated to surface pressure (Sawada et al. 1999). Fish caught at a depth of 90 m will experience a 9-atmosphere (1 atmosphere = 101.325 kPa) reduction in pressure. As pressure is reduced, gas within a swimbladder is expected to expand according to Boyle's law (Ona 1990; Mukai and Iida 1996). Freezing fish has also been shown to distort swimbladder shape (Koumoundouros et al. 2000). These potential changes in the shape or orientation of the swimbladder are expected to influence the TS of a fish (Foote 1980*b*; Ona 1990). Ex situ backscatter measurements and backscatter model predictions from this study used live specimens acclimated to surface pressure. One potential problem with our ex situ measurements was that fish were lowered to a depth of 4–6 m after being acclimated to surface pressure. It is possible that the increase in pressure reduced the volume and potentially changed the shape of the swimbladder, which could influence backscatter measurements. This effect was most likely minimal, as experiments on kokanee (*Oncorhynchus nerka*) found differences in TS were small (approximately 1 dB) with a depth change from 5 to 10 m (Mukai and Iida 1996). We believe that our ex situ TS measurements are representative of unrestrained Pacific hake.

Compared with the ex situ measurements, the KRM backscatter model overestimates the TS of most hake, especially at near-horizontal orientations. Overestimates of TS predictions have been observed in other model-to-measurement comparisons (e.g., Horne et al. 2000; Kang and Hwang 2003; Lilja et al. 2004). Owing to the complexity of sound scattering from a biological target, there are numerous potential causes for these discrepancies. As previously mentioned, lowering the fish to 4–6 m during experiments may have changed the volume and shape of the swimbladder. The radiographs used to image each fish's swimbladder were taken at the surface. It is possible that radiographs of swimbladders were not representative of the fish at depth. Another explanation is that the density (ρ) and sound speed (c) values used in backscatter model calculations were not appropriate for Pacific hake, as they have not been measured for Pacific hake flesh or the swimbladder. Values used in this study matched those used in backscatter models of Atlantic cod (Clay and Horne 1994). Differences in the resulting reflection coefficient values can result in TS differences within the fish body of up to 10 dB (Horne and Jech 2005). The backscatter model also assumes that ρ and c values are homogenous throughout the fish body. This assumption ignores differences in density and speed of sound through other backscattering organs such as skeletal elements or gonads. Since the fish body has been shown to contribute only 5%–10% of the total backscatter in swimbladdered fish (Foote 1980*c*), variation in predicted TS due to inaccurate g and h values in the fish body will not dominate predicted whole fish backscatter intensities. Finally, Foote and Francis (2002) have suggested that the KRM model assumption of finite cylinders excludes diffraction of sound through the swimbladder. Diffraction can cause acoustic waves to have different phases than predicted, which could result in additional constructive or destructive interference. Comparisons between the KRM and a boundary-element model, which includes diffraction, found no significant differences in predictions from the two models (Foote and Francis 2002). Additional comparisons between backscatter models and empirical TS measurements will help explain discrepancies between models and measurements and should provide insight on how biological organisms scatter sound.

Given the observed differences between our Pacific hake TS measurements and those estimated with the backscatter model and measurements from previous studies, we were interested in how our results compared with species with similar morphological characteristics. The in situ and ex situ TS measurements from this study were lower than those previously measured for walleye pollock (*Theragra chalcogramma*) (Williamson and Traynor 1984; Traynor 1996), but were similar to in situ measurements and backscatter model predictions for the southern blue whiting (*Micromesistius australis*) (McClatchie et al. 1996*b*; McClatchie et al. 1998). Likewise, the in situ and ex situ TS-to-length regressions developed for hake had lower intercepts (–74.0 and –73.1 dB) than the regression currently used for walleye pollock (20 log(L) – 66), but was comparable with the regression used for southern blue whiting (21.72 × log(L) – 72.80). Even though these other species belong to different families than Pacific hake, they are all in the same order (i.e., Gadiformes) and have similar external morphologies. Given that the swimbladder is the major source of backscatter (Foote 1980*c*), we hypothesized that the observed interspecific TS differences are due to variations in swimbladder morphometry. This hypothesis was investigated by comparing swimbladder measurements from radiographs of Pacific hake and walleye pollock with similar SLs (within 1 cm). No radiographs of southern blue whiting were available for comparison. Walleye pollock swimbladders (measured by Hazen 2003) had an average of 1.8 times the dorsal surface area of Pacific hake swimbladders (Henderson 2005). A two-tailed *t* test found that these distributions were significantly different ($t_{[0.05\ (2),\ 9]} = 1.00$, $p \ll 0.05$). This result provides support for the hypothesis that the lower observed TS values of species such as Pacific hake and southern blue whiting may be due to differences in swimbladder morphology.

The validity of forcing the slopes of all fish TS-to-length regressions through 20 has been questioned (McClatchie et al. 2003). Results from this study suggest that a slope of 20 is appropriate for Pacific hake, with the caveat that the in situ TS-to-length regression used in this study does not contain measurements of fish smaller than 30 cm. The slope of the TS-to-length regression based on KRM backscatter model predictions, which includes hake as small as 20 cm, also does not significantly differ from 20. As backscatter model predictions of adult fish show fair agreement with ex situ measurements, it is believed that model predictions for juvenile fish are also reasonable. Even though backscatter models support the use of 20 in the TS-to-length regression, it is essential to add TS measurements from fish smaller than 30 cm to the in situ TS-to-length regression.

Additional effort should be allocated to measuring TS values of juvenile Pacific hake. Even though the adult European perch (*Perca fluviatilis*) TS-to-length relationship was not significantly different than that of juveniles (Frouzova and Kubecka 2004), it is possible that changes in Pacific hake TS are not linear with growth (cf. Abe et al. 2004). Pacific hake have an allometric growth pattern, reaching 70%–75% of their maximum length and 50% of their maximum weight by age 4 (Dark 1975). Growth of scattering structures, such as the swimbladder, may also be allometric. If true, then the current TS-to-length relationship may not be accurate for all length ranges, and a single regression may not be an appropriate representation of the acoustic size to fish length relationship for Pacific hake.

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