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Fish orientation is consistently identified as a major influence on fish target strength (TS). Generally, orientation is defined as the tilt angle of the fish with respect to the acoustic transducer, whereas a more accurate definition includes tilt, roll, and yaw. Thus far, the influences of roll and yaw on fish TS have only been examined cursorily. We used *in situ* single-target data to create fish tracks, to estimate fish tilt and yaw, and correlated these estimates with TS. The results show that tilt, yaw, and beam position have a significant influence on fish TS. To investigate further how yaw and beam position affect TS, we calculated the expected backscatter from each fish within simulated fish aggregations using a backscatter model. The TS of individual fish at 38 and 120 kHz varied by as much as 11 and 19 dB with changes in yaw and beam position. Altering the fish's tilt, yaw, and beam position resulted in TS differences of 14 and 26 dB at 38 and 120 kHz, respectively. Orientation had a minimal influence on an aggregation's average TS if the aggregation had a variable tilt-angle distribution and was dispersed throughout the acoustic beam.

Keywords: beam position, orientation, target strength, target tracking, yaw.

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Introduction

The importance of accurate estimates of target strength (TS) for acoustic-based population estimates is well known and documented. Factors influencing TS include animal length, orientation, feeding state, and reproductive state (Love, 1971; Nakken and Olsen, 1977; Ona, 1990; Horne, 2003). Difficulty in measuring each of these variables led MacLennan and Simmonds (1992) to state that, "target strength must be considered a stochastic parameter". However, improvements in the analysis of acoustic data and backscatter modelling have increased our understanding of how different variables influence TS. Backscatter models allow the manipulation of individual variables, which in turn facilitates quantification of their effects on TS (Hazen and Horne, 2004). Here, we use a numerical-backscatter model and *in situ* target-tracking measurements to investigate how tilt and swimming direction (i.e. yaw) combined with position in the acoustic beam can influence the TS of a fish.

Orientation has repeatedly been shown to influence TS (Nakken and Olsen, 1977; Foote, 1980a; Hazen and Horne, 2004). In those papers, "orientation" generally refers to the fish's tilt angle when orientation also consists of yaw and roll. Relatively few studies have investigated the influence of these factors on fish TS. Studies conducted using tethered fish in rotatable frames found that yaw (Love, 1977) and roll (Nakken and Olsen, 1977) have a significant influence on TS. Dahl and Mathisen (1983) used tethered fish in a river to illustrate that small (10°) changes in side-aspect angles of salmon could result in large (3–8 dB) changes in TS. Zedel *et al.* (2005) found differences of 5 dB in the TS of fish swimming in opposite directions from an ADCP beam, but cautioned that there may be large differences between ADCP backscatter measurements and measurements from a downward-looking echosounder. Except for Zedel *et al.* (2005), the influence of yaw and roll on fish TS has only been measured for fish aligned with the acoustic axis. Restricting fish to the acoustic axis removes the potential bias associated with the beam pattern of the transducer (Traynor and Ehrenberg, 1979), but the measurements may not be representative of fish swimming through an acoustic beam. To understand how beam position and yaw may influence acoustic-based population estimates, it is necessary to measure, or to model, backscatter from fish spread throughout the main lobe (i.e. half-power points) of the acoustic beam.

The effect of yaw on TS is expected to be minimal when the target is on the acoustic axis, and to increase with greater distances off the axis. As a fish moves away from the acoustic axis, the combination of beam position and yaw increases the effective tilt angle of the fish (Clay and Horne, 1995). To illustrate by example, two identical fish at equal distances from the acoustic axis are swimming towards or away from a transducer (Figure 1). Despite these fish being the same length and having the same tilt angle relative to horizontal, they will have equal but opposite tilt angles relative to the acoustic beam. Therefore, the fish swimming away

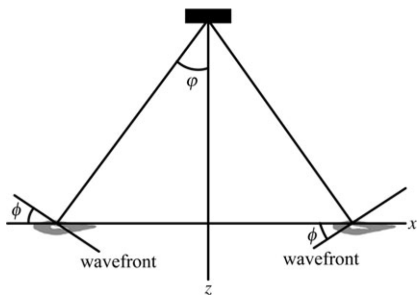

Figure 1. Effective tilt angle (ϕ) of a fish attributable to swimming direction and beam position. Psi (φ) is the equivalent beam angle of the transducer. The white area within the fish represents the swimbladder.

from the transducer will have a relatively greater TS because the incident beam angle is nearly orthogonal to the dorsal surface of the swimbladder.

To understand how the combination of beam position and orientation potentially influences individual and ensemble TSs, we used *in situ* measurements of TS and backscatter model estimates. *In situ* single-target detections of Pacific hake (*Merluccius productus*) were combined into tracks (i.e. multiple detections of the same fish), and used to tabulate frequency distributions of fish orientation. Tilt angles can be inferred from *in situ* target tracks if there is minimal ping-to-ping variability in fish behaviour and a fish is not tilted while swimming (Torgersen and Kaartvedt, 2001; McQuinn and Winger, 2003). Multiple detections of the same fish can also be used to estimate yaw. To quantify how orientation and beam position can influence average TS, we simulated fish distributions throughout an acoustic beam and tabulated ensemble TSs using the Kirchhoff–Ray mode (KRM) backscatter model.

Methods

Target tracking

Before identifying target tracks, single targets must be detected from *in situ* TS measurements. These were collected as part of the National Marine Fisheries Service's (NMFS) Pacific hake acoustic-trawl surveys in 1992, 1995, 1998, and 2001 aboard the RV "Miller Freeman" (Wilson and Guttormsen, 1997; Wilson *et al.*, 2000; Guttormsen *et al.*, 2003). In all years, the echosounder was calibrated using 60 mm (38 kHz) and 23 mm (120 kHz) copper spheres. Transceiver settings from each survey are listed in Table 1. Values of TS were collected using a SIMRAD 38 kHz split-beam EK500 echosounder (Bodholt *et al.*, 1989) as the vessel drifted over low-density fish aggregations. Owing to the dense daytime aggregations of Pacific hake, all measurements of TS were collected at night. The species composition of the aggregation was sampled before the drift using an Aleutian wing-trawl midwater net. If time allowed, a second trawl was conducted after the acoustic measurements had been collected to verify that the species composition and length frequencies had not changed. To provide more confidence that the measurements were restricted to hake, trawl catches had to be a minimum of 85% hake by weight to be included in the study. In all, 13 drift periods were selected for this study (Table 2). Length distributions from trawl catches associated with these 13 drifts had narrow ranges, with CVs ranging from 4.49% to 20.76%. All trawl catch length distributions were unimodal, with one exception. Hake caught during trawl 47 in 1998 had an average length of 39 cm, but 9.1% of the hake catch consisted of fish ranging in length from 18 cm to 25 cm. Length frequency histograms from each drift period are presented in Henderson (2005).

Single targets were detected using two software packages. They were initially identified and processed by the NMFS Alaska Fisheries Science Center using BI–500 software (Foote *et al.*, 1991). Sonardata's Echoview (v. 3.25) was used to identify targets located within the depth range sampled by the midwater trawl. A single-target threshold of −62 dB was used for all years except 1992, when the threshold was set to −60 dB. The minimum and maximum echolengths were 0.6 and 1.8 ms, respectively, except for 1992 when they were set at 0.8 and 1.8 ms. Maximum TS compensation was set at 3 dB to restrict echoes to those within the main lobe of the acoustic beam, and to minimize bias against smaller targets at the edge of the beam (Traynor and Ehrenberg, 1979).

Single targets were combined into target tracks using the target-tracking algorithm in Echoview. This algorithm, based on Blackman (1986), predicts a target's three-dimensional position at the time of the next ping, based on its current position and

Table 1. Transceiver settings for the 38 kHz echosounder used during the NMFS *in situ* target strength measurements.

Transceiver settings	1992	1995	1998	2001
Transducer depth (m)	0	9.15	9.15	9.15
Sound velocity (m s^{-1})	1 471	1 471	1 471	1 471
Absorption (dB km^{-1})	10	10	10	10
Power (W)	2 000	2 000	2 000	2 000
Pulse length	1.024	1.024	1.024	1.024
Alongship angle sensitivity	21.9	21.9	21.9	21.9
Athwartship angle sensitivity	21.9	21.9	21.9	21.9
Two-way beam angle (dB)	−20.6	−20.6	−20.6	−20.7
Sv gain (dB)	27.5	27.1	27.1	25.5
TS gain (dB)	27.4	27.3	27.1	25.8
Alongship 3 db beamwidth (dg)	7.2	7.2	6.7	6.9
Athwartship 3 db beamwidth (dg)	7.2	7.2	6.7	6.8
Alongship offset (dg)	−0.1	−0.9	−0.9	−0.8
Athwartship offset (dg)	−0.2	−0.2	−0.2	−0.3

Table 2. Description of trawl catches associated with drift periods used to detect single targets. These single targets were then used to create individual fish tracks.

Year	Trawl	Percentage hake by weight	Average length (cm)	Length CV	Total number of single targets	Single targets within tracks	Target tracks	Tilt and yaw estimates
1992	56	96.9	46.99	5.08	8 502	310	88	222
	57	96.3						
1995	80	88	48.37	4.49	3 778	279	77	202
	81	94.7						
	84	88.9	48.79	5.02	9 422	752	202	550
	85	98.5						
1998	16	97	30.90	20.77	13 572	173	55	118
	47	99.4	38.51	17.95	4 963	0	0	0
	60	97.7	40.52	12.11	8 862	47	15	32
	61	94						
	64	96.3	41.65	12.82	6 585	63	20	43
	65	97.6						
	74	99.9	41.23	8.05	4 070	107	34	73
2001	10	99.9	33.90	10.84	1 937	26	8	18
	12	92.9						
	37	99.9	47.25	9.36	4 442	88	27	61
	38	99.9						
	49	97.5	48.81	5.98	2 856	133	39	94
	50	96.6						
	52	84.7	48.92	7.08	1 776	170	47	123
	53	96.8						
	82	94.8	50.34	6.61	2 767	126	38	88
	83	99.1						

velocity. A target was added to a track if its position was within the acceptable volume gate, which was centred at the predicted location. The volume of the gate was calculated by the exclusion distances, which we set as 1 m for the major and minor axes, and 0.4 m in range. To be included in a track, a target could not be separated from the previous target by more than three pings. Targets not included within a track were used to start a new track. A track needed to contain at least three targets to be considered valid. The reader should consult the Echoview help-menu (Echoview, 2005) for algorithm equations and further discussion of target-tracking methods.

To ensure that any movement attributed to a fish was not due to vessel motion, we corrected for the alongship vessel displacement. Following the methods of McQuinn and Winger (2003), a target's position was corrected by subtracting the vessel displacement, calculated by Echoview using the vessel log distance, from the alongship change in target position. This transformation corrects for vessel drift, but does not correct for vessel pitch, roll, or heave. As measurements of TS were not conducted in rough seas (N. Williamson, pers. comm.), these factors were assumed to have a minimal influence on tracking results (Torgersen and Kaartvedt, 2001; McQuinn and Winger, 2003).

The last step before calculating tilt and yaw using target tracks was to estimate each track's tortuosity. The tortuosity of a track is the total distance travelled by a target divided by the straight-line distance from the first to the last position in that track. This value was used to assess the linearity of the swimming path of a fish. A linear track has a tortuosity value of 1, and tortuosity values increase as a target's path becomes more convoluted. Because we calculate tilt and yaw based on changes in the position of a fish, we assume that there is no deviation from the ping-to-ping swimming path of a tracked target. To increase confidence in our estimates of tilt and yaw, we eliminated tracks with tortuosity values >1.2. A value of 1.2 was arbitrarily chosen to represent linear swimming behaviour, based on the examination of 1536 tracks with tortuosity values ranging from 1 to 26.15. Using this criterion, 650 tracks from 12 of the original 13 drift periods were selected for analysis.

For each tracked fish, beam position was determined using echo-phase differences among the four split-beam quadrants (Bodholt and Solli, 1992). After correcting for vessel displacement, tilt and yaw of a fish were calculated based on the targets' change in three-dimensional position, using

$$\text{tilt} = \sin^{-1}\frac{\Delta z}{\sqrt{(\Delta x^2 + \Delta y^2 + \Delta z^2)}}, \quad (1)$$

and

$$\text{yaw} = \tan^{-1}\frac{\Delta y}{\Delta x}, \quad (2)$$

where Δx is the target's change in alongship position, Δy the target's change in athwartship position, and Δz the target's change in depth. As Equation (2) calculates yaw from -90° to 90°, yaw was converted to a 360° scale using the sign of Δx and Δy. For example, if both Δx and Δy were negative, then 180° would be added to the absolute value of the calculated yaw. Estimates of tilt and yaw were divided into 5° bins, and probability density functions (PDFs) were compiled for each drift period.

To determine the influence of tilt, yaw, and distance-off-axis (DOA) on measurements of TS, a linear model was developed. Data for each factor were standardized (subtract the mean and divide by the s.d.) to allow for direct comparison among factors within the model. The most appropriate linear model was determined using a stepwise selection based on the Akaike information criterion (AIC). In this approach, model terms were systematically added and removed to find the most parsimonious model with the best fit based on deviance (Akaike, 1973).

Simulations

We used five simulations to investigate the influence of tilt, yaw, and beam position on fish TS: *in situ*, orientation and beam position, schooling, shoaling, and tilt angle/ standard deviation (s.d.). In each simulation, the KRM-backscatter model was used to calculate the expected values of TS for 5000 fish at various orientations and beam positions (Table 3). The incident beam angle was calculated using random or fixed values of tilt, yaw, roll, and three-dimensional position within the acoustic beam (Medwin and Clay, 1998; Figure 1). In our simulations, we assume that the roll of each fish is zero (cf. Horne, 2003).

The KRM model was used to calculate the expected backscatter from a fish based on the incident angle of an acoustic wave. The KRM model (Clay and Horne, 1994) combines the breathing mode and the Kirchhoff approximation to estimate the intensity of sound reflected from an object using acoustic impedances (i.e. sound speed, g, and density, h, contrasts) of the fish body and swimbladder (Table 4). Dorsal and lateral radiographs from live fish were used to image swimbladder and body morphology. Tracings of these radiographs were divided into 1 mm fluid-filled (fish body) and gas-filled (swimbladder) cylinders that were elliptically interpolated to form a three-dimensional digital representation of the fish. The KRM model estimates backscatter from each cylinder based on the size of the cylinder, the cylinder's orientation with respect to the incident acoustic wave, and the carrier frequency. The backscatter from the fish body and swimbladder are summed coherently to estimate backscatter from the fish. All values of TS were calculated as reduced scattering lengths (RSL), which is a non-dimensional, linear measure of backscatter. RSL is equivalent to the square root of the backscattering cross section (σ_{bs}) divided by the length (L) of the fish in metres. RSL is converted to TS using

$$\mathrm{TS} = 20\log(\mathrm{RSL}) + 20\log(L). \quad (3)$$

For more detail regarding equations and methods used in the KRM model, the reader is referred to Clay and Horne (1994).

Continuous ranges of tilt and roll angles, incremented in 2° steps, were used in each simulation (Table 3). All simulations, except for the first, used backscatter-model predictions from a single fish 47 cm long. This fish was chosen because it was close to the average length (44 cm) of all hake caught in trawls associated with the TS measurements (Table 2). In the first simulation, which recreates *in situ* conditions, the entire length range of fish caught in trawls was represented in the backscatter-model predictions. Three fish were used to model different length ranges: a 24 cm fish was used for the range of 19–41 cm, the 47 cm fish (as used in the other simulations) for the 42–62 cm range, and a 60 cm fish for the 63–72 cm range because that was the largest hake radiographed before conducting these simulations. To model fish at lengths different from their actual lengths, fish bodies and swimbladders were linearly scaled in all dimensions.

In situ

The first simulation used *in situ* tilt, yaw, and depth distributions from target-tracking data to create TS distributions. Tilt, yaw, and depth values were randomly selected from target-tracking frequency distributions for each factor. To reduce bias attributable to small sample sizes, a TS measurement period needed at least 50 estimates of tilt and yaw from target-track data points. The x and y positions of fish within the beam were randomly selected based on depth (0–200 m) and a 3 dB beam width of 7.2°. The distance from the acoustic axis ranged between 0 and 12.5 m, the radius of a 7.2° beam at 200 m. Fish length was randomly selected based on the trawl-catch length distribution (Table 2). A Kolmogorov–Smirnov goodness-of-fit test was used to compare TS distributions from the *in situ* simulation with real *in situ* TS measurements.

Orientation and beam position

To quantify the influence of yaw and beam position on fish TS, an individual fish was rotated 360° at six fixed-beam positions. For each degree of rotation, the expected TS was calculated at 38 and 120 kHz. To investigate how the combination of a fish's tilt angle, yaw, and beam position influenced TS, this simulation included tilt angles of 5° head down, 0° (i.e. horizontal), and 5° head up.

Schooling vs. shoaling

If yaw influences the TSs of individual fish, then fish behaviour should influence an aggregation's average TS. Average TS values

Table 3. Settings for the five simulations used to investigate the influence of tilt, yaw, and beam position on fish TS.

Simulation	Tilt	Yaw	x-position	y-position	z-position	Length	
In situ	Distribution based on *in situ* tracks	Distribution based on *in situ* tracks	Random within 3 dB	Random within 3 dB	Tracking PDF	Trawl distributions	
Yaw and beam position	Fixed (−5°, 0°, 5°)	Fixed (0° − 360°)	Fixed (0, 2.5, 5, 7.5, 10, and 12.5 m)	Fixed (0 m)	Fixed (200 m)	Fixed (47 cm)	
Shoaling	Fixed (−10°, −5°, 0°, 5°, 10°)	Random	Random at a fixed radius (0, 2.5, 5, 7.5, 10, 12.5 m)		Fixed (200 m)	Fixed (47 cm)	
Schooling	Fixed (−10°, −5°, 0°, 5°, 10°)	Fixed (270°)	Random at a fixed radius (0, 2.5, 5, 7.5, 10, and 12.5 m)			Fixed (200 m)	Fixed (47 cm)
Tilt angle/s.d.	Normal distribution (μ = −10°, 0°, 10°; s^2 = 5, 10, 20)	Random	Random within 3 dB	Random within 3 dB	Fixed (200 m)	Fixed (47 cm)	

Table 4. Density (ρ) and speed of sound (c) estimates used in the backscatter model.

Medium	ρ (kg m^{-3})	c (m s^{-1})	$g = \rho_2/\rho_1$	$h = c_2/c_1$
Water	1 026	1 488	–	–
Fish body	1 070	1 570	1.04	1.06
Swimbladder	7.44	335	0.007	0.21

The values of g and h values are the ratios between density and speed of sound of two media with an interface (i.e. water and fish body, or fish body and swimbladder).

were calculated for simulated aggregations that were schooling (i.e. polarized yaw) and shoaling (i.e. random yaw) at 38 kHz. Tilt was held constant at five different angles ($-10°$, $-5°$, $0°$, $5°$, $10°$), the distance from the acoustic axis was fixed at six different radii values (0, 2, 5, 7.5, 10, and 12.5 m), and yaw was either assigned randomly (shoaling) or fixed (schooling). The TS distribution of a schooling aggregation (simulation 3) was compared with that of a shoaling aggregation (simulation 4) using a Kolmogorov–Smirnov goodness-of-fit test.

Tilt angle/s.d.

The final simulation was designed to illustrate how tilt distributions can influence an aggregation's TS distribution. Random yaw and beam positions were convolved with truncated Gaussian tilt distributions, with means of $-10°$, $0°$, and $10°$ and s.d.s of $5°$, $10°$, and $20°$. These tilt distributions were selected to represent the tilt-angle distributions observed for many fish species (McClatchie *et al.*, 1996). An ANOVA, followed by a Tukey's test for honestly significant differences, was used to determine the combinations of tilt angle and tilt s.d. that resulted in significantly different average TSs.

Results

Target-tracking

In all, 650 tracks, comprising 2274 single targets, were detected from the 12 TS measurement periods (Table 2). The mean number of single targets per track was 3.5, and the s.d. 0.95. In all, 1624 estimates of fish tilt and yaw were calculated from these tracks.

Target-tracking, tilt-angle distributions were similar among TS measurement periods (Figure 2). Except for the drift between hauls 84 and 85 in 1995, all tilt-angle distributions were skewed "head up". Mean tilt angles ranged from $-2.19°$ to $19.57°$, with values of s.d. ranging from $9.07°$ to $21.89°$. Two TS measurement periods, between hauls 80 and 81 and between hauls 84 and 85 in 1995, had slightly negative tilt medians of $-0.30°$ and $-0.64°$. Other tilt medians ranged from $0.17°$ through $17.10°$. Combining all hauls, the mean tilt angle was $4.21°$, with an s.d. of $19.26°$ and a median of $0.47°$ (Figure 3).

Figure 4 shows the distribution of swimming directions relative to the vessel heading. Proportions at each $5°$ yaw bin were relatively evenly distributed between 1% and 6% of the total. Most samples had a dominant mode at $0°$ and/or $180°$ that may be an artefact of the assumption that the vessel only moves in an alongship direction. Three drifts (between hauls 60 and 61 in 1998, between hauls 64 and 65 in 1998, and between hauls 10 and 12 in 2001) had dominant modes that were $\geq$10% of the total. Each of these drifts contained $<$50 yaw estimates. The low sample sizes allowed three to five yaw estimates in a single bin to skew the distributions and were therefore excluded from further analyses.

A linear model was developed using 1624 estimates of tilt, yaw, and DOA as independent variables, and the associated TSs as the dependent variable. Based on AIC, the most parsimonious linear model with the lowest deviance was

$$\mathrm{TS} = -46.25 - 0.95\mathrm{tilt} + 0.55\mathrm{yaw} + 2.15\mathrm{DOA} + 0.53\mathrm{yaw} : \mathrm{DOA}, \quad (4)$$

where the colon indicates an interaction effect between yaw and DOA. Tilt and the interaction between yaw and DOA both had a significant influence on fish TS ($p < 0.05$) (Table 5). The individual significance of yaw and DOA in the model should not be interpreted because the interaction term was significant. The overall r^2 value from the linear model was 0.069.

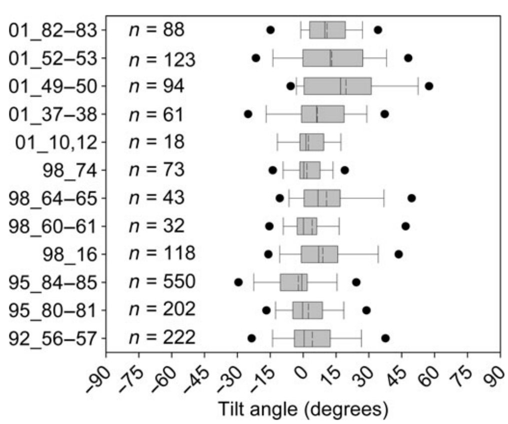

Figure 2. Tilt-angle distributions of Pacific hake calculated using individual fish tracks from 12 TS measurement periods. The measurement period is read as the year, underscore, followed by the trawls associated with the TS measurements. The solid line within the box is the median, the dashed line is the mean, error bars are the 25th and 75th percentiles, and closed circles are the 5th and 95th percentiles.

Simulations

Backscatter model

Results from Pacific hake backscatter model show that backscatter intensities and directivities differ between fish lengths and acoustic

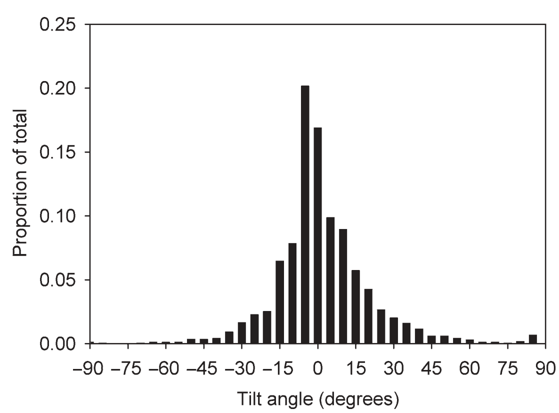

Figure 3. Tilt-angle PDF based on 12 single-target detection periods (n = 1624).

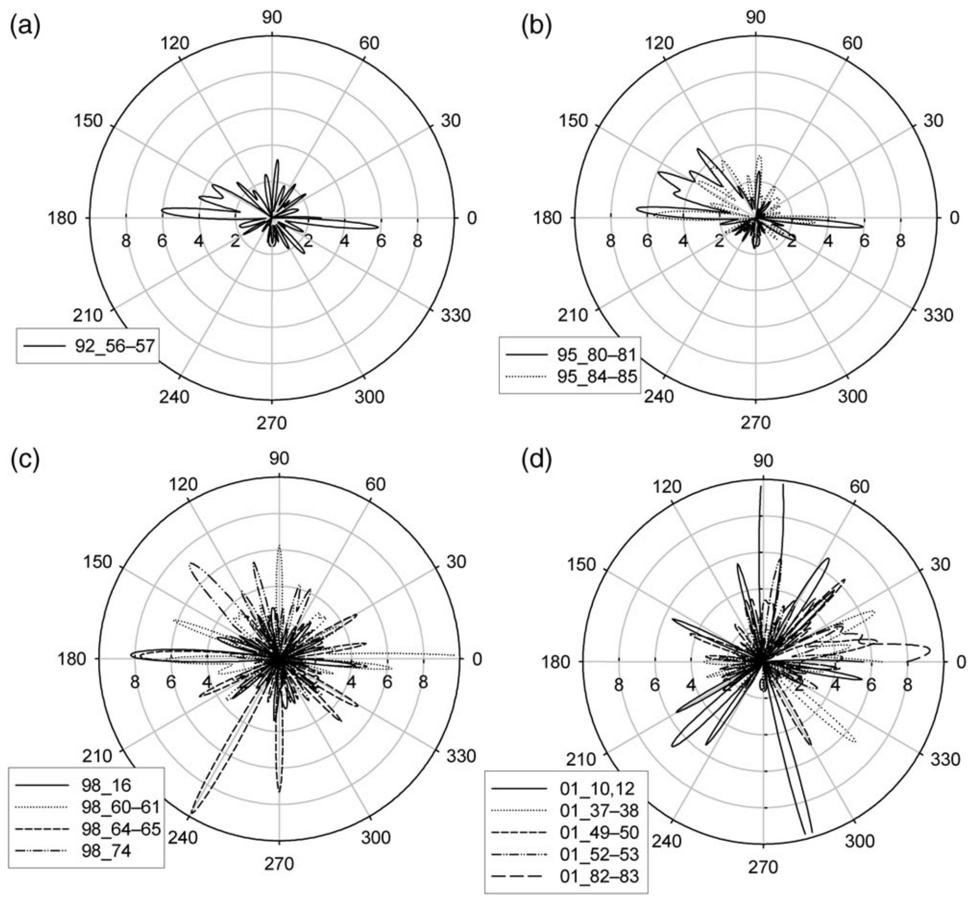

Figure 4. Yaw-angle PDFs for target detection periods from (a) 1992, (b) 1995, (c) 1998, and (d) 2001.

Table 5. Results of a linear regression model using *in situ* tilt, yaw, and DOA observations as independent variables, and TS measurements as the dependent variable.

Variable	Value	s.c.	*t*-value	*p*-value
Intercept	−46.2497	0.2310	−200.1949	0.0000
Tilt	−0.9448	0.2325	−4.0635	0.0001
Yaw	0.5539	0.2328	2.3794	0.0175
DOA	2.1458	0.2323	9.2368	0.0000
Yaw:DOA	0.5331	0.2348	2.2703	0.0233

The most appropriate linear model was determined using AIC criteria (see text).

frequencies. Because of the greater directivity at higher frequencies, the 120 kHz backscatter ambits (Figure 5b and d) are more complex than the ambits of fish modelled at 38 kHz (Figure 5a and c). Large fish (Figure 5c and d) reflect more energy and are more directional than small fish (Figure 5a and b), at both frequencies. Maximum predicted backscatter from the dorsal aspect was at a slightly "head-down" tilt, corresponding to the angle of the swimbladder. The predicted TS of small (20–24 cm) fish ranged from −35.86 to −79.34 dB, depending on the tilt of the fish relative to the transducer. The average range of TS values for small fish was 34.89 dB. Predicted TS values for large (42–66 cm) fish ranged from −23.69 to −74.67 dB, with an average range of 39.29 dB among individual fish.

In situ

The *in situ* simulations, which were designed to reproduce measured *in situ* TS distributions based on fish length and orientation, resulted in TS ranges similar to those observed during *in situ* measurements (Figure 6). The minimum and maximum simulated TS values were approximately −24 and −62 dB. As with *in situ* TS measurements, the TS distributions from this simulation were bimodal. A Kolmogorov–Smirnov goodness-of-fit test found that in eight out of nine comparisons, the simulated distributions were not significantly ($p > 0.05$) different from the measured distributions. However, examination of the frequency histograms revealed differences between modal locations and average TS. Average measured values of TS differed from average simulated values of TS by 1.31–9.01 dB (Figure 7). The average difference between these two distributions was 5.55 dB, similar to the 3–5 dB difference observed between the backscatter model predictions and *ex situ* TS measurements for Pacific hake (Henderson and Horne, 2007).

Orientation and beam position

Changes in the swimming direction of a fish resulted in TS differences, regardless of the tilt angle. Figure 8 is a polar plot that summarizes the effect of yaw and beam position on TS at three different tilt angles (5° head down, horizontal, and 5° head up). Predicted values of TS were contoured at increasing distance from the acoustic axis, but still within the main lobe of the

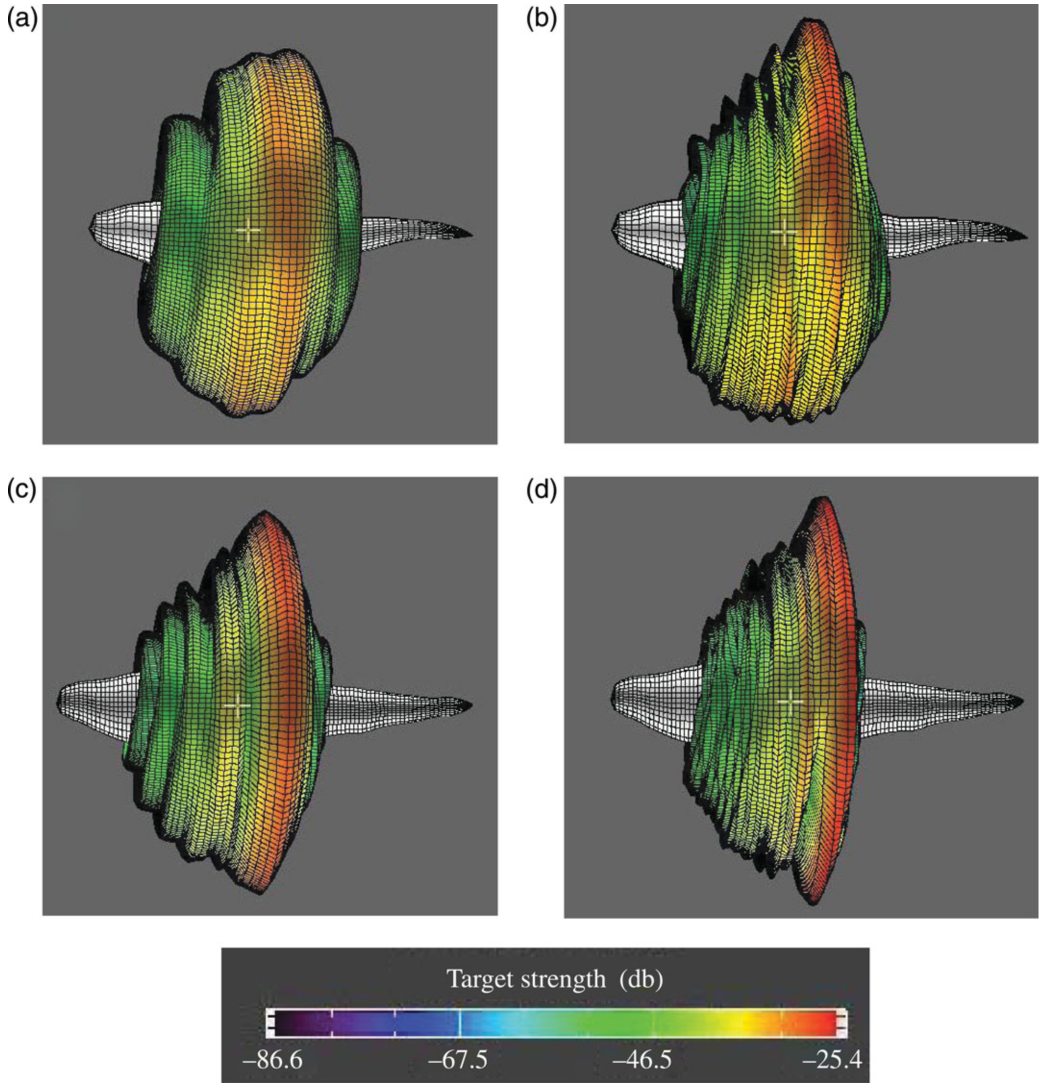

Figure 5. Expected backscatter based on tilt and roll for (a) a 24 cm fish at 38 kHz, (b) a 24 cm fish at 120 kHz, (c) a 47 cm fish at 38 kHz, and (d) a 47 cm fish at 120 kHz.

transducer (Figure 9). The largest TS differences were found when a fish was orientated perpendicular to the vessel (yaw 90° or 270°). In contrast, when a fish was aligned in the same as or the opposite direction to the vessel (yaw 0° or 180°), the TS was equal at all beam positions (Figure 8). A fish directly on the acoustic axis always had the same TS regardless of yaw. As a fish moves farther from the acoustic axis, the greater the influence yaw will have on TS. This effect is generally more pronounced at 120 kHz than at 38 kHz. At 38 kHz, a fish with a tilt angle of 5° "head down", 0°, or 5° "head up" had maximum TS differences of 7, 11, and 5 dB with changes in yaw and beam position (Figure 9a–c), respectively. At the same tilt angles, a fish measured at 120 kHz had maximum TS differences of 10, 19, and 5 dB with changes in yaw and beam position (Figure 9d and e).

Tilting the fish 5° "head up" and 5° "head down" resulted in even bigger changes in TS for a fish. The backscatter model predicted TS differences as large as 14 dB at 38 kHz, and as large as 26 dB at 120 kHz (Figure 9). Because the orientation of the swimbladder is different from that of the fish body, the influence of yaw and DOA on TS is not symmetrical at tilt angles of 5° "head down" and 5° "head up". As the fish assumes a 5° "head-down" tilt, the swimbladder becomes more normal with respect to the acoustic beam. A "head-down" tilt generally results in greater values of TS than a fish with a "head-up" tilt, regardless of yaw.

Schooling vs. shoaling

Although the combination of yaw and beam position has a big effect on the TS of an individual fish, the TS distribution of a shoaling (random yaw) aggregation was similar to that of a schooling (fixed yaw) aggregation. Each fish in the schooling aggregation had a yaw of 270° (orthogonal to vessel heading). A yaw of 270° was selected based on the results of the orientation and beam position simulation, which indicated that yaw and beam position had the greatest influence on TS when a fish was swimming perpendicular to the vessel (yaw 90° or 270°). Average values of TS

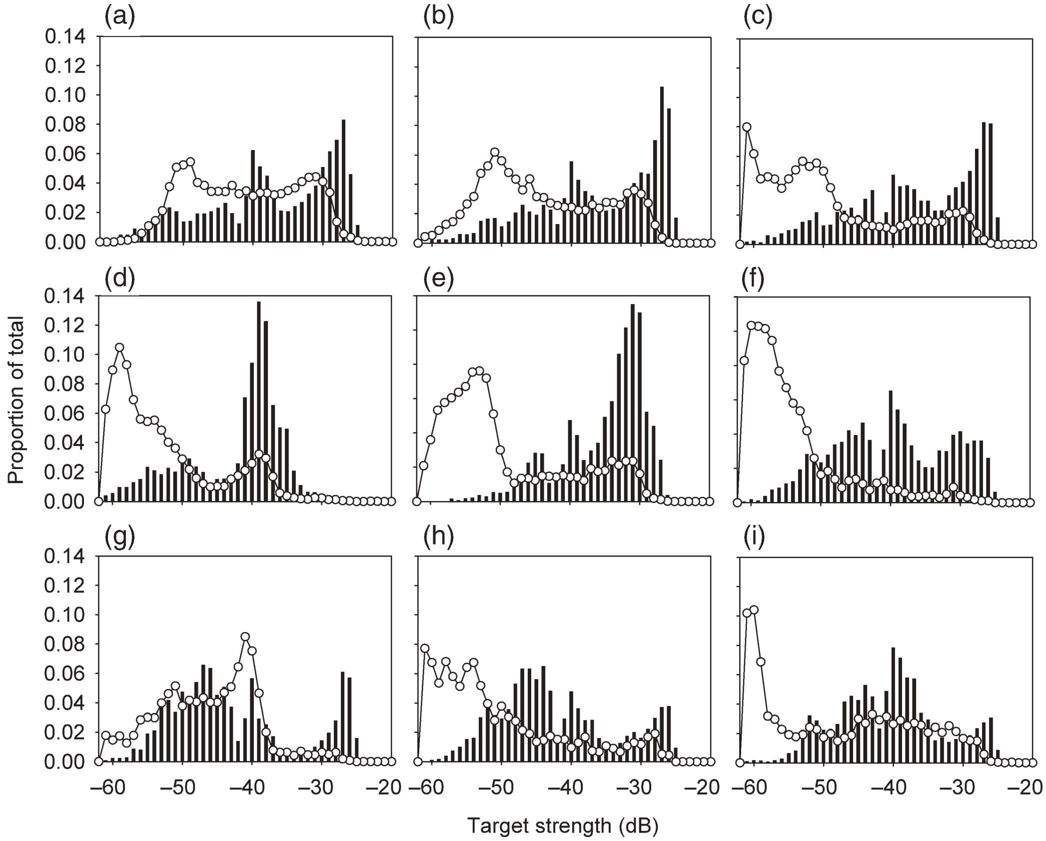

Figure 6. Simulated TS distributions (black bars), estimated using a backscatter model and *in situ* orientations based on fish tracks, for (a) 1992 hauls 56–57, (b) 1995 hauls 80–81, (c) 1995 hauls 84–85, (d) 1998 haul 16, (e) 1998 haul 74, (f) 2001 hauls 37–38, (g) 2001 hauls 49–50, (h) 2001 hauls 52–53, and (i) 2001 hauls 82–83. The white circles are *in situ* TS distributions from the same measurement period.

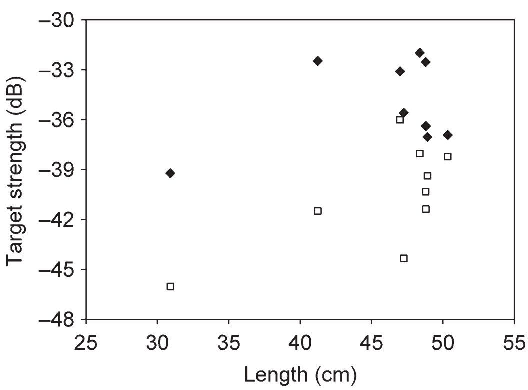

Figure 7. Comparison of average TS and length for *in situ* single target detections (open squares) and *in situ* simulations (solid diamonds), based on tilt, yaw, and beam-position estimates calculated from individual fish tracks.

from the shoaling aggregation were consistently similar to those of the schooling aggregation, regardless of the ensemble's average tilt angle or beam position (Figure 10). Combining estimates from all tilt angles and beam positions, the average TS of a shoaling aggregation was −31.27 dB, compared with an average TS of −31.24 dB for a schooling aggregation. The TS distributions from these two aggregations were not significantly different ($p = 0.14$) based on a Kolmogorov–Smirnov goodness-of-fit test.

Tilt angle/s.d.

The average TS of an aggregation is significantly influenced by the tilt-angle distribution. If the s.d. of this factor is low, then the average tilt angle has a big influence on average TS. With a tilt s.d. of 5°, average estimates of TS at tilt angles of −10°, 0°, and 10° differed by as much as 8.69 dB (Figure 11). As tilt s.d. increased, the importance of average tilt angle on TS decreased. With a tilt-angle s.d. of 20°, average estimates of TS differed by a maximum of 1.27 dB at tilt angles of −10°, 0°, and 10°. An ANOVA, followed by a Tukey's test, found that with an s.d. of 20°, average values of TS were not significantly different ($\alpha > 0.05$) at tilt angles of −10° and 0°. At an s.d. of 10° or less, TS distributions differed significantly at every tilt angle. Regardless of the average tilt angle or its s.d., individual TS values ranged over >20 dB (Figure 11a–i).

Discussion

The swimming direction of a fish can have a great influence on TS if the fish is not directly on the acoustic axis. This effect is most pronounced when a fish enters or exits the acoustic beam on a trajectory that passes through the acoustic axis. In such a situation, the incident acoustic beam strikes the fish on the head or tail, effectively changing the tilt angle of that fish. Simulation results found that as a fish moves away from the acoustic axis, swimming direction has a greater effect on TS. The predicted 11 dB (at 38 kHz) and 19 dB (at 120 kHz) changes in fish TS attributable to changes in yaw and beam angle were consistent with *in situ* TS

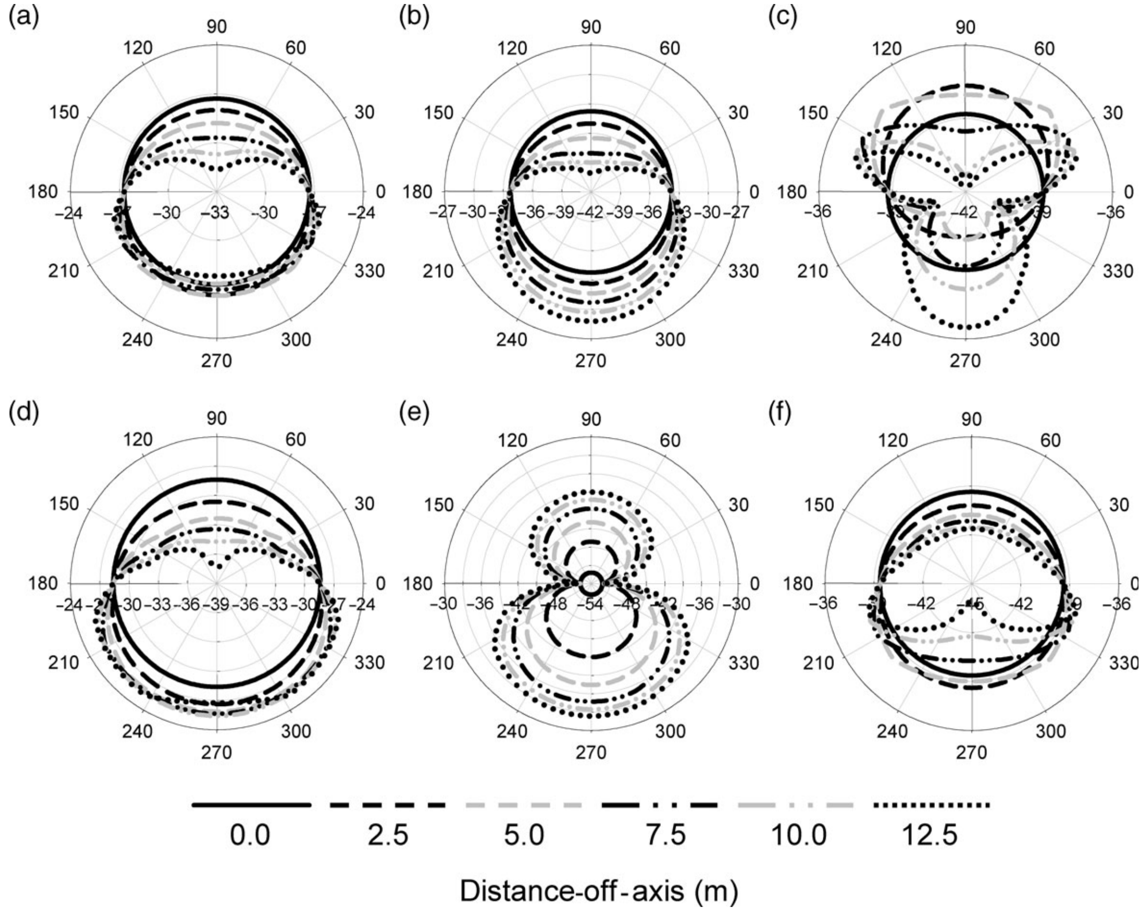

Figure 8. Polar plots of fish TS estimates with changes in fish yaw and DOA. Tilt and carrier frequency are (a) $-5°$ and 38 kHz, (b) 0° and 38 kHz, (c) 5° and 38 kHz, (d) $-5°$ and 120 kHz, (e) 0° and 120 kHz, and (f) 5° and 120 kHz. Each radial ring denotes a TS difference of 3 dB. Note that each plot has a different TS scale.

measurements. The regression model developed using *in situ* TS data identified tilt, yaw, and distance from the acoustic axis as significant factors influencing the TS. Changes in individual values of TS, caused by changes in orientation, help explain the multimodal TS distributions observed for fish species such as walleye pollock (*Theragra chalcogramma*; Williamson and Traynor, 1984), herring (*Clupea harengus*; Huse and Ona, 1996), Atlantic cod (*Gadus morhua*; Hammond, 1997), hoki (*Macruronus novaezelandiae*; Cordue *et al*., 2001), and capelin (*Mallotus villosus*; Jørgensen and Olsen, 2002).

Although TS differences were large for an individual fish, comparison of TS distributions from simulated aggregations with a fixed (schooling) or random yaw (shoaling) showed no significant differences if fish were dispersed within the acoustic beam. When we designed these simulations, we hypothesized that changes in TSs of individuals within an aggregation would be reflected in the average target strength of that aggregation. We attribute the contrary results to the numerous combinations of tilt, yaw, and beam position that resulted in the same TS. For example, an incident angle insonifying a fish 2.5 m to the stern of the transducer with a tilt angle of 0° and a yaw angle of 90° matches the incident angle insonifying a fish 2.5 m to the port of the transducer with a tilt angle of 0° and a yaw angle of 180°. Because those fish are insonified at the same incident angle, they will have the same TS. As a result of these non-unique combinations, an aggregation of fish dispersed throughout the beam will produce essentially the same TS distribution, regardless of the aggregation's yaw distribution.

This study focused on the influence of yaw and beam position on fish TS, but as far as we know this is also the first study that has estimated *in situ* tilt-angle distributions of Pacific hake. The calculated tilt-angle distributions are similar to those expected for other gadoids (McClatchie *et al*., 1996). However, there may be concerns regarding the accuracy of our tilt-angle estimates. To calculate tilt angles, we assumed that the movement of the vessel was restricted to an alongship direction, because we had no data on vessel heading, pitch, roll, or heave. Some studies (Torgersen and Kaartvedt, 2001; McQuinn and Winger, 2003) found that if conditions are calm, then a vessel's pitch and roll should not influence tilt-angle estimates based on target tracks. We are unable to confirm this assumption with our data. Another potential bias in our tilt-angle estimates may result from the single target-detection algorithm, which detects the targets used in forming tracks. Targets with larger tilt angles were detected less often as the fish moved away from the acoustic axis (Figure 12). The lack of TS measurements from fish at greater tilt angles may be due to a bias against targets with smaller values of TS, which has been noted before (Barange *et al*., 1993; Koslow *et al*., 1997; Bertrand *et al*., 1999). Without independent confirmation, however, our tilt-angle estimates may not be completely representative of Pacific hake *in situ* swimming behaviour.

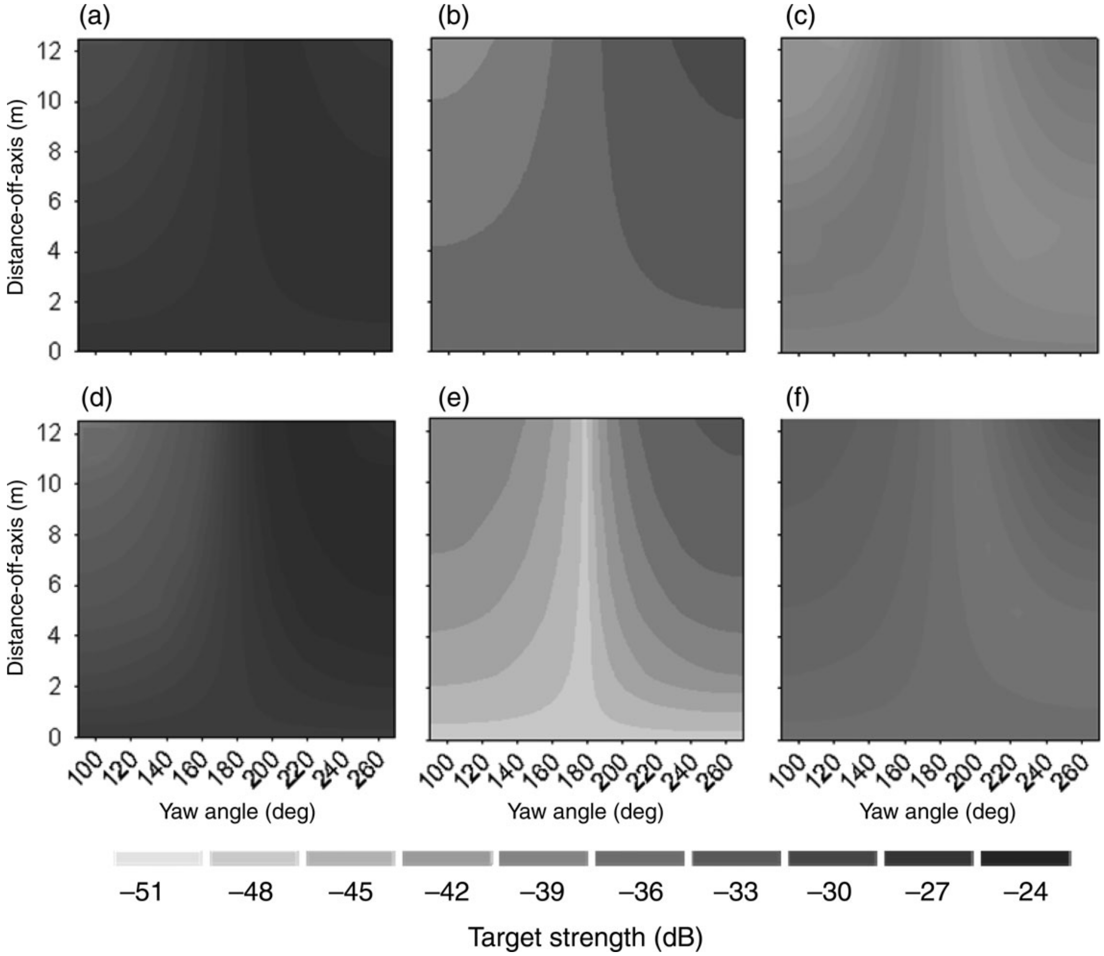

Figure 9. Contour plots of the predicted influence of yaw and DOA for a 47 cm fish modelled at (a) -5° tilt and 38 kHz, (b) 0° tilt and 38 kHz, (c) 5° tilt and 38 kHz, (d) -5° tilt and 120 kHz, (e) 0° tilt and 120 kHz, and (f) 5° tilt and 120 kHz. Yaw angles were only plotted from 90° to 270° because the expected TS is symmetrical on either side of the saggital axis of a fish.

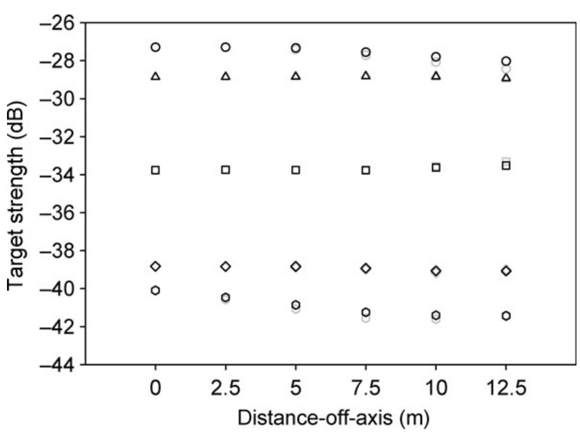

Figure 10. Comparison of average values of TS at various combinations of tilt and DOA for shoaling (grey symbols) and schooling (black symbols) aggregations. In some instances, shoaling and schooling symbols overlap perfectly, so it appears that there is only one symbol. Each point represents a simulation of 5000 fish with a fork length of 47 cm. Tilt angles are -10° (triangles), -5° (circles), 0° (squares), 5° (diamonds), and 10° (hexagons).

Tilt angle had a significant influence on TS based on *in situ* measurements and backscatter-model simulations. This influence was reduced, however, as the tilt-angle s.d. increased. At an s.d. of 20°, there were minimal differences in the aggregation average TS regardless of mean tilt angle. Where tilt s.d. was 10° or less, as expected for an aggregation exhibiting uniform avoidance (McClatchie *et al.*, 1996), the resulting average TS was significantly influenced by the mean tilt angle of that aggregation. This result has important implications for *in situ* TS measurements used to determine average acoustic size. Accurate TS estimates depend on the absence of uniform avoidance behaviours away from the sampling platform (i.e. vessel) or any other stimulus (Blaxter and Batty, 1990; Gerlotto and Fréon, 1992; Fernandes *et al.*, 2000). As target-tracking software continues to improve, it is proposed that tilt angles of individual fish within aggregations be measured in real time to ensure that changes in fish behaviour do not bias the estimates of TS.

The results of this study have shown that a large sample size of individual fish and TS is necessary to estimate accurately the average acoustic size of individual fish within an aggregation. Owing to the "greater-than-20-" dB TS differences observed for

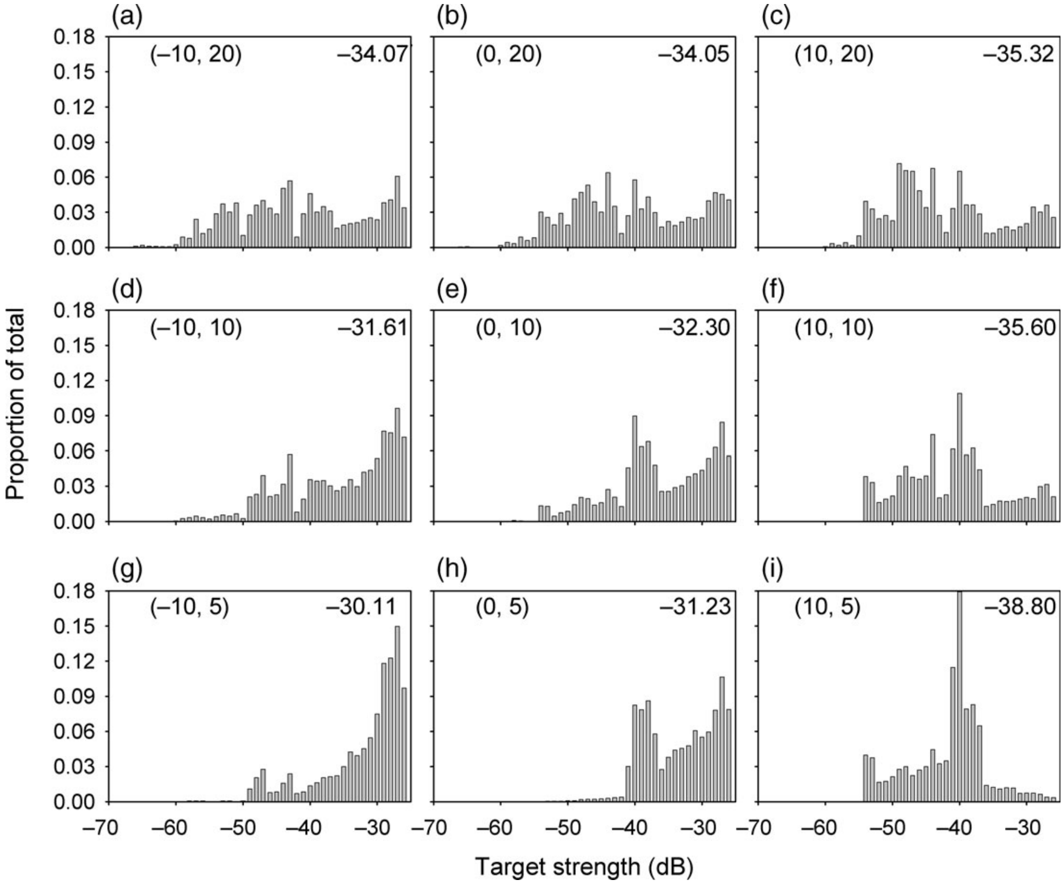

Figure 11. Target-strength histograms of simulated aggregations with different Gaussian tilt-angle distributions. The numbers in parentheses are the mean and the s.d. of the tilt-angle distribution. The number to the right is the average TS of the simulated aggregation.

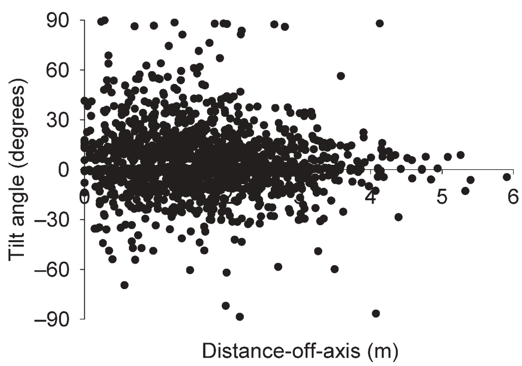

Figure 12. Tilt-angle estimates as a function of a target's distance from the acoustic axis.

individual fish, small sample sizes could significantly skew average estimates of TS. For example, fish on the periphery of an aggregation may have a different size distribution (DeBlois and Rose, 1995), or adopt different orientations (Foote, 1980b; MacLennan and Simmonds, 1992) from those within the aggregation. If sample sizes are sufficiently high, and fish are dispersed throughout the beam and swimming normally (i.e. no vessel avoidance or attraction), then the influence of orientation on average TS estimates will be minimal.

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