Tilt angle and target strength: target tracking of Atlantic cod (*Gadus morhua*) during trawling

Ian H. McQuinn and Paul D. Winger

Vertical orientation (tilt angle) is known to affect the target strength (TS) of ensonified fish and is a large component of the variability inherent in acoustic-biomass estimates. To measure the effects of changes in tilt angle on TS during diel vertical migrations, a concentration of migrating Atlantic cod (*Gadus morhua*) was observed acoustically from a research vessel over several days. Single-target data were collected from a split-beam echosounder and were subsequently tracked, corrected for vessel orientation and movement, and analysed for 3-dimensional displacement (speed and direction). The results revealed a large variability in TS and several patterns of swimming behaviour from random to directed orientation and movement, with changes in both vertical and horizontal displacements and inferred orientation. These behavioural patterns and their affects on TS were analysed as a function of "time-since-sunset". Regular diel orientation patterns were observed as cod rose from the ocean bottom in the evening, increasing their tilt angle, and descended at sunrise to regain the ocean floor. Standardized TS (B_{20}) was found to be highly correlated with tilt angle. This relationship can be used to correct for the diel changes in the TS of these migrating cod as a function of the *in situ*-measured tilt angle and thus to improve the accuracy of acoustic-biomass estimation.

I. H. McQuinn: Department of Fisheries and Oceans, Maurice Lamontagne Institute, C.P. 1000, 850 route de la Mer, Mont-Joli, Québec, Canada G5H 3Z4. P. D. Winger: Biopsychology Program, Departments of Biology and Psychology, Memorial University of Newfoundland, St. Johns, Newfoundland, Canada A1B 3X9. Correspondence to I. H. McQuinn; e-mail: mcquinni@dfo-mpo.gc.ca.

Introduction

Variability in the incident angle between the acoustic-wave front and the dorsal aspect of fish targets (aspect angle) is one of the most important factors influencing *in situ*, target-strength (TS) estimates (Aglen, 1994) because of the highly directive scattering of many fish species. Since the orientation and stability of vertical echosounder transducers are controllable and measurable to a large extent, the vertical orientation or tilt angle of the fish targets becomes the dominant unknown. Unfortunately, fish-tilt angle can be a very unstable parameter over which investigators have the least control and, in most cases, the least information. The fact that fish vary their vertical orientation with time causes variability among repeated TS measurements of individual fish and increases the statistical variability of mean *in situ* TS estimates. However, more serious than increased variability is the effect of oriented-fish behaviours that shift the mean tilt angle and therefore introduce systematic bias

into TS estimation. Many acoustic applications assume tilt angle to be constant and at maximum dorsal aspect, even though small departures from this assumption can have major repercussions on fish-biomass estimates (Foote, 1980; Olsen *et al.*, 1983; Buerkle, 1987).

The development of target-tracking software over the past decade has made it possible to measure the swimming behaviour of fish *in situ* using information readily available from a split-beam echosounder. This technique provides a non-intrusive method of collecting and analysing data on the sequential, 3-dimensional (3-D) position of single targets for the study of fish behaviour in various ecological settings (Brede *et al.*, 1990). Although the 3-D position information from split-beam TS data is considerably more precise than previous technologies (e.g. single beam), the method has been criticized for weaknesses associated with the discrimination between single and multiple targets (Soule *et al.*, 1995). Under certain conditions, the common algorithms used to identify single targets can fail,

accepting multiple targets with erratic amplitude and phase information.

One means of circumventing the problem of multiple targets is that of tracking a single target over a series of pings, thereby identifying the target as a single fish through an analysis of its "behaviour" and its interaction with other tracked targets. Target tracking also has the advantage of generating information on swimming performance, such as speed and direction, as well as 3-D orientation, including tilt angle. These target-tracking techniques have been exploited extensively in the riverine environment from fixed or scanning horizontal systems, where the tracking of migrating species such as salmon has enabled the identification of individual fish for population assessment through target counting (Mulligan, 2000). However, they have been less frequently used vertically in the marine environment, mainly because of the problems associated with the motion of the acoustic platform (pitch, roll, and heave) and horizontal displacement. Various studies have reported target-tracking results from slowly drifting vessels (Huse and Ona, 1996; Torgersen and Kaartvedt, 2001) or autonomous buoys (Godø et al., 1999). The present paper describes a study where individual fish were tracked from a trawling vessel and estimates were made of various parameters on their swimming behaviour including tilt angle while the vessel's displacement was controlled. The objective was to measure the swimming angle of cod through target tracking and to relate this to their TS and length distributions over a diel vertical-migration cycle to determine a tilt-angle-dependent length–TS relationship.

Materials and methods

Single-target data were collected from a large, homogeneous distribution of Atlantic cod (*Gadus morhua* L.) along the West Coast of Newfoundland in May, 1998 (Table 1) during their annual spawning migration into the Gulf of St. Lawrence (McQuinn et al., 1999). The acoustic platform was the CCGS "Teleost", a 63-m research trawler equipped with a SIMRAD EK500 scientific echosounder coupled to a hull-mounted, 38 kHz 7° split-beam transducer. Raw acoustic-sample data were collected in the HAC standard format (Simard et al., 1997) using the CH1 software (Simard et al., 1998) and analysed with the CH2 echo-integration package (Simard et al., 2000). Tracking data were collected as filtered, single-target detections from the serial port of the EK500. Filter parameters (minimum TS, maximum echo duration, and maximum gain compensation) were broad to allow a high number of accepted targets (Table 2), since erroneous detections (i.e. multiple targets) would be scrutinized and eliminated during post-processing. Vessel position was determined from Global Positioning System (GPS) data collected at 2-s intervals. During the study, the weather conditions were ideal, with several days of completely calm seas, eliminating the need

to correct the split-beam angle data for irregular vessel motion (pitch, roll, and heave).

Single-target data were collected during trawling (pelagic and bottom), so the vessel speed was significantly reduced ($1.5–2.5 \, \mathrm{m \, s^{-1}}$) from the normal survey speed ($5.5 \, \mathrm{m \, s^{-1}}$) allowing for longer tracks (minimum = 3; maximum = 50 pings per target) and a high spatial and temporal correspondence between acoustic-target and catch-data collection. A total of nine pelagic- and bottom-trawl sets were analysed, covering the nighttime hours from 21:00 h to 05:00 h over five days. In all, over 1800 tracks were identified as cod and analysed for behavioural characteristics, from a total of nearly 37 000 echoes. Tracks with a mean TS ≤ -45 dB were considered to be non-cod and were eliminated from further analyses.

All single targets were analysed in post-processing using Fish Eye target-tracking and Fish Tales track-editing software (Carousel Computer Consultants). The 3-D Cartesian coordinates (X,Y,Z) were determined from the alongship (θ) and athwartship (φ) angles and the range (r) which were supplied by the EK500.

$$x = z \tan(\theta)$$

$$y = z \tan(\varphi)$$

$$z = \sqrt{r^2 - (x^2 + y^2)}.$$

Each track was visually scrutinized for internal consistency in the spatial and temporal displacement of the single targets and subsequently edited where inconsistencies were detected, i.e. when erratic displacement and TS values were detected.

As noted earlier, calm seas eliminated the need to correct these coordinates for vessel pitch, roll, and heave. However, to remove the effect of "alongship" vessel displacement, the position of the vessel relative to the fish echo was also determined by converting the latitude and longitude positions from the GPS to Cartesian coordinates using a Lambert projection. Vessel displacement (VD) was then determined between each position coordinate from time t to t + i

$$VD = \sqrt{\left(X_{t+i} - X_t\right)^2 + \left(Y_{t+i} - Y_t\right)^2}$$

where i is the step interval. To correct for the GPS position-to-position error or "jitter", the step interval was increased until a regular pattern was obtained in the estimated position-to-position vessel speed, which is sensitive to position errors. The estimated vessel displacement between pings was then subtracted from the "alongship" fish displacement (in X), yielding the net ping-to-ping fish position and displacement.

From these data, several behavioural parameters were estimated, assuming that ping-to-ping changes in X, Y, and Z positions were the result of active swimming. Swimming speed was calculated as the average of the ping-to-ping fish displacements over time. The displacement between positions was assumed to be in a straight line and therefore swimming speeds are likely to represent minimum

Table 1. Details of trawl catches, target tracks, and the estimated mean behavioural characteristics (tilt angle, geographic and relative fish trajectories, horizontal angular deviation, vertical range and height, swimming speed) of migrating Atlantic cod (*Gadus morhua* L.) off the West Coast of Newfoundland.

Set no.	Date (d-m-yr)	Local time (h:min)	Type	Vessel speed (m s⁻¹)	Cod in catch (% wt)	No. of cod	Mean cod length (cm)	No. of echoes	No. of tracks	Mean TS (dB)	B_{20} (dB)	Tilt angle (deg)	Geographic fish trajectory (deg)	Relative fish trajectory (deg)	Horizontal angular deviation (deg)	Vertical range (m)	Vertical height (m)	Swimming speed (m s⁻¹)
7a	07/05/1998	04:39	Bottom	1.32	98.5	204	45.78	4296	217	−30.3	−63.5	1.19	159.5	287.0	97.3*	203.8	23.9	1.60
7b	07/05/1998	05:04	Bottom						119	−30.8	−64.0	−0.58	63.0	37.5	39.6*	207.1	16.9	2.01
9a	08/05/1998	00:10	Pelagic	2.66	100.0	111	53.41	6462	502	−33.2	−67.8	6.64	284.7	82.2	101.1*	154.7	–	0.86
9b	08/05/1998	00:50	Pelagic	2.18				1826	81	−33.6	−68.1	5.00	245.7	50.8	114.6	155.7	17.7	1.03
11	08/05/1998	22:43	Pelagic	2.67	100.0	194	47.99	5807	–	−35.2	−68.1	7.94	–	–	–		–	–
17	09/05/1998	21:14	Bottom	1.71	95.9	116	40.31	438	41	−32.3	−64.4	2.30	354.2	351.8	109.3	181.4	9.4	0.98
29	10/05/1998	22:12	Bottom	2.01	78.2	58	41.60	1199	58	−33.7	−66.1	3.37	301.0	298.4	116.9	209.2	28.8	1.19
30a	10/05/1998	23:24	Bottom	1.29	34.3	241	46.39	7423	177	−32.2	−65.5	2.86	5.5	353.8	110.7*	187.2	24.4	1.15
30b	10/05/1998	23:54	Bottom						67	−30.7	−64.0	1.41	23.5	154.8	154.4	187.0	28.8	0.96
31	11/05/1998	00:45	Bottom	1.71	94.7	117	46.41	2856	138	−32.2	−65.5	2.93	352.2	289.6	132.6	179.8	25.9	0.90
32	11/05/1998	03:48	Bottom	1.38	96.1	140	45.71	977	38	−32.9	−66.1	2.36	96.1	106.3	77.1*	188.4	–	
43	12/05/1998	22:37	Pelagic	2.63	98.8	190	49.47	5605	388	−35.7	−69.5	10.35	305.3	273.5	73.7*	159.8	40.3	0.67
Total						1371		36889	1826									

*Distribution of horizontal trajectories significantly different ($p < 0.01$) from random according to Rayleigh test (Batschelet, 1981).

Table 2. Echosounder settings used to select single targets from the SIMRAD EK500.

Parameter	Setting
Pulse duration (ms)	1.0
Minimum uncompensated TS (dB)	−60
Minimum echo/pulse duration ratio	0.8
Maximum echo/pulse duration ratio	1.8
Maximum gain compensation (dB)	6.0
Maximum phase jitter (phase steps)	2.0
Detection range (m)	5 to bottom

estimates. Fish orientation was defined as the direction of the resultant horizontal (X–Y) and vertical (Z = tilt angle) trajectories, where the mean and angular deviation was calculated from the sum of the individual ping-to-ping vectors (Batschelet, 1981).

Trawl-catch data

Catch data were sampled for species composition and catch weight. Atlantic cod were measured for individual fork length (mm) and weight (g). The length/TS relationship was estimated using the mean length from the catch samples and the mean TS (average backscattering cross-section converted to dB) from the corresponding fish-track samples by the equation

$$TS = 20 \log L + B_{20} \tag{1}$$

where L is fork length in centimetres.

Results

Trawl catches

The analysis of the trawl-catch samples revealed, from their maturity stages, that these cod were grouped in prespawning concentrations and ranged in length from 15 to 95 cm, primarily between 20 and 65 cm, with mean lengths per sample from 40.3 to 53.4 cm (Table 1). Echograms showed that during the daytime hours they were distributed on or very close to the seafloor, making individual target identification impossible. At night, they rose to be distributed throughout the water column up to 50–60 m off bottom (McQuinn *et al.*, 1999) consistently, and were easily resolvable as single targets (Figure 1). The catches were fairly homogeneous, consisting primarily of cod (95–100% by weight) with the exception of samples 29 and 30, which contained 78 and 34% cod, respectively (Table 1). The remainder of these two samples was juvenile redfish (<17 cm), which were easily distinguishable from the cod echoes on the echograms and in the target data, being much smaller than the mature cod.

Behavioural parameters of fish tracks

Over 1800 tracks were identified and scrutinized from nearly 37 000 echoes, yielding from 41 to 502 tracks per sample (Table 1), and from 3 to ∼50 echoes per track. The average TS per sample estimated from the mean of the target tracks was between −35.7 and −30.3 dB. The mean vertical range of the cod tracks was between 150 and 210 m, which corresponded to a mean off-bottom height between 9 and 40 m.

Estimates of swimming speed and direction revealed several behavioural patterns; from random to directed orientation and movement, both vertical and horizontal migrations and a large variability in TS (Table 1). These behavioural patterns and their effects on TS were analysed as a function of time after sunset (Figure 2). Regular diel-orientation patterns were observed. Cod rose from the ocean bottom in the evening, increasing their tilt angle to between 2° and 4° head-up, with occasional periods of increased tilt up to 10° during the night (e.g. sample 43), and descended at sunrise to regain the ocean floor.

Behavioural influences on TS

When mean standardized TS (B_{20} from Equation (1)) from all cod tracks was plotted against mean fish length from the trawl samples, without consideration for behavioural factors, there was a large spread of estimates (−63.5 to −69.5 dB) with possibly even a downward dependence on fish length (Figure 3). It would be difficult to assume from this figure that B_{20} is a constant. However, there was a clear relationship between B_{20} and the measured tilt angle (Figure 4). This figure includes those samples that were separated between two time intervals due to a noticeable change in swimming behaviour during trawling. Even when there was a significant change in tilt angle between intervals within a sample (e.g. sets 30a and 30b), the relationship holds well, following the general pattern shown by previous studies of a decreasing TS as tilt angle increases (Olsen *et al.*, 1983). In the present study, we observed a 6-dB decrease between 0° and 10° head-up, which corresponds to that predicted by modelling (J. Horne, unpublished data). We have fitted empirically a polynomial regression through these points, giving the relationship

$$B_{20} = -63.4 + 0.478A_T - 0.762A_T^2 + 0.131A_T^3$$
$$- 0.0065A_T^4 \quad (r^2 = 0.95, \ p = 0.0001)$$

for tilt angles (A_T) > 0, although other modelled relationships based on swimbladder shape and orientation may be more appropriate.

Physical influences on TS

Modelling and experimental studies have shown the effects on swimbladder volume, shape, acoustic cross-section, and, ultimately, TS induced by the change in pressure following a vertical migration (Harden-Jones and Scholes, 1985; Ona, 1990; Arnold and Greer Walker, 1992). It is generally agreed that changes in the volume of a cod's swimbladder resulting from changes in ambient pressure follow Boyle's
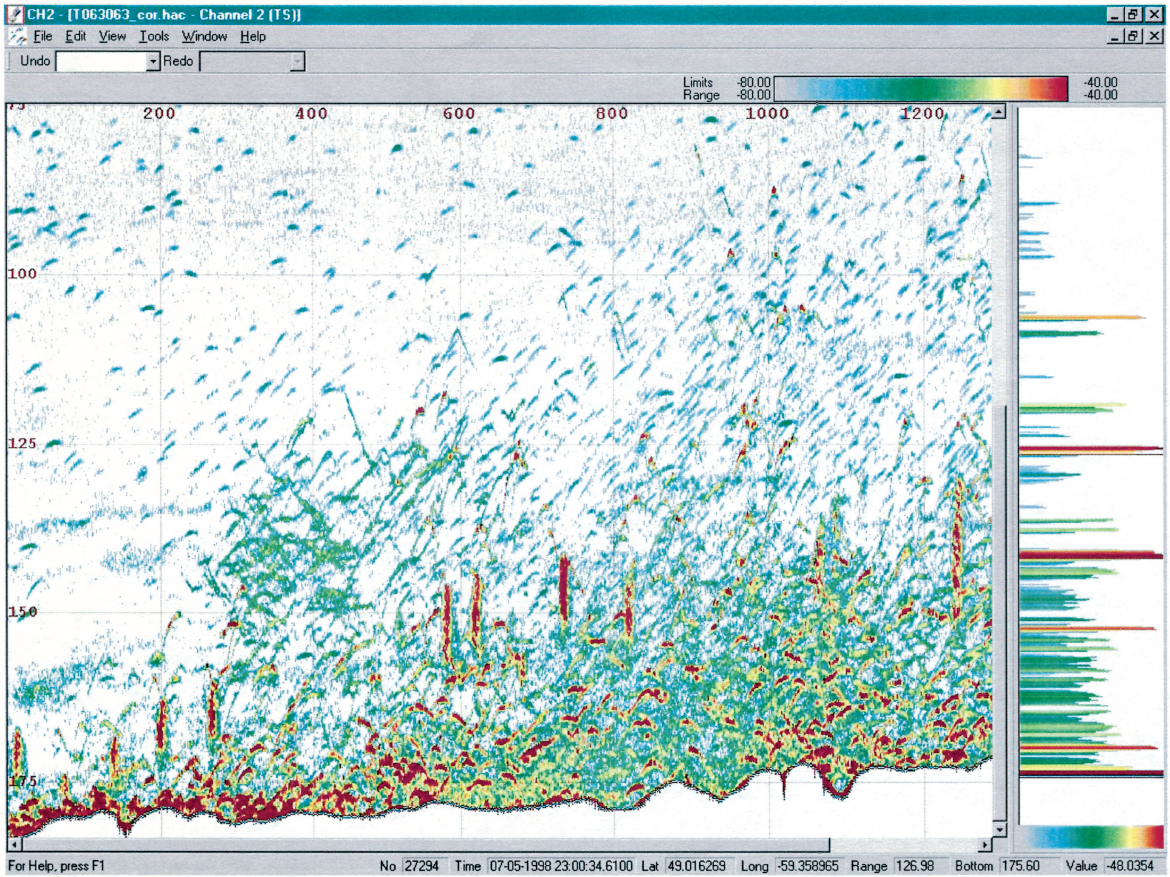
Figure 1. An echogram of Atlantic cod (*Gadus morhua* L.) (dark echoes) rising off the bottom at sunset along the west coast of Newfoundland (19:51–20:45 local time).
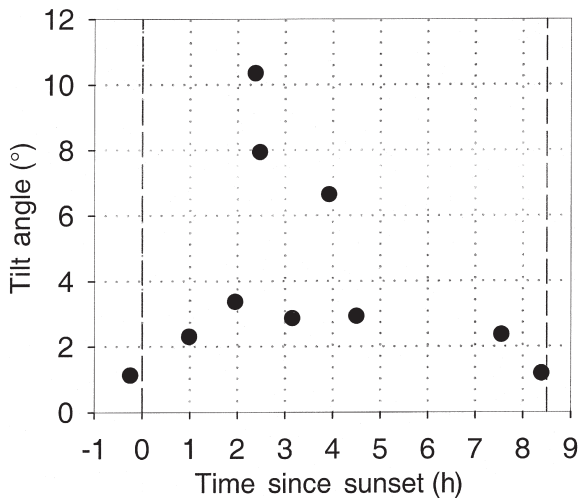

Figure 2. Mean tilt angle versus "time-since-sunset" (20:25 local time) for Atlantic cod (*Gadus morhua* L.) off western Newfoundland. Dashed reference lines indicate sunset and sunrise, respectively.
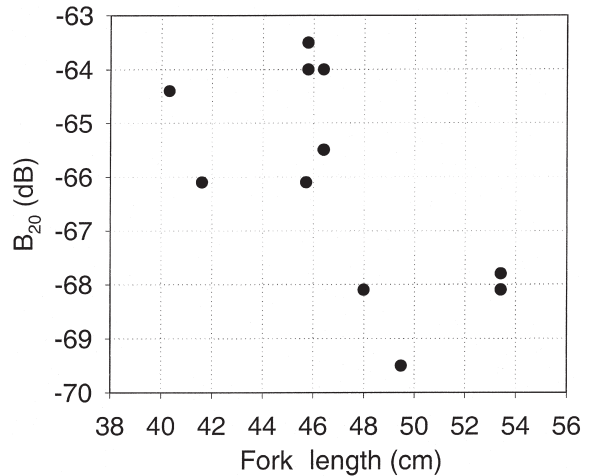

Figure 3. A scatterplot of estimated T intercepts (B_{20}) from TS–length relationships determined from catches and tracked targets of Atlantic cod (*Gadus morhua* L.).
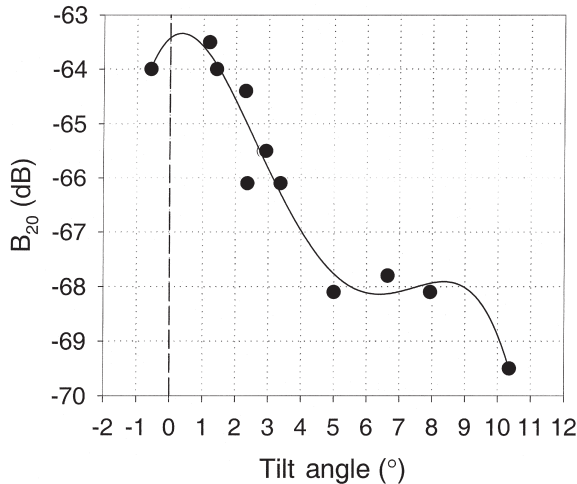
Figure 4. A relationship showing the dependence of standardized TS (B_{20}) on tilt angle in Atlantic cod (*Gadus morhua* L.).
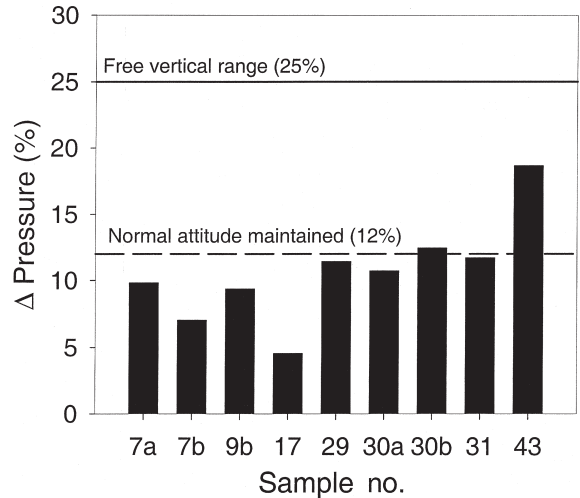

Figure 5. The estimated change in pressure exerted on Atlantic cod (*Gadus morhua* L.) following an ascent from the seafloor to the average off-bottom height for each sample. Reference lines indicate the limit of the free vertical range (solid line) and the limit at which normal attitude can be maintained through fin movements (dashed line).

Law, at least initially before the fish is able to compensate for the pressure change, either by resorbing gas after rising or secreting gas after sinking. Here, we use the model of Harden-Jones and Scholes (1981) to demonstrate the relative importance of this effect on the cod in the present study. As the fish rise from the bottom at night from say, 200 to 160 m (i.e. the maximum observed mean height off-bottom = 40 m), the pressure decreases on the swimbladder, which then expands according to the equation

$$V_2 = \frac{V_1 \times P_1}{P_2}$$

where P_1 and P_2 are the pressures in absolute atmospheres at the initial and final depths, respectively. If we assume an initial swimbladder volume (V_1) of 50 ml (Harden-Jones and Scholes, 1981), the final volume (V_2) will be 61.8 ml, an increase of 11.8 ml, or 23.5%. Harden-Jones and Scholes (1985) concluded that cod maintained "normal horizontal attitude" with reductions in pressure of up to 12% simply through pectoral-fin and tail-fin movements. Assuming no gas resorption, in only one case in the present study did the calculated pressure reductions exceed 12% and in no case did they exceed the free vertical range (25%) beyond which cod would rise uncontrollably (Figure 5).

We can also estimate the time required for cod to adapt to a change in depth using the study of Harden-Jones and Scholes (1985). They used empirical measurements backed by theoretical considerations to estimate the adaptation time (t) required for cod to resorb gas from a swimbladder following a decrease in depth (Table 3). From their formula, $t = 254\ln(P_1/P_2)$, a 50-cm cod will require 54 min to resorb the excess gas, regaining the initial swimbladder volume, if it migrated from 200 to 160 m. From these calculations, we show that in every case it would have taken these cod less time to adapt to their observed height off the bottom than the elapsed time since sunset, when, presumably, they

began their vertical migration (Figure 6). Therefore, if these cod were not already neutrally buoyant when they arrived at the observed mean off-bottom height, as surmised by Arnold and Greer Walker (1992), they would have had ample time to become so before being ensonified by our echosounder.

To estimate the effect of decreasing pressure on a change in TS (Table 3), we have assumed a simple cylindrical model (Harden-Jones and Scholes, 1981)

$$TS = 10 \log \frac{rl^2}{2\lambda}$$

where r is swim bladder radius (m), l is swimbladder length (held constant = 0.125 m), and $\lambda = 0.05$ m. Even assuming that these fish made no volume compensation by resorbing gas, our calculations show the change in TS to be marginal (0.10–0.45 dB), compared to the effects of changes in tilt angle on TS.

Discussion

Acoustic TS has been described as a dynamic variable (Traynor, 1984; Mitson and Holliday, 1990); *in situ* measurements often exhibit large variances and estimated length–TS relationships differ significantly among studies (McClatchie *et al.*, 1996). This is at least partly due to the variable conditions under which these measurements are made. Vessel motion on uneven seas can affect the incident angle of the sounder beam on the target. However, many studies have pointed out the importance of fish behaviour as it affects fish directivity and the measured

Table 3. Estimated changes in swimbladder volume (V_2) and TS, and the resulting adaptation time required for Atlantic cod (*Gadus morhua* L.) to resorb excess swimbladder gas (Harden-Jones and Scholes, 1985) following a vertical migration assuming a 50-ml volume at start depth.

	Physical parameters								
Set no.	Start depth (m)	End depth (m)	Mean height (m)	V_2 (ml)	ΔV (ml)	Difference (%)	Adaption time (min)	Time since sunset (min)	ΔTS (dB)
7a	233.8	209.8	23.9	55.4	5.4	10.9	26.2	503	0.22
7b	230.0	213.1	16.9	53.8	3.8	7.6	18.5	529	0.16
9b	179.4	161.7	17.7	55.2	5.2	10.3	24.9	275	0.21
17	196.8	187.4	9.4	52.4	2.4	4.8	11.8	59	0.10
29	242.2	213.4	28.8	56.4	6.4	12.9	30.8	117	0.26
30a	217.6	193.2	24.4	56.0	6.0	12.0	28.8	189	0.25
30b	221.8	193.0	28.8	57.1	7.1	14.2	33.7	219	0.29
31	211.5	185.6	25.9	56.6	6.6	13.2	31.6	270	0.27
43	205.7	165.5	40.3	61.5	11.5	22.9	52.5	142	0.45

TS (Aglen, 1994; Godø and Michaelsen, 2000), although better understanding of the problem over the past few decades has not brought about obvious and easily applicable solutions. The range of possible fish behaviours which affect TS is simply too vast to be predicted. We know, for example, that sometimes fish react to survey vessels (Gerlotto and Fréon, 1992; Misund *et al.*, 1996) and sometimes not (Fernandes *et al.*, 2000), depending on physical factors such as vessel noise, topography, and depth, as well as factors intrinsic to the fish, such as reaction threshold and swimming capacity. Without the ability to predict fish behaviour under all possible survey conditions, the capacity to predict the appropriate TS relationship will remain elusive. While modelling can explain the effects of the physical environment on the

swimbladder, what is required is the ability to measure the behavioural parameters that affect the orientation distribution of fish under survey conditions. With modern echosounders, it is possible to measure *in situ* target strengths and tilt angles (Foote, 1980) and use these measurements to determine correction factors for this dynamic variable (Mitson and Holliday, 1990).

The present study has demonstrated that, under the proper conditions, it is possible to measure some key fish behaviours using scientific echosounders on a moving vessel and to incorporate a tilt-angle-dependent term (B_{20}) into the length–TS relationship. The estimation of *in situ* tilt angles reduces the variance of TS measurements by averaging over the within-individual variance and, by correcting for the directivity of the fish targets, leads to more accurate biomass estimates. Estimating tilt angle in this manner assumes that the displacement of the fish is due to active swimming in the direction of the measured displacement, i.e. the fish movement is not passive displacement by currents or non-neutral buoyancy. Although we made no measurements, current velocities estimated from a 3-D circulation model of the Gulf of St. Lawrence in the study area, on these dates, and at these depths were on average $0.06 \, \mathrm{m \, s^{-1}}$ with peak velocities of $0.14 \, \mathrm{m \, s^{-1}}$ (F. Saucier, unpublished data). Mean swimming velocities were around 0.7–$2.0 \, \mathrm{m \, s^{-1}}$, and were therefore significantly higher than the estimated current velocities. Further, results from the present study have shown that vertical drift due to non-neutral buoyancy was unlikely to have caused a significant passive displacement of these cod.

Accuracy of the B_{20} estimates also depends upon the accuracy of the biological sampling. We used both bottom and pelagic trawling to sample the biological factors (size distributions, maturity, fatness, etc.) relevant to the TS–length dependence. Any difference in size selectivity between the two gears would affect the B_{20} estimates. For example, the mean length for the pelagic-trawl samples was systematically higher than for the bottom-trawl samples. If
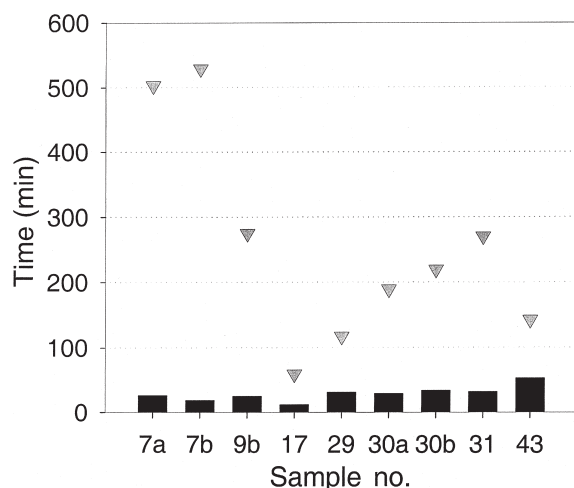

Figure 6. The estimated time required for Atlantic cod (*Gadus morhua* L.) to adapt to neutral buoyancy following an ascent from the seafloor to the average off-bottom height (solid bars) compared to the actual "time-since-sunset" (triangles) for each sample.

this was due to a selectivity bias towards larger cod with the pelagic trawl, the result would exaggerate the relationship in Figure 4. However, when the cod were mostly in midwater, thus necessitating use of the pelagic trawl, the tilt angles were the most extreme, and the TS estimates were the lowest. Knowledge of selectivity ogives should help to reduce any effect of gear sampling bias.

Target tracking can also be used for other studies on fish behaviour, such as vessel avoidance, as well as the study of horizontal and vertical migrations using information on swimming speed and direction (Godø *et al.*, 1999; Torgersen and Kaartvedt, 2001). For example, we have seen that when the cod rose off the bottom at night they retained on average a positive tilt angle (head-up) throughout the night, swimming at $0.7–1.6\,\mathrm{m\,s^{-1}}$. It is possible that these fish remained slightly negatively buoyant throughout the night, requiring them to swim upward to combat sinking, similar to that observed for mackerel (He and Wardle, 1986) and herring (Huse and Ona, 1996). Curiously, those samples showing a noticeably higher average tilt angle for the cod included concentrations of smaller targets, most likely shrimp, capelin, or juvenile redfish, overlapping the cod targets. This noticeable change in tilt angle may well represent a change in swimming behaviour due to active feeding on those prey items, possibly attacking from below. From an analysis of their stomach fullness (D. Chabot, unpublished data), the cod were actively feeding at the time of the study. Remaining neutrally or slightly negatively buoyant while in midwater would also ensure that these cod would not exceed their free vertical range and rise uncontrollably to the surface (Harden-Jones and Scholes, 1981; Arnold and Greer Walker, 1992), and would facilitate a rapid descent to the bottom if required. It is common among many fish species, both pelagic and demersal, that a startle reaction, e.g. to an approaching noisy vessel or trawl, elicits a fast-diving response (Olsen, 1990; Ona and Godø, 1990). This behaviour was seen at the end of set no. 7 (samples 7a and 7b), when the deck lights and winches were turned on to haul back the trawl. The mean tilt angle of the cod tracks decreased from $1.2°$ to $-0.6°$, the swimming direction changed from $160°$ to $63°$ and became more polarized, i.e. the angular deviation (Batschelet, 1981) decreased from $97.3°$ to $39.6°$, and the swimming speed increased from 1.6 to $2.0\,\mathrm{m\,s^{-1}}$ (Table 1). Further analysis may reveal other behaviours, both natural and avoidance-related.

Acknowledgements

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