

# Variations in the target strength of Atlantic cod during vertical migration

George A. Rose

Rose, G. A. 2009. Variations in the target strength of Atlantic cod during vertical migration. – ICES Journal of Marine Science, 66: 1205 – 1211.

Experiments conducted at sea in June 1999 and January 2000 indicated that the mean target strength ( $TS$ ) of Atlantic cod (*Gadus morhua*) varies not just with length, but also with pressure (depth) and fish orientation, particularly during vertical migration. In June, when fish were migrating and spawning, vertical migration was pronounced, extending up to 150 m off the seabed, and the associated  $TS$  declined by as much as 5 dB. In January, when the fish were located nearer the seabed, mean  $TS$  was more stable and matched a conventional model of  $TS$  vs. length [ $L$ , cm; i.e.  $TS = 20 \log(L) - 66$ ] based on measurements of *ex situ* fish orientated horizontally and positioned at close range. This paper demonstrates that mean  $TS$  is inversely related ( $p < 0.05$ ) to the range off the seabed ( $r$ , m), which includes 90% of fish. Based on this finding, a new multivariate  $TS$  model is proposed:  $TS = 20 \log(L) - 65 - 0.05 r$ . In this model,  $r$  is a proxy for swimbladder volume and fish orientation. A survey in May 2007 found that cod (mean  $L = 63$  cm) dispersed in such a way that single targets could be resolved up to 100 m from the seabed. Measurements of  $TS$  of *in situ* individual fish ( $TS_{\text{individual}}$ ) and mean  $TS$  inferred from a comparison of area-backscattering coefficients ( $s_a$ ) and count-based densities ( $TS_{\text{indirect}}$ ) were positively correlated with a slope not different from unity. Means of these  $TS$  estimates were  $-32.4$  and  $-32.2$  dB, respectively, or  $\sim 2.3$  dB less than that predicted by the conventional model. In contrast, the new multivariate model predicts  $TS = -32.5$  dB, which is nearly identical with the means of  $TS_{\text{individual}}$  and  $TS_{\text{indirect}}$ .

**Keywords:** acoustic surveys, Atlantic cod, Smith Sound, target strength, vertical migration.

Received 8 August 2008; accepted 9 January 2009; advance access publication 20 April 2009.

G. A. Rose: Fisheries Conservation Group, Marine Institute of Memorial University, PO Box 4920, St John's, NL, Canada A1C5R3. tel: +1 709 778 0482; fax: +1 709 778 0669; e-mail: grose@mi.mun.ca.

## Introduction

Many marine fish surveyed using acoustic methods undertake vertical migrations that move them from the seabed well into the pelagic zone (Harden-Jones, 1968; Levenez and Petit, 1990; Rose, 1993). Such migrations may vary with season and the physiological cycles of the fish. It has been known for many years that vertical migrations in fish may have strong effects on the acoustic-scattering properties of both individuals and aggregations of fish (Foote, 1980), as a consequence of several factors: (i) swimbladder volume vs. pressure (Harden-Jones and Scholes, 1981; Arnold and Walker, 1992), (ii) fish orientation while swimming (Nakken and Olsen, 1977; McQuinn and Winger, 2003), and (iii) fish physiology and condition (Ona, 1990; Thorne and Thomas, 1990). Some of these factors reduce and others increase the acoustic target strength ( $TS$ ). Despite such known variations, mean  $TS$  with fish size is still commonly used to scale area-backscattering coefficients ( $s_a$ ) to estimate fish density or biomass. In fact, the literature is replete with empirical and theoretical models of  $TS$  vs. size (typically length;  $L$ ) relationships for many species (Simmonds and MacLennan, 2005).

In the coastal waters of Newfoundland and the Gulf of St Lawrence, Atlantic cod (*Gadus morhua*) have been surveyed and researched acoustically for many years (Rose and Leggett, 1989; Rose, 1993, 2003; McQuinn *et al.*, 2005). Despite ample evidence of variation in  $TS$  measurements of *in situ* cod, fish biomass or numbers have been estimated using empirical  $TS$  vs.  $L$  models

(e.g. Rose and Porter, 1996). The same has been true in the Barents Sea, where cod are surveyed using acoustic methods (Hjellvik *et al.*, 2004).

Recent surveys of cod conducted during different seasons and under different conditions of vertical migration have highlighted the uncertainty (systematic and random error) introduced in estimates of biomass when using simple  $TS$  vs.  $L$  models. These surveys also provided an opportunity to conduct experiments to quantify variation in  $TS$ . In particular, diel and seasonal variations in the vertical distribution and swimming behaviour of cod were studied, as well as their effects on  $s_a$  and  $TS$ .

In theory, fish moving to shallower depths should exhibit increases in  $TS$  because of pressure decreases and the resultant increases in swimbladder volumes, as per Boyle's Law (Harden-Jones and Scholes, 1981). Vertical movements might also cause decreases in  $TS$  because of non-horizontal swimming behaviour. Traditionally, this variability and the resulting uncertainty has been accepted (Hjellvik *et al.*, 2004) or mitigated by restricting surveys to the same season each year and the same time of day (Rose, 2003). However, the recent requirement of year-round acoustic surveys for ecosystem-based studies of cod disallows these approaches, and stresses the need for more accurate and precise  $TS$  models, perhaps with more variables. The purpose of this research is to quantify the influences of vertical migrations of cod in coastal Newfoundland waters on their  $TS$ .

Methods

Surveys of spawning and overwintering cod were conducted in Smith Sound, Trinity Bay, Newfoundland, from the CCGS “Teleost” in June 1999 and January 2000, respectively. Measurements of volume-backscattering strength ( $S_v$ ) and  $TS$  were made with a calibrated 38 kHz echosounder (Simrad EK500) and a hull-mounted, split-beam transducer (ES38B; see Table 1 for settings). The echosounder transmitted once per second. Once during each survey, the ship remained stationary for a period of 24–30 h directly over a large concentration of fish. Before and after these periods, the ship surveyed a larger area surrounding and including the fish. The surveys indicated that the fish aggregation did not move much horizontally during the periods that the ship was stationary. Cod were caught after each experiment using a Campelen 1800 research trawl (McCallum and Walsh, 1996). All catches were 100% cod.

Another survey of cod in Smith Sound was conducted with the 15 m vessel “Coastal Explorer” in May 2007. Again,  $S_v$  and  $TS$  were measured with a calibrated EK500 and a hull-mounted ES38B (see Rose, 2003, for details of the survey design). During this survey, most of the acoustically detected cod could be resolved individually at distances up to 100 m off the seabed. There were only a few fish located near the seabed, suggesting that there were also only a few fish in the dead zone (Ona and Mitson, 1996). These data provided good measurements of  $TS$  of *in situ* cod ( $TS_{\text{individual}}$ ) and fish tracks that allow measures of their numerical densities. Comparison of these density estimates with those derived from the echo-integration method give indirect estimates of mean  $TS$  of *in situ* cod ( $TS_{\text{indirect}}$ ). Fishing on acoustic targets was done during this survey, but mean fork lengths are reported for cod caught in a January 2007 survey in Smith Sound.

The acoustic data were analysed using Echoview software (Myriax Inc., Hobart, Australia). The seabed was identified in the echograms by experienced personnel. For the first two stationary experiments, the volume-backscattering coefficients ( $S_v$ ) were integrated in 5 m deep  $\times$  10 min long bins. The  $S_v$  from the May 2007 survey were integrated in 5 m deep  $\times$  100 m long bins.

**Table 1.** Settings for the echosounder (Simrad EK500) with 38 kHz, split-beam transducer (ES38B) during June 1999 and January 2000.

Transducer depth (m)	6 (1)
Absorption coefficient ( $\text{dB km}^{-1}$ )	10
Pulse length (ms)	Medium = one
Bandwidth (kHz)	Auto
Maximum power (W)	2 000
Two-way beam angle (dB)	−20.6 (−20.5)
$S_v$ transducer gain (dB)	25.8 (−26.3)
$TS$ transducer gain (dB)	26.0 (−26.3)
Angle sensitivity alongship	21.9
Angle sensitivity athwartship	21.9
3 dB beam width alongship ( $^\circ$ )	7.0 (6.9)
3 dB beam width athwartship( $^\circ$ )	6.8
Alongship offset ( $^\circ$ )	−0.16 (0.06)
Athwartship offset ( $^\circ$ )	−0.16 (−0.02)
Bottom minimum threshold (dB)	−48
$TS$ minimum (dB)	−60
Minimum echo length factor	0.8
Maximum echo length factor	1.8
Maximum gain compensation (dB)	4.0
Maximum phase deviation ( $^\circ$ )	2.0

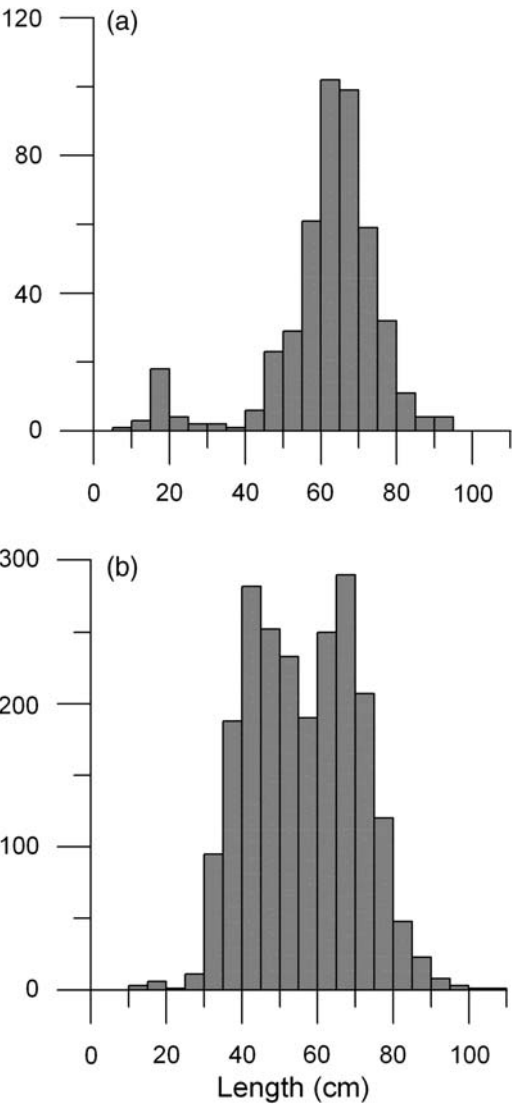
Some settings (in parentheses) differed in May 2007.

For all three studies, the respective  $TS$  measurements were averaged in bins of the same size.

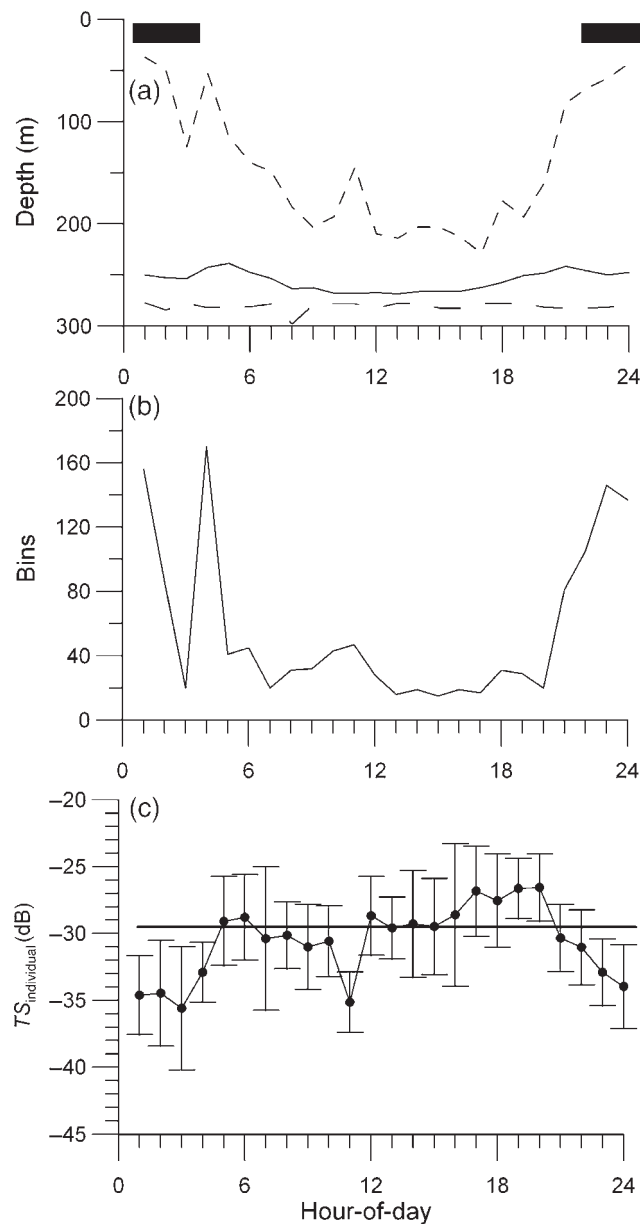
Following Ona and Mitson (1996), the  $s_a$  were corrected for the dead zone by extrapolating the mean  $S_v$  in the 5 m above the detected seabed throughout the depth of the dead zone. Following Gauthier and Rose (2001), if the volume density of fish ( $N_v$ ) exceeded empirically determined thresholds,  $TS$  were omitted from those bins (Sawada *et al.*, 1993). Additionally, the depth distributions of cod were calculated by weighting the mid-depth of the bins by the associated  $s_a$  for each hour. Statistical analyses were performed using Systat (Systat Inc., San Jose, USA).

Results

In June 1999, the distribution of cod  $L$  was bimodal with a mean  $L = 65$  cm; the dominant mode ranged from 40 to 95 cm (Figure 1a). These fish moved 50–150 m vertically (Figures 2a and 3a and b). From these data, 13 887  $TS_{\text{individual}}$  measurements were grouped into 2939 bins; of these, 1354 were acceptable with  $N_v < 0.1 \text{ fish m}^3$  (Figure 2b). Grouped by hour, mean  $TS_{\text{individual}}$  were

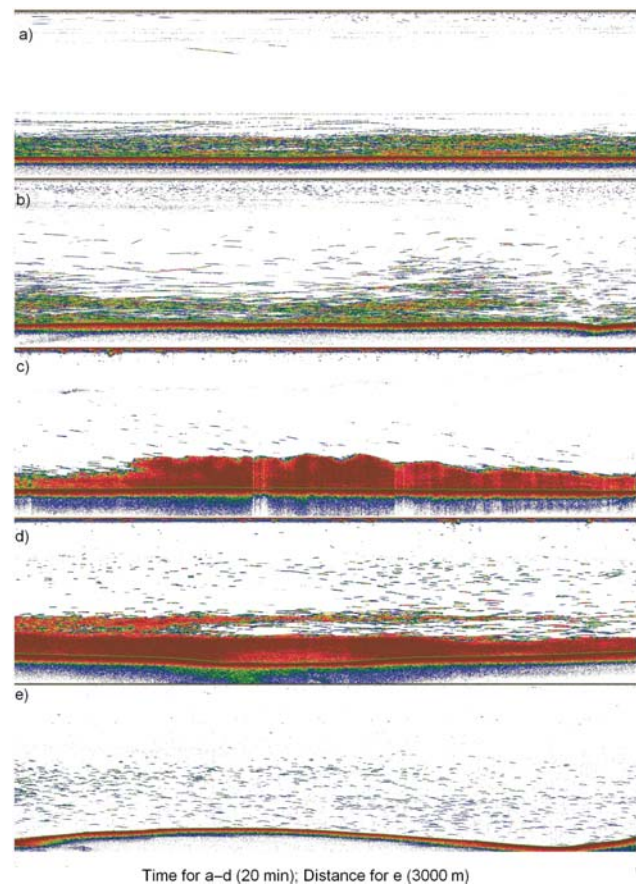


**Figure 1.** Length distribution of cod sampled during (a) June 1999 and (b) January 2000 in Smith Sound.



**Figure 2.** Data from June 1999: (a) depth distribution of cod, maximum vertical range (short dash line),  $s_v$ -weighted mean depth (solid line), and maximum depth (long dash line); (b) number of bins containing valid  $TS_{\text{individual}}$  measurements ( $N_v < 0.1 \text{ fish m}^{-3}$ ); and (c)  $TS_{\text{individual}}$  measurements (mean and s.e.) vs. predicted TS from Equation (1) (straight line; Rose and Porter, 1996). Night-time is indicated (black bars).

largest during the daytime when the fish were within 25 m of the seabed, and closely matched model predictions (Figure 2c). At night, the fish were much more pelagic, and mean  $TS_{\text{individual}}$  declined as much as 5 dB. The mean TS for tracked fish, weighted by the number of measures in each track, was very similar to the mean  $TS_{\text{individual}}$ , and they too declined up to 5 dB as the fish migrated vertically (Figure 4a). The numbers of tracked fish were much larger by night than by day (Figure 4b). The vertical distance that individual tracked fish moved was larger and more variable as the fish moved farther from the seabed (Figure 4c).

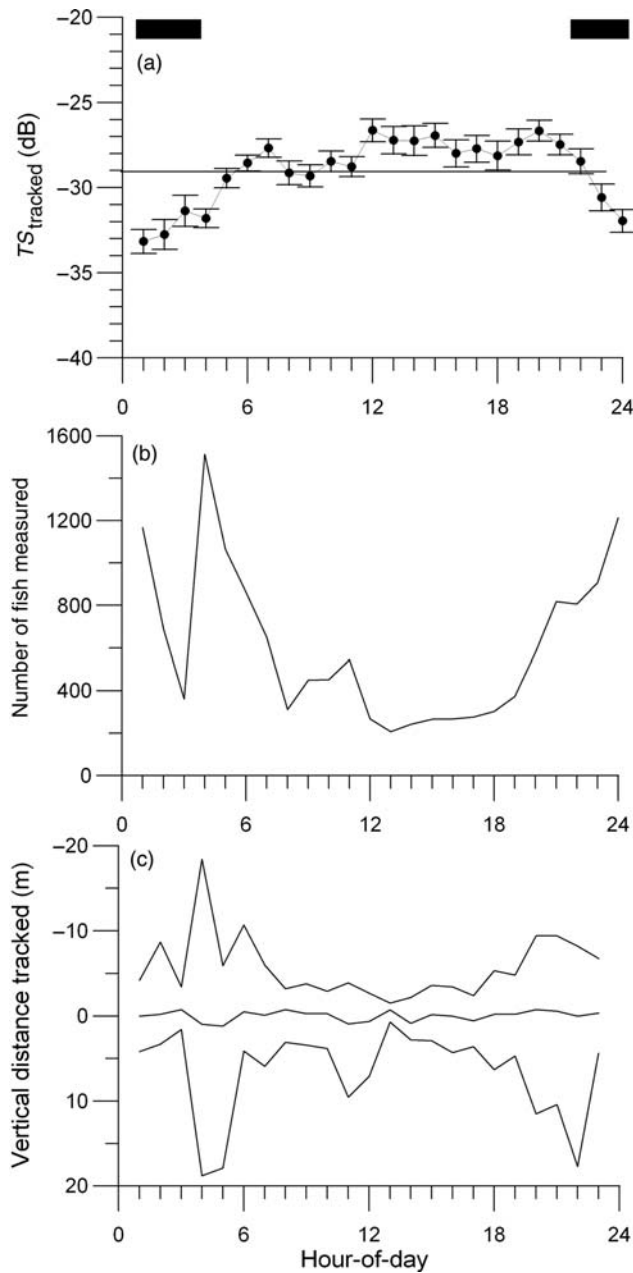


**Figure 3.** Echograms from the sea surface to below the seabed (38 kHz  $S_v$  vs. depth and time) with minimum  $S_v = -75 \text{ dB}$ : 10 June 1999, seabed = 278 m, (a) daytime 09:40–10:00 h and (b) night-time 04:07–04:27 h; 6 January 2000, seabed = 159 m, (c) daytime 07:17–07:37 h and (d) night-time 04:55–05:15 h; and 8 May 2007, seabed = 300 m, horizontal distance 3000 m, (e) daytime 09:45 h.

In January 2000, the unimodal distribution of cod  $L$  ranged from 30 to 100 cm, with a mean  $L = 55 \text{ cm}$  (Figure 1b). These fish moved only 25–40 m vertically (Figures 3c and d and 5a). From these data, 10 203  $TS_{\text{individual}}$  measurements were grouped into 2275 bins; of these, only 157 were acceptable, with  $N_v$  between 0.04 and  $1.0 \text{ fish m}^{-3}$  (Figure 5b). The lower limit rejected TS values obtained from large zooplankton, later confirmed in images from a camera deployed on an ROV. Grouped by hour, mean  $TS_{\text{individual}}$  were largest by day and matched model predictions (Figure 5c). Measurements of the mean TS of tracked fish were too few by day to be reported.

The mean TS values for tracked fish, weighted by the number of measures in each track, were very similar to the mean  $TS_{\text{individual}}$  and model predictions of TS, except during daylight, when only a few fish were tracked and measurement uncertainty was large (Figure 6a). As with solitary measurements of individual targets, the numbers of tracked fish were much larger during the hours of darkness (Figure 6b). Tracked fish moved vertically only 2–3 m in January compared with 10–20 m in June (Figure 6c).

The range above the seabed that encompassed 90% of the cod backscatter ( $r$ , m) was significantly correlated with the mean  $TS_{\text{individual}}$  in June 1999 (Figure 7). Using  $r$  as a proxy for the combined effects of  $\theta$  and changes in swimbladder volume with



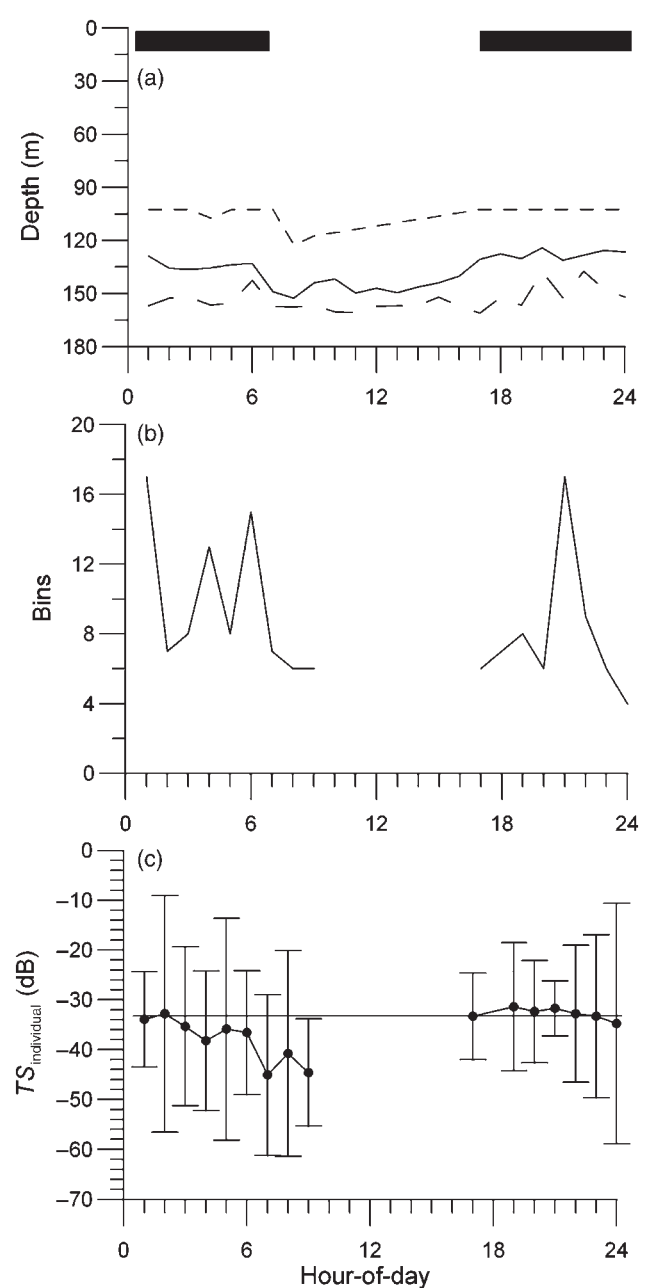
**Figure 4.** Summary of tracked fish from June 1999: (a)  $TS_{\text{tracked}}$  (mean, s.e.) weighted by number of measures of each fish [solid straight line is the prediction from Equation (1)]; (b) number of fish measured; and (c) vertical distance (m) tracked, indicating limits of values and mean (—, upwards; +, downwards). Night-time is indicated (black bars).

pressure, the regression slope (Figure 8) was added to the  $TS$  vs.  $L$  equation from Rose and Porter (1996):

$$TS = 20 \log(L) - 65, \quad (1)$$

resulting in a new multivariate  $TS$  model:

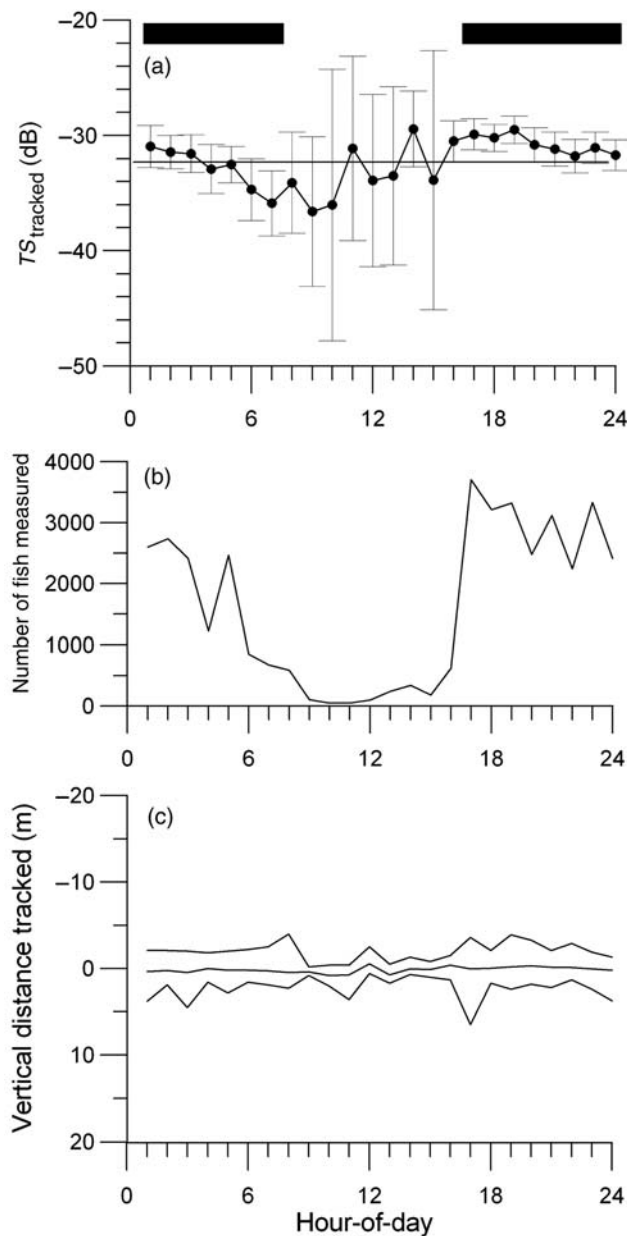
$$TS = 20 \log(L) - 65 - 0.05r. \quad (2)$$



**Figure 5.** Data associated with  $TS_{\text{individual}}$  measurements from January 2000: (a) depth distribution of cod, maximum vertical range (short dash line),  $s_a$ -weighted mean depth (solid line), and maximum depth (long dash line); (b) number of 5 m by 10 min bins containing valid  $TS_{\text{individual}}$  measures; and (c)  $TS_{\text{individual}}$  (mean and s.e.) where  $0.04 < N_v < 1 \text{ fish m}^{-3}$  with  $TS$  predicted from Equation (1) (straight line; Rose and Porter, 1996). Night-time is indicated (black bars).

The data supporting Equation (2) were not extrapolated if  $r$  was in the range 20–100 m.

Equation (2) was used to estimate cod biomass from a survey on 8 May 2007 where the cod were pelagic and had low  $s_a$  (Figure 3e). Estimates of  $TS_{\text{indirect}}$  were highly variable throughout the survey, but the slope of the regression of  $TS_{\text{indirect}}$  on  $TS_{\text{individual}}$  did not differ significantly from unity, and their means were virtually equal (mean  $TS_{\text{indirect}} = -32.2 \text{ dB}$ ; mean

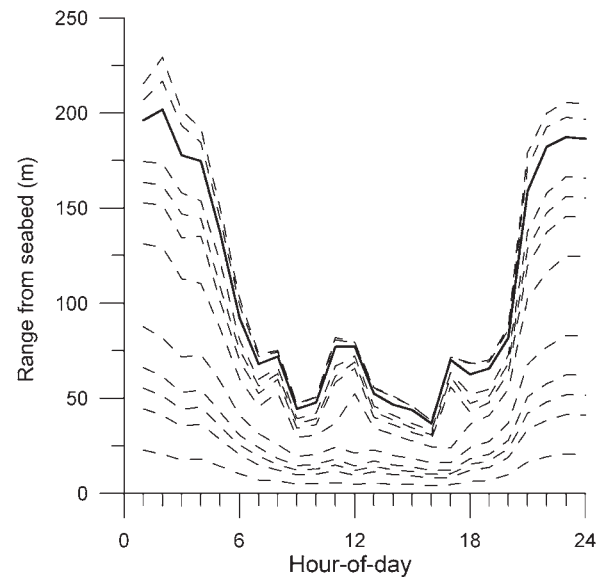


**Figure 6.** Summary of tracked fish from January 2000: (a)  $TS_{\text{tracked}}$  (mean, s.e.) weighted by the number of measures of each fish [solid straight line is the prediction from Equation (1)]; (b) number of fish measured; and (c) vertical distance tracked (m), indicating limits of values and mean (–, upwards; +, downwards). Night-time is indicated (black bars).

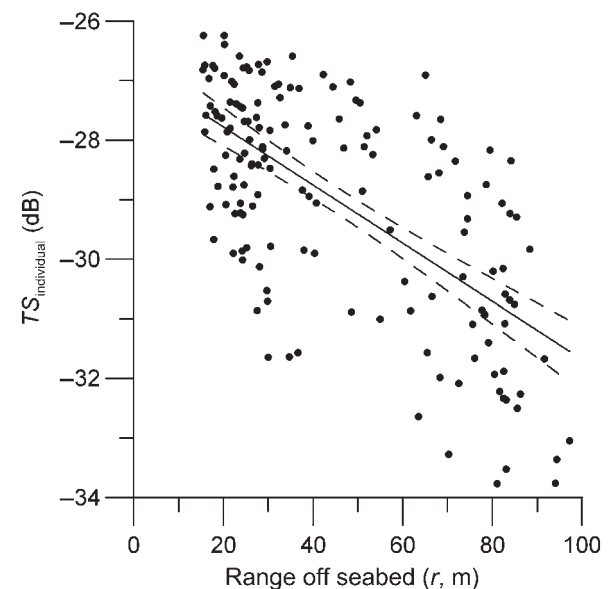
$TS_{\text{individual}} = -32.4$  dB; paired  $t$ -test,  $p > 0.05$ ; Figure 9). These means are, respectively, 2.4 and 2.2 dB, less than that predicted by Equation (1) (i.e.  $TS = -30.0$  dB for  $L = 63$  cm). By comparison, these means are 0.2 and 0 dB different from that predicted by Equation (2) (i.e.  $TS = -32.5$  dB for mean  $L = 63$  cm).

## Discussion

This analysis confirms that the  $TS$  of Atlantic cod is modulated by fish behaviour. Therefore, models of  $TS$  vs.  $L$  (Rose and Porter, 1996; Simmonds and MacLennan, 2005, and references therein)

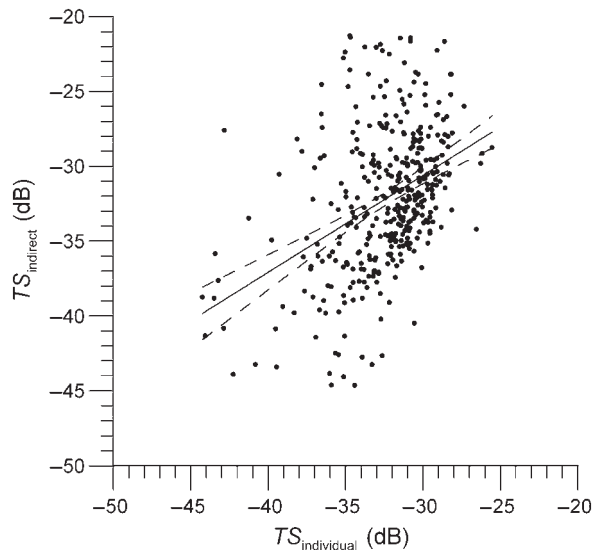


**Figure 7.** Depth distribution of  $s_a$  attributed to cod vs. local hour in June 1999. Dashed lines are the upper ranges that include 5, 10, 20, 30, 40, 50, 60, 70, 80, 95, and 100% of  $s_a$  measured from the seabed; solid line includes 90%.



**Figure 8.** Range off the seabed that contains 90% of the  $s_a$  attributed to cod ( $r$ , m) over 10 min intervals, and mean  $TS_{\text{individual}}$  (dB), in June 1999. The regression equation is  $TS = -0.05r - 26.8$  ( $n = 155$ ,  $r^2 = 0.42$ ,  $p < 0.05$ ).

do not account for these variations and may contribute uncertainty, generally negative bias, in estimates of abundance reaching, perhaps, 4–5 dB or >300% negative bias. In one example in this study, the use of Equation (1) resulted in an underestimation of cod biomass of 40–45%. Similarly, Hjellvik *et al.* (2004) established declines of up to 50% in the Barents Sea biomass during night-time for estimates derived using  $TS$  vs.  $L$  models for cod and other species. Notwithstanding these provocative findings,



**Figure 9.** Regression of 19 382 measurements of  $TS_{\text{indirect}}$  on 158 136  $TS_{\text{individual}}$ , each averaged in 379 bins of 100 pings each from a survey of Smith Sound on 8 May 2007. The mean  $TS_{\text{indirect}} = -32.4$  dB, mean  $TS_{\text{individual}} = -32.2$  dB, and  $TS_{\text{indirect}} = 0.7 TS_{\text{individual}} - 11.2$  ( $p < 0.05$ ; the slope does not differ from 1,  $p > 0.05$ ).

$TS$  vs.  $L$  models for cod provide acceptable uncertainty in estimates of cod biomass surveyed at all hours during winter, when fish are less active and do not undertake extensive vertical migrations.

Because  $TS$  declines as cod migrate upwards from the seabed, the effect of  $\theta$  dominates from the effect of bladder expansion with decreased pressure (Harden-Jones and Scholes, 1981). Bladder expansion probably occurs as cod migrate 100–150 m vertically (Arnold and Walker, 1992), and all else being equal,  $TS$  should increase. However, this increase with decreasing pressure is apparently more than offset by a decrease in  $TS$  when cod change  $\theta$  during migrations. In *ex situ* experimentation, Nakken and Olsen (1977) and Rose and Porter (1996) demonstrated that changes in  $\theta$  could vary cod  $TS$  by 10–20 dB. Resolving these two countering influences is beyond the scope of this paper. However, it could be done by solving physics-based scattering models with estimates of  $\theta$  from fish-track data and comparing these results with concomitant measurements of  $TS$  of *in situ* cod.

Following vertical ascents, the  $TS_{\text{individual}}$  did not increase as expected if fish regained a more dorsal aspect. Perhaps, on average, cod do not swim horizontally while pelagic. Observations with a camera from an ROV support this interpretation. Some  $TS_{\text{individual}}$  measured by day, particularly in June, were larger, but within 1 s.e. of those predicted by Equation (1). Nevertheless, there may be some random error from undersampling or systematic measurement error because of the inclusion of some multiple targets.

It is well known that fish migrate vertically (Godø and Wespestad, 1993; Gauthier and Rose, 2002). This study reveals that such behaviour by cod has a large diel component, but that it differs seasonally. However, it is not exclusively a diel phenomenon. At times, such as when transiting, or as was evident at around 11:00 on June 1999 (Figures 2 and 4, respectively), cod migrate vertically outside the usual diel pattern.

Typically, uncertainty is managed in any time-series of cod abundance measurements by standardizing the survey timing and  $TS$  model (Simmonds and MacLennan, 2005; Kalikhman and Yudanov, 2006). This is true for surveys in coastal Newfoundland, which inspired this study. They are traditionally conducted only in January and February, when the vertical fish distribution is most stable (Rose, 2003). Recently, however, ecosystem-based studies of cod required surveys to be conducted throughout the year. Also, for surveys in the Barents Sea, intra-survey or interyear variations in vertical distributions of cod could introduce significant uncertainty (bias and imprecision) in the acoustically derived, cod-biomass estimates (Hjellvik *et al.*, 2004).

This study demonstrates that in addition to cod size,  $TS$  is modulated by fish-swimbladder volume and orientation during vertical migrations. This conclusion could be relevant to other vertically migrating species with swimbladders that exhibit pronounced acoustic directivity at the survey frequency. Use of a multivariate model could account for temporal and spatial variations in  $TS$ , thereby reducing uncertainty in the biomass estimates. This study constitutes a step in that direction by providing a model of  $TS$  vs. cod length and range from the seabed, a proxy for fish-swimbladder volume and orientation during vertical migrations.

## Acknowledgements

Appreciation is extended to the crews of the RV “Coastal Explorer” and CCGS “Teleost”, Chris Stevens and Chris Lang of the Northwest Atlantic Fisheries Centre, and Wade Hiscock of the Marine Institute, Memorial University, for technical assistance. April Smith, working under the Women in Science and Engineering programme at Memorial University, did the time-consuming work of fish tracking. Funding was provided by the NSERC grants to the author and to the Chair in Fisheries Conservation by the Department of Fisheries and Oceans Canada and the Newfoundland and Labrador Department of Fisheries and Aquaculture.

## References

- Arnold, G. P., and Walker, M. G. 1992. Vertical movements of cod (*Gadus morhua* L) in the open sea and the hydrostatic function of the swimbladder. *ICES Journal of Marine Science*, 49: 357–372.
- Foot, K. G. 1980. Effect of fish behaviour on echo energy: the need for measurements of orientation distributions. *ICES Journal of Marine Science*, 39: 193–201.
- Gauthier, S., and Rose, G. A. 2001. Diagnostic tools for unbiased *in situ* target strength estimation. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 2149–2155.
- Gauthier, S., and Rose, G. A. 2002. Acoustic observation of diel vertical migration and shoaling behaviour in Atlantic redfishes. *Journal of Fish Biology*, 61: 1135–1153.
- Godø, O. R., and Wespestad, V. G. 1993. Monitoring changes in abundance of gadoids with varying availability to trawl and acoustic surveys. *ICES Journal of Marine Science*, 50: 39–51.
- Harden-Jones, F. R. 1968. *Fish Migration*. Edward Arnold Publishers Ltd, London.
- Harden-Jones, F. R., and Scholes, P. 1981. The swimbladder, vertical movements, and the target strength of fish. In *Meeting on Hydroacoustical Methods for the Estimation of Marine Fish Populations*, pp. 157–181. Ed. by J. B. Suomala. The Charles Stark Draper Laboratory, Inc., Cambridge, MA.

- Hjellvik, V., Godø, O. R., and Tjøstheim, D. 2004. Diurnal variation in acoustic densities: why do we see less in the dark? *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 2237–2254.
- Kalikhman, I. L., and Yudanov, K. I. 2006. *Acoustic Fish Reconnaissance*. Taylor and Francis, Boca Raton, FL, USA. 245 pp.
- Levenez, J. J. G. F., and Petit, D. 1990. Reaction of tropical coastal pelagic species to artificial lighting and implications for the assessment of abundance by echo integration. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 189: 128–134.
- McCallum, B., and Walsh, S. J. 1996. Groundfish survey trawls used at the Northwest Atlantic Fisheries Centre, 1971–present. *NAFO Science Council Studies*, pp. 93–104.
- McQuinn, I. H., Simard, Y., Stroud, T. W. F., Beaulieu, J.-L., and Walsh, S. J. 2005. An adaptive, integrated “acoustic-trawl” survey design for Atlantic cod (*Gadus morhua*) with estimation of the acoustic and trawl dead zones. *ICES Journal of Marine Science*, 62: 93–106.
- McQuinn, I. H., and Winger, P. D. 2003. Tilt angle and target strength: target tracking of Atlantic cod (*Gadus morhua*) during trawling. *ICES Journal of Marine Science*, 60: 575–583.
- Nakken, O., and Olsen, K. 1977. Target strength measurements of fish. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 170: 52–69.
- Ona, E. 1990. Physiological factors causing natural variations in acoustic target strength of fish. *Journal of the Marine Biological Association of the UK*, 70: 107–127.
- Ona, E., and Mitson, R. B. 1996. Acoustic sampling and signal processing near the seabed: the deadzone revisited. *ICES Journal of Marine Science*, 53: 677–690.
- Rose, G. A. 1993. Cod spawning on a migration highway in the North-west Atlantic. *Nature*, 266: 458–461.
- Rose, G. A. 2003. Monitoring coastal northern cod: towards an optimal survey of Smith Sound, Newfoundland. *ICES Journal of Marine Science*, 60: 453–462.
- Rose, G. A., and Leggett, W. C. 1989. Interactive effects of geophysically-forced sea temperatures and prey abundance on mesoscale coastal distributions of a marine predator, Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 46: 1904–1913.
- Rose, G. A., and Porter, D. 1996. Target-strength studies on Atlantic cod (*Gadus morhua*) in Newfoundland waters. *ICES Journal of Marine Science*, 53: 259–265.
- Sawada, K., Furusawa, M., and Williamson, N. J. 1993. Conditions for the precise measurement of fish target strength *in situ*. *Fisheries Science*, 20: 15–21.
- Simmonds, E. J., and MacLennan, D. 2005. *Fisheries Acoustics. Theory and Practice*, 2nd edn. Blackwell Science, Oxford, UK.
- Thorne, R. E., and Thomas, G. L. 1990. Acoustic observations of gas bubble release by Pacific herring (*Clupea harengus pallasii*). *Canadian Journal of Fisheries and Aquatic Sciences*, 47: 1920–1928.

doi:10.1093/icesjms/fsp085