

IN SITU MEASUREMENTS OF THE ACOUSTIC TARGET STRENGTH OF CAPE HORSE MACKEREL *TRACHURUS TRACHURUS CAPENSIS* OFF NAMIBIA

B. E. AXELSEN*, G. BAULETH-D'ALMEIDA† and A. KANANDJEMBO†

The acoustic target strength (*TS*) of Cape horse mackerel *Trachurus trachurus capensis* was measured *in situ* at 38 kHz during two surveys over the Namibian continental shelf in 1998 and 1999 using a SIMRAD EK500 echosounder/ES38D submersible split-beam transducer. Scattered aggregations of horse mackerel 100–200 m deep were ensouffled. The transducer was lowered to a depth of 85–140 m in order to resolve single targets at short ranges (5–50 m). Individual fish were tracked using specially developed software. Samples of ensouffled fish were obtained using pelagic and demersal trawls; the former was fitted with a codend Multisampler for depth-specific sampling. Recorded *TS* estimates were low, producing b_{20} -values ranging from -77.5 to -74.9 dB (-76.0 dB \pm 1.3), considerably lower than published estimates for horse mackerel (-73.4 dB < b_{20} < -65.2 dB). An explanation for the weak acoustic backscattering may be swimbladder compression. Surface-projected b_{20} values, which were computed using the depth of each target and the scattering area reduction rate previously found for herring ($\gamma = -0.29$), corresponded to -72.6 dB. This value is close to the *TS* constant of -72 dB currently applied for horse mackerel in Namibian and Angolan waters.

Key words: acoustic, Benguela, Cape horse mackerel, *in situ*, Namibia, target strength

Hydroacoustic surveying is the principal means of estimating the abundance of pelagic fish in the Benguela system off the west coast of southern Africa. The biomass of Cape horse mackerel *Trachurus trachurus capensis* along the Namibian coast has been monitored acoustically since 1990. The main advantages of the acoustic method are its ability to sample large volumes of water with relatively little effort and the high sample resolution obtained in both horizontal and vertical planes. Conversion from acoustic densities to absolute abundance requires knowledge of the acoustic backscattering properties of the target species, specifically the mean dorsal aspect target strength (*TS*; e.g. MacLennan and Simmonds 1992). Measurements of *TS* must be averaged in the intensity or squared amplitude domain (Love 1971, McCartney and Stubbs 1971, Foote 1980a):

$$TS = 10 \log\left(\frac{\sigma}{4\pi}\right) \text{ (dB)} \quad (1)$$

where σ is the acoustic cross-section in m². Using a regression of log fish length against *TS* from a number of datasets, Foote (1980a) found that, although the intercept varied between 16 and 24, it seldom deviated significantly from 20 at 38 kHz, indicating that σ is proportional to the squared total fish length (*L*) at that frequency (Love 1977):

$$TS = 20 \log L + b_{20} \text{ (dB)} \quad (2)$$

The *TS* of Cape horse mackerel has been investigated from survey data (Barange and Hampton 1994, Barange *et al.* 1996, Lillo *et al.* 1996, Gutiérrez and MacLennan 1998, Svellingen and Ona 1999), volumetric considerations of the swimbladder (Torres *et al.* 1984) and back calculation from integration values and independent estimations of target densities (the comparison method; Misund *et al.* 1997). However, there are large variations in the reported b_{20} constants, and there is currently no species-specific *TS* expression available for Cape horse mackerel that is conclusively supported in the literature. Foote (1987) recommended the use of $b_{20} = -67.5$ dB for physoclist (closed swimbladder) fish, but he also reported considerable inter-species variation (± 3 dB) for this group. The equation currently applied for horse mackerel off Namibia and Angola (*T. t. capensis* and *T. trecae* respectively):

$$TS = 20 \log L - 72 \text{ (dB)} \quad (3)$$

was originally derived for clupeoids (Foote *et al.* 1986, Foote 1987). The use of Equation 3 for horse mackerel therefore disregards the general recommendations from Foote (1987), implying that the acoustic scattering properties of horse mackerel resemble those of the

* Institute of Marine Research, P.O. Box 1870 Nordnes, 5817 Bergen, Norway. Email: bjorna@imr.no

† Ministry of Fisheries and Marine Resources, P.O. Box 912, Swakopmund, Namibia

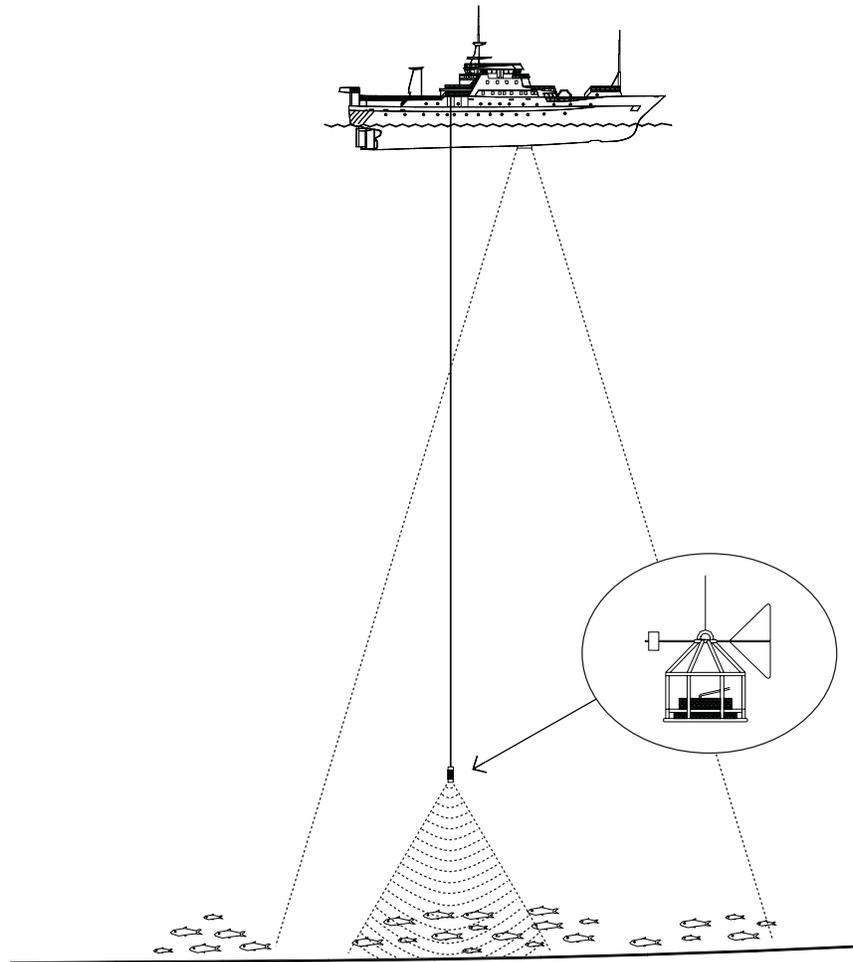


Fig. 1: Experimental set-up during the target strength measurements, showing the acoustic beams of the hull-mounted and the submersible transducers. The steel housing of the submersible transducer is enlarged

clupeoid group rather than physoclists. Whereas physoclistous horse mackerel can regulate swimbladder volume through gas secretion and resorption (e.g. Torres *et al.* 1984), clupeoids are physostomes (open swimbladder) and depend on gasping air at the surface to regulate swimbladder volume (e.g. Blaxter and Batty 1984, Nøttestad 1998). At 38 kHz, the swimbladder constitutes as much as 90–95% of the acoustic scattering of fish (Foote 1980b, Ona 1990) and its volume and shape significantly influence the *TS* of

the fish (Olsen and Ahlquist 1996). Physiological factors such as fat content can also affect fish *TS* (Ona 1990). If horse mackerel maintain neutral buoyancy with depth, they would be expected to have a higher, less depth-dependent, *TS* than physostomes. To the authors' knowledge, swimbladder compression has not been reported for horse mackerel. This study explores the justification for the use of Equation 3 and the possibility that swimbladder compression is not, or only in part, compensated in Cape horse mackerel.

Table I: Technical specifications and calibration parameters for the echosounder system used during the target strength measurements

Specification	
Echosounder model (Simrad)	EK 500
Transducer model (Simrad)	ES 38 D
Carrier frequency (kHz)	38
Transmission effect (kW; on the terminals)	2.0
Estimated speed of sound (m s ⁻¹)	1 500
Absorption coefficient (dB km ⁻¹)	10
Pulse duration (ms ⁻¹)	1.0
Band width (kHz)	3.8
Angle sensitivity (dB)	21.9
Vertical resolution (cm)	10
Equivalent transmission angle (dB)	-21.0
TS gain (dB; transducer)	24.3
Min. TS threshold, (dB) transducer (October 1998)	-55
Min. TS threshold, (dB) transducer (May 1999)	-70
3 dB beam width (°)	6.7/6.7
Alongship offset (°)	-0.02
Athwartship offset (°)	0.12

MATERIAL AND METHODS

High-resolution *TS* measurements of Cape horse mackerel were conducted *in situ* during two surveys (in October 1998 and May 1999) on board the RV *Dr Fridtjof Nansen* over the Namibian continental shelf between 17°29'S, 11°31'E and 18°57'S, 11°35'E. A total of five series of *TS* measurements were made. Reference fish samples were obtained by targeted trawling.

Fish sampling

Both pelagic (Åkrehamn) and demersal (Gisund Super) sampling trawls were used. Thyborøn 125 combi otter boards (7.41 m², 2 030 kg) were used for both trawl types. The codend mesh size was 24 mm (stretched mesh). During both surveys, fish samples were taken in the study area prior to the *TS* measurements to confirm that the observed scattering layers consisted of monospecific aggregations of Cape horse mackerel, and that the length ranges were reasonably narrow. The *TS* measurements were conducted in the vicinity of where the initial trawls were taken. After each *TS* measurement series, reference trawls were taken through the scattering layers at the depth of the *TS* measurements. Tows were made from the position of the vessel at the end of the measurements in directions opposite to the drifting directions. A remote-controlled multiple codend system fitted to the pelagic trawl – the Multisampler (Engås *et al.* 1997) – permitted discrete sampling from three different

depths without contamination from other depths during each deployment. This system was utilized to sample the scattering layers and to check for non-target scatterers below and above the layers.

Measurements of *TS*

A SIMRAD EK 500 echosounder (Bodholt *et al.* 1989 – software version 5.1) connected to an ES38B keel-mounted 38 kHz split-beam transducer was used to locate suitable fish aggregations. The *TS* measurements were conducted using a second EK 500 unit running an ES 38D submersible 38 kHz split-beam transducer (Svellingen and Ona 1999). This transducer was mounted in a weight-balanced steel housing (Fig. 1) to ensure vertical signal transmission. The transducer was oil-filled and depth-compensated. Split-beam transducers produce estimates of alongship and athwartship offset angles, allowing compensation for loss of echo energy according to the two-way beam pattern (Foote *et al.* 1986).

A standard split-beam calibration of the echosounder was carried out prior to the *TS* measurements in October 1998 at about 10 m deep using SIMRAD LOBE software. Unfortunately, weather conditions did not permit a repeat calibration during the May 1999 survey, but the system has proved stable over time (*TS* gain between 24.20 and 24.30 dB), and consequently no appreciable changes were suspected during the experiments. Technical specifications and calibration parameters are listed in Table I. When a suitable scattering layer of horse mackerel was located, the vessel was stopped and the transducer was lowered to about 5 m above the horse mackerel layer, so minimizing the reverberation volume. Submersible transducers should ideally be calibrated at the depth of deployment, but this was not feasible in the present study because of unfavourable weather conditions and variable fish depths. However, changes in ambient pressure should not affect the performance of pressure-stabilized transducers to critical extents. Time of reception, compensated and uncompensated *TS*, range, and alongship (α) and athwartship (β) offset angles were recorded from the EK 500 serial port and stored on a computer. Corresponding *S_v* echograms were printed for a range interval of 5–50 m from the transducer.

All *TS* measurements were taken at night and were initiated whenever targeted trawling indicated monospecific aggregations of horse mackerel (85–97% of the catch by mass, Table II). Table III summarizes the sampling details for each measurement series. The measurements in October 1998 were conducted on loose aggregations of horse mackerel 90–120 m deep (bottom depth 120 m). The transducer was then low-

Table II: Catch composition and catch rates of the trawl reference samples. Note that both *TS* Series 4 and 5 are referenced to the last net sample

Parameter/species	Date			
	October 1998		May 1999	
Series number	1	2	3	4 & 5
Trawl type	DEM	DEM	MS	MS
Tow duration (min)	26	16	12	11
	<i>Catch rate (kg h⁻¹)</i>			
<i>T. trachurus capensis</i>	2 071	2 286	626	47
<i>Aequora aequora</i>	508			
<i>Argyrosomus hololepidotus</i>		116		
<i>Raja alba</i>	84			
<i>Squalus megalops</i>		21		
<i>Atractoscion aequidens</i>	11	28		
<i>Pterothrissus belloci</i>	3.2	28		
<i>Chelidonichthys capensis</i>	12	13	6.9	
<i>Dentex macrophthalmus</i>			8.6	
<i>Merluccius capensis</i>	10	12	3.2	8.6
<i>Callorhynchus capensis</i>	8.2			
Other demersal species	8.6	27.6	0	0
Total	2 715	2 510	647	56
Percentage <i>T. trachurus capensis</i>	*94 (76)	91	97	85

* Disregarding *A. aequora*, total in parenthesis
 DEM = Demersal trawl
 MS = Multisampler (pelagic trawl)

ered to about 5 m above the upper border of the scattering layer (85 m deep), some 35 m above the bottom. Operating at 25–50 m range, single fish at the boundary of the layer were readily resolved as single targets. However, weather conditions were not ideal for *TS* measurements, with prevailing winds of 27 knots and 2 m swells, which necessitated using the

side-thrusters for the vessel to stay in position. The deck lights were switched on during the first measurement series, but were shut off during all subsequent experiments. During the experiments in May 1999, good weather and loose aggregations of horse mackerel in midwater provided optimal conditions for *TS* measurements. The final measurements were

Table III: Time, location and general sea conditions during the five target strength (*TS*) measurement series. Note that Series 5 was recorded at dawn, as the fish were migrating towards the bottom

Parameter	Date				
	16 October 1998	17 October 1998	24 May 1999	26 May 1999	26 May 1999
Series number	1	2	3	4	5
Time	16:00–20:00	23:00–01:45	22:15–02:45	02:30–04:45	04:45–07:00
Location	17°45'S 11°39'E	17°45'S 11°40'E	17°29'S 11°31'E	18°57'S 11°35'E	18°57'S 11°35'E
Bottom depth (m)	120	120	160	277	277
Transducer depth (m)	85	85	110	140	140
Mean fish depth (m)	99.8	97.4	129.8	171.8	174.4
Aggregation depth (m)	90–120	90–120	130–160	150–200	150–270
Aggregation type	Loose layer	Loose layer	Loose layer	Scattered	Dispersed
Sea state	Rough	Rough	Satisfactory	Good	Good
Weather conditions	Overcast	Overcast	Dense fog	Misty	Misty
Use of side-thrusters	Yes	Yes	No	No	No
Use of deck-lights	Yes	No	No	No	No

Table IV: Criteria for acceptance of echo-traces during the split-beam target tracking

Criterion	Value
Max. off-axis angle to target θ (°)	5
Min. range (from transducer to fish) (m)	5
Max. range (from transducer to fish) (m)	50
Min. distance from fish to bottom (m)	5
Min. number of pings in each trace	5
Max. number of missing echoes in one track	0
Max. distance between consecutive pings in a track (cm)	10

recorded at dawn, as the fish began their downward migration towards the bottom.

Analysis

All horse mackerel in small catches, or randomly selected subsamples of at least 200 fish from larger catches, were analysed. Total fish length was measured to the nearest cm below. The root mean square total length (*RMSL*) of the fish in each sample was calculated from the number of fish (n_i) in each 1-cm length group (l_i):

$$RMSL = \sqrt{\frac{\sum (n_i \times l_i^2)}{\sum n_i}} \quad (4)$$

Despite recent improvements to the *TS* detection algorithm in the EK 500 software (e.g. Soule *et al.* 1995, 1997), multiple echoes may still be accepted as single target echoes, positively biasing *TS* measurements (Hewitt and Demer 1991). However, if the density of the ensonified population is low compared with the reverberation volume, information on the spatial position of targets within the beam can be used to track individual targets (Zhao 1996). In the present study, fish-tracking procedures were used to exclude potential multiples included by the EK 500 *TS* detection algorithm and to group the data into respective traces. The criteria applied in the tracking procedure are summarized in Table IV. The azimuth angle between the target and the acoustic axis (θ) used in the tracking procedure was calculated as:

$$\theta = \left| \arcsin\left(\frac{d}{r}\right) \right| \quad (5)$$

where d is the horizontal distance from the acoustic axis to the target and r is the target range. The fish tilt angle (γ) can then be estimated as:

$$\gamma = \arctan\left[\frac{\Delta z}{\Delta h}\right] \quad (6)$$

where Δz and Δh are the movements in the vertical and horizontal planes respectively. However, for γ to approximate the actual tilt angle, the vertical resolution of the EK 500 receiver should be 2 cm or less; the receiver used in this study had a standard digital sampling distance of 10 cm at 38 kHz. Instead, the cumulative track angle, or the angle between the start and end points of each fish trace (η), was used as a proxy for the tilt angle (Vabø 1999):

$$\eta = \arctan\left[\frac{\sum_i^{n-1} \Delta z_i}{\sum_i^{n-1} |\Delta h_i|}\right] \quad (7)$$

where Δz_i and Δh_i respectively denote the vertical and horizontal movements of the fish from ping number i to ping number $i+1$ for all n pings in a trace. All *TS* averaging was carried out in the intensity domain by rearranging Equation 1. In order for each fish, or trace, to contribute equally to the overall mean, the mean within-track *TS* was calculated for each trace and averaged over all traces. The b_{20} constant for each *TS* measurement series was then estimated:

$$b_{20} = \overline{TS} - 20 \log(RMSL + 0.5) \quad (8)$$

where \overline{TS} is the mean overall *TS* for each measurement series. The addition of 0.5 is on account of measuring the total fish length to the nearest cm below.

Modelling swimbladder compression

Physoclists have *rete mirabilae* that enable them to produce and resorb gas, and hence to compensate for compression of the swimbladder during vertical migrations (Tytler and Blaxter 1973, Blaxter and Tytler 1978, Harden Jones and Scholes 1985). It is generally assumed that physoclists maintain neutral buoyancy throughout their depth range, so the *TS* can be properly estimated with Equation 1. However, the processes of producing and resorbing gas to respectively inflate (Blaxter and Tytler 1978) or deflate (Tytler and Blaxter 1973) the swimbladder in such fish can take 5 h or more, so the justification for the use of Equation 1 may therefore be compromised.

Wardle *et al.* (1996) demonstrated that caged, near-surface-dwelling horse mackerel were neutrally buoyant, but their swimbladder compression has not been studied. Horse mackerel are fast-swimming (Wardle

et al. 1996, Dreimere *et al.* 1999) and have large pectoral fins that provide an upward lift while swimming, so they should not need to be neutrally buoyant to maintain their preferred depth. Negative buoyancy is advantageous for rapid vertical predator avoidance (Blaxter 1985), and horse mackerel could utilize this to avoid predators such as hake *Merluccius capensis* (Pillar and Wilkinson 1995, Pillar and Barange 1998) and marine mammals (Hammond *et al.* 1994, McKinnon 1994). Some pre-dators such as dolphins use echolocation to detect their prey (Au and Martin 1989), and uncompensated swimbladder compression causing reduced *TS* in horse mackerel could be beneficial in terms of reduced conspicuousness to acoustically mediated predators. The *TS* function currently applied for horse mackerel in Namibia and Angola ($b_{20} = -72$ dB), originally derived for the physostomous herring *Clupea harengus*, is chosen because the acoustic properties of horse mackerel are believed to be closer to those of herring than to those of gadoids and other physoclists. Building on this assumption, surface-projected *TS* values were computed using the depth of each trace and the scattering area reduction rate found for herring (Vabø 1999), or $\gamma = -0.29$ in the model:

$$TS_z = TS_0 + 10 \log\left(1 + \frac{z}{10}\right)^\gamma \quad (9)$$

$$\sigma_z = \sigma_0 \left(1 + \frac{z}{10}\right)^\gamma, \quad (10)$$

where TS_z and σ_z are *TS* and backscattering cross-section at depth z , and TS_0 and σ_0 are the corresponding surface projections. The model is based on the assumptions that the swimbladder volume (v) decreases according to Boyle's Law, as expressed by

$$v_z = v_0 \left(1 + \frac{z}{10}\right)^{-1}. \quad (11)$$

Consequently, γ can have values of between 0 and -1, or respectively zero and maximum depth dependency, depending on the relative reduction of the swimbladder in the vertical plane. In a sphere that maintains its shape during compression, $\gamma = -2/3$. The backscattering area reduction rate in herring of $\gamma = -0.29$ therefore corresponds to a moderate reduction in scattering area, meaning that the swimbladder contracts relatively more in the vertical plane than in the horizontal plane (Blaxter 1979). If the buoyancy changes with depth, tilt angles are likely to also change (Vabø 1999), modulating the effect of swimbladder compression on *TS*. It is therefore difficult to predict which model will best describe the overall effects of changes in ambient pressure on *TS*. In the present study, the herring

model is used, because it is considered to be the most appropriate currently available for Cape horse mackerel.

RESULTS

Fish samples

During the October 1998 survey, horse mackerel formed a layer close to the bottom during trawling the *TS* measurements. Because vessel avoidance has a vertical component in Cape horse mackerel (Misund and Aglen 1992, Barange and Hampton 1994), demersal trawling is often the best sampling strategy when the fish are close to the bottom. Consequently, bottom trawl samples taken immediately after *TS* measurements were used as biological reference samples for measurements in Series 1 and 2. However, during the May 1999 survey, horse mackerel were scattered in midwater during the experiments. Samples were then obtained using a pelagic trawl fitted with the codend Multisampler. Sample 3 consisted almost entirely of horse mackerel, whereas the last sample, which was used for *TS* measurement Series 4 and 5, contained some hake *Merluccius capensis* (Table II). The sample length ranges of the horse mackerel were reasonably narrow ($SD = 1.2-2.2$ cm) relative to the average total fish length of 17.2–26.7 cm.

Most horse mackerel caught during the experiments in October 1998 were immature or maturing, with empty or near-empty stomachs. Although *TS* may be affected by fish buoyancy, fat content, gonad development and other physiological factors (Ona 1990), the *TS* of the fish sampled would not have been appreciably affected by deformation (dorso-ventral compression) of the swimbladder by the gonads or the stomach. By comparison, horse mackerel sampled in May 1999 were recovering or spent, so the *TS* of these fish could not have been affected by swimbladder deformation. Therefore, differences in gonad development between 1998 and 1999 could only have accounted for relatively small differences in *TS*.

Split-beam target tracking

Figure 2 shows an *Sv* echogram of ensoufied horse mackerel that were aggregated just above the bottom. The vertical movement of the transducer as a result of large swells caused the wave-shape of the echo traces. This movement, however, would not have appreciably affected the *TS* measurements, because only the range and not the transmission angle differs between pings, and the range variation is relatively small (<1 m). High

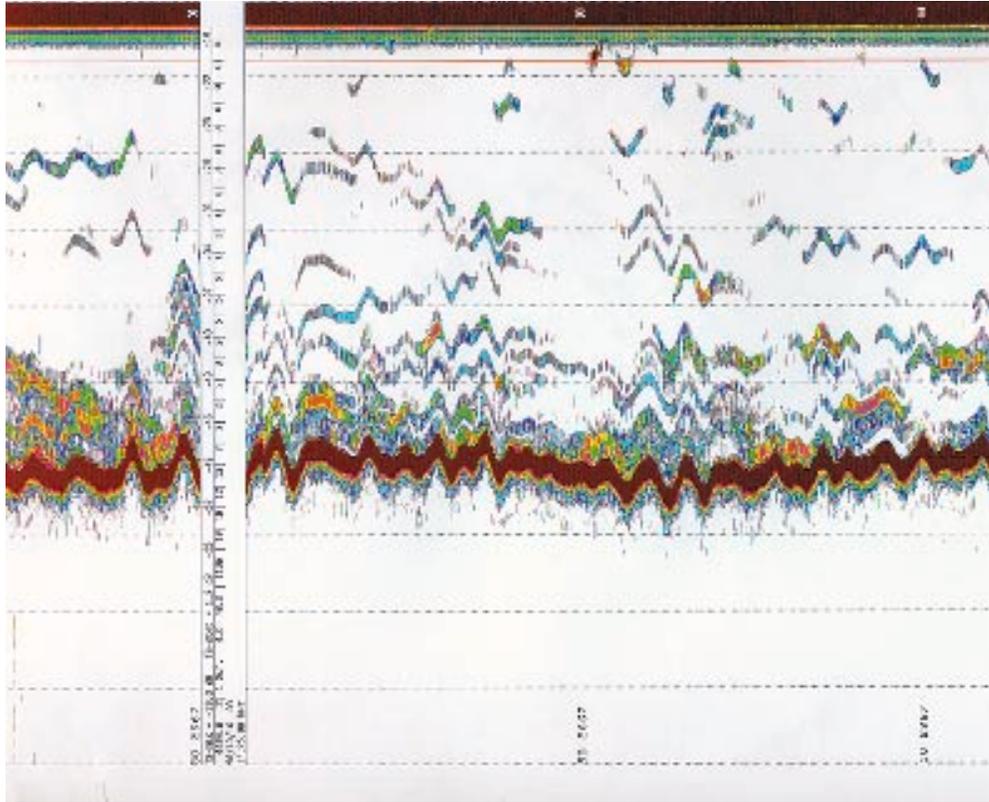


Fig. 2: Sv echogram at 38 kHz recorded using the submersible transducer in October 1998. The ensouffied Cape horse mackerel were aggregated near the bottom (120 m) during this experiment

positive and negative tilt angle estimates (Equation 7) may, however, have been somewhat over-represented. Table V summarizes the results from the split-beam tracking analyses for all five series, including mean TS ,

fish length and b_{20} constants. The TS histograms in Figure 3 show that the mean within-track TS ranged from -67 to -32 dB for corresponding total fish lengths of 10–29 cm, averaging between -45.9 and -49.5 dB.

Table V: Results from the target tracking analysis and root mean square lengths (RMSL)

Series number	1	2	3	4	5
Number of accepted traces	550	316	1 177	312	395
Mean pings/trace	8.0	7.6	6.8	7.6	8.2
Mean σ (cm ²)	3.24	1.41	1.25	2.58	1.81
Mean TS (dB)	-45.9	-49.5	-48.8	-46.9	-48.4
Min. total length (cm)	12	10	21	22	22
Max. total length (cm)	22	23	29	28	28
Mean total length (cm)	17.2	18.0	26.7	25.1	25.1
RMSL (cm)	17.3	18.1	26.8	25.2	25.2
n	291	351	182	64	64
Point-based b_{20} (dB)	-70.9	-74.9	-77.5	-75.1	-76.6

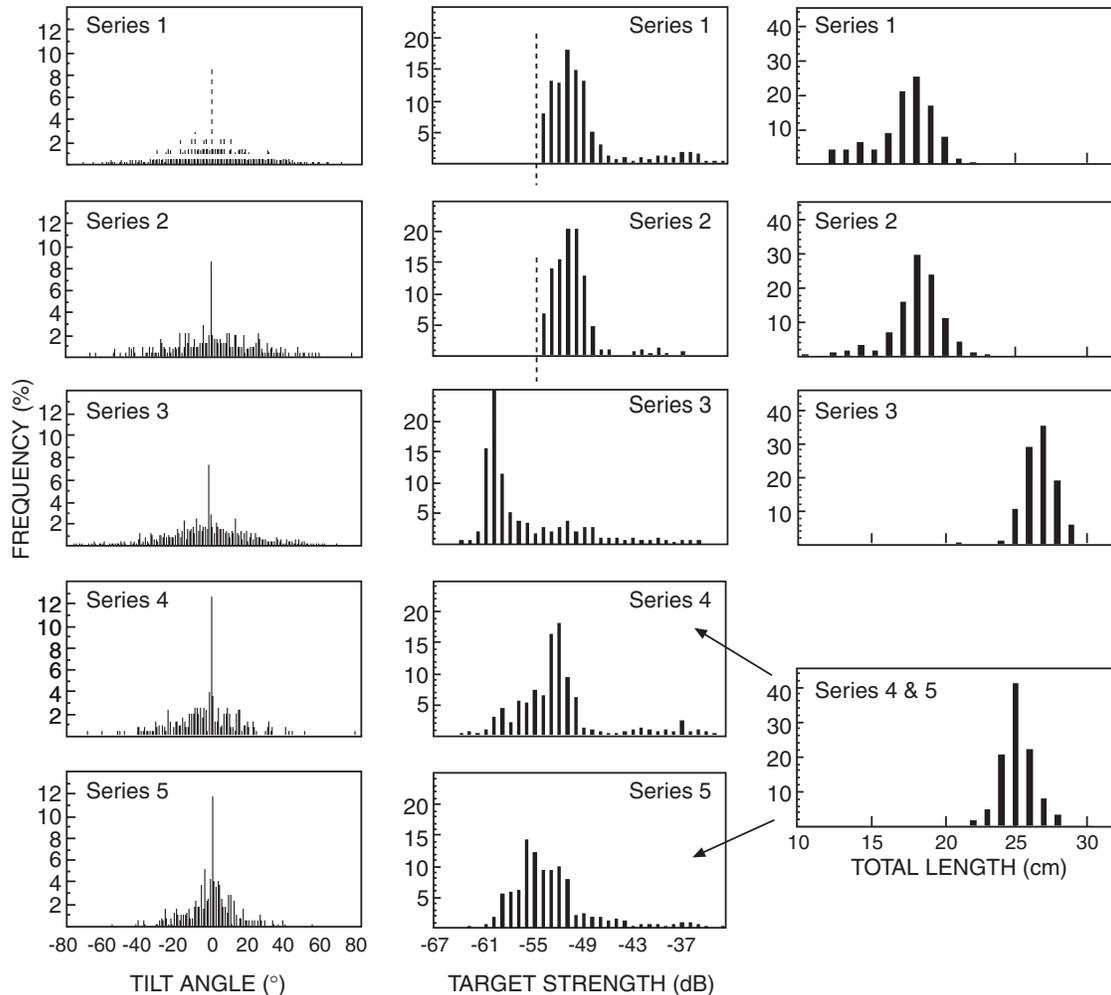


Fig. 3: Frequency of the estimated tilt-angle and mean within-trace *TS* distributions from the target-tracking procedure, including the total length distributions from the reference trawl samples. Dotted lines indicate the minimum *TS* threshold applied during data acquisition. Note that the length distribution from the last reference trawl sample is used as reference for both Series 4 and 5

The *TS* distribution patterns were similar in all experiments, except for Series 3, although the fish in the trawls were larger in Series 4 and 5 (25.1 cm) than in Series 1 and 2 (17.2 and 18.0 cm respectively). The *TS* distribution in Series 3 was skewed to the left (Fig. 3). The estimated tilt angles ranged from -80 to 80° , but were centred on 0° ($14^\circ < SD < 26^\circ$) in all series, indi-

cating that the fish did not undertake rapid vertical migrations during the experiments.

Effects of swimbladder compression on *TS*

The surface-projected *TS* estimates using the back-

Table VI: Back-calculation of surface projected target strength (TS) values and corresponding b_{20} estimates using four different back-scattering area reduction models ($RMSL$ = root mean square length; γ = area reduction rate of the back-scattering cross-section σ with depth, $\gamma = 0$ and $\gamma = 1$ corresponding to respectively no and maximum pressure dependency

Parameter	Series number					Mean $\pm SD$	
	1	2	3	4	5	Series 1–5	Series 2–5
Mean depth of fish (m)	99.8	97.4	129.8	171.8	174.4		
RMSL (m)	17.3	18.1	26.8	25.2	25.2		
TS (dB)							
$\gamma = 0$	-45.9	-49.5	-48.8	-46.9	-48.4		
$\gamma = -0.29$	-42.8	-46.5	-45.4	-43.2	-44.7		
$\gamma = -0.4$	-41.7	-45.4	-44.1	-41.8	-43.3		
$\gamma = -0.5$	-40.6	-44.3	-42.9	-40.5	-42.1		
$\gamma = -0.67$	-38.9	-42.6	-41.0	-38.4	-39.9		
b_{20} (dB)							
$\gamma = 0$	-70.9	-74.9	-77.5	-75.1	-76.6	-75.0 ± 2.6	-76.0 ± 1.3
$\gamma = -0.29$	-67.8	-71.9	-74.1	-71.4	-72.9	-71.6 ± 2.4	-72.6 ± 1.2
$\gamma = -0.4$	-66.7	-70.8	-72.8	-70.0	-71.5	-70.4 ± 2.3	-71.3 ± 1.2
$\gamma = -0.5$	-65.6	-69.7	-71.7	-68.7	-70.2	-69.2 ± 2.3	-70.1 ± 1.2
$\gamma = -0.67$	-63.9	-68.0	-69.7	-66.6	-68.1	-67.3 ± 2.2	-68.1 ± 1.3

scattering area reduction rate for herring $\gamma = -0.29$ are listed in Table VI. Three other models ($\gamma = -0.4$, $\gamma = -0.5$, $\gamma = -0.67$) are included for comparison. The surface projected TS values, and the corresponding b_{20} values, were between 3.0 and 3.7 dB lower than the respective measurements ($\gamma = 0$), translating to an average reduction of 3.4 dB over the five series using the herring model. The surface projections conform to the TS function currently applied for horse mackerel in Namibia and Angola.

DISCUSSION

The main advantage of a submersible over a hull- or keel-mounted transducer is the ability to resolve fish layers and shoals into single targets by reducing the pulse volume, so lessening the probability of multiple echoes being accepted as single fish targets (Foote 1987, Hewitt and Demer 1991, Barange *et al.* 1996, Soule *et al.* 1995, 1997). Reducing the distance between the transducer and a fish aggregation also increases the signal-to-noise ratio, and hence the detectability of weak targets. The target-tracking method used in this study isolated fish traces and therefore removed scattering from dense plankton aggregations (Stanton *et al.* 1996), which can be erroneously interpreted as fish echoes, so further reducing the risk of multiple target errors (Anon. 1999).

During the October 1998 survey, there was some

drift of the ship, which caused the angle of the transducer cable to deviate up to about 20° from vertical. It was assumed, however, that the transmission angle was nearly vertical, because the transducer was hanging freely in a weight-balanced housing. However, if the transmission angle was affected, TS values would have been negatively biased. Using equipment similar to that used here, Ona and Svellingen (1998) found that the transmission angles deviated $<4^\circ$ at about 30° cable angles. Therefore, although some negative bias may have affected the present results, it is expected to be small.

The side-thrusters of the vessel produced noise that may have caused fish avoidance, but it would have been considerably less at the depth of the recordings than at the surface. The use of deck lights during the recording of TS in Series 1 may have caused the fish to polarize (Ona and Toresen 1988, Koike *et al.* 1991), because horse mackerel react strongly to light (Koike *et al.* 1991, Barange and Hampton 1994). Polarization increases the dorsal aspect TS (Table V; MacLennan and Simmonds 1992), so this series should therefore be viewed in isolation.

Jellyfish *Aequora aequora* were present in the first reference sample (Table II). Because jellyfish are usually most abundant near the surface (Brierley *et al.* 2001, Sparks *et al.* 2001), they were probably caught during shooting and hauling. Apart from jellyfish and horse mackerel, the majority of the remaining species caught with the bottom trawl were typical bottom dwellers that did not occupy the acoustically

Table VII: Overview of published values of the b_{20} relevant for horse mackerel

Species or group	Method	b_{20}	Reference
<i>T. trachurus</i>	Comparison method	-73.4	Misund <i>et al.</i> (1997)
Clupeoids	Various <i>in situ</i> methods	-71.9	Foote (1987)
<i>T. symmetricus murphyi</i>	<i>In situ</i> survey data	-68.9	Lillo <i>et al.</i> (1996)
<i>T. symmetricus murphyi</i>	<i>In situ</i> survey data	-68.2	Gutiérrez and MacLennan (1998)
Physoclists	Various <i>in situ</i> methods	-67.5	Foote (1987)
<i>T. trachurus capensis</i>	<i>In situ</i> survey data	-66.8	Barange <i>et al.</i> (1996)
<i>T. trachurus capensis</i>	<i>In situ</i> survey data	-66.8	Svellingen and Ona, 1999
<i>T. symmetricus murphyi</i>	Swimbladder volume	-66.7*	Torres <i>et al.</i> (1984)
<i>T. trachurus capensis</i>	<i>In situ</i> survey data	-65.2	Svellingen and Ona (1999)

* This value was calculated in the present study for the two reported groups of fish averaging 38.7 and 31.4 cm total length

sampled volume (5–25 m above bottom). Some small hake were, however, caught in the last reference sample and, because the degree of mixing is somewhat high for *TS* measurement purposes, care must be taken when interpreting the results.

Mesh selection in the codend can be excluded as a possible source of bias for the horse mackerel size structures because the small mesh size of the trawl retains juveniles as small as 5 cm. Size-dependent avoidance in front of the net and mesh selection in the large-meshed panels in the mouth of the trawl (e.g. Everson and Miller 1999) may, however, have caused a bias. When estimating mean fish length, the sample range should be narrow to reduce trawl-sampling error. This criterion is satisfied in the last two samples, in which there was only one cohort present, but a smaller cohort (<15 cm) was present in the first two samples, and the sample ranges were somewhat high for *TS* purposes (Fig. 3).

TS measurements

During the October 1998 survey, the minimum *TS* threshold was set to -55 dB, but it was adjusted to -70 dB in the May 1999 survey (Table I). The low *TS* values recorded suggest that this threshold may have caused a loss of observations in the lower range of *TS* distributions of Series 1 and 2 (Fig. 3). The minimum *TS* threshold should have been about -70 dB to ensure proper coverage of the distribution range and to eliminate threshold-induced bias (Weimer and Ehrenberg 1975).

The b_{20} estimates (Table V) suggest low *TS* for horse mackerel compared with values in the literature, which vary greatly (Table VII). Some of this variation is likely attributable to methodological differences. Several studies have estimated *TS* values from survey data (Barange *et al.* 1996, Lillo *et al.* 1996, Gutiérrez and MacLennan 1998, Svellingen and Ona 1999), which may be positively biased as a result of multiple

echoes. Barange *et al.* (1996) attempted to overcome this problem by visual scrutiny of the *TS* distributions, assigning weak distributional modes to the target species and stronger, more elusive, modes to multiple echoes of the targets, subsequently removing the stronger mode from the dataset. However, unbiased *TS* data may be bi- or polymodal. It may even be argued that polymodality should be expected, even for populations with unimodal size distributions (Williamson and Traynor 1984, Zhao 1996). Using a Simrad EK 500, Zhao (1996) demonstrated that the mean within-track *TS* of a single, freely swimming 34 cm herring was extremely variable (25 dB trace-to-trace variation) at several discrete frequencies (18, 38 and 120 kHz). That author also demonstrated that polymodality is a general characteristic for *TS* distributions originating from a single fish over time and cautioned against linking distributional modes in *TS* distributions to given size-groups (Rudstam *et al.* 1999).

A common problem when extracting *TS* detections from survey data is that the distance between where the trawl samples were taken and the *TS* measurements may be too large for validation purposes. Torres *et al.* (1984), on the other hand, derived *TS* values from tank experiments and compared swimbladder volume with fish length. Because of the large impact that fish behaviour may have on *TS* (Foote 1978, 1987), *in situ* techniques are generally preferable whenever possible (Foote 1987, MacLennan and Simmonds 1992). The *ex situ* approach has, however, the advantage of a controlled experimental set-up, but it should be supplemented with empirical observations to validate predictions. Another approach is to back-calculate the average acoustic backscattering cross-section from acoustic densities (area backscattering coefficient s_A) and independent measures of animal densities, usually referred to as the comparison method (MacLennan and Simmonds 1992, Misund and Beltestad 1995, Misund *et al.* 1997). That technique is based on echo integrals and is therefore not affected by multiple target errors, but it is more sensitive to fish avoidance effects. When

applied in situations in which entire fish aggregations can be caught, e.g. purse-seining (Misund and Beltestad 1995, Misund et al. 1997), the risk of size- or species-selective sampling is much reduced. However, it is difficult to obtain accurate estimations of the animal densities, particularly if the fish are dispersed (Misund and Beltestad 1995). Higher *TS* should be expected when fish are schooling than when dispersed (Foote 1987), because of higher degrees of synchronization and polarization (Pitcher 1983) and hence more uniform tilt-angle distributions (Blaxter and Batty 1990).

Studies based on survey data or on caged fish report higher *TS* values than those based on *in situ* experiments (Table VII). During surveys, it is difficult to trace individual fish in order to reduce bias from multiple echoes, because each fish are only briefly present within the acoustic beam. Long detection ranges further increase the risk of accepting multiple echoes, as well as eliminating weaker echoes, which results in higher *TS* estimates. The targets may be located within the high-resolution range of hull-mounted transducers during surveying, but the influence of the vessel may in such situations represent another source of bias; positive if the fish polarize underneath the vessel and negative if the fish dive.

Angular orientation and swimbladder compression

The lower-than-expected b_{20} estimates found in the present study may be attributable to the angular orientation of the fish (Foote 1978, Vabø 1999) and uncompensated vertical movements (Harden Jones and Scholes 1985, Blaxter and Batty 1990) producing a depth dependency in *TS* (Brawn 1969, Vabø 1999). The angular orientation of fish relative to the transducer considerably affects the acoustic backscattering, producing the characteristic angle sensitivity diagrams (e.g. Nakken and Olsen 1977). Fish populations will therefore produce different *TS* distributions for different types of behaviour (Zhao 1996). In the present study, the tilt angle distributions were similar to wide normal distributions with a peak on 0°, which seems reasonable in the absence of vertical migrations. During Series 5, the fish migrated downwards, and a negatively skewed tilt-angle distribution would have been expected. However, the 100 m descent lasted for about 30 minutes and may not have required steep swimming angles, particularly if the fish were negatively buoyant. The tilt angles in Series 5 had a narrower distributional range ($SD = 14^\circ$) than the others ($SD 19\text{--}26^\circ$), suggesting a higher degree of polarization, consistent with downward migration. Some variation in *TS* between the series may be anticipated from the differences in angular distributions, but the behaviour of the fish seemed

similar between the series. The present measurements were obtained from fish 100–200 m deep, so another possible explanation for the weak *TS* recorded may be that it is depth-dependent as a result of swimbladder compression and/or alternation of swimming angles with depth. The fast-swimming nature of horse mackerel, combined with their large pectoral fins, may reduce their need to produce gas to stay neutrally buoyant. Conversely, negative buoyancy might be advantageous during rapid vertical movements, which is a characteristic for horse mackerel, and reduced *TS* would reduce conspicuousness versus acoustically mediated predators.

CONCLUSIONS

The *TS* estimates for the horse mackerel under study ($-77.5 \text{ dB} < b_{20} < -74.9 \text{ dB}$) are markedly lower than the *TS*-to-length relationship currently applied in biomass surveys off Namibia and Angola ($b_{20} = -72 \text{ dB}$) and those reported in the literature for *Trachurus* spp. ($-73.4 \text{ dB} < b_{20} < -65.2 \text{ dB}$). Surface-projected *TS* values, compensated for swimbladder compression as observed in herring, conform to the current *TS* function for horse mackerel off Namibia and Angola. If the *TS*-to-length relationship derived here is considered realistic, and if depth dependency is appropriate, current biomass estimates of horse mackerel off Namibia and Angola could be considerably underestimated, possibly by as much as one-half depending on the depth of the fish. However, further studies are required to verify the results reported here, particularly with regard to the hypothesis that the *TS* in the physoclistous horse mackerel is depth-dependent. Further quantification of this is required before any changes to the current survey method are recommended.

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