



Acoustic target strength (TS) of argentine anchovy (*Engraulis anchoita*): the nighttime scattering layer

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Engraulis anchoita is a physostomous fish with a dual chambered swimbladder (sb). *In situ* target strength (TS) measurements on this species are only possible at night, when anchovies disperse forming a scattering layer near the sea surface. A survey data series comprising more than 50000 single target detections, recorded from 1995 to 2008, was analyzed in order to study the species specific TS at 38 kHz. A TS vs. fish total length (L) equation was obtained from the *in situ* measurements ($TS = 31.9 \log L - 82.4 \text{ dB}$; $r^2 = 0.78$). When the slope of the regression line was forced to 20 into the TS equation, the resulting value for the constant term (b_{20}) was -68.6 dB . In any case, these results indicate an average difference of +3 dB (higher TS values) when compared with the general model suggested for *clupeoid* fish. The TS measurements obtained inside the nighttime sound scattering layer exhibited a negative trend with depth. An empirical depth dependence term for the anchovy TS equation was obtained through a three parameter least square fitting of the data [$TS = 31.3 \log L - 79.6 \text{ dB} - 4.74 \log(1 + z/10)$; $r^2 = 0.74$]. Anatomical data obtained through high resolution X-Ray Computed Tomography was employed as input for a Prolate Spheroidal Model (PSM). Theoretical TS vs. tilt angle functions were obtained considering the compression of the sb at different depths and under the assumption of different contraction rates. The TS functions were then averaged over different fish tilt angle distributions and used to derive theoretical depth dependence curves of average fish TS. The implications of the adopted sb contraction rate and tilt angle distribution are discussed by comparing the modelled TS(z) curves against the empirical data.

Keywords: depth dependence, *Engraulis anchoita*, fish target strength, *in situ* measurements, physostomous fish, TS modelling.

Introduction

Argentine anchovy (*Engraulis anchoita*) is the main pelagic fish species inhabiting the South Western Atlantic Ocean (SWAO). The size of this fish population exceeds several million tons and comprises two stocks: The northern stock (the larger one) is also known as the Bonarenses stock and occupies the shelf waters from southern Brazil to central Argentina (24° S–41° S); while the southern stock, known as the Patagonian stock, is located off the Patagonian coast (42° S–48° S). Main spawning activity of the

species occurs from September to December (Cousseau and Perrotta, 2013). Regular acoustic surveys are carried out annually during the austral spring (October–December) by the National Institute of Fisheries Research of Argentina (INIDEP), in order to perform the assessment of both anchovy stocks. Anchovy surveys have also been carried out occasionally during the austral winter (May–July).

During daytime Argentine anchovy forms compact and very dense schools and thus the collection of single target echoes with

narrow band echosounders is very difficult, if not impossible. These compact schools distribute over most of the water column during the day, from near the sea surface to 70 m depth, approximately. It is only at night that anchovy schools break up, forming a layer of dispersed fish near the sea surface that may extend over tenths of nautical miles. At sunrise, the fish layer regroups into smaller aggregations that quickly develop into small compact schools. Slight variations of this schooling pattern can be observed at other times along their migration cycle (Nion and Castaldo, 1982), but maximum dispersal of the individuals always occur at night and near the sea surface.

This springtime behaviour (nighttime dispersal) is probably related to the spent activity of the species, since most of the spent takes place at night. Feeding activity seems to be very low at the time of spent (Pájaro *et al.*, 1997; Pájaro, 2002). The only food present in the stomach contents indicates a moderate feeding activity on small prey, as small copepods and fish eggs, which is accomplished by filtering. Former studies on the seasonal variation of fat content for the northern stock indicate higher values for the winter period (July–August) compared to spring (Aizpun *et al.*, 1979). A detailed description of the oceanographic conditions in the area is out of the scope of this article but perhaps it is worth to note that at the time of spawning (southern spring to summer) a strong thermocline is present over most of the anchovy distribution area (Baldoni *et al.*, 2015). This physical stratification seems to have implications on the geographical distribution of the stocks and probably also on the observed behaviour (Hansen *et al.*, 2001; Martos *et al.*, 2005).

The general TS vs. fish length (L) equation, developed for *physostomous* fish in Foote (1987), was adopted at the beginning of this survey series (1993) in order to convert the survey echointegration values (NASC) into fish densities (MacLennan and Simmonds, 1992) and hence to provide absolute biomass estimates of the anchovy stocks. However, the need of a species specific TS equation has been a recognized issue for a long time. Even if the acoustic estimates are used as a relative index of fish abundance, a different slope of the TS vs. L relationship could lead to an error in the predicted trend of the stock size. More recently, higher TS values than those predicted by the generalized equation have been reported for *clupeoids* (Ona, 2003; Zhao *et al.*, 2008; Amakasu *et al.*, 2010), hence confirming the necessity of investigating the subject.

The anchovy nighttime scattering layer extends vertically from near the sea surface (5–10 m depth) down to the upper limit of the spring–summer thermocline (35–45 depth) (Baldoni *et al.*, 2015). Occasionally, the density of fish in this scattering layer is low enough as to permit the detection of single targets acoustically, allowing for the collection of *in situ* fish target strength data. In 1995, with the introduction in Argentina of the first split-beam echosounder, the collection of TS data with calibrated instruments become an integral part of every anchovy survey. This paper summarizes some of the results compiled during 15 years of surveying the species acoustically. *In situ* target strength measurements and concurrent pelagic trawling data obtained at the nocturnal scattering layer were selected from this survey data series and utilized to construct a species-specific TS vs. L relationship to be used in echointegration surveys.

As a *physostomous* fish, TS of *Engraulis anchoita* is expected to exhibit a negative trend with depth due to swimbladder (sb) compression. Different results have been reported for *physostomous* fish species, based on both experimental and theoretical work and

different contraction rates of the fish sb dimensions have been suggested as the possible explanations (Ona 2003; Gorska and Ona 2003a; Gorska and Ona 2003b; Zhao *et al.*, 2008). In this paper, we paid special attention to this subject and in order to obtain an experimental depth correction term for the TS equation, we fitted a three parameter equation to the *in situ* TS data. Additionally, we studied the anatomy of the anchovy sb by X-ray Computed Tomography (CT scanning) in order to simulate fish TS functions through a Prolate Spheroidal Model (PSM; Prario *et al.*, 2015). We used PSM simulations to study the variation of the average TS with depth, by considering different contraction rates of the sb dimensions and also different behaviour modes (different tilt angle pdf's). Different theoretical explanations for the observed depth dependence of the *in situ* TS data are proposed. However, we consider our results on the TS of the Argentine anchovy are valid only for the nighttime situation (fish scattered at night and near the sea surface). There is evidence for instance, of a very different depth dependence associated to the sound scattering recorded from the daytime (compact) schools of anchovy. This is the subject of another ongoing study.

Materials and methods

The surveys, the instrumentation, and the data

The data were collected onboard the *R/V's Cap. Oca Balda* and *Dr E. Holmberg*, two 65 m length stern trawlers operated by INIDEP. The vessels were equipped with *SIMRAD EK500* echosounders operating at 38, 120, and 200 kHz. The scientific echosounders were calibrated with standard targets at least once a year and according to the procedures recommended in Foote (1987). Only the split-beam 38 kHz data were employed for this study and the most relevant echosounder settings are shown in Table 1. The trawl stations were carried out at irregular intervals along the survey trackline and their location was based on the interpretation of the echorecordings and the surveyed distance from the previous trawl station. Other regular survey activities included of CTD casts and plankton tows with different nets for the collection of anchovy eggs and the accompanying zooplankton. Additional information of this survey series can be found in Madirolas *et al.* (2013).

This survey series is primarily intended to provide point estimates of the Argentine anchovy abundance. The surveys are carried out annually from October to December at the peak of the spawning season, when most of the stock can be surveyed in the shortest time. The survey area extends to about 45 000 and 27 000 nmi², for the northern and southern stocks, respectively, and each survey takes approximately 3 weeks to be completed. Acoustic and pelagic trawling data obtained at 16 different anchovy surveys were analyzed for this study. The data series comprises the surveys carried out between 1995 and 2008. Figure 1 shows the surveyed area and the typical layout of the surveys trackline.

Acoustic data files were recorded with the Bergen Echo Integrator (BEI) software (Foote *et al.*, 1991), which is the software routinely utilized onboard INIDEP's research vessels for fish stock assessment since 1995. Myriax Echoview v4.10 software (Higginbottom *et al.*, 2000) was utilized for post-processing the *in situ* TS measurements. Two different pelagic trawls were used: a NICHIMO type midwater trawl (22 m headrope with rectangular doors 2.5 m²–270 kg) and an ENGEL type trawl (31 m headrope with Suberkrup doors 4.5 m²–900 kg) were utilized for the

Table 1. Echosounder settings and single target detection parameters.

SIMRAD EK500 echosounder with ES38-B split-beam transducer	
Firmware version	v5.33
Frequency	38 kHz
Pulse length	1 ms
Output power	2000 W
Bandwidth	Auto (Wide)
TS Tr. Gain	27.5–23.3 dB*
Ping-rate	2 pps
Min./Max. Echo Length	0.5 ms/1.5 ms
Max. Gain Comp.	6.0 dB
Max. phase deviation	0.8°
TS min. value	−70 dB
Echoview software	
Filter angles (Minor/Major)	±3.5°
TS threshold	−70 dB
Min. pulse length	0.5 ms
Max. pulse length	1.5 ms
Max. angle SD (Minor/Major)	0.8°
Min. echoes per track	3 (w/max. 1 missing ping)

*Depending on vessel/year.

pelagic hauls. In all cases, a cod-end liner of 20 mm mesh size was employed.

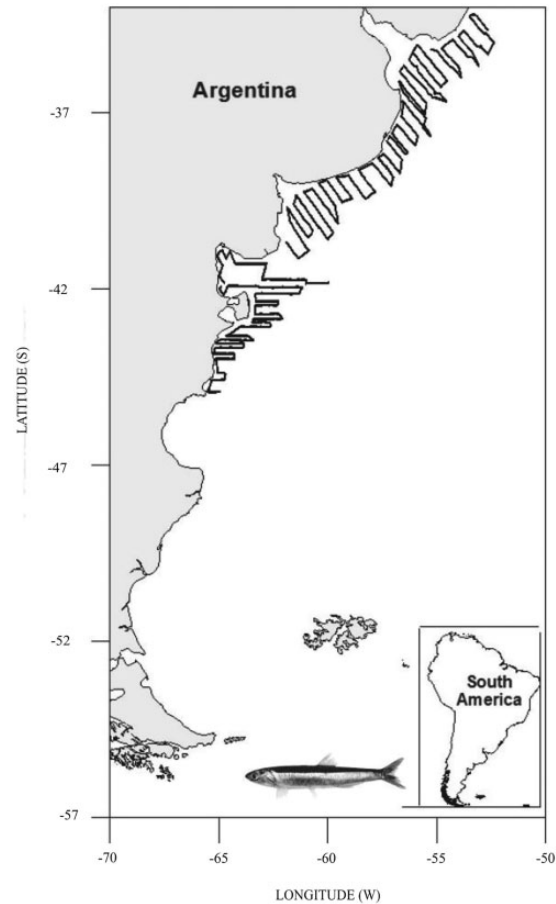
The *in situ* target strength measurements were collected only at night, with the vessel slowly sailing over the subsurface fish scattering layer. The lighting on deck was kept to a minimum. Only TS data corresponding to those trawl stations where the presence of *Engraulis anchoita* accounted for at least 90% of the total catch were accepted. The risk of failure of the single target discriminators (pulse duration and phase variation) was raised in Soule *et al.* (1997) and hence it is of common practice to limit TS data collection to those situations with low fish density. This is quantified in terms of the expected number of fish per sampling volume unit in Ona (1999), according to the formula:

$$N = \frac{s_A \left(\frac{c\tau}{2}\right) R^2 \Omega_D}{4\pi 10^{TS/10} \Delta_z (1852)^2} \quad (1)$$

where s_A (m^2/nm^2) is the nautical area scattering coefficient of the fish layer, c (m/sec) is the sound speed, τ (ms) is the pulse duration, R (m) is the average depth, Ω (sr) is the transducer equivalent beam angle, and Δ_z (m) is the depth interval occupied by the fish layer. Hence, the data set was further limited to those trawl stations with a value of $N \leq 0.1$.

Fish sampling data

As stated before, the daytime compact schools of anchovy merge after sunset into a nighttime scattering layer that may have a horizontal extension of up to several nautical miles. The spatial structures of these layers are very homogeneous. In all cases, trawling was accomplished across the whole vertical extent of the scattering layer and hence, the obtained samples integrate vertically the size distribution of fish within the layer. The *in situ* measurements were collected immediately before, during or immediately after the trawl station used as reference for fish size distribution. Hence, a reasonable correspondence is expected between the obtained fish sample and the collected acoustic data. The whole catch obtained in each trawl station was sorted into species and

**Figure 1.** The anchovy surveys in Argentina.

the total weight per species was obtained. A fish sample of 200 individuals was randomly taken from the catch of the target species (anchovy) and these fish were subjected to the regular fish sampling routine, comprising individual fish length and weight measurement, stomach content, and sexual maturity determination, gonad extraction for fish reproduction studies, and otoliths extraction for age determination.

In situ TS data processing

Both, BEI data files containing pre-processed EK500 single target data (E_x data telegrams) and EK500 raw data (W_x and B_x data telegrams) were employed for the TS analysis. In order to extract the single target echoes from the raw data files, a 40 log equalized echogram was created from the echo amplitude raw data (W_x telegrams) and combined with the angle raw data (B_x telegram) to create virtual echograms containing only single target echoes (Higginbottom *et al.*, 2000). The acceptance criteria for the single target detections were established according to the general principles of echo pulse duration and phase variation (Ona, 1999). A minimum threshold value of -70 dB was applied to both, the pre-processed and the raw data (virtual) single target echograms to exclude the acoustic contribution from noise and most of the smaller plankton. A transducer beam angle window of $\pm 3.5^\circ$ was also applied to the single target detections, in order to avoid a

possible bias to the larger TS values, due to the decrease of the signal to noise ratio (S/N) towards the exterior sections of the sound beam (Ona *et al.*, 1996). The most relevant parameters utilized for single target detection are shown in Table 1.

The theoretical TS function (TS vs. fish tilt angle) was computed at 38 kHz with the PSM in order to obtain a rough but objective TS threshold criteria to be applied to the *in situ* data. As a rough reference, we modelled the TS functions for an adult fish ($L \approx 15$ cm) and a juvenile ($L \approx 10$ cm) at 20 m depth and obtained maximum and minimum values of -39 and -60 dB for the adult fish and -43 and -68 dB for the juveniles. In order to further reduce the probability of acceptance of multiple target echoes, the resulting single targets obtained in both, pre-processed and virtual echograms, were grouped into fish tracks (Ona and Hansen, 1991). The maximum value of each track (highest echo amplitude) was evaluated and the whole track, i.e., all single echoes contained in the track, was rejected if its maximum did not lie between the maximum and minimum values of the simulated TS function. This procedure was undertaken to further exclude unwanted contributions from other organisms, as it may be the case for some larger zooplankton (mainly salps) and some larger fish (mainly hake). We believe that this track based process of thresholding helps to preserve the extreme but true TS values (min. and max.) of the target species, instead of simply “cutting” the tails of the TS distribution, as it is the case when a threshold value is applied directly on the single target echoes distribution. Finally, the single target echoes contained in the thresholded fish tracks were extracted in order to calculate the corresponding average TS of the experiment in the linear domain.

The maximum relative error (MRE) associated to the mean TS of each selected experiment was estimated using the standard error (SE) and the number of echoes in each experiment. The TS data were fitted with an exponential function in order to evaluate the relationship between the number of single target echoes and the expected MRE of the averaged TS (Figure 2). This analysis suggested that a reasonably low variance in $\langle TS \rangle$ could be expected when the number of accepted single target echoes was higher than 500. In this way, a total of 16 trawl stations from the 1995–2008 survey series were selected as suitable *in situ* experiments to be used for the subsequent TS analysis. For each considered experiment, the obtained single targets echoes were averaged in the linear domain and then converted to TS in dB are 1 m^2 , according to the definition:

$$\langle TS \rangle = 10 \log_{10} \langle \sigma_{bs} \rangle \quad (2)$$

where σ_{bs} is the equivalent back-scattering cross-section in m^2 and $\langle TS \rangle$ is the mean fish target strength (Clay and Medwin, 1977).

Depth dependence analysis of the experimental data

To smooth the experimental TS vs. depth data, each experiment was stratified by depth using a running mean criterion (Hastie and Tibshirani, 1990). The TS measurements were grouped into depth layers or bins, defined as a mobile depth window of 3 m height that was shifted in 0.1 m steps across the water column. The resulting bins were then used for grouping the TS data and to compute the average TS of each bin. Furthermore, to minimize noise in the computation of these averages, only those bins containing 50 or more single-target echoes were considered for the

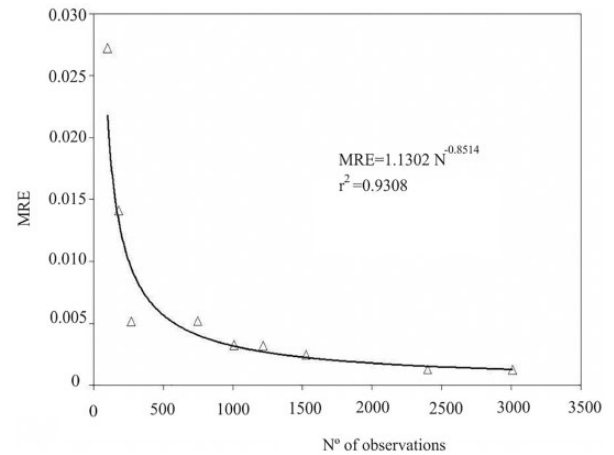


Figure 2. Maximum Relative Error (MRE) of the mean TS as a function of the number of observations (single target echoes).

depth dependence analysis. In order to limit the variability of the data for the depth dependence analysis, either due to experimental artefacts or due to unusual fish behaviours, those noisier experiments whose TS data laid consistently outside ± 1 SE of the fitted relationship were discarded for the construction of the $TS(L, z)$ model. Trawling at each experiment site integrated vertically all the fish in the scattering layer and thus the corresponding average fish length was associated to all the depth bins of the experiment, i.e. it was assumed there was no stratification of the fish length with depth inside the fish scattering layer. In this way, we obtained the data triplets (TS, z, L) for the subsequent depth dependence analysis. All depth values are referred to the sea surface level.

TS modelling

In order to study the morphology of the anchovy sb, several individuals were transferred to acclimatization tanks installed onboard to allow for the adaptation of fish to the surface pressure conditions. After an acclimatization period of 12 h, the specimens exhibiting a normal swimming behaviour were individually anesthetized by immersion in a tray containing a benzocaine-ethanol solution dissolved in sea water. No bubbles release was observed during anaesthesia. After a 5 min immersion in the anaesthetic solution, each specimen was measured (length and weight) and shock-frozen by sinking it into a container with liquid nitrogen. The frozen specimens were immediately transferred to a freezer (-20°C) for a few days, until they were brought to a medical facility for CT scanning. This was performed in the lateral plane of the fish and with a scanning resolution of 1.5 mm. The resulting data files (.DICOM files, NEMA PS3/ISO 12052) were used for image segmentation with ITK-SNAP software (Yushkevich *et al.*, 2006) in order to resolve the sb from the rest of the body tissues. The sb anatomical measurements, necessary as input for the PSM, were obtained from the segmented image by means of Netfabb v6.0 software (<http://www.netfabb.com/>).

A modified version of the PSM (Furusawa, 1988) presented in Prario *et al.* (2015) was used to simulate anchovy TS. The simulation considered the coherent addition (in the linear domain) of the sound backscattering produced by three scatterers: the two main chambers of the anchovy sb (soft spheroids) and the fish

Table 2. Fish length and TS statistics for the 16 selected experiments.

Exp.	Date	Time (GMT)	N [1/m ³]	<L> [cm]	C.V. [%]	Tracks	Targets	<z> [m]	<TS> [dB]	TS _{mode} [dB]	C.V. [%]
E1	16/10/1995	03:00	0.064	15.2	9.3	154	780	23.1	-45.3	-42.5	12.4
E2	13/10/1995	02:00	0.099	13.5	6.0	297	1171	18.3	-46.1	-42.0	12.4
E3	26/10/1996	00:00	0.050	14.8	10.2	390	1306	31.6	-44.5	-43.0	9.7
E4	18/05/1998	05:00	0.046	14.9	11.5	398	2002	8.2	-45.5	-42.0	12.5
E5	13/12/1998	06:00	0.072	14.2	6.0	1182	5154	17.9	-46.6	-44.0	12.4
E6	03/11/2003	03:00	0.107	12.3	12.3	2298	9290	14.4	-48.1	-48.0	9.1
E7	05/11/2003	01:00	0.057	13.9	15.1	507	2990	18.8	-47.0	-48.0	11.3
E8	06/11/2003	01:00	0.073	11.0	14.5	270	909	16.7	-48.6	-50.0	9.9
E9	07/11/2003	02:00	0.037	16.4	5.9	1135	5180	18.4	-44.7	-41.0	13.6
E10	14/07/2003	01:00	0.035	14.6	13.7	171	1744	17.1	-46.0	-45.0	10.0
E11	08/11/2003	03:00	0.040	15.9	6.9	663	2355	14.7	-42.9	-42.0	11.4
E12	23/10/2004	00:00	0.053	15.2	7.2	1530	5696	11.7	-43.1	-41.0	10.9
E13	02/10/2004	03:00	0.048	15.0	5.5	636	2925	14.7	-44.3	-43.0	11.3
E14	02/10/2004	02:00	0.041	16.2	7.2	266	915	19.4	-43.4	-42.0	11.5
E15	24/10/2004	00:00	0.038	17.0	4.7	1054	4113	26.5	-43.3	-42.0	13.2
E16	05/11/2008	00:00	0.043	15.6	4.5	958	3778	21.8	-44.8	-43.0	13.4

body (fluid spheroid). The contributions from other minor gas filled cavities, as the auditory channels, were assumed to be negligible and disregarded. The PSM model requires the dimensions of each prolate spheroid as inputs. These dimensions were obtained with the following assumptions: the widths of the equivalent soft spheroids were given to obtain an equal dorsal area to each of the measured sb chambers; the lengths of the soft spheroids were equalled to the measured chamber lengths; the width of the equivalent fluid spheroid was derived by assuming its volume to equal the measured fish body volume and equalling the length of the fluid spheroid to the measured body standard length. The sound speed and density contrasts used for modelling the fish body were 1.04 (Gorska and Ona, 2003a) and 1.058 (Taylor, 1921; Massa *et al.*, 2007 for 10% of fat content), respectively, while pressure-release boundary conditions were used for both sb chambers.

Results

An empirical TS vs. L relationship

The data selection criteria resulted in 16 accepted experiments of *in situ* TS measurements. These experiments correspond to nine different surveys of this series. The catches were composed almost exclusively of anchovy. The minimum and maximum fish length values recorded in the experiments were 8.2 and 19.8 cm, respectively. The average L obtained in each experiment ranged from 11.0 to 17.0 cm. The variability of fish size in the samples was not very high (CV < 15%). The length distributions were typically unimodal and the mode was rather narrow in most cases. In the few cases where a second mode was present, this was very small compared to the main one. However, the presence of few individuals with sizes far from the modal value was frequent. Table 2 summarizes the statistics of L for each experiment.

The single target selection criteria applied to the data resulted in a total of 11 909 selected fish tracks which comprised 50 308 single target echoes. The obtained TS distributions were unimodal and the modes ranged from -41.0 to -50.0 dB. Table 2 summarizes the fish TS statistics corresponding to each experiment. Figure 3 shows two examples (juveniles and adult fish) of the obtained L distributions and the associated TS values.

The average value of fish TS obtained in each of the 16 selected experiments is plotted against its corresponding average fish total length in Figure 4. Experiments E4 and E10 (wintering anchovy)

were also included in the analysis (Figure 4) since no significant differences were observed when compared with the bulk of the TS data (springtime spawning). In order to obtain a TS vs. L relationship, a nonlinear fitting (StatSoft, Inc., 2011) was performed to the (TS, L) data pairs and a good correlation was found ($r^2 = 0.78$). The following values for the parameters a and b were obtained:

$$TS(L) = 31.9 \log L - 82.4 \text{ dB} \quad (3)$$

where L (cm) is the fish total length. The obtained relationship is plotted as a solid line in Figure 4 and the range interval corresponding to a ± 1 standard error (SE) is shown as a shadowed band, centred in the average values of the fitted equation.

To facilitate the comparison with previously reported TS vs. L relationships, the slope of the obtained fitting curve [Equation (3)] was forced to a coefficient equal to 20. Consequently, the new constant term obtained (b_{20}) was -68.6 dB:

$$TS_{b_{20}}(L) = 20 \log L - 68.6 \text{ dB} \quad (4)$$

The 20-forced fitting curve [Equation (4)] is shown in Figure 4 as a dotted line. The general TS equation proposed for *clupeoid* fish in Foote (1987) is also included in the same figure for its comparison (see dashed line). Whatever the adopted value for the constant term of the equation (free fitting or slope forced to 20), higher values of TS were obtained for the whole size range of Argentine anchovy as compared with the generalized empirical equation for *clupeoids*.

Depth dependence of the empirical TS data

Most of the experiments showed a clear trend of decreasing TS with depth. However, the data in a few experiments (E4, E11, and E15) exhibited a rather noisy pattern and were excluded for the depth dependence analysis. This is exemplified in Figure 5 (A: accepted experiment and B: rejected data). The deeper limit of the TS data was also slightly truncated in some of the remaining experiments due to a sudden change in the TS values observed in the vicinity of the thermocline. This process resulted in approximately 30 000 accepted fish single echo measurements averaged into 1493 data triplets (depth bins) of TS, L, and z. The depth

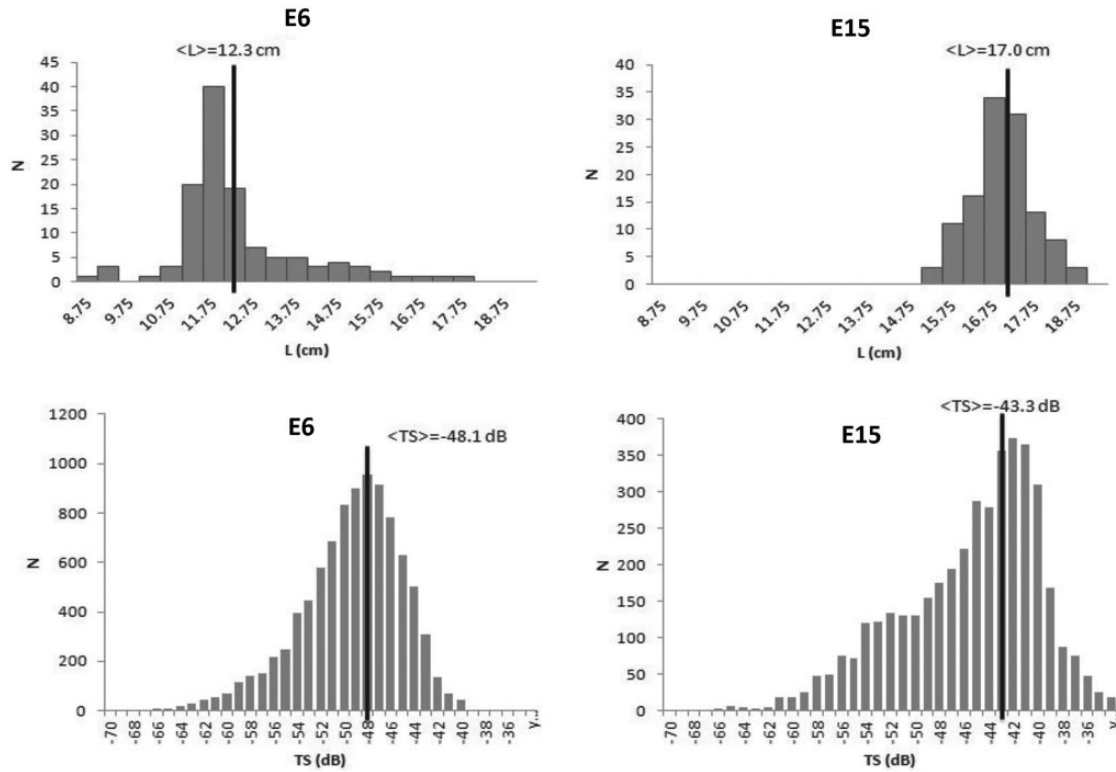


Figure 3. Two examples of anchovy total length (L) and corresponding TS distributions as found in the experiments utilized for this study.

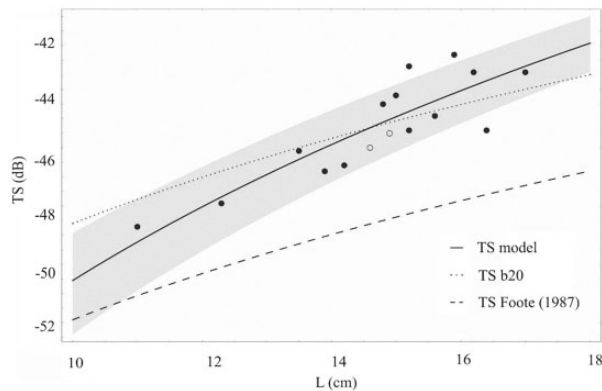


Figure 4. $\langle TS \rangle$ vs. fish total length (L) relationship. Bold solid line = free fitting equation; shadowed band = free fitting ± 1 SE ; dotted line = equation with slope forced to 20; dashed line = Foote (1987) equation. The two empty circles correspond to the wintering anchovy surveys (E4 and E10).

dependence of TS was then quantified through a nonlinear surface fitting to the data triplets (StatSoft, Inc., 2011). To facilitate the comparison with previous works, we used the three parameters (a_z , b_z , and γ) equation proposed in Zhao et al. (2008) and a good correlation was found ($r^2=0.74$):

$$TS(L, z) = 31.3 \log L - 79.6 - 4.74 \log \left(1 + \frac{z}{10} \right) \quad (5)$$

where z is the fish depth in m. Equation (5) is plotted in Figure 6 as a function of depth and the fish length is visualized as

curves of constant L. Table 3 summarizes the obtained fitting results.

The anatomy of *Engraulis anchoita* sb

Engraulis anchoita has a dual chambered sb and the two chambers are linked via a sphincter. The anterior (smaller) chamber presents two channels connected to the auditory system while the posterior (larger) chamber has two ducts, a pneumatic duct connected to the digestive system and a posterior duct connected to the exterior. Figure 7A sketches the anatomy of the sb (Pons, 2006). It has to be noted that Argentine anchovy has a very delicate sb and decompression can easily cause sb rupture or major morphological distortions. Only a few specimens endured the acclimatization period and showed no signs of sb over inflation or rupture. Unfortunately, these specimens were all of similar size ($L \approx 15$ cm) and hence it was not possible to establish any relationship between the sb dimensions and fish size. Figure 7B shows a side aspect X-ray image of one of the surface adapted specimens. This specimen ($L=14.7$ cm total length) was judged as the most representative of the true anatomy of the *Engraulis anchoita* sb and hence we based all our TS simulations on the anatomical measurements taken on that specimen. Table 4 contains the most relevant anatomical features extracted from the X-ray analysis of the specimen. Figure 7C shows a 3D rendering of the sb as obtained after segmentation of the CT images.

Theoretical modelling of the anchovy TS

We employed the anatomical parameters extracted from the CT scanning as input for the PSM simulations. In order to simulate the variation of anchovy TS with depth, we computed the sizes of

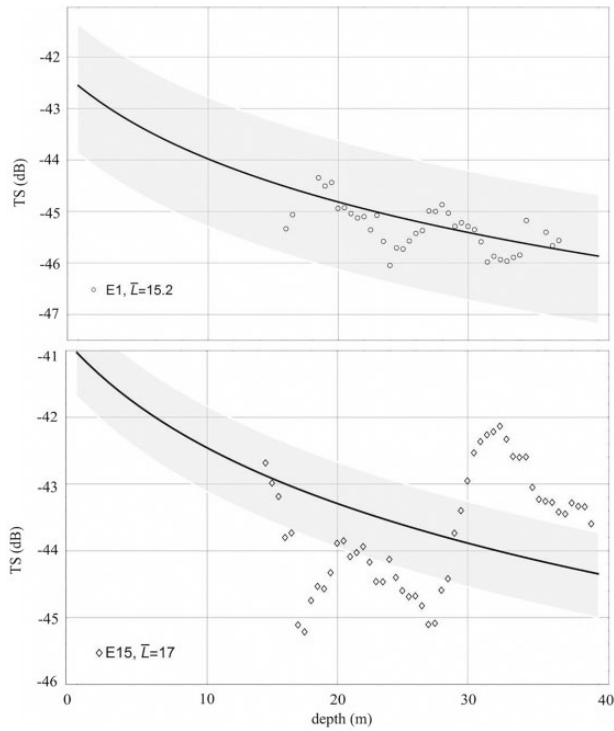


Figure 5. Illustration of the data selection criteria utilized for the depth dependence analysis. (A) Example of an accepted experiment (E1); (B) Rejected data (E15). (solid line= curve from Equation (5); shadowed band= ± 1 SE).

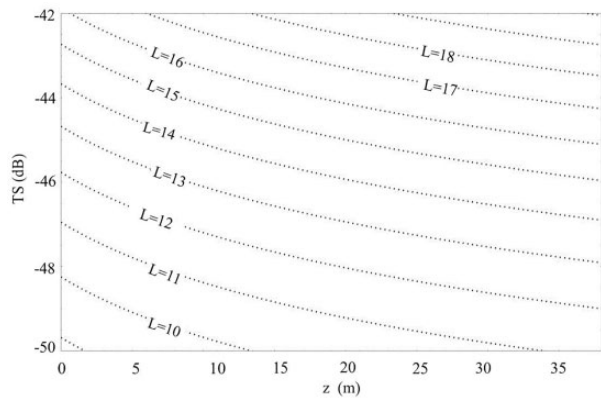


Figure 6. Anchovy TS as a function of fish total length and depth. Each curve represents the variation of TS with depth for a given value of fish length.

Table 3. Statistics of the fitted equation parameters.

Parameter	Fitted value	Std. error	Lo. Conf. Limit (95%)	Up. Conf. Limit (95%)	r^2
a	31.9	4.56	22.10	41.67	0.78
b	-82.4	5.32	-93.85	-71.02	
b_{20}	-68.6	-	-	-	-
a_z	31.3	0.49	30.4	32.3	
b_z	-79.6	0.55	-80.7	-78.5	0.74
γ	-0.474	0.03	-0.53	-0.42	

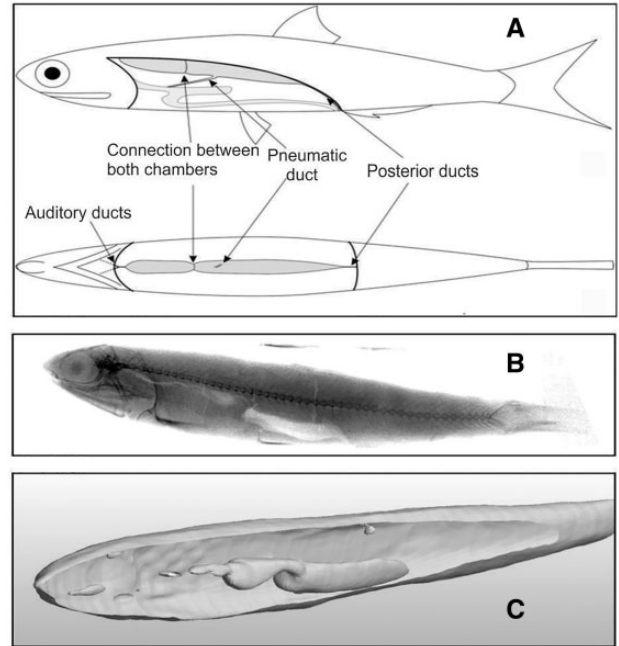


Figure 7. The anatomy of the *Engraulis anchoita* swimbladder. (a) Sketches indicating the different pneumatic structures (*). (b) Side aspect X-ray image showing the two main chambers. (c) The segmented image of the anchovy sb after X-ray scanning of the specimen. (*) redrawn from Pons (2006).

the two soft spheroids (the sb chambers of the selected specimen, $L= 14.7$ cm) at 10 m intervals, from 0 m to 40 m depth. We also considered three different contraction rate patterns of the sb dimensions: (a) isotropic compression (sb diameter and length are allowed to compress freely); (b) an intermediate situation where the sb diameter is allowed to compress more than its length; and (c) sb compression occurs in the transversal plane only (sb length is kept constant). The spheroids dimensions were derived according to the equations proposed in Gorska and Ona (2003a):

$$a_{sb}(z) = a_{sb}(\theta)(1 + z/10)^{-\alpha} \quad (6)$$

$$l_{sb}(z) = l_{sb}(\theta)(1 + z/10)^{-\beta} \quad (7)$$

where $a_{sb}(\theta)$ and $l_{sb}(\theta)$ are the sb diameter and length at the sea surface, respectively, and α and β are their corresponding contraction rates. Hence, the three sb contraction rates considered above were expressed as: (a) $\alpha = 1/3$, $\beta = 1/3$; (b) $\alpha = 0.37$, $\beta = 0.26$, and (c) $\alpha = 1/2$, $\beta = 0$, respectively. Next we used the PSM to compute the TS vs. tilt angle function according to each condition of the sb (contraction rate pattern and depth stratum). An example of the resulting spheroids and the corresponding TS functions is presented in Figure 8, where the contributions of the sb, the body and the whole fish are shown separately. The example presented in the Figure corresponds to the selected specimen ($L= 14.7$ cm) situated at 20 m depth, which is the average depth of the *in situ* TS measurements. The effects of the three considered sb contraction rates at this particular depth are shown.

In order to study the depth dependence of the anchovy TS, the obtained TS functions were then averaged over different fish tilt

Table 4. Anatomical parameters of the fish body and sb chambers, obtained through CT scanning.

Fish body	
Total length	14.7 cm
Standard length	12.1 cm
Max. width	1.6 cm
Max. height	2.0 cm
Volume	26.1 cm ³
Surface (total)	65.5 cm ²
Equivalent spheroid width (*)	2.0 cm
sb—anterior chamber	
Max. length	1.27 cm
Max. width	0.49 cm
Max. height	0.53 cm
Volume	0.12 cm ³
Surface (total)	1.63 cm ²
Surface (dorsal)	0.61 cm ²
Equivalent spheroid width (**)	0.38 cm
Vertical offset (***)	0.10 cm
Horizontal offset (***)	1.4 cm
Longitudinal angle	5°
sb—posterior chamber	
Max. length	2.70 cm
Max. width	0.55 cm
Max. height	0.70 cm
Volume	0.42 cm ³
Surface (total)	4.12 cm ²
Surface (dorsal)	2.37 cm ²
Equivalent spheroid width (**)	0.70 cm
Vertical offset (***)	0.35 cm
Horizontal offset (***)	-0.70 cm
Longitudinal angle	5°

The selected anchovy specimen (total length = 14.7 cm) has been previously adapted to the hydrostatic pressure conditions of sea surface.

*Obtained for spheroid volume = body volume and spheroid length = body std. length.

**Obtained for spheroid dorsal surface area = sb dorsal surface area and spheroid length = sb length.

***Coordinates of the geometrical centroid of the chamber relative to the centroid of the fish body.

angle pdf's. The process of averaging TS functions is very sensitive to the selection of the fish tilt angle distribution (Foote, 1980), which is unknown in our case. However, some assumptions can be formulated. During the acclimatization process, all death and anesthetized anchovies sunk immediately to the bottom of the tank. Hence, we assume that fish near the sea surface were in a slightly negative buoyancy condition and then, a neutral or slightly head up position (positive modal tilt angle) can be expected. A rather broad tilt angle distribution has been noted for other clupeoid fish at night. Huse and Ona (1996) reported nighttime patterns characterized by positive tilt angles and broad distributions for *Clupea harengus*. Aoki and Inagaki (1988) also reported positive tilt angles and broad distributions for *Engraulis japonicus* at depths ranging from 20 to 40 m. Therefore, we conclude that positive tilt angles (head up) with rather broad pdf's (large values of sd) can be expected for the anchovies at the nighttime scattering layer. Consequently, we averaged the TS functions of our fish by assuming tilt angle distributions with positive modal values (0°, 5°, 10°, 15°, and 20°) and rather high sd values (10°, 20°, and 30°). Gaussian distributions were considered in all cases. We utilized an averaging angular interval equal to ± 3 sd or

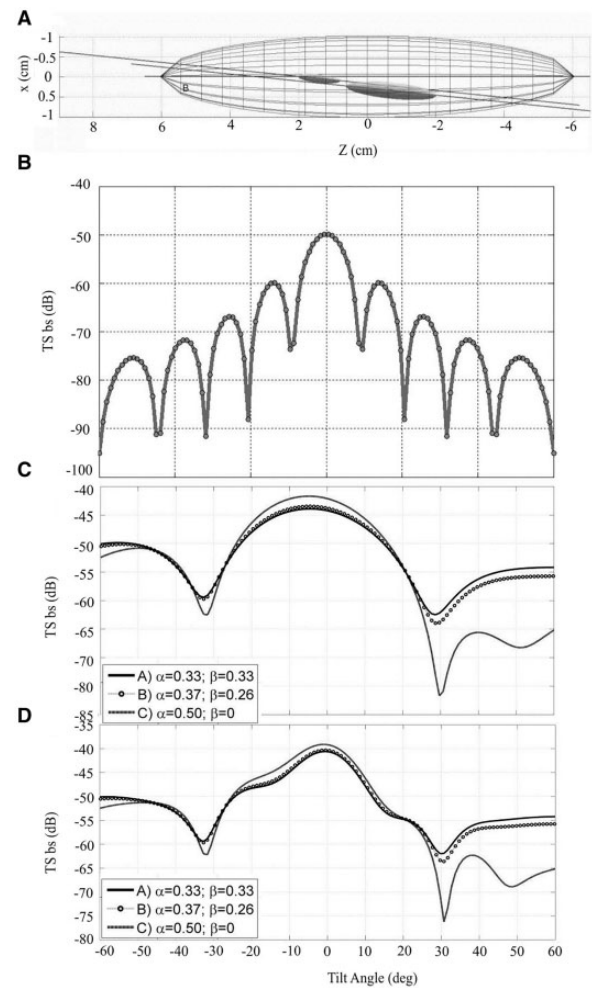


Figure 8. PSM simulation of the sound scattering function at 38 kHz for an anchovy of 14.7 cm total length exposed at 3 atm of hydrostatic pressure (20 m depth). The effects of the three considered sb compression rates are shown. The simulation computes the coherent addition of the three main scattering sources. (A) Model sketch of the three spheroids associated to each scatterer, (B) Contribution from the fish body; (C) Contribution from the two sb chambers; (D) Fish total sound scattering.

$\pm 60^\circ$, whichever occurred first and we centred this interval at the modal value. Figure 9 is included in order to evaluate the effect of the averaging angular interval as a function of the pdf parameters.

Cartesian pairs of the form (TS, z) were computed from the PSM for the different combinations of compression rate patterns (α and β) and tilt angle pdf's (μ and sd). These values were used to fit theoretical curves of TS(z) according to the general equation proposed in Ona (2003), which essentially represents Equation (5) for a given fish length ($L=14.7$ cm in our case):

$$\sigma(z) = \sigma_0(1 + z/10)^{-\gamma} \quad (8)$$

$$TS(z) = 10 \log(\sigma_z) \quad (9)$$

where $\sigma(z)$ is the mean-backscattering cross-section at depth z , equal to σ_0 at the sea surface and γ is the estimated

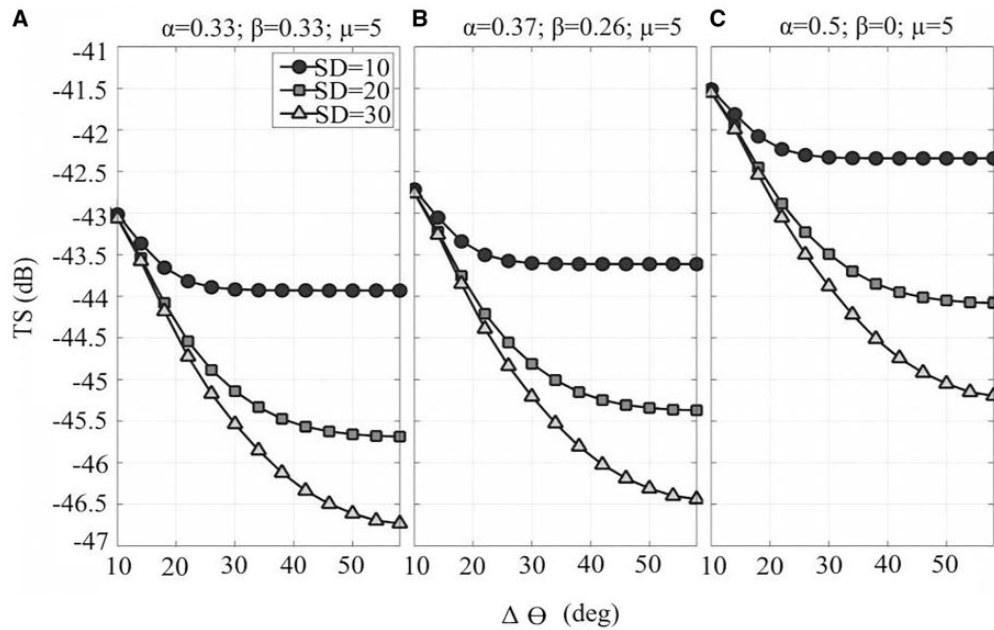


Figure 9. The effects of the angular interval ($\Delta\theta$) employed for averaging TS functions. The Figure corresponds to the reference specimen ($L=14.7$ cm) with its sb compressed at 20 m depth and according to the three considered sb contraction rates.

contraction-rate parameter of the fish sb (0.67 for a free spherical balloon in a high frequency regime).

We explored two theoretical scenarios in order to explain the observed reduction of TS with depth: the first scenario assumes that all the TS depth dependence is caused by the sb contraction only and that no behavioural changes occur with depth, i.e. it assumes the tilt angle pdf (μ and sd) remains constant all across the depth range of fish. In order to test this hypothesis, the obtained average TS values were used to fit theoretical curves of $TS(z)$. The theoretical curves were then compared with the empirically observed depth dependence, expressed by Equation (5) evaluated at $L=14.7$ cm. In this scenario, the theoretical curve that best matched Equation (5) corresponded to the combination: $\alpha=0.37$, $\beta=0.26$, and $N(5,20)$. This is shown in Figure 10 together with the experimental curve [Equation (5)]. Other theoretical curves obtained under the same scenario are also included in the Figure for comparison. These other combinations of parameters produced curves with a different slope (different γ) and/or required very large tilt angles to match the experimental curve, which is believed to represent an unlikely fish behaviour. The second scenario assumes the observed depth dependence of TS is explained by a combination of the sb contraction and a fish behavioural component, characterized by a progressive increase of the modal tilt angle (increasing μ) across the entire fish depth range. We computed the pairs (TS, z) for the different combinations of parameters and found the experimental curve can also be reproduced if we assumed a sb contraction rate defined by $\alpha=0.5$, $\beta=0$, and a tilt angle pdf defined by $N(\mu,20)$, with the modal tilt (μ) varying from $\mu=3^\circ$ at 0 m depth to $\mu=18^\circ$ at 40 m depth. This is shown in Figure 11. A certain function $\mu(z)$ is implicit under this scenario. We did not obtain $\mu(z)$ explicitly but as it can be seen in Figure 11, the change in the fish tilt angle with depth is expected to be non linear (increasing trend with depth). Other combination of parameters (α , β , and sd) did not match

the experimental curve within the whole depth range of fish and/or required unlikely values of μ .

Discussion and conclusions

The *in situ* data

The information collected fulfils the recommendations formulated by most authors in regard to the *in situ* fish TS measurements. In general terms, the fish length exhibited a unimodal and rather narrow length distribution, as reflected by the low values of the coefficient of variation (C.V., Table 2). The procedure employed for the selection of single targets should guarantee a reasonably low probability of inclusion of echoes originated by more than one fish (multiple targets). The addition of a second stage of thresholding, based on the fish tracks statistics (the maximum TS value of the track), is expected to contribute to the rejection of unwanted (weaker) targets without compromising the lower tail of the anchovy TS distributions. It has been noted (Zhao, 1996) that the tracked echo data (the single targets extracted from fish tracks) recorded in a TS experiment with captive herring, may bias the average TS positively, as compared to the average value obtained directly from the raw data (single target echoes). However, the same author states that when a minimum of only three single target echoes are required to form a fish track and when the data is logged from non-stationary platforms, this bias should be significantly reduced. In fact we built the tracks with a minimum of three single target echoes and the ship was drifting or slowly sailing (1–3 kn) during the *in situ* TS measurements and hence, it should not be a concern here. It is also worth to be mentioned that in contrast with the findings of Zhao (1996), we did not find significant differences between the average TS obtained from the tracked echo data and the average values of the fish tracks. However, we utilized the tracked echo data and not the average of the tracks for our study, since the objective of this work was to provide a TS equation for the echointegration

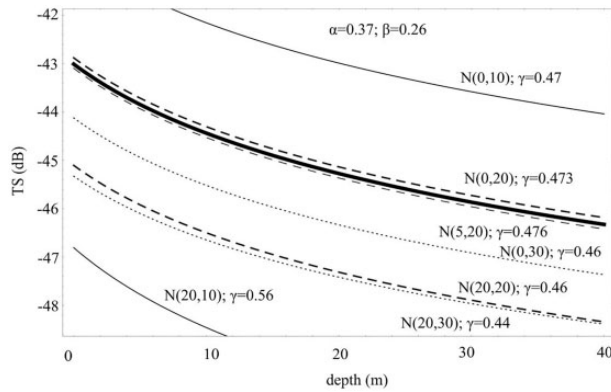


Figure 10. Theoretical depth dependence of anchovy TS under the first considered scenario: Contraction of the sb dimensions only (no behavioral response with depth). Bold solid line: experimental curve [Equation (5)]; Thin solid lines, bold dashed lines and dotted lines: simulated curves for $sd = 10^\circ$, $sd = 20^\circ$ and $sd = 30^\circ$, respectively. The theoretical curve that best matched the experimental data was obtained for the combination $\alpha = 0.37$, $\beta = 0.26$ and $N(5,20)$ (thin dashed line).

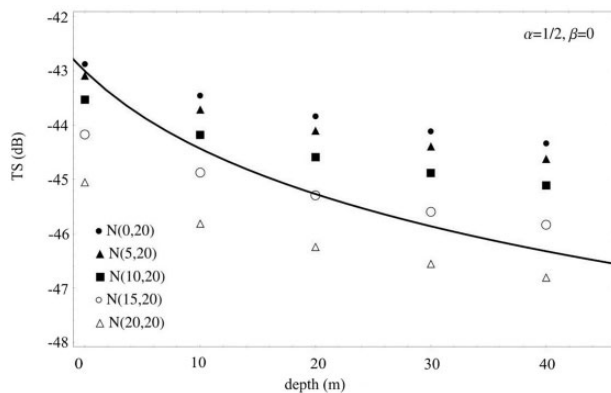


Figure 11. Theoretical depth dependence of anchovy TS under the second considered scenario: Contraction of the sb dimensions and modal tilt angle (μ) increasing with depth. Best match of the experimental data was obtained for sb contraction rate $\alpha = 0.5$, $\beta = 0$, $sd = 20^\circ$ and modal tilt (μ) varying from 3° (0 m depth) to approx. 18° (40 m depth).

surveys and hence it has to be based on the individual contributions of fish to the echointegration values (Dawson and Karp, 1990; Ona, 1999; Zhao, 1996). Therefore, we believe that in our case the tracked echo data (the single target echoes extracted from the selected fish tracks) was the best option for estimating the average TS in the experiments.

Another source of variability in determining the TS of fish relates to its physiological condition (Ona, 1990). Most of the surveys were carried out in the same season of the year (spring spawning) and hence it is expected that physiological factors such as gonad development and stomach and fat content affected our *in situ* TS experiments in a similar way. The available data prevented us to study possible seasonal variations in the anchovy TS. However, two of the experiments were carried out in wintertime (E4 and E10) and both fit well within the observed variability of the other experiments (springtime). The value of the gonado-

somatic index (GSI) for wintering anchovies is about half the springtime spawning. The opposite is observed for the fat content: wintering anchovies have as much as twice the fat content when compared to spring spawning individuals (Aizpun *et al.*, 1979). Therefore, it could be speculated the good fitting of the wintertime data when laid over the springtime TS data, is due to some sort of mutual cancelling effect between gonad development and fat content. Fish behaviour can dramatically affect the fish TS, mainly through changes in the fish tilt angle. As noted before, the fish behaviour at the nighttime scattering layer is possibly conditioned by spawning, while feeding activity is very low and mostly accomplished by filtering few and very small organisms. The other known anchovy feeding strategy is by actively preying on larger zooplankton, which in turn could lead to a different pattern of fish tilt angle occurring perhaps in specific feeding areas along their migration route. Nevertheless, further research including a broader experimental window, both in time and space, is needed to verify the influence of physiological and behavioural factors on the TS of Argentine anchovy.

The TS vs. fish length relationship

Very few results on the TS of *Engraulidae* fish have been published. Our results suggest higher TS values compared to the generalized model proposed in Foote (1987) for *Clupeoids* ($b_{20} = -71.9$ dB). However, this model was mostly based on herring data and did not include any species of *Engraulids*. Ona (2003) raised the issue of higher TS values also for herring as compared to the generalized model. In regard to *Engraulids*, Barange *et al.* (1996) reported TS values for *Engraulis capensis* that are even lower ($b_{20} = -76$ dB) than those predicted by the generalized model. Barange and coauthors emphasize the potential risk of a positive bias caused by the acceptance of erroneously high TS values, originated by the additive interference of echoes from closely aggregated fish (multiple target echoes). In any case, it is improbable that our results were biased by this cause because our data complied with the recommendations made in Ona (1999) (see values of N in Table 2) and also because of the consistency observed between the results of the different experiments ($r^2 = 0.78$). Therefore, it is difficult to believe that the constructive interference of multiple echoes could positively bias the average TS in a similar amount at every experiment. On the other side, Kang *et al.* (2009) suggested a TS for *Engraulis japonicus* somewhat higher ($b_{20} = -65.8$ dB) than ours. While the average TS obtained in the referenced study can be questioned due to the possibility of abnormal fish tilt angle distributions (tethered specimens by line and hook), their measured TS vs. tilt angle function agrees quite well with our PSM predictions for *Engraulis anchoita* of similar size. In other study, Sawada *et al.* (2009) obtained an average value of TS close to -46 dB for *Engraulis japonicus* of 10.6 cm (standard length) by employing a combined acoustical-optical towed system. This result is in close agreement with our study. Finally, Zhao *et al.* (2008) report an average value of TS close to -51 dB for *Engraulis japonicus* of 10.6 cm (fish total length), which also agrees well with our results.

As a whole, our TS vs. L equation seems to be in agreement with the most recent works carried out on *Engraulids*, particularly the ones for *Engraulis japonicus*, suggesting TS values higher than those originally assumed. The theoretical simulations we made with the PSM also support the idea of rather high TS for the Argentine anchovy. Whether or not the observed discrepancy

with the studies on the South African anchovy reflects a very specific TS or if this can just be explained by methodological issues, still remains a question. Surprisingly, given the limitations of the technology that was available at the time, our present results on the TS of *Engraulis anchoita* closely agreed with those presented in [Madirolas \(1991\)](#), where a TS of -51.3 dB was proposed for anchovies of 10.2 cm (total length), based on *in situ* measurements performed with single beam transducers and processed manually by means of the Craig and Forbes algorithm ([Craig and Forbes, 1969](#)).

The depth dependence of TS

Our *in situ* TS data obtained from the nighttime fish scattering layer exhibited a negative trend with depth. We fitted a depth dependent TS equation to the experimental data in the same way as proposed by other authors [[Equation \(5\)](#)] and found a depth dependant coefficient $\gamma = 0.474$ ($r^2 = 0.74$). This value of γ is very close to the contraction rate of a spheroid with its longer axis maintained constant ($\gamma = 0.5$), i.e. allowing for the sb transversal compression only. Our results agree with the findings of [Fassler et al. \(2009\)](#) who demonstrated the asymmetrical compression of the sb in another physostomous fish (*Clupea harengus*) but are slightly different from the ones reported by [Zhao et al. \(2008\)](#), where the free balloon hypothesis ($\gamma = 0.67$) is proposed for *Engraulis japonicus*.

A few experiments had to be discarded because of a noisier TS(z) relationship. Whether or not this unusual trend should be interpreted as distinct behaviour or simply as noise was not studied and these data were discarded for the depth dependence analysis. We did so because of we aimed to obtain a depth dependent term based on what we interpret as “typical” fish behaviour. It was also observed that many of the experiments showed a sudden change in the TS(z) trend near the deepest limit of the scattering layer, i.e. close to the depth of the thermocline (≈ 40 m). It may be speculated if this sudden change could indicate a modification in the behavioural pattern of anchovy (tilt angle distribution), triggered by the sharp changes in temperature and density occurring at the thermocline. However, this behaviour only affected a few (deepest) meters of the scattering layer and hence these data were not considered for the present analysis, since we aimed to obtain an empirical equation that is suitable for the major part of the anchovy scattering layer.

The sb volume of a physostome fish decreases with depth due to the Boyle’s principle and this may have a direct impact on TS. The most obvious effect of depth is the sb dorsal area decreases as a consequence of its volume reduction. However, the contraction of the sb may trigger secondary effects. Among these, we know the fish will experience a decrease in buoyancy and they may react to this with an increase of their swimming tilt angle, in order to generate more hydrodynamic lift and hence avoiding sinking. The use of the sb as a buoyancy regulatory organ is generally accepted ([Horne, 1975](#)) and the hydrodynamic consequences of the swimming tilt angle have already been studied ([Strand et al., 2005](#)). Among other authors, [Huse and Ona \(1996\)](#) consider the possibility of a varying tilt angle as the response of a physostomous species (herring) to changes in fish buoyancy caused by the sb compression. In this work, we have employed theoretical modelling to explore possible mechanisms that explain the depth dependence observed in the *in situ* TS data of *Engraulis anchoita*. Different combinations of sb contraction rates and fish tilt angle

pdfs were considered and we found two possible explanations. The first one suggests the hypothesis of a slightly asymmetrical sb contraction pattern as the only mechanism responsible for the reduction in the observed TS. The second explanation we have proposed, puts forward the hypothesis of a combination of sb contraction in the transversal plane only plus a gradual increase of the modal tilt angle across the fish depth range. Both theoretical explanations implied the anisotropic contraction of the sb ($\alpha > \beta$) and also a rather broad fish tilt angle pdf. Whether or not the observed reduction in anchovy TS is caused by the sb compression only or by a combination the two effects is still a question and detailed *in situ* observations of the fish tilt angle distribution at different depths and under different conditions (day and night) would be necessary to answer this question accurately.

The data utilized for the TS analysis comprises 15 years of surveying the two different stocks of the target species (*Engraulis anchoita*). After rigorous acceptance criteria, 16 different *in situ* experiments were selected and analyzed. The obtained TS(L,z) equation showed a good correlation factor ($r^2 = 0.74$). This relationship was obtained for the size range 11–16 cm, which corresponds to age classes 1–4 and account for over 90% of the total biomass of the Argentine anchovy population ([Garciaarena et al., 2016](#); [Orlando et al., 2016](#)). However, acoustic assessment surveys of anchovy are carried on a “24 hours a day” working schedule and the survey cumulated s_A values are similar for both periods, day and night. Hence, we expect the application of the new TS vs. length relationship will decrease the nighttime biomass estimates by a factor close to 0.5 but, as stated before, we consider [Equation \(5\)](#) may not be representative of the daytime situation, where a stronger depth dependence of TS might be expected and thus causing a possible increase in the daytime biomass estimates. Whether or not a daytime corrected TS will partially compensate for the decrease in the nighttime estimate of the abundance, cannot be yet confirmed. Additional work on this issue is currently on going.

A good portion of the global fish biomass is composed of *Engraulids* and many of these stocks are being subject of intense fishing activity by the commercial fleets ([Whitehead, 1985](#)). In most cases, these fish play a major role in their respective marine ecosystems ([Bakun, 2006](#)). A close monitoring of these stocks is of central importance and hence more studies on the acoustical properties of this fish family are key to ensure the unbiased estimation of their abundance.

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