

Estimation of target strength of *Sardina pilchardus* and *Sardinella aurita* by theoretical approach

Salaheddine El Ayoubi¹ · Kamal Mamza¹ · Tadanori Fujino^{2,3} · Koki Abe⁴ · Kazuo Amakasu⁵ · Kazushi Miyashita⁶

Abstract The target strength (TS) patterns of *Sardina pilchardus* and *Sardinella aurita* at 38 and 120 kHz were estimated by a prolate-spheroid model, using measurements of swimbladder length and width. The ratio of swimbladder length to total length (TL) was similar in both species, however the ratio of swimbladder width to TL was smaller and more variable for *S. aurita*. Assuming a normal distribution of fish swimming orientation angle (θ_{fish}) with mean \pm standard deviation (SD) of $0 \pm 10^\circ$, the normalized (by TL) average TS (b_{20}) was estimated to be -64.0 dB (38 kHz) and -65.2 dB (120 kHz) for *S. pilchardus*, and -66.2 dB (38 kHz) and -67.2 dB (120 kHz) for *S. aurita*. Compared with currently applied b_{20} values at 38 kHz, our results under four different θ_{fish} assumptions ($0 \pm 10^\circ$, $0 \pm 15^\circ$, $-5 \pm 10^\circ$, and $-5 \pm 15^\circ$) were 6-9 dB higher for *S. pilchardus* and 5-7 dB higher for *S. aurita*. This suggests four- to eightfold overestimation risk for *S. pilchardus* and three- to fivefold overestimation risk for *S. aurita* when using the currently applied b_{20} values.

Keywords *Sardina pilchardus* · *Sardinella aurita* · Target strength · Theoretical approach · Prolate spheroid model

✉ Tadanori Fujino

tadanori@nagasaki-u.ac.jp

¹ Institut National de Recherche Halieutique, Lot N°11 nouveau port, Agadir 80010, Morocco

² Marino Forum 21, 5F Hagaromo-building 1-5-2 Hatchobori Chuo-ku Tokyo 104-0032, Japan

³ Present address: Center for International Collaborative Research, Nagasaki University, 1-12-4, Sakamoto, Nagasaki-shi, Nagasaki 852-8523, Japan

⁴ National Research Institute of Fisheries Engineering, Fisheries Research Agency, 7620-7 Hasaki Kamisu-shi Ibaraki 314-0408, Japan

⁵ Research Center for Advanced Science and Technology, Tokyo University of Marine Science and Technology, 4-5-7 Konan Minato-ku Tokyo 108-8477, Japan

⁶ Field Science Center for Northern Biosphere, Hokkaido University, 20-5 Bente-cho, Hakodate-shi, Hokkaido 040-0051, Japan

Introduction

Sardina pilchardus and *Sardinella aurita* are clupeoid species widely found in the eastern Atlantic Ocean, being important targets for purse seine fisheries [1, 2]. *S. pilchardus* is found in the northeastern Atlantic, extending from the southern Celtic Sea and North Sea to Mauritania and Senegal, with residual populations also off The Azores, Madeira, and The Canary Islands [3]. *S. aurita* has a rather wide distribution, on both the eastern and western coast of the Atlantic Ocean [4]. Their catch is especially important in the northwest African region; over one million tons were landed annually from 2006 to 2010, dominating the small pelagic species catch in Morocco, Mauritania, and Senegal [1, 2].

To assess the abundance of these two species, acoustic surveys have been carried out for nearly three decades by European and western African countries [1, 2, 5]. An acoustic survey collects the acoustic backscattering strength from fish schools, and converts it to density using target strength (TS), the intensity of sound backscattering from a single fish [6]. TS is known to be species specific and varies with several physical and biological factors such as fish swimming orientation angle, length, depth, carrier frequency, and physiology [6-9]. In general, swimming orientation angle is known to be the largest source of variation [6, 7], and the TS at a certain frequency under natural swimming orientation angle is expressed as a function of fish length (L) in the form $TS = a \log L + b$, where a is the slope and b is the intercept. Assuming that the backscattering cross-section, which is the linear value of TS, is proportional to the square of fish length, $TS = 20 \log L + b_{20}$ is applied in many species [6].

Regarding *S. pilchardus*, b_{20} values ranging from -67.2 to -66.4 dB were found by in situ TS measurements at 38 kHz along the coast of Morocco [10]. This seems to be different from the lower b_{20} value of -70.5 dB found by in situ TS measurements at 38 kHz for *Sardinops ocellatus* [11], a sardine species found off South Africa. Currently, European and African countries apply b_{20} values ranging from -72.6 to -70.5 dB for *S. pilchardus* [12], which mainly refers to values of *Clupea harengus* [13-15]. Similarly, a b_{20} value of -71.9 dB from *C. harengus* [15] is applied in Morocco for *S. aurita*, as species-specific TS knowledge is lacking. As a TS difference of several dB will result in a severalfold difference in abundance estimation (e.g., twofold for 3 dB), reasonable species-specific TS- L relationships should be applied for acoustic data analysis for both *S. pilchardus* and *S. aurita*.

In this study, we examined the TS of *S. pilchardus* and *S. aurita* by a theoretical approach using an acoustic backscattering model. Both species are physostomes [16, 17], i.e., fishes with an open swimbladder. The swimbladder represents 90-95 % of the acoustic backscattering from the dorsal direction of the fish [18], so the TS for a fish can be considered to be close to the TS from the swimbladder. Several types of swimbladder backscattering models have been applied to estimate the TS from fish, including the Kirchhoff approximation (KA) model [19], Kirchhoff ray mode (KRM) model [20], deformed-cylinder model (DCM) [21], and prolate-spheroid model (PSM) [22]. Among these models, the KA, KRM, and DCM need detailed swimbladder shapes for their calculation, while the PSM approximates the swimbladder shape as a prolate spheroid and uses its major and minor axes for the calculation. In the present study, we could not obtain detailed swimbladder shapes, such as the stereoscopic structure of the swimbladder, as we relied on swimbladder measurements from the ventral-side visual of the swimbladder dimensions. As the application of KA, KRM, and DCM was difficult,

we applied the PSM for TS estimation. By estimating the TS using the PSM under several swimming orientation angle assumptions, we intend to determine whether presently applied TS values [13-15] for *S. pilchardus* and *S. aurita* are reasonable, and indicate the potential TS difference between these two species.

Materials and methods

Collection of fish samples and swimbladder observations

Fresh fish samples of *S. pilchardus* ($N = 45$) and *S. aurita* ($N = 64$) were collected in the major purse seine fishing port at Agadir, Morocco. Shortly after landing of the fish, fresh samples in good condition were selected and their total length (TL) measured. The fish were then dissected from mouth to anus without damaging the swimbladder. After carefully removing the internal organs around the swimbladder, the length from the nose point to the head end of the swimbladder (swimbladder start length, SBS), swimbladder length (SBL), and swimbladder width (SBW) (see Fig. 1) were measured by digital caliper. Samples in which the swimbladder was damaged or had completely collapsed were excluded from the measurements.

For *S. pilchardus*, 13 additional live, anesthetized samples were also used to observe swimbladders adapted to surface water pressure and free from capture stresses. These samples were collected by a pelagic trawl (opening $20 \times 30 \text{ m}^2$) of the R.V. Al Amir Moulay Abdallah (298 t), and were stored in a seawater circulating tank (1 m long \times 1 m wide \times 0.7 m deep) for over 2 weeks. Shortly before measurement, the fish were gently transferred to a solution of 1 % 2-phenoxyethanol seawater for anesthetization and then measured in the same way as for the fresh samples (Fig. 1). Note that no obvious release of gas from the anal or pneumatic duct was observed during dissection or swimbladder measurements. Similarly, no obvious swimbladder dilation due to removal of the internal organs was observed.

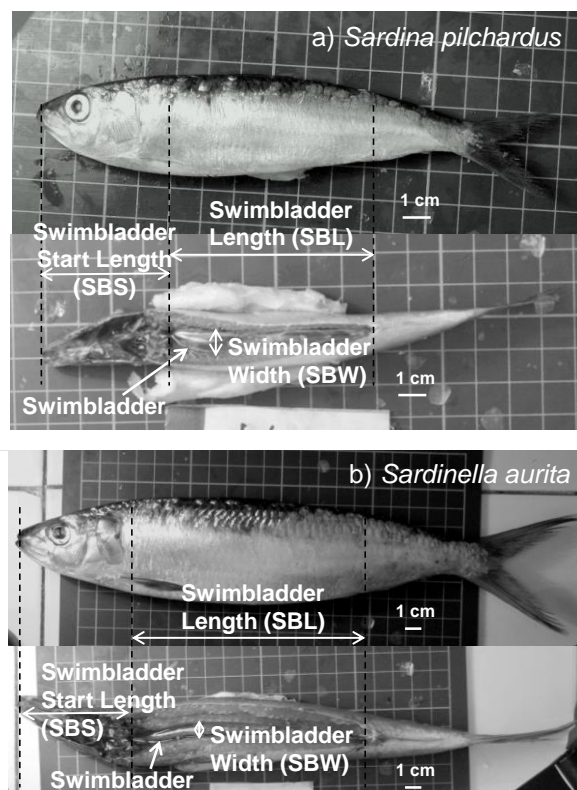


Fig. 1 Swimbladder measurements of a) *S. pilchardus* and b) *S. aurita* from the lateral side and dissected ventral side

Target strength estimation using a prolate spheroid model

In the PSM, TS can be expressed as a function of f , θ_{sb} , a , b , and c . f is the frequency, which was set 38 and 120 kHz. θ_{sb} is the swimbladder orientation angle (-90° , head down; 0° , horizontal; 90° , head up). a and b are the major and minor radii of the spheroid, respectively, being equal to half the SBL and SBW values obtained by the swimbladder measurements. c is the speed of sound in the surrounding water and was set to 1500 m/s in this study. TS was calculated for each θ_{sb} value, but θ_{sb} is not the same as the fish swimming orientation angle (θ_{fish}) because the swimbladder axis is not parallel to the body axis. Therefore, the swimbladder tilt angle θ_{sb_tilt} , which is the angle between the body axis and swimbladder axes, was taken into account as $\theta_{sb} = \theta_{fish} - \theta_{sb_tilt}$. As θ_{sb_tilt} was difficult to measure by dissection, we assumed that θ_{sb_tilt} was 6° for *S. pilchardus* after Machias and Tsimenides [16] and 10° for *S. aurita* after Whitehead and Blaxter [17]. After TS estimation for θ_{fish} from -90° to 90° in 1° steps, the average TS (TS_{avg}) under natural θ_{fish} was derived following the method of Foote [23], which assumes that θ_{fish} follows a normal distribution. Regarding daytime θ_{fish} of Clupeiformes, Ona [24] reported $-3.9 \pm 12.8^\circ$ and $0.2 \pm 11.9^\circ$ at different depth for *C. harengus*. Similarly, Amakasu et al. [25] referred $-3.7 \pm 8.6^\circ$, derived from observation of *Engraulis japonicus*. In this study, we considered a combination of average 0° (horizontal) and -5° (slightly head down) with standard deviation set at 10° and 15° , and assumed four patterns, namely $0 \pm 10^\circ$, $0 \pm 15^\circ$, $-5 \pm 10^\circ$, and $-5 \pm 15^\circ$, to estimate the daytime TS. Finally, after confirming the proportional growth of the swimbladder and body length, the TS_{avg} -TL relationship was fit using the following equation:

$$TS_{avg} = 20 \log TL + b_{20}, \quad (1)$$

where TL is total length (cm) and b_{20} is the normalized TS_{avg} by length (cm).

Results

Swimbladder morphology

Both *S. pilchardus* and *S. aurita* showed a smooth ellipsoidal-shaped swimbladder (Fig. 1). Table 1 presents the measured range of TL, the ratio of SBS to TL, the ratio of SBL to TL, and the ratio of SBW to SBL (aspect ratio). For *S. pilchardus* with TL in the range of 10-20 cm and *S. aurita* with TL in the range of 17-35 cm, the mean ratio of SBS to TL was identical (0.21). Similarly, the mean ratio of SBL to TL was identical (0.40) for both species, indicating that the relative position of the swimbladder to the fish body was the same in these two species. However, the aspect ratio for the two species was different, namely 0.09 for *S. pilchardus* and 0.07 for *S. aurita*, indicating narrower swimbladder shape for *S. aurita* compared with *S. pilchardus*.

Figure 2 shows the relationships between SBL and SBW versus TL for *S. pilchardus* and *S. aurita*, as well as *Engraulis japonicus* from Amakasu et al. [25] for comparison. Both SBL and SBW had positive correlation ($P \leq 0.001$) with TL for *S. pilchardus* and *S. aurita*, indicating proportional development of the swimbladder with the fish body. The relationship between SBL and TL was similar in both species, showing crossover of the plots in the overlapping TL range (Fig. 2a, 17-20 cm). Compared with *E. japonicus*, the regression line for the two studied species was located higher, indicating a greater ratio of SBL to TL compared with *E. japonicus*. For *S. pilchardus*, crossover of the plots for the live and fresh samples was observed (Fig. 2a).

The relationship between SBW and TL differed between *S. pilchardus* and *S. aurita*, showing larger values for

S. pilchardus in the overlapping TL range (Fig. 2b, 17-20 cm). For *S. aurita*, high variation was observed: for *S. pilchardus*, SBW values were not observed to overlap for TL differences of 10 cm (e.g., 10 to 20 cm), whereas *S. aurita* showed overlapping SBW values for such differences (e.g., 20 to 30 cm). The regression line for *E. japonicus* was located above the measurements for *S. aurita* but overlapped with the SBW of *S. pilchardus*. For *S. pilchardus*, crossover of the plots for the live and fresh samples was observed (Fig. 2b).

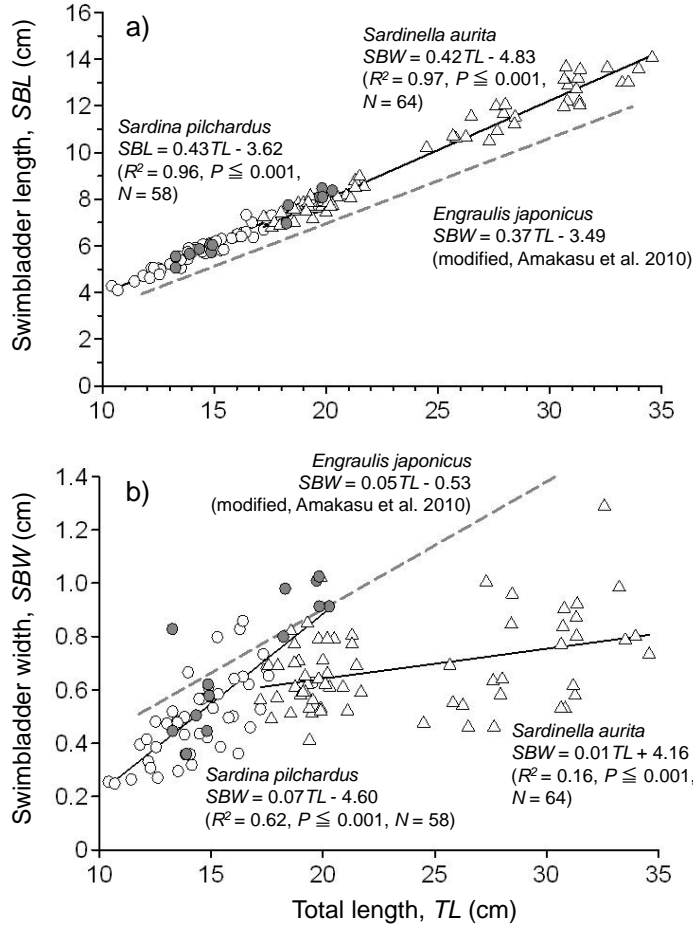


Fig. 2 a Relationship between TL and SBL for *S. pilchardus* and *S. aurita*. **b** Relationship between TL and SBW for *S. pilchardus* and *S. aurita*. Unfilled circle indicates *S. pilchardus* measurements from fresh (dead) specimens; grey circle indicates *S. pilchardus* measurements from live, anesthetized specimens. Unfilled triangle indicates *S. aurita* measurements from dead specimens. Grey broken line indicates the relationship for *E. japonicus* modified from Amakasu et al. [25]

Table 1 Range of TL, ratio of SBS and SBL to TL, and ratio of SBW to SBL (aspect ratio) for *S. pilchardus* and *S. aurita*

Species	N	TL (cm)	SBS / TL	SBL / TL	SBW / SBL
<i>Sardina pilchardus</i>	58	10.4-20.3	0.21 ± 0.01 (0.2-0.23)	0.40 ± 0.01 (0.37-0.45)	0.09 ± 0.02 (0.05-0.16)
<i>Sardinella aurita</i>	64	17.2-34.6	0.21 ± 0.02 (0.17-0.24)	0.40 ± 0.02 (0.37-0.44)	0.07 ± 0.01 (0.04-0.12)

Target strength

Figure 3 shows example relationships between TS and θ_{fish} (TS patterns), for three different swimbladder sizes at 38 and 120 kHz. The maximum TS values were similar or slightly higher at 120 compared with 38 kHz. The response of the TS to θ_{fish} was more sensitive at 120 kHz compared with 38 kHz, showing a steep decrease from the maximum TS with varying θ_{fish} .

Table 2 presents the b_{20} values calculated for four different θ_{fish} distributions, namely normal distributions with

mean \pm SD of $0 \pm 10^\circ$, $0 \pm 15^\circ$, $-5 \pm 10^\circ$ or $-5 \pm 15^\circ$. The b_{20} values for *S. pilchardus* ranged from -65.0 to -63.5 dB at 38 kHz and from -66.4 to -64.6 dB at 120 kHz. For *S. aurita*, the b_{20} values ranged from -66.8 to -65.0 dB at 38 kHz and from -67.9 to -65.9 dB at 120 kHz. Among the four θ_{fish} distributions, b_{20} was highest for mean \pm SD of $-5 \pm 10^\circ$, lowest for $0 \pm 15^\circ$, and intermediate for $0 \pm 10^\circ$. Comparing the two frequencies, b_{20} was higher at 38 than 120 kHz, showing a 1.1-1.4 dB difference for *S. pilchardus* and 0.9-1.1 dB difference for *S. aurita* (Table 2), reflecting the different TS patterns in Fig. 3. Comparing the two species, b_{20} for *S. pilchardus* was 1.4-2.2 dB higher than for *S. aurita* at 38 kHz and 1.1- 2.1 dB higher at 120 kHz.

Figure 4 shows the relationship between TS_{avg} and TL for *S. pilchardus* and *S. aurita* for a θ_{fish} distribution with mean \pm SD of $0 \pm 10^\circ$, together with that of *E. japonicas* for comparison (modified from Amakasu et al. [25]: scale length converted to TL). Among the three species, *S. pilchardus* had the highest TS_{avg} , *E. japonicus* was intermediate, and *S. aurita* was lowest at 38 kHz. At 120 kHz, *S. pilchardus* and *E. japonicus* showed similar TS_{avg} -TL relationships, while *S. aurita* had lower TS_{avg} than *S. pilchardus* and *E. japonicus*.

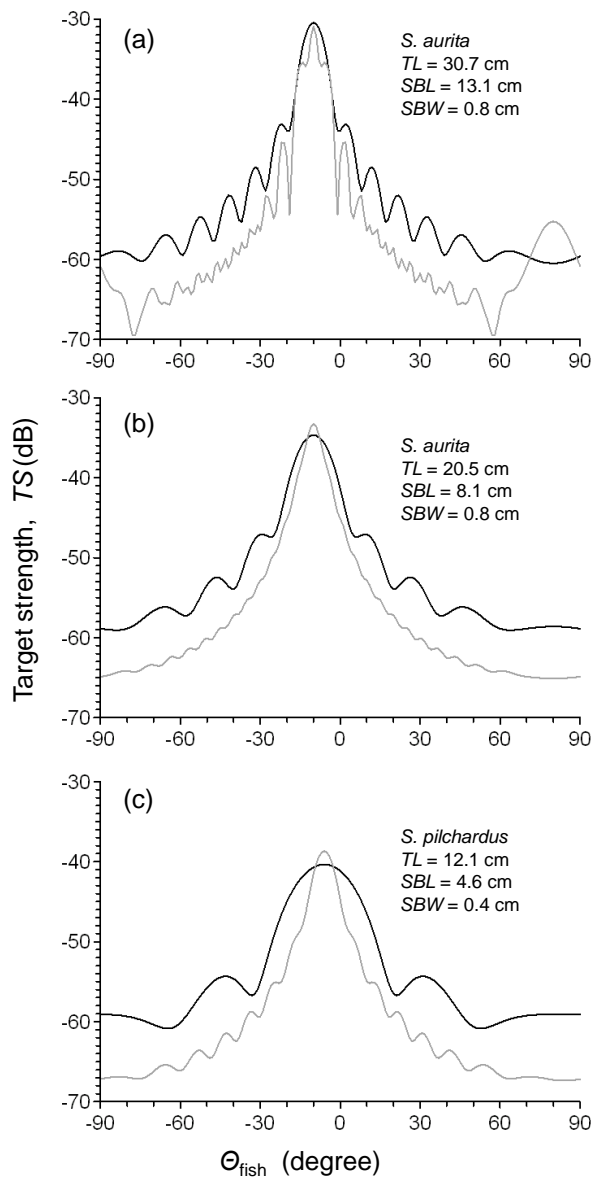


Fig. 3 Example relationships between TS and θ_{fish} at 38 kHz (black line) and 120 kHz (grey line) for: **a** *S. aurita* with TL = 30.7 cm, SBL = 13.1 cm, and SBW = 0.8 cm; **b** *S. aurita* with TL = 20.5 cm, SBL = 8.1 cm, and SBW = 0.8 cm; **c** *S. pilchardus* with TL = 12.1 cm, SBL = 4.6 cm, and SBW = 0.4 cm

Table 2 Normalized average TS (b_{20} of $TS_{avg} = 20\log_{10}TL + b_{20}$) of *S. pilchardus* and *S. aurita* at four different fish swimming orientation angle (θ_{fish}) distributions

Distribution of θ_{fish} (average, standard deviation)	<i>Sardina pilchardus</i>		<i>Sardinella aurita</i>	
	38 kHz	120 kHz	38 kHz	120 kHz
(0, 10)	-64.0	-65.2	-66.2	-67.3
(0, 15)	-65.0	-66.4	-66.8	-67.9
(-5, 10)	-63.5	-64.6	-65.0	-65.9
(-5, 15)	-64.8	-66.1	-66.2	-67.2

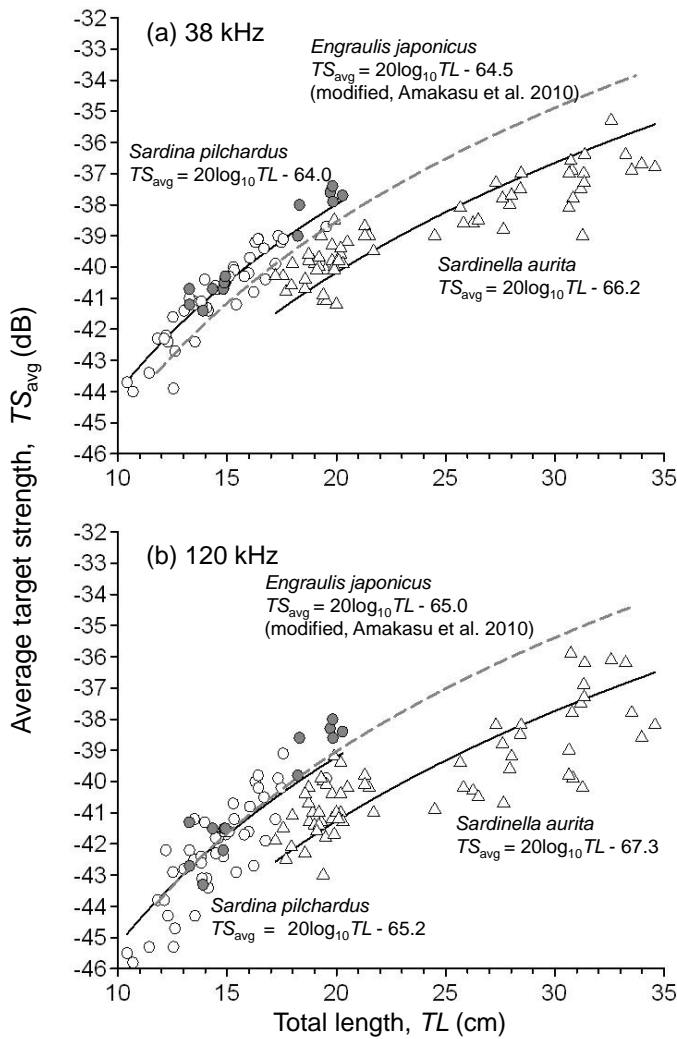


Fig. 4 Relationship between average TS (TS_{avg}) and TL for *S. pilchardus* and *S. aurita* at **a** 38 kHz and **b** 120 kHz. *Unfilled circle* indicates *S. pilchardus* TS estimated from dead specimens, *grey circle* indicates *S. pilchardus* TS estimated from live, anesthetized specimens. *Unfilled triangle* indicates *S. aurita* TS estimated from dead specimens. TS_{avg} values were calculated assuming a normal distribution of swimming tilt angle with average of 0° and standard deviation of 10° . *Grey broken line* indicates the relationship for *E. japonicus* modified from Amakasu et al. [25]

Discussion

The results of the present study indicate b_{20} values ranging from -65.0 to -63.5 dB at 38 kHz for *S. pilchardus* under four θ_{fish} distributions (Table 2). Compared with b_{20} values reported for *S. pilchardus* off Morocco (-67.2 to -66.4 dB [10]) and currently applied b_{20} values for *S. pilchardus*, using values from *Clupea harengus* (-72.6 to -71.9 dB [13-15]) or *Sardinops ocellatus* (-70.5 dB [11]), our results are rather close to the b_{20} values for *S.*

pilchardus obtained by in situ measurements off Morocco [10].

The dB difference between the b_{20} values reported for *S. pilchardus* off Morocco and our result is 1.4-3.7 dB. Possible reasons for the higher b_{20} indicated in our study compared with the b_{20} values obtained for *S. pilchardus* off Morocco could be the effect of θ_{fish} distributions, depth, and physiology. In the present study, we considered daytime θ_{fish} distributions and applied horizontal (0°) or slightly head-down (-5°) mean θ_{fish} with standard deviation of 10° or 15° . However, the in situ measurements of *S. pilchardus* off Morocco were conducted at nighttime, meaning that θ_{fish} is likely to be different and have greater standard deviation compared with daytime [26-29]. A greater deviation in θ_{fish} results in a lower TS value (see Table 2), thus nighttime TS would be several dB lower compared with daytime [30-32]. For pelagic fish, Edwards and Armstrong [30] reported 2-3 dB lower TS at nighttime for caged herring. Similarly, Edwards and Armstrong [31] reported 4-5 dB lower TS for caged mackerel. This difference in diurnal θ_{fish} distributions seems to explain well the dB difference between our result and the nighttime b_{20} values measured for *S. pilchardus* off Morocco [10].

Regarding depth and physiology, Ona reported that both affect the TS of *C. harengus* and described the effects via the following equation [9]:

$$TS = 20\log L - 2.3\log(1 + z/10) - 65.4 + 0.24(\text{GSI}) \quad (2)$$

where L is fish body length (cm), z is swimming depth (m), and GSI is gonadosomatic index. In situ TS measurement of *S. pilchardus* off Morocco was conducted at a depth range of 10-35 m [10], hence it could give 0.7-1.5 dB higher b_{20} values at the surface when applying Eq. (2). Considering that our sample had swimbladder condition close to that at the surface, based on the overlapping measurements for live and fresh samples (Fig. 2), this 0.7-1.5 dB difference could also explain our relatively high b_{20} values. Regarding GSI, no information was obtained in the present study or in the report off Morocco [10], however studies on *S. pilchardus* showed GSI up to 6-6.6 [33, 34]. Applying Eq. (2), this would give a variation of up to ± 1.4 -1.6 dB. In summary, in situ TS measurements off Morocco (b_{20} of -67.2 to -66.4 dB [10]) could be 2-3 dB higher at daytime compared with nighttime and the effect of depth could also give a 0.7-1.5 dB higher b_{20} value at the surface. The effect of GSI is unknown but assumed to result in a variation of up to 1.4-1.6 dB. Given these factors, the 1.4-3.7 dB difference between our result and the nighttime b_{20} values measured for *S. pilchardus* off Morocco [10] can be explained, indicating that our b_{20} would be natural for *S. pilchardus* in daytime.

Our results seem more convincing in comparison with TS studies of *E. japonicus*, also a Clupeiformes physostome, which has a relationship between swimbladder size and TL that is not so different from *S. pilchardus* (Fig. 2). The nighttime in situ TS of *E. japonicus* is reported as -68.3 dB (b_{20} , 12 m, 25 m depth [35]) and -67.6 dB (b_{20} , 10-45 m depth [36]), which is close to the nighttime in situ TS of *S. pilchardus* (b_{20} , -67.2 to -66.4 dB, 10-35 m [10]). Daytime reports are 2-4 dB higher; a tank experiment using live *E. japonicus* specimens during daytime (confirmed to the author) showed b_{20} of -65.8 dB [37], and b_{20} of -64.5 dB was obtained using quick killed live samples with assumption of θ_{fish} distribution at $0 \pm 10^\circ$ (mean \pm SD) [25]. Considering the similar swimbladder size to *S. pilchardus* and the 2-4 dB difference in the b_{20} values obtained for *E. japonicus* by nighttime in situ TS measurements and in daytime [25, 37], again our b_{20} values for *S. pilchardus* (-65.0 to -63.5 dB) seem reasonable for daytime.

Regarding *S. aurita*, the TS would be rather low compared with *S. pilchardus*. The swimbladder of *S.*

pilchardus and *S. aurita* had similar SBL and swimbladder start position (identical ratios of SBL to TL and SBS to TL), but the SBW of *S. aurita* showed greater variation and was smaller than for *S. pilchardus* (Table 1; Fig. 2). Smaller SBW was reflected in the TS estimation (Fig. 4; Table 2); the b_{20} for *S. aurita* for each θ_{fish} distribution was 1.4-2.2 dB less at 38 kHz and 1.1-2.1 dB less at 120 kHz (Table 2) compared with *S. pilchardus*. This indicates that the TS of *S. aurita* could potentially be 1-2 dB lower compared with *S. pilchardus*.

In future work, more data on swimbladder tilt angle ($\theta_{\text{sb_tilt}}$) should be collected to verify the TS difference between *S. pilchardus* and *S. aurita*, as the present study applied this value from references [16, 17]. Observation methods such as soft X-rays [38] would enable more precise measurement of SBW and $\theta_{\text{sb_tilt}}$ in the fish body, and provide the stereoscopic structure of the swimbladder, allowing application of theoretical models that take into account more details of the swimbladder structure [19-21]. Collection of tank-stored live *S. aurita* would be preferable, as the high variation in SBW (Fig. 2) could be due to either natural differences among individuals or the nature of the swimbladder, which is possibly fragile and more affected by the capture process compared with *S. pilchardus*. Meanwhile, considering the risk of overestimation by more than three- or fourfold if using the presently applied values (dB difference: *S. pilchardus* 6-9 dB, *S. aurita* 5-7 dB), revision of the TS value found in the present study (e.g., the $\theta_{\text{fish}} 0 \pm 10^\circ$ assumption) with the depth contraction parameter of Ona [9] should be applied for *S. pilchardus* and *S. aurita*.

Acknowledgements We thank the technicians of the Institut National de Recherche Halieutique (INRH) Agadir regional center for collection of fish samples in Agadir, Dr. Atsushi Kawabata for providing measurement data of *E. japonicus*, and the captain and crew of R.V. Al Amir Moulay Abdallah for keeping live *S. pilchardus* on board the vessel. The work was conducted under the Morocco-Japan cooperative project, “Capacity development of fisheries resource monitoring for the sustainable management of small pelagic resources in the Kingdom of Morocco” that involved cooperation between INRH and the Japan International Cooperation Agency (JICA). We are also grateful for the scientific support provided by Hokkaido University throughout the project.

References

1. FAO (2013) Report of the FAO Working Group on the Assessment of Small Pelagic Fish off Northwest Africa. Casablanca, Morocco, 24-28 May 2011. FAO Fisheries and Aquaculture Report No. 1026. Rome
2. FAO (2013) Report of the FAO Working Group on the Assessment of Small Pelagic Fish off Northwest Africa. Dakar, Senegal 21-25 May 2012. FAO Fisheries and Aquaculture Report No. 1036. Rome
3. Parrish RH, Serra R, Grant WS (1989) The monotypic sardines, *Sardina* and *Sardinops*: their taxonomy, distribution, stock structure, and zoogeography. *Can J Fish Aquat Sci* 46: 2019-2036
4. Bard FX, Koranteg KA (1995) Dynamics and use of sardinella resources from upwelling off Ghana and Ivory Coast. ORSTOM, Paris
5. ICES (2012) Report of the Working Group on Small Pelagic Fishes, their Ecosystems and Climate Impact (WGSPEC), 27 February - 2 March 2012, Fuengirola, Spain. ICES CM 2012/SSGEF: 10
6. Simmonds EJ, MacLennan DN (2005) Fisheries Acoustics: Theory and Practice. Blackwell Science, Oxford, United Kingdom

7. Hazen EL, Horne JK (2003) A method for evaluating the effects of biological factors on fish target strength. ICES J Mar Sci, 60: 555-562
8. Ona E (1990) Physiological factors causing natural variations in acoustic target strength of fish. J Mar Biol Assoc UK, 70: 107-127
9. Ona E (2003) An expanded target strength relationship for herring. ICES J Mar Sci 60: 493-499
10. Svellingen I, Ona E (1999) A summary of target strength observations on fishes from the shelf off West Africa. Joint Meeting of ASA/EAA/DEGA. J Acoust Soc Am 105(2)
11. Barange M, Hampton I, Soule M. (1996) Empirical determination of in situ target strengths of three loosely aggregated pelagic fish species. ICES J Mar Sci 53: 225-232
12. ICES (2011) Report of the Working Group on Acoustic and Egg Surveys for Sardine and Anchovy in ICES Areas VIII and IX (WGACEGG), 22-26 November 2010, ICES CM 2010/SSGESST: 24
13. Degnbol P, Lassen H, Staehr KJ (1985) *In-situ* determination of target strength of herring and sprat at 38 and 120 kHz. Dana 5: 45-54
14. ICES (1982) Report of the 1982 Planning Group on ICES-Coordinated Herring and Sprat Acoustic Surveys. ICES Document CM 1982/H: 04
15. Foote KG (1987) Fish target strengths for use in echo integrator surveys. J Acoust Soc Am 82(3): 981-987
16. Machias A, Tsimenides N (1996) Anatomical and physiological factors affecting the swim-bladder cross-section of the sardine *Sardina pilchardus*. Can J Fish Aquat Sci 53: 280-287
17. Whitehead PJP, Blaxter JHS. (1989) Swimbladder form in clupeoid fishes. Zool J Linnean Soc 97: 299-372
18. Foote KG (1980) Importance of swimbladder in acoustic scattering by fish: A comparison of gadoid and mackerel target strengths. J Acoust Soc Am 67(6): 393-396
19. Foote KG (1985) Rather-high-frequency sound scattering by swimbladdered fish. J Acoust Soc Am 78: 688-700
20. Clay CS, Horne JK (1994) Acoustic models of fish : the Atlantic cod (*Gadus morhua*). J Acoust Soc Am, 96: 1661-1668
21. Ye Z, Furusawa M (1995) Modeling of target strength of swimbladder fish at high frequencies. J Acoust Soc Jpn 16: 371-379
22. Furusawa M (1988) Prolate spheroidal models for predicting general trends of fish target strength. J Acoust Soc Jpn 9: 13-24
23. Foote KG (1980) Averaging of fish target strength functions. J Acoust Soc Am 67(2): 504-515
24. Ona E (1984) Tilt angle measurements on herring. ICES CM 1984/B: 19
25. Amakasu K, Sadayasu K, Abe K, Takao Y, Sawada K, Ishii K (2010) Swimbladder shape and relationship between target strength and body length of Japanese Anchovy (*Engraulis japonicus*). The Journal of the Marine Acoustics Society of Japan 37: 46-59 (**in Japanese with English abstract and captions**)
26. Beltestad AK (1973) Feeding behaviour and vertical migration in 0-group herring (*Clupea harengus* L.) in relation to light intensity. Candidata realium thesis, University of Bergen, Norway (**in Norwegian**)
27. Edwards JI, Armstrong F, Magurran AE, Pitcher TJ (1984) Herring, mackerel and sprat target strength experiments with behavioural observations. ICES CM 1984/B: 34
28. Foote KG, Ona E (1985) Tilt angles of schooling penned saithe. ICES CM 1985/B: 26

29. Huse I, Ona E (1996) Tilt angle distribution and swimming speed of overwintering Norwegian spring-spawning herring. ICES J Mar Sci 53: 863-873
30. Edwards JI, Armstrong F (1983) Measurement of the target strength of live herring and mackerel. FAO Fish. Rep 300: 69-77
31. Edwards I, Armstrong F (1983) Target strength measurements on herring, sprat and mackerel. ICES CM 1983/B: 23
32. Traynor JJ, Williamson NJ (1983) Target strength measurements of walleye pollock (*Theragra chalcogramma*) and a simulation study of the dual beam method. FAO Fish Rep 300: 112-124.
33. Amenzoui K, Ferhan-Tachinante F, Yahyaoui A, Kifani S, Mesfioui AH (2006) Analysis of the cycle of reproduction of *Sardina pilchardus* (Walbaum, 1792) off the Moroccan Atlantic coast. C R Biol 329: 892-901
34. Pešić A, Đurović M, Joksimović A, Regner S, Simonović P, Glamuzina B (2010) Some reproductive patterns of the sardine, *Sardina pilchardus* (Walbaum, 1792), in Boka Kotorska Bay (Montenegro, southern Adriatic Sea) Acta Adriat 51(2): 159-168
35. Sawada K, Takahashi H, Abe K, Ichii T, Watanabe K, Takao Y (2009) Target-strength, length, and tilt-angle measurements of Pacific saury (*Cololabis saria*) and Japanese anchovy (*Engraulis japonicus*) using an acoustic-optical system, ICES J Mar Sci 66: 1212-1218
36. Zhao X, Wang Y, Dai F (2008) Depth-dependent target strength of anchovy (*Engraulis japonicus*) measured in situ. ICES J Mar Sci 65: 882-888.
37. Kang D, Cho S, Lee C, Myoung JG, Na J (2009) Ex situ target-strength measurements of Japanese anchovy (*Engraulis japonicus*) in the coastal Northwest Pacific. ICES J Mar Sci 66: 1219-1224
38. Sawada K, Ye Z, Kieser R, McFarlane GA, Miyanoohana Y, Furusawa M (1999) Target strength measurements and modeling of walleye pollock and Pacific hake. Fish Sci 65: 193-205