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Fisheries Research 75 (2005) 86–96
FISHERIES RESEARCH
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Target strength of some European fish species and its dependence on fish body parameters

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Received 15 December 2004; received in revised form 19 April 2005; accepted 28 April 2005

Abstract

The dependence of maximum, minimum and mean target strength (TS), in both horizontal and vertical planes, on the body length, weight and swimbladder volume of European freshwater fish species (trout-*Salmo trutta*, perch-*Perca fluviatilis*, bream-*Abramis brama*, roach-*Rutilus rutilus*, carp-*Cyprinus carpio* and bleak-*Alburnus alburnus*) was studied. TS was measured with a split-beam echosounder operating at 120 kHz. The orientation of the fish towards the transducer was found to be the most important parameter that affected the TS. Body length and fish species were less important and variations in swimbladder volume contributed little. Regression models for TS, length, weight and swimbladder volume were fitted to the data for both individual fish species and pooled for all species. The side aspect in the lateral plane gave the strongest echo for all fish species except trout. Here, the dorso-ventral aspect gave the most intensive echoes.

Keywords: Target strength; Fish; Freshwater; Acoustics

1. Introduction

The importance of hydroacoustics for the study of fish density, biomass and behaviour in shallow inland waters is widely recognized. However, unbiased conversion from acoustic parameters, such as target strength (TS) to the parameters familiar to fisheries biologists, such as length and weight, is still not a routine procedure. This is particularly true for multi-species communities of European freshwater fish. A number of studies have described the relationship between TS and the real size of individual species, in particular for commercially important fish, such as Salmonidae (Dahl and Mathisen, 1983; Lilja et al., 2000), non-European freshwater fish (Love, 1969; Shibata, 1971) and marine fish (Love, 1977; Naken and Olsen, 1977; Buerkle and Sreedharan, 1981; Miyahonana et al., 1990). Much less attention has been paid to

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doi:10.1016/j.fishres.2005.04.011

other European freshwater fish (Borisenko et al., 1989; Kubecka, 1994; Kubecka and Duncan, 1998; Lilja et al., 2000; Frouzova and Kubecka, 2004). Moreover, the relationship between TS and real body size is affected not only by the species of fish but also by other factors, such as mode of observation. In particular, relationships between target strength and real fish size, based on various body aspects of freshwater fish ensonified horizontally, has not been satisfactorily elucidated.

The target strength of an individual fish depends on the morphological parameters of its body, such as length, weight, fat content, gonad development and presence, size and type of swimbladder (Ona, 1990; Hazen and Horne, 2003). Also aspect—the orientation of the fish's body axis in relation to the sound beam is at least as important as these morphological parameters. Target strength changes dramatically during a change of aspect. During one turn of the fish's body around dorso-ventral or lateral axis, the target strength-aspect function has a well defined maximum which, according to MacLennan and Simmonds (1992), can be used for comparisons of different fish species and size. Theoretically, the same can apply to the function's minimum.

This paper presents sets of equations which can be used for estimation of the length, weight or swimbladder volume from mean target strength of individual European freshwater fish species and from their target strength at maximum and minimum aspects in both the horizontal and vertical planes. The relationships presented are for both fish species pooled and for individual species. These relationships were derived for a frequency of 120 kHz which is progressively more used in freshwater hydroacoustic research, but for which empirical data about relationships between real body size and TS are rare.

2. Methods and material

2.1. Material

All data were collected during the summer and autumn of 2000 in a concrete pond about 12 m × 5 m × 2 m in size (length × width × depth) using a "fish rotating carousel" (Fig. 1).

The fish used in the experiment were caught by fyke nets in a tributary of Rimov reservoir (Czech Republic) or, in the case of trout and carp, brought from local fish farms. Fish from the families Salmonidae-brown trout (*Salmo trutta*), Percidae-perch (*Perca fluviatilis*) and Cyprinidae-bream (*Abramis brama*), roach (*Rutilus rutilus*), carp (*Cyprinus carpio*) and bleak (*Alburnus alburnus*) were measured. All these fish have swimbladders. Trout and perch have a one-chambered swimbladder, while the others have two-chambers. Body shape differs among these three families: while the

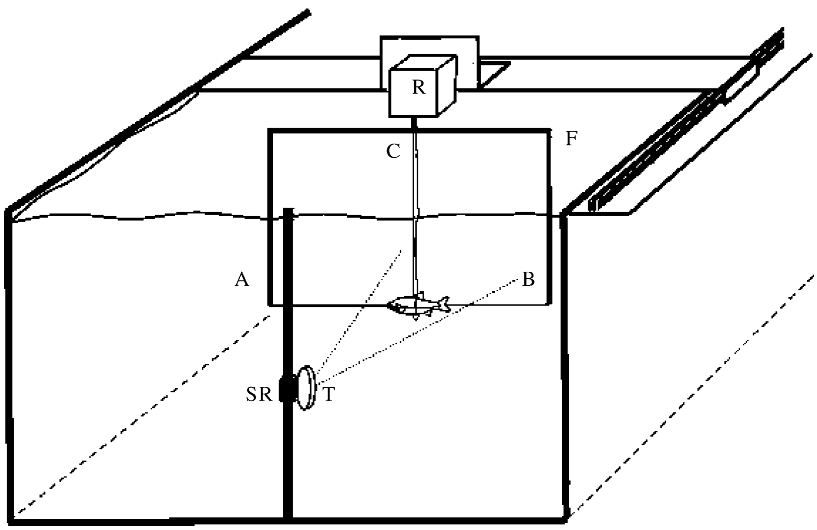

Fig. 1. The scheme of "fish rotating carousel". The fish was hung on the frame (F) and centered with the help of the sonar rotator (SR) in the acoustic beam (T, transducer). The frame, with fish was fixed, on rotator (R) which turned the whole frame around its axis.

trout body shape is fusiform, others have bodies more (bream, carp) or less (perch) laterally compressed. The fish used ranged from 72 to 710 mm in total length and from 4 to 6913 g in body mass. The species and size ranges selected cover the normal variability of the fish commonly found in freshwater reservoirs in central Europe.

2.2. Experimental setup

All fish were stored for up to 2 days in an aerated 1000 l tank before the experiment. The tank was shaded over the top to minimize stress and disturbance of the fish. Each fish was anesthetized with MS 222 (Sandoz) directly before the experiment and its total length, fork length, standard length and weight were measured. No natural biological functions were available for the fish during experiment. The fish was then carefully mounted in the carousel (Fig. 1). Four 0.3 mm fishing lines were sewn on to the jaw, tail, spine and belly of the fish. The head and tail lines were stretched to the carousel's vertical metal rods sticking down into the water at points A and B in Fig. 1. The spine and belly lines were attached to the frame's horizontal rig above the water (point C). For yawing (in the horizontal plane), three of the lines, to the points A–C were used as drawn in Fig. 1; for tilting (in the vertical plane) all four lines were used, with both spine and belly lines gently stretched to point C. The head and tail lines supported the fish while the spine and belly lines were used to hold the fish straight, either upright or lying on its side in the water. The fish was swung a little to release the residual gas from the oral cavity. The frame, with the fish, was then mounted on the rotator with either the side or the dorsal aspect of the fish facing towards the transducer, defined as 90°. The distance between the fish and the transducer was about 6 m. The transducer's pan and tilt were trimmed so that it could "see" the fish exactly on the acoustic axis. The fish's head was mounted to the left as seen from the transducer. With the carousel always rotating anticlockwise, all fish thus produced the same side, head, side, tail sequence. Several turns were recorded with the fish first in the horizontal plane (yawing) and then several times with fish in the dorsoventral plane, so that all the fish produced the same ventral, head, dorsal, tail sequences. The echosounder and the fish rotor were started simultaneously. One complete rotation took about 4 min. With a ping rate of 10 ping/s, 2400 measurements were obtained from each aspect cycle.

The swimbladder volume was measured after completion of the acoustic measurements. The fish was killed by cutting the vertebral canal behind the head and then dissected under water. A funnel and a volumetric cylinder full of water, placed above the fish, collected and measured the gas from the swimbladder and body cavity when the fish was cut open.

2.3. Acoustic equipment and measurement

A Simrad EY 500 split beam echosounder recorded the acoustic data. The echosounder was equipped with an ES120-4 elliptical transducer (120 kHz sound frequency with a nominal beam angle of $9.1 \times 4.3°$). The transducer was mounted on a remotely controlled Subatlantic pan and tilt rotator with the 'along ship' axis facing vertical in the water. The echosounder was set to store echo, trace, sample angle and sample power telegrams with a ping-rate of 10 ping/s. The duration of the transmitted pulse was 0.1 ms and the bandwidth was set to 12 kHz (wide). The telegrams for storage of echograms were set to record 250 echo samples with a range of 15 m and with the TVG 40logR indicating a point spread model. Attennuation coefficient was set to 6 dB km^{-1} (Francois and Garrison, 1982). The echosounder's single-echo-detector parameters were set to accept echoes with a minimum value, −72 dB (threshold); minimum echo length, 0.8 and maximum echo length, 1.5 times the transmitted pulse length. Maximum gain comp, 5 dB and maximum phase deviation, 10. See the SIMRAD manual (1994) for further explanations of these criteria. We applied this wide setting in order to ensure as that as many as possible detections from the fish were captured. The echosounder system was calibrated every day with a 23 mm copper calibration sphere estimated to have a TS of −40.6 dB, the reference target was in the same distance like the experimental targets—about 6 m, peak noise background in TS level was about −75 dB.

2.4. Data processing

Echo data were processed with Sonar5-Pro (Balk and Lindem, 2003) and with MS Excel software. In all cases, the echoes from two or more complete turns were processed.

Sonar5-Pro extracted echo and trace telegrams to generate amplitude and single echo detection echograms. We roughly separated single echo detections of fish from noise detections (fluctuations in the background reverberation), and detections of the carousel's vertical metal rods, with Sonar5-Pro's manual tracker and exported to Excel the values of TS, range, 'along ship' and 'athwart ship' positions, from each fish detection. A second cleaning was then carried out by accepting only detections within $\pm 3^\circ$ on the 'athwart' axis and $\pm 2^\circ$ on the 'along ship' axis. Statistical post-processing (descriptive statistics, correlations, regressions, and *t*-tests) was also carried out in Excel 6.

The echo of the head and tail aspect of small fish was difficult to detect with the single echo detector due to a poor signal-to-noise ratio. In the SED-echogram the horizontal line of detections from the fish could show gaps for several pings. In the amplitude (Amp-echogram), however, the horizontal line of echoes could still be seen. Hence, the information for the missing detections was available, although not obtainable with the single echo detector. An alternative method was therefore developed and implemented in Sonar5-Pro to extract the missing detections. A thin pelagic layer was manually placed to cover only the range between rising and falling echo intensities of the fish echo, as seen in Sonar5-Pro's Amp-echogram, and an oscilloscope window was activated in 'peak mode' (Balk and Lindem, 2003). When asked to analyze the selected layer, the oscilloscope's peak detector registered and plotted the strongest echo with its TS, range and ping number. Since the Amp-echogram was recorded with 40logR, and since the fish was mounted on the acoustic axis, the detected peaks fully represent the TS of the fish.

Echo intensities from two body aspects (maximum side or dorsal and ventral, minimum head and tail) of two body planes—horizontal (yawing or lateral plane) and vertical (tilting or dorso-ventral plane) in addition, in both planes, mean TS values were considered. Mean TS was defined as the average reflection intensity collected during one complete turn of the fish body. The definitions of the side, head and tail aspects are described in Fig. 2. The maximum and minimum TS values were recorded in every side or head/tail aspect record. TS of all records within 3 dB around the maximum or minimum values were averaged. In the vertical plane, dorsal and ventral TS was defined as the mean value of the highest 3 dB in the dorsal or ventral peak. The minimum tail and head aspect TS was estimated in the same way as in the horizontal (lateral, yawing) plane. In this context, it is also necessary to explain the term maximum side, ventral or dorsal aspect. The full side, dorsal, ventral, head and tail aspects may not be the aspects that occur the maximum or minimum sound reflections (Kubecka, 1994). Instead, the maxima and minima may be located a few degrees away (3–18° according to Blaxter and Batty, 1990; Benoit-Bird and Kelley, 2003). The off-angles depend on the morphological characteristics of the fish body. The main determinant is the shape of the swimbladder and its placement within the body. This is not only species dependent, but may vary among individuals of the same

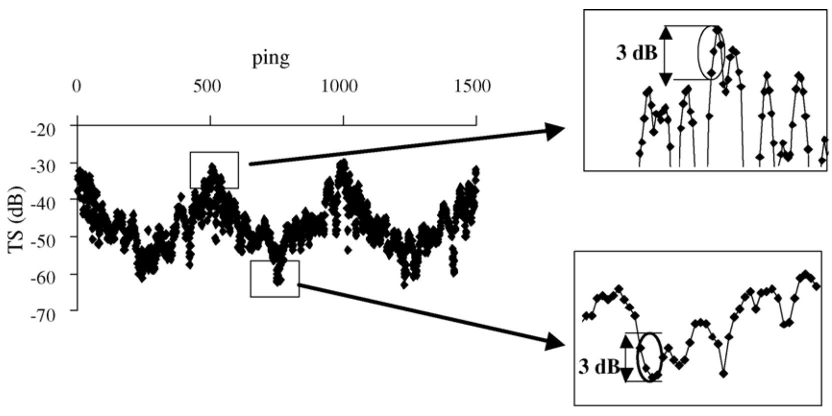

Fig. 2. An example of the calculation of TS maxima and minima of bleak; total length, 202 mm; weight, 64 g.

species (Blaxter and Batty, 1990). In agreement with these authors we always used maximum or minimum TS values for the next processing, regardless of the fact that they were not exactly a TS of the full aspect (90 or 270°).

The dependence between the expected fish TS and length, TS and wet weight, and TS and swimbladder volume was modeled with the traditional $TS = a \log x + b$ regression formula, where a and b are constants for a given fish species and relationship, and x is the length, weight or swimbladder volume of the fish.

To find out how these three factors influence TS, a three-way ANOVA was applied. Significance and the proportion of variability explained by these factors were tested. The proportion of the total variability explained by the individual factors was calculated as the sum of squares accounted for by the individual factors as a percentage of the total sum of squares (Sokal and Rohlf, 1995). General linear models tested the effect of various treatments on individual factors while the other factors worked as co-variables. Three-way ANOVA and general linear models were computed with the statistical software package SPSS 11.0.

3. Results

At first, differences between TS values of the two maximum side aspects from one fish turning in the horizontal plane were tested (paired t-test, $p > 0.05$). No significant difference was found, so both these maximum aspects were used in the next processing without distinguishing if they were obtained from the left or right side of the body. Likewise, the TS values of head and tail aspects were tested and were also found not to be significantly different, so the head and tail aspects were also combined for further processing as the minimum head–tail aspect. Similarly, maximum (dorsal and ventral) and minimum (head and tail) TS values in the vertical plane were tested and no significant differences were found so both maximum dorsal and maximum ventral TS values and minimum head and minimum tail TS values were combined for further processing as the maximum dorso-ventral TS and minimum head–tail TS.

Three-way ANOVA was used to test the influence of species, length, and aspect (maximum side or maximum dorso-ventral and minimum head–tail aspect) on the resulting TS. Comparison of these factors investigated separately by ANOVA (Table 1) indicated that both aspects, TL and species contributed significantly to the resulting TS. In both the horizontal and vertical planes, the largest proportion of TS variability (83 and 84%) was explained by the aspect (position of the body axis with respect to the beam axis). The total length (TL) explained a smaller portion of the variability and species made the smallest contribution to total TS variability (Table 1), in both planes.

We pooled all the TS versus size (length and weight) registrations and calculated general regressions for maximum and minimum aspects and mean TS in the lateral (horizontal) and dorso-ventral (vertical) planes.

Table 1
The effect of fish species, total length, and body aspect on resulting TS value

Parameter	Horizontal				Vertical			
	Sum of square	d.f.	p	%	Sum of square	d.f.	p	%
Fish species	995.6	5	***	4.9	141.3	5	*	1.2
Total length (TL)	1944.6	45	**	9.6	1243.6	30	**	11.1
Aspect	16777.9	1	***	83.0	9342.0	1	***	83.7
Species × TL	6.2	2	ns	0.1	14.9	2	ns	0.1
Species × aspect	148.4	5	*	0.7	137.0	5	ns	1.28
TL × aspect	278.1	45	ns	1.3	260.2	30	ns	2.3
Species × TL × aspect	13.5	2	ns	0.1	10.1	2	ns	0.1
Error	41.4	8	–	0.2	7.2	4	–	0.1
Corrected total	20206.1	–	–	–	11156.5	–	–	–

d.f., degree of freedom; %, percentage of total variability.
* Means p value < 0.05.
** Means p value < 0.01.
*** Means p value < 0.001.

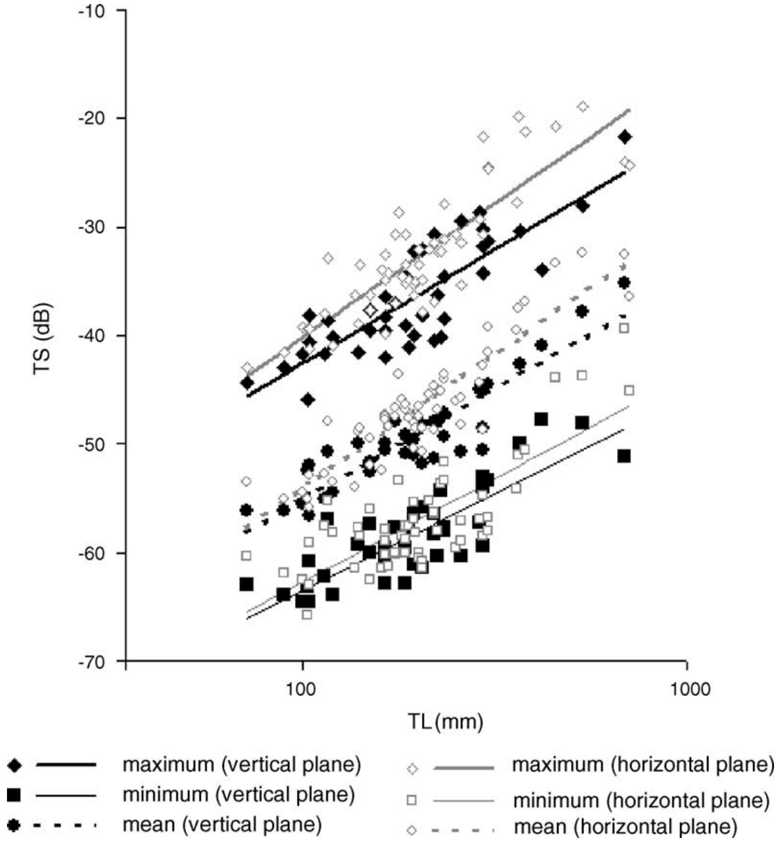

Fig. 3. Comparison of the regression curves of maximum, minimum and mean TS values obtained during fish rotation in horizontal and vertical planes. Points represent data, lines represent linear regression models.

The side aspect of the pooled fish was the aspect with the strongest reflection (Fig. 3) and is significantly different from the reflection of the maximum dorso-ventral aspect (Univariate Analysis of Variance, $p < 0.001$, total length used as co-variable). Further, the mean TS in the horizontal plane was stronger than the reflection of the mean TS in the vertical plane with a significant difference between them (Univariate

Table 2
Regression analyses of maximum, minimum and mean target strength (TS) in dB, of pooled fish species, on fish total/fork/standard body length (L) in mm in both horizontal and vertical planes according to equation $\mathrm{TS} = a \log L + b$

	a	b	R
Horizontal plane ($N = 56$)			
Side	24.71/24.55/24.15	−89.63/−88.39/−86.51	0.8576/0.8393/0.8361
Head–tail	19.14/19.43/19.29	−101.08/−101.07/−99.98	0.7813/0.7816/0.7858
Mean	24.73/24.64/24.26	−103.61/−102.51/−100.68	0.9055/0.8888/0.8861
Vertical plane $N = 40$			
Dorso-ventral	21.15/21.43/21.44	−84.95/−84.87/−84.05	0.8275/0.8458/0.8513
Head–tail	17.87/17.40/17.10	−99.30/−97.64/−96.30	0.82368/0.8092/0.8002
Mean	20.45/19.86/19.65	−96.13/−94.14/−92.87	0.9073/0.8894/0.8848

Table 3
Regression analyses of target strength (TS) in dB on fish wet weight (W) in g in the order maximum TS/minimum TS/mean TS in both horizontal and vertical plane, according to equation TS = $a \log W + b$

	N	*a*	*b*	*R*	Range of weight (g)
Horizontal					
All fish pooled	56	7.28/6.10/7.48	−47.00/−68.97/−61.32	0.8284/0.8165/0.8978	4–6913
Roach	9	11.48/0.81/6.83	−52.00/−58.47/−58.14	0.8459/0.1557/0.9132	16–289
Trout	10	5.63/2.37/3.90	−46.68/−62.82/−57.83	0.9379/0.6111/0.9116	4–269
Perch	9	7.35/4.31/7.13	−46.04/−66.49/−61.55	0.8659/0.5353/0.9428	10–330
Carp	13	8.36/9.04/8.52	−52.04/−75.80/−64.50	0.9211/0.9448/0.9474	56–6913
Bream	10	10.95/7.36/9.46	−53.31/−72.44/−64.32	0.8626/0.8403/0.924	41–499
Vertical					
All fish pooled	40	5.40/5.48/5.70	−47.11/−68.87/−60.43	0.7252/0.8096/0.8899	4–6010
Roach	8	5.97/4.40/5.65	−47.62/−65.27/−58.85	0.9040/0.6896/0.9457	16–289
Trout	11	8.01/3.40/3.62	−48.76/−66.56/−58.56	0.9617/0.7513/0.9010	4–269
Perch	5	9.91/4.34/6.33	−53.51/−67.71/−61.28	0.9657/0.9539/0.9428	10–330
Carp	11	9.22/5.73/7.84	−59.77/−69.73/−65.69	0.9539/0.8513/0.9762	56–6010

Analysis of Variance, $p = 0.001$). On the other hand, the reflections of the head–tail aspects in the vertical and horizontal planes were not significantly different (Univariate Analysis of Variance, $p = 0.249$). Table 2 presents the regressions for length and all body aspects in both planes of the pooled fish species, while Tables 3 and 4 present regressions for wet weight and swimbladder volumes of the pooled fish and of individual fish species.

Fig. 3 demonstrates the trend of increasing range between maximum and minimum TS with increasing body size. The range between the curves of maximum and minimum TS of pooled fish in the horizontal plane ranged from 22 dB (for the smallest fish) to 27 dB (for the largest fish) and in the vertical plane from 17 to 20 dB. For individual species, the biggest difference between maximum and minimum TS in the horizontal plane was found for roach, and in the vertical plane for trout.

Table 5 shows the regression coefficients for the length–TS relationships of individual species. When the transducer was facing the side aspect, roach gave the strongest echo, followed by bream, perch and carp. The weakest echoes in this aspect were produced by the trout. In contrast, when facing the transducer with the dorso-ventral aspect, trout gave the strongest echo followed by perch and roach. Carp produced the weakest echo. It is interesting to note that the mean and head–tail values for trout and perch are weaker than those of the other species in both planes. Moreover, TS of the trout's maximum dorso-ventral aspect was higher than TS of its maximum side aspect, which was different from the results for the other species (see Fig. 4).

Table 4
Regression analyses of target strength (TS) in dB on fish swimbladder volume (SBV) in ml in the order maximum TS (side aspect or dorso-ventral aspect)/minimum TS (head and tail aspect)/mean TS in both horizontal and vertical plane, according to equation TS = $a \log \mathrm{SBV} + b$

	N	*a*	*b*	*R*	Range of volume (ml)
Horizontal					
All fish pooled	36	6.47/4.77/6.44	−37.86/−60.57/−51.48	0.8434/0.7265/0.9192	0.1–400
Roach	8	10.00/0.44/6.06	−38.82/−57.75/−50.34	0.8883/0.7240/0.9376	1.2–30
Trout	8	4.84/1.77/3.22	−37.57/−58.66/−51.33	0.9372/0.6433/0.8140	0.1–6.5
Carp	11	8.95/9.87/9.39	−42.61/−65.74/−55.16	0.9588/0.8210/0.9800	3.5–400
Vertical					
All fish pooled	32	4.37/4.48/5.23	−39.07/−60.94/−52.45	0.6389/0.8035/0.9123	0.1–400
Roach	7	5.17/4.23/5.05	−40.75/−60.23/−52.36	0.8462/0.1161/0.9270	1.2–30
Trout	9	6.62/2.60/2.80	−35.15/−60.81/−52.22	0.9006/0.5506/0.9124	0.1–6.5
Carp	10	9.43/5.55/8.07	−48.82/−62.43/−56.50	0.9358/0.9550/0.9782	3.5–400

Table 5
Regression analyses of maximum, minimum and mean target strength (TS) in dB on fish total body length (TL) in mm, for individual species, in both horizontal and vertical plane, according to equation TS = a log TL + b

	N	a	b	R	Range of total body length(mm)
Horizontal					
Roach	9	33.55/2.49/20.66	−107.51/−62.66/−92.76	0.8299/0.1604/0.9264	117–305
Trout	10	17.25/6.77/11.82	−75.48/−73.87/−77.50	0.9421/0.5729/0.9061	72–259
Perch	9	24.98/15.36/24.65	−88.98/−93.20/−104.10	0.8840/0.5727/0.8083	101–290
Carp	13	25.27/27.47/25.76	−92.06/−119.43/−105.32	0.9172/0.9457/0.9443	140–710
Bream	10	33.03/20.97/27.91	−108.36/−106.51/−110.46	0.8894/0.8183/0.9346	168–380
Vertical					
Roach	8	18.11/12.87/17.02	−77.96/−86.55/− 87.37	0.8984/0.6612/0.9329	117–305
Trout	10	24.40/10.43/10.96	−89.44/−83.99/−76.79	0.9647/0.7590/0.8984	72–259
Perch	5	33.11/14.57/20.96	−110.68/−92.65/−97.05	0.9671/0.9601/0.9359	101–290
Carp	10	28.17/17.56/23.97	−104.68/−97.78/−103.90	0.9531/0.8540/0.9756	140–690

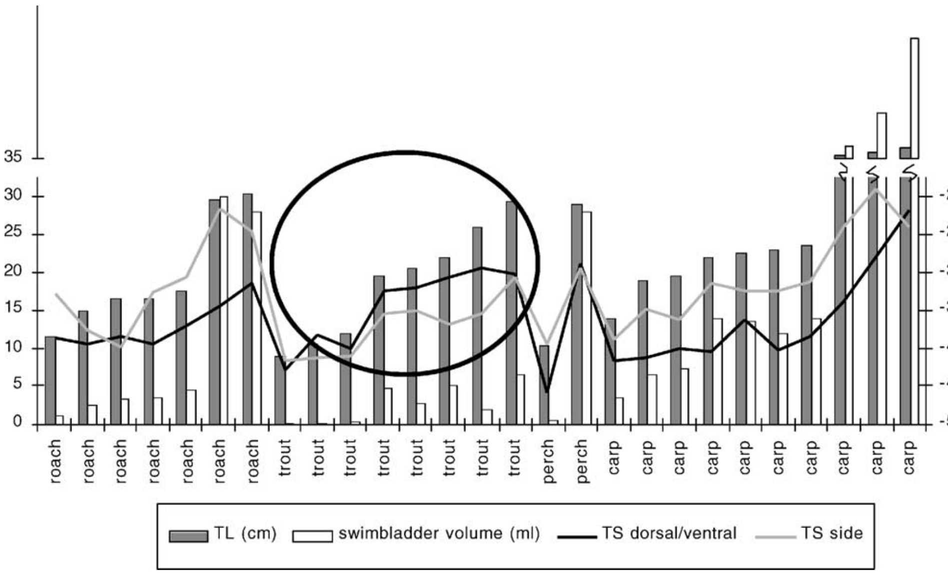

Fig. 4. Comparison of the fish body length, swimbladder volume (left axis) and maximum side and dorso-ventral TS (right axis) of individual fish. The oval indicates trout for which the maximum dorso-ventral TS is stronger than the maximum side TS.

Table 6
Comparison of the effects of total length (TL), fish weight (W), swimbladder volume (SBV) and fish species on maximum TS in vertical and horizontal planes by generalized linear model

Parameter	Vertical				Horizontal			
	Sum of square	d.f.	Percentage of variance	p	Sum of square	d.f.	percentage of variance	p
TL	120.3	1	68.4	***	423	1	78.9	***
W	0.8	1	0.5	ns	1.7	1	0.3	ns
SBV	0.2	1	0.1	ns	0.3	1	0.1	ns
Species	54.5	3	31.0	***	111.3	3	20.8	**

Sum of squares, degree of freedom (d.f.), percentage of total variance explained.
** Significance of individual factors is given mean p value < 0.01.
*** Significance of individual factors is given mean p value < 0.001.

Table 6 compares the effect of species, length, weight and swimbladder volume on maximum TS. In this comparison, only two parameters, length and species showed significant effects on the TS. Length explained most of the variability and, hence, with a known aspect, length is the major predictor of TS.

Both length, weight and swimbladder volume are related to the physical size of the fish and each of these factors proved to correlate significantly ($p < 0.01$) with TS when evaluated separately ($r = 0.914$, 0.755 and 0.782 for length, weight and swim-bladder volume, respectively). From partial correlation, however, length was the only significant ($p < 0.01$) factor ($r = 0.829$).

4. Discussion

Of the factors tested (Table 1), the position of the fish body axis with respect to the axis of the sound beam (fish body aspect) proved to have the most significant effect on the TS (explaining 83% of the data variability in the horizontal plane and 84% in the vertical plane), followed by length (14 and 12%) and species (0.2 and 0.6%).

The fish body aspect apparently depends on the mode of observation, which is commonly vertical or horizontal. It is obvious that while in the horizontal plane the fish may be visible at all angles during one turn of its body around its dorso-ventral axis, while in the vertical plane of observation some tilt aspects occur more often than others, and some aspects, such as the head or tail aspect rarely occur. In the vertical plane, the aspect, and consequently resulting TS of the fish, is more predictable than in a horizontal view and it is influenced mainly by fish behaviour (Torgersen and Kaartvedt, 2001). A different swimming pattern is expected, for example, from a single fish and a fish in a shoal (Blaxter and Batty, 1990) and it can differ also during day and night for some fish species (Axenrot et al., 2004). In practice this means that, for example, the TS of a 300 mm long roach varies in the horizontal plane from 24 to 57 dB depending on its current aspect in relation to the transducer. The range between maximum (side aspect) and minimum (head or tail aspect) TS is 23 dB. In the vertical plane, the range between maximum (dorsal or ventral aspect) and minimum (head or tail aspect) TS is 19 dB. However, under natural conditions fish do not occur in all potential positions and therefore the TS in vertical plane changes maximally by about 13 dB (Čech and Kubečka, 2002).

Among the effects on TS of individual morphological parameters of the fish body, total fish length (TL) was shown to be the most important predictor of TS (Table 6). TL shows a significant effect on TS even when constrained by swimbladder volume and weight. In contrast, swimbladder volume when constrained by TL shows no significant effect on TS (Fig. 4), which seems to contradict the general belief that the swimbladder is responsible for most of the backscattering by a fish body (Foote, 1980). However, it must be taken into account that backscattering also rather depends more on the area of the fish body, which may reflect the acoustic beam, rather than on body volume. The same may be valid also for the swimbladder (Blaxter and Batty, 1990). Hence, body length may appear statistically more important just because it correlates more closely to the area of the body. In contrast, the relationship between swimbladder volume and swimbladder area, which is active in sound reflection, may be much more complex because of inter- and intra-specific differences in the shape of the swimbladder. Our study only indicated that its volume is not the best indicator of the effect of the swimbladder on TS. This is also supported by the results of Gauthier and Rose (2002) and of Knudsen and Gjelland (2004) who studied changes of TS with expected changes in swimbladder volume at different depths and established that these TS changes are minor. The study of Benoit-Bird et al. (2003) also showed that differences in the volume of the swimbladder in six snapper species did not cause differences in TS.

When we compare our results with the general, multi-species regressions of various authors TS–length relationships are similar (Fig. 5). On the other hand, the TS–length relationship for maximum dorso-ventral aspect is different among different authors. This pattern is in agreement with our finding that species of fish is more important for TS variability in the vertical than in the horizontal plane of observation (Table 1). However, in both cases, the species effect is quite low (species accounts for only 0.2 and 0.6% of the total variability). Some authors (Foote, 1979; McClatchie et al., 1996) object to pooling fish species but our study has indicated that the role of fish species on TS variability can be low in the case when morphological differences of pooled species are not pronounced. Moreover,

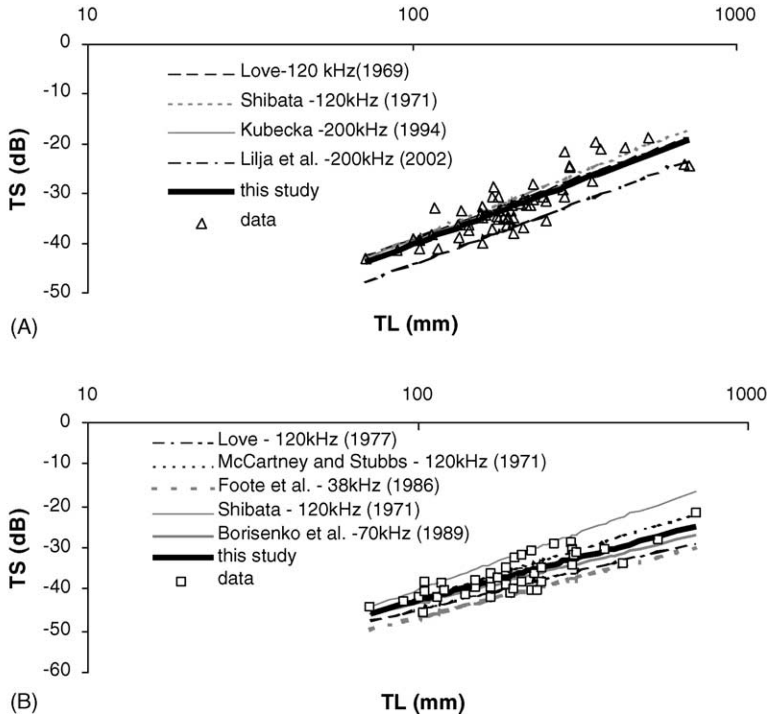

Fig. 5. Comparison of data from this study with some commonly used TS–length relationships from the literature (Love, 1969, 1977; Shibata, 1971; McCartney and Stubbs, 1971; Foote et al., 1986; Borisenko et al., 1989; Kubecka, 1994). A, side aspect; B, dorsal aspect.

in freshwater hydroacoustics it is still not possible to distinguish individual species and fish stocks in open freshwaters are usually mixtures of several common species (Vašek et al., 2004). Under such circumstances some general equations describing the relationships between body size and target strength should be useful.

Nevertheless, some differences between particular species do exist. That the weakest echoes are due to trout is in agreement with the observations of Kubecka and Duncan (1998) and Lilja et al. (2000) and we can speculate that body shape and swimbladder anatomy (single versus two-chambered) may be most important for inter-species differences.

Acknowledgements

This study was supported by Grants NO. Z6017912 and S6017004 of the Czech Academy of Sciences. The authors thank Mr. Zdenek Prachar, Mr. Petr Dvorak and Mr. Jaroslav Fuksa for their field assistance and also express their appreciation to Dr. Milan Hladik and two fish farms in South Bohemia—in Kaplice and in Hluboka—for the fish supply. Authors thank also Dr. Mary Burgis for careful editing of the English text. Great thanks also go to Dr. Martin Cech for stimulating discussion. Authors thank also two anonymous referees and the editor for inspiriting comments.

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