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Sinusoidal cycling swimming pattern of reservoir fishes

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A circular split-beam transducer (7°, nominal angle), fixed on the bottom close to the deepest point (*c.* 36 m) of the Rimov Reservoir and beaming up towards the surface showed that most fishes stayed in the epilimnion during the summer. The majority (83%) of larger fish individuals (136–359 mm L_S; maximum target strength, TS_{max}, ranged from − 42·2 to − 34·1 dB) in open water performed very characteristic sinusoidal movements in the vertical plane during July and August. As they crossed the sonar beam (3–4 m wide), the fishes changed their depth several times (frequency 1·3–10·1 cycles min^{-1}) with amplitude of 19–321 cm. The trajectory of fish vertical oscillations was in many cases greater than the trajectory of their horizontal movement. Fishes started to swim up-and-down after sunrise and continued doing so during daytime. The sinusoidal movement pattern was replaced by direct movement before sunset. A number of descriptive parameters of up-and-down movement is proposed and their ranges are given. Variation of target strength indicates active changes of fish tilt (30° on average) in transient phases of the sinusoidal cycle rather than changes of swim bladder volume. Up-and-down fish swimming is likely to be an efficient way of visual inspecting a larger volume of the epilimnion for prey, mainly large zooplankton (*Daphnia*, *Leptodora*), whose epilimnetic density in the Rimov Reservoir is low and patchy in summer time.

Key words: Rimov Reservoir; sinusoidal swimming; echosounder; facultatively planktivorous fishes.

INTRODUCTION

Over short time periods (seconds to minutes) fishes are usually believed to swim more or less horizontally with the functional dorsal part of the body facing the surface and being forced forward mainly by the action of the caudal fin (Videler, 1993; Webb, 1993*a*,*b*). In European lakes and reservoirs exhibiting summer-time temperature and oxygen stratification, fishes seem to inhabit the surface depth strata of the water column (Bohl, 1980; Goldspink, 1990; Brabrand & Faafeng, 1993; Imbrock *et al.*, 1996) and it is difficult to study their behaviour and distribution using conventional vertical echosounding with a boat-mounted transducer emitting ultrasonic waves towards the bottom (Kubečka & Wittingerova, 1998). Due to the distribution of fishes in the epilimnion, a bottom mounted transducer (Thorne, 1983; Thorne *et al.*, 1990; Arrhenius *et al.*, 2000) should be used to study fish behaviour in the pelagic zone.

The present study tested the assumption that the classical concept of fish swimming applies rather rarely during warm periods of the year and that most

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*Author to whom correspondence should be addressed. Tel.: +42 03 87 77 58 70; fax: +42 03 85 30 02 48; email: carcharhinusleucas@yahoo.com open-water reservoir fishes use a sinusoidal trajectory of swimming in the vertical plane. A detailed description of the sinusoidal swimming pattern was undertaken and considered in relation to known and theoretical information concerning swimming and foraging behaviour.

STUDY AREA

The study was carried out in the canyon-shaped meso- to eutrophic Rimov Reservoir, Czech Republic (48°50′ N; 14°30′ E, 170 km south of Prague). It has an area of 210 ha, a volume of 33×10^6 m^3 and maximum depth of 45 m. The Rimov Reservoir was built by damming the River Malse, which is the main reservoir tributary. The average water retention time (reservoir volume divided by the tributary discharge) varies from 80 to 180 days (Seda & Kubečka, 1997).

The fish assemblage of the Rimov Reservoir comprises 34 fish species and five hybrids. Only a few fish species, roach *Rutilus rutilus* (L.), common bream *Abramis brama* (L.), bleak *Alburnus alburnus* (L.), perch *Perca fluviatilis* L., ruffe *Gymnocephalus cernuus* (L.) reach ecologically significant population levels in the reservoir (Seda & Kubečka, 1997; Kubečka *et al.*, 1998; Vasek *et al.*, 2000).

MATERIALS AND METHODS

Fish swimming behaviour was examined in relation to environmental conditions in the reservoir. Characteristic periods of the annual cycle of the reservoir reflecting biotic (biomass, size and species composition of zooplankton and phytoplankton) and abiotic (thermal and oxygen stratification and destratification of the water column) conditions were chosen (Seda & Kubečka, 1997; Seda *et al.*, 2000). Acoustic data were collected during late July, mid-August and mid-November 1998 and late May 1999.

The investigation was carried out using a SIMRAD EY 500 split-beam scientific echosounder, using a frequency of 120 KHz. The echosounder was controlled by a personal computer (Chicony 486DX). The transducer used (SIMRAD ES120-7G) had a circular beam pattern with a nominal angle of 7·1°. The transducer was fixed on the bottom (depth *c.* 36 m) close to the deepest point of the reservoir beaming up towards the water surface, recording open-water fishes, mainly in the epilimnetic and upper hypolimnetic layers (Fig. 1). Acoustic data were stored on the hard disk of the computer for later analysis. The whole sonar system was calibrated with a standard calibration tungsten carbide sphere of 36 mm diameter (Foote *et al.*, 1987). Stratification variables (temperature in ° C and dissolved oxygen concentration in mg l^{-1}) were measured with a calibrated WTW OXI 196 probe.

Four levels of acoustic data filtering were used: (1) The threshold for the primary noise filtering of the up-looking record during fieldwork was set to a minimal target strength (TS) of -70 dB (MacLennan & Simmonds, 1992); (2) a second filtering procedure was applied in the postprocessing software SIMRAD EP 500. The threshold for secondary filtering was set at -65 or -59 dB according to the observed noise levels; (3) individual fish hits were tracked together to form whole fish records using the tracking facility of EP 500. The configuration of the tracking facility was as follows: minimal number of detections to track a fish (hits in beam) was set to two; maximal range between detections was set to 10 cm (system ping rate 10 pings s^{-1}); maximal number of missing pings per track (ping gap) was set to 1. The EP 500 tracking facility was not originally designed for tracking of fishes with more than 10 hits and the fish record was segmented in several shorter segments. A special macro in Microsoft Excel was programmed for joining segments belonging to one fish; (4) the last level of filtering was intended to distinguish overlapping multiple targets and accidental non-fish targets remaining from previous

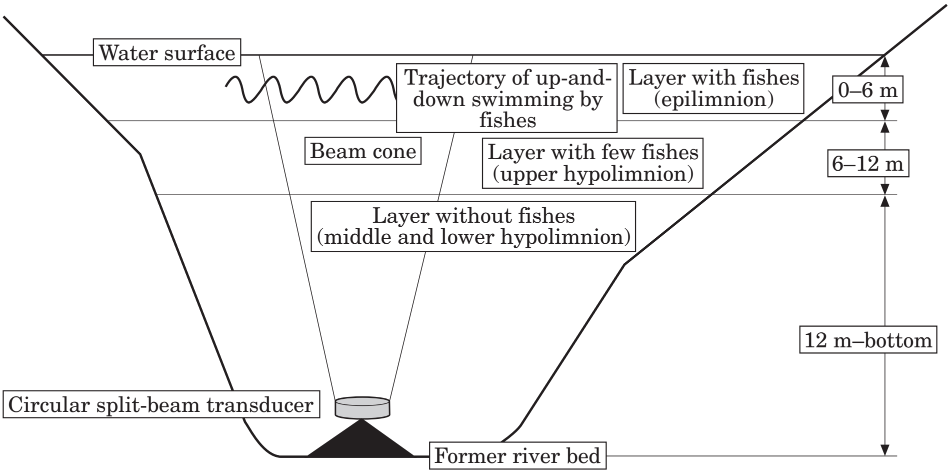

FIG. 1. The deployment of the bottom-mounted surface-facing transducer in the dam part of the Rimov Reservoir, together with a schematic view of stratification and fish records during summer 1998 observations.

filtering levels (visual analysis). This filtering, as well as the calculation of fish trajectories, was carried out in Microsoft Excel.

By knowing the three dimensional trajectory of fishes, it was possible to unambiguously distinguish between cycling and non-cycling fishes. Only fishes executing a clear vertical cycling pattern (no straight swimming) with at least one complete sinusoidal cycle (two turning points, descending and ascending phase) within the beam were considered as cycling fishes. Distinguishing between straight and sinusoid swimming pattern was easy, because sinusoidal swimming was rather symmetric [Fig. 2(a)], without straight trajectories. There were no hybrid trajectories between sinusoid and straight pattern. Records of swimming patterns were of different quality mostly with respect to what part of the beam was crossed by the fish. Fishes crossing just margins of the beam were not included in the analysis. The same applies to overlapping records, which did not satisfy single target criteria necessary for extracting complete acoustic information. Some fish records were clearly sinusoidal, but their three dimensional track was not tracked sufficiently due to limitations in the tracking facility of the SIMRAD EP 500 software. These fishes were counted as cycling but not included in the detailed analysis of sinusoidal swimming pattern. Fishes smaller than -45 dB (<100 mm standard length, L_S; Love, 1971) never exhibited sinusoidal swimming. Smaller fishes (0+ and 1+ years) were well distinguished by size from larger fishes as there were no records between -48 and -44 dB. Of nearly 700 acoustic target trajectories recorded, only the best 201 cycling records were chosen for detailed study of the up-and-down swimming pattern. Twenty-nine parameters describing the sinusoidal swimming pattern were recognized (Appendix).

Data were analysed using linear and non-linear regression and *t*-tests (Wilkinson, 1990).

RESULTS

During the daytime in summer (July and August recorded between 0515 and 2030 hours), a sinusoidal swimming pattern (regular up-and-down movements while the fish crossed the sonar beam) was observed for 83% of fishes >100 mm (target strength > -45 dB) in Rimov Reservoir. Remaining fishes >100 mm in the open water had two different swimming modes. Either they were too close to the surface to be able to follow a sinusoidal trajectory (inhabiting the uppermost

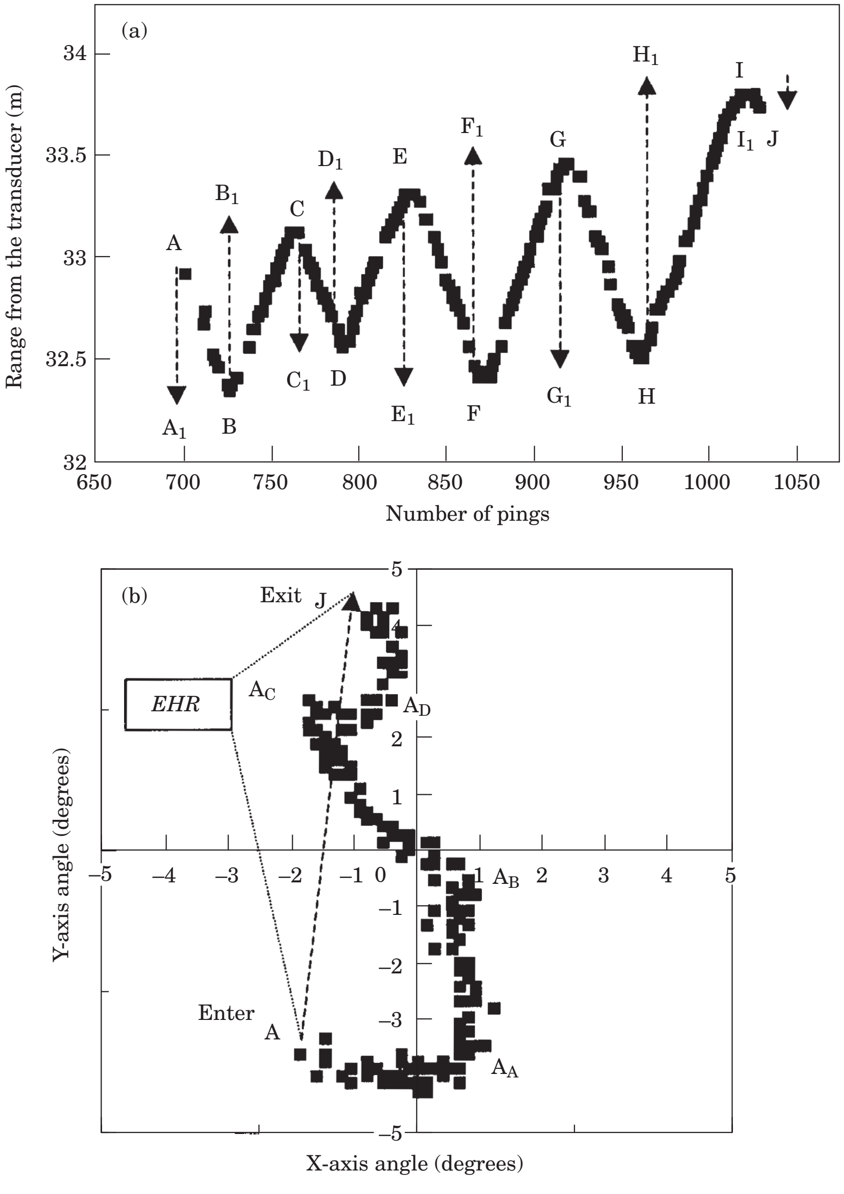

FIG. 2. Subsequent positions of sinusoidally swimming fish moving across the ultrasonic beam. The descriptive parameters of the trajectory of this particular fish: D_{aver}=3·03 m, L_S=221 mm, CT=66 s, E_{no}=202 pings, RC_{no}=4, FC=3·6 cycles min^{-1}, SS=14·7 cm s^{-1}, RSC=243 cm, DSC=17 s, A_{max}=96 cm, A_{min}=57 cm, A_{aver}=81 cm, VR=693 cm, HR=681 cm, EHR=387 cm, TSD=972 cm, IH=1·76, IV=1·79, IFM=0·40, IHS=0·98, IT=0·89 (for explanation of parameters see Appendix). (a) Swimming trajectory in the vertical plane (side view). B, C, D, E, F, G, H and I, turning points; A, entry of the fish to the beam cone; J, exit of the fish from the beam cone; A_1, B_1, C_1, D_1, E_1, F_1, G_1, H_1 and I_1, auxiliary points to measure the *VR* parameter. (b) Swimming trajectory in the horizontal plane (top view) with entry (A) and exit (J) from the beam cone. A_A, A_B, A_C and A_D, auxiliary points to measure the *HR* parameter and comparison with *EHR* parameter. X-axis, angular distance from the beam axis in one horizontal plane. Y-axis, angular distance from the beam axis in second horizontal plane.

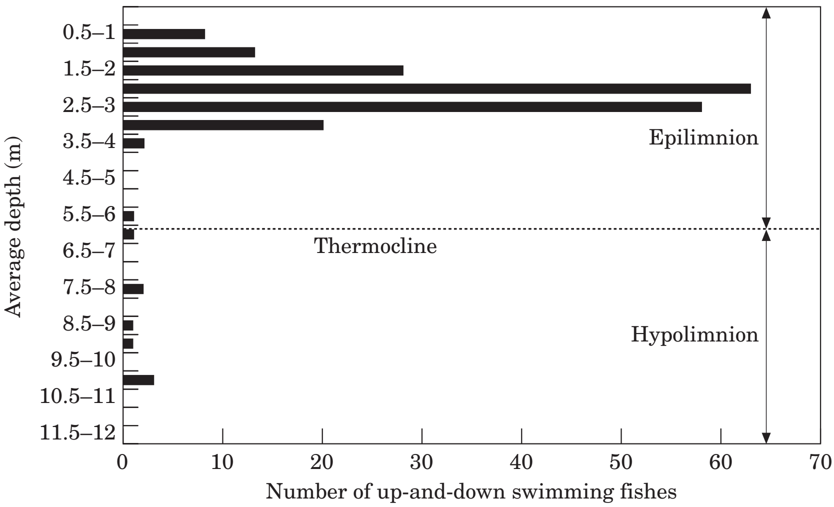

FIG. 3. Average summer depth of up-and-down swimming fishes in the open water of the Rimov Reservoir. The distribution of the epilimnion, hypolimnion and thermocline are given.

0·5 m below the water surface; 6% of fish records) or they swam straight just below the thermocline (depth range 7–12 m; 11% of fish records).

The main stock of up-and-down swimming fishes was observed mostly in the depth (D_{aver}) range between 0·5–4 m of the water column in the upper and middle layers of the epilimnion (Fig. 3). A few sinusoidally swimming individuals were recorded below this down to a depth of 10·5 m (i.e. below the thermocline) in the upper layers of the hypolimnion. Table I gives the mean, S.D. and minimum and maximum value of the parameters describing the sinusoidal movement pattern. There was no influence of fish size ($P>0·05$) or time of the day on swimming depth of a fish ($P>0·05$).

The up-and-down swimming mode was found for fishes with the TS_{max} range from $-42·2$ to $-34·1$ dB, which when converted into fish length using the general equation of Love (1971) gave a predicted length range of 136 to 359 mm L_S (Fig. 4). Average L_S was 228 mm. The length frequency distribution corresponds to common sizes of three dominant fish species of the Rimov Reservoir: bleak, roach and common bream (Vasek *et al.*, 2000). The up-and-down swimming pattern was not found for fishes <136 mm.

The average amplitude (A_{aver}) of the observed sinusoidal movement, the vertical range between the lowermost and the uppermost position of up-and-down swimming fishes, ranged for individual fish from 19 to 321 cm [Fig. 5(a)]. Average amplitude for all sinusoidal movements was 98 cm. Most cycles had amplitudes of *c.* 1 m, but the distribution was slightly asymmetric with some individuals performing cycles with an amplitude >2 m. Even with the smallest amplitude recorded, regular change of depth occurred, and the trajectory was clearly sinusoidal (vertical range resolution of the sonar system was 0·03 m). The size of average amplitude was not dependent on fish length ($P>0·05$).

The frequency of cycling (FC) ranged from 1·3 to 10·1 cycles min^{-1} [Fig. 5(b)]. The average frequency of cycling was nearly 4 cycles min^{-1}, but the distribution was skewed towards slower cycling (mode=3 cycles min^{-1}). The frequency of

TABLE I. Mean, S.D., maximal and minimal values for individual parameters describing sinusoidal movement of open water fishes in Rimov Reservoir during the summer (n=201). For explanation of parameters see Appendix

Parameter	Mean	S.D.	Min.	Max.
^{1}Average target strength of sinusoidally swimming fish (dB) (TS_{aver})	−43·2	2·4	−48·3	−37·5
^{2}Average fish depth in sampled water column (m) (D_{aver})	3·0	1·46	0·57	10·35
^{3}Recorded time of day (min) (RT)	1227		522	2027
^{4}Crossing time (s) (CT)	39	21	15	154
^{5}Number of recorded pings (E_{no})	98	57	39	401
^{6}Number of recorded sinusoidal cycles (RC_{no})	2·3	1·2	1·0	7·5
^{7}Maximal amplitude of sinusoidal trajectory (cm) (A_{max})	112	52	23	345
^{8}Minimal amplitude of sinusoidal trajectory (cm) (A_{min})	84	49	17	321
^{9}Average amplitude of sinusoidal trajectory (cm) (A_{aver})	98	46	19	321
^{10}Vertical range (cm) (VR)	402	247	57	1266
^{11}Horizontal range (cm) (HR)	450	163	91	998
^{12}Effective horizontal range (cm) (EHR)	306	88	47	468
^{13}Total recorded swimming distance (cm) (TSD)	617	265	130	1590
^{14}Swimming speed (cm s^{-1}) (SS)	17·7	6·2	9·9	42·0
^{15}Frequency of cycling (cycles min^{-1}) (FC)	3·9	1·5	1·3	10·1
^{16}Range of sinusoidal cycle (cm) (RSC)	298	104	102	662
^{17}Duration of sinusoidal cycle (s) (DSC)	18	7	6	45
^{18}Horizontal index (IH)	1·55	0·79	1·0	9·25
^{19}Vertical index (IV)	1·39	0·96	0·21	6·5
^{20}Index of forward movement (IFM)	0·55	0·17	0·10	0·95
^{21}Index of horizontal swimming (IHS)	1·45	0·88	0·34	5·70
^{22}Average TS in uppermost position of sinusoidal cycle (dB) (TS_{upper})	−38·1	1·6	−42·7	−33·7
^{23}Average TS in lowermost position of sinusoidal cycle (dB) (TS_{lower})	−38·1	1·7	−41·8	−34·1
^{24}Average TS in descending phase of sinusoidal cycle (dB) (TS_{desc})	−44·5	3·7	−51·8	−32·4
^{25}Average TS in ascending phase of sinusoidal cycle (dB) (TS_{asc})	−45·7	2·7	−52·3	−39·6
^{26}Average TS in top (uppermost and lowermost) positions of sinusoidal cycle (dB) (TS_{max})	−38·1	1·6	−42·2	−34·2
^{27}Average TS in transient (descending and ascending) phase of sinusoidal cycle (dB) ($TS_{desc\ \&\ asc}$)	−45·1	2·7	−51·1	−37·3
^{28}Tilting index (IT)	0·85	0·05	0·69	1·00
^{29}Estimate fish length (mm) (L_S)	228	44	136	359

cycling decreased significantly with increasing amplitude (Fig. 6). Larger fishes had higher frequency of cycling (regression analysis; $F_{1,199}$=22·86, P<0·01).

The range of sinusoidal cycle (RSC), the wavelength of the trajectory of sinusoidal movement, was from 102 to 662 cm [Fig. 5(c)]. Average range of the sinusoidal cycle was 298 cm. The range of the sinusoidal cycle decreased significantly with rising frequency of cycling (Fig. 7).

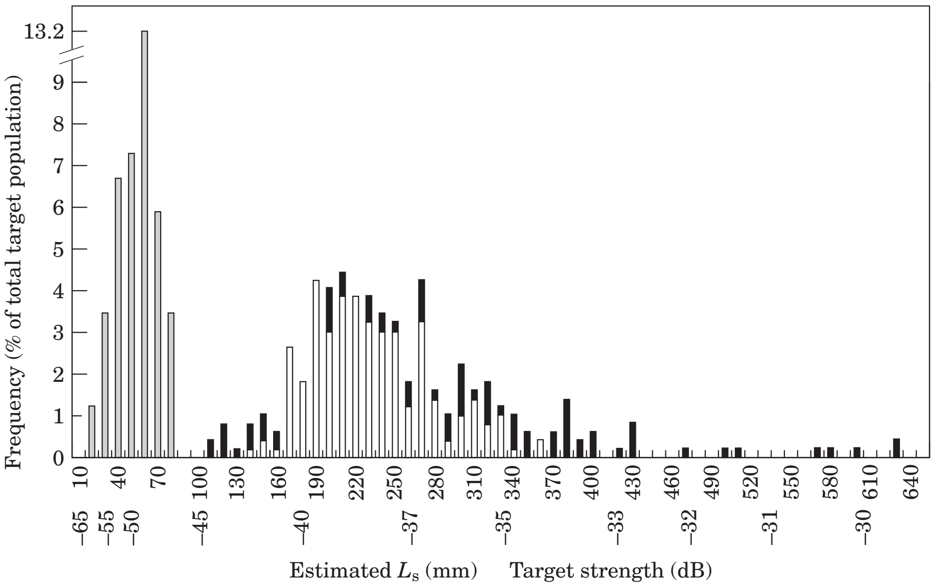

FIG. 4. Frequency distribution of *TS* and estimated lengths of all tracked fishes (*TS*: L_S conversion according to Love, 1971) recorded in the open water of the Rimov Reservoir during July and August 1998. ■, non-cycling fishes >+1 years; □, cycling fishes >+1 years; ▨, juvenile (+0 and +1 years) non-cycling fishes. Juvenile fish <100 mm L_S did not show a sinusoidal swimming pattern. The majority of the larger fishes exhibited a sinusoidal pattern during daytime. Some non-cycling fishes overlapped in size with the cycling population, while others were clearly larger (predatory fishes) or smaller (juveniles).

The duration of a sinusoidal cycle (*DSC*) was on average 18 s, with a range of values from 6 to 46 s [Fig. 5(d)].

The average swimming speed (*SS*) of the fishes executing sinusoidal swimming was 17·7 cm s^{-1} (0·6 km h^{-1}). The maximal swimming speed was 42 cm s^{-1} (1·5 km h^{-1}) and the minimal swimming speed was 9·9 cm s^{-1} (0·35 km h^{-1}) [Fig. 5(e)]. The distribution was highly asymmetric with only a few individuals swimming at speeds >30 cm s^{-1} (>1 km h^{-1}). A significant linear increase of swimming speed with increase of fish length was observed (Fig. 8).

The average value of the horizontal index (*IH*) was 1·55 (the fishes swam in the horizontal plane 1·55 times further from entry point to exit point of the beam compared to the vector connecting enter point and exit point) [Fig. 5(f)]. The minimal value for *IH* was 1·00 (direct forward movement; $HR=EHR$). By contrast the maximal value for *IH* was 9·25 (nearly no forward movement, the fish was swimming in the horizontal plane almost in the circle).

The average value of the vertical index (*IV*) was 1·39 (the fish swam in vertical plane 1·39 times further from entry point to exit point of the beam compared to the vector connecting entry point and exit point) [Fig. 5(f)]. The minimal value for *IV* was 0·21 (displaying low amplitude of the sinusoidal trajectory or low frequency of cycling). The maximal value for *IV* was 6·51 (showing highly extensive movement of up-and-down swimming fishes in the vertical plane, $VR \gg EHR$). Smaller up-and-down swimming fishes swam significantly more extensively in the vertical plane than did larger fishes (regression analysis; $F_{1,199}=27{\cdot}99$, $P<0{\cdot}01$).

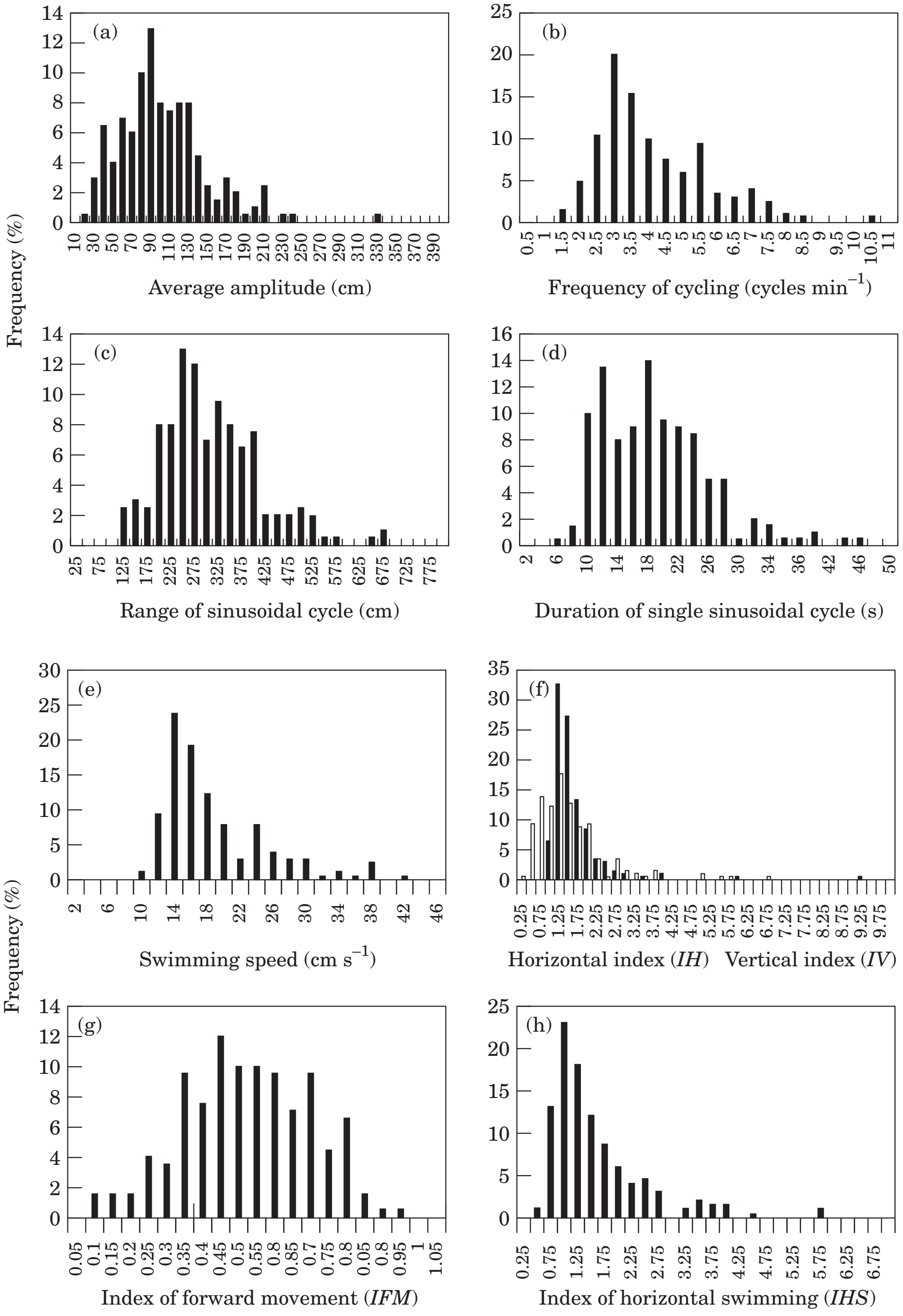
Frequency (%)
(a)
0 2 4 6 8 10 12 14
10 30 50 70 90 110 130 150 170 190 210 230 250 270 290 310 330 350 370 390
Average amplitude (cm)
(b)
0 5 10 15 20 25
0.5 1 1.5 2 2.5 3 3.5 4 4.5 5 5.5 6 6.5 7 7.5 8 8.5 9 9.5 10 10.5 11
Frequency of cycling (cycles min^{-1})
(c)
0 2 4 6 8 10 12 14
25 75 125 175 225 275 325 375 425 475 525 575 625 675 725 775
Range of sinusoidal cycle (cm)
(d)
0 2 4 6 8 10 12 14 16
2 6 10 14 18 22 26 30 34 36 42 46 50
Duration of single sinusoidal cycle (s)
Frequency (%)
(e)
0 5 10 15 20 25 30
2 6 10 14 18 22 26 30 34 38 42 46
Swimming speed (cm s^{-1})
(f)
0 5 10 15 20 25 30 35
0.25 0.75 1.25 1.75 2.25 2.75 3.25 3.75 4.25 4.75 5.25 5.75 6.25 6.75 7.25 7.75 8.25 8.75 9.25 9.75
Horizontal index (*IH*) Vertical index (*IV*)
(g)
0 2 4 6 8 10 12 14
0.05 0.1 0.15 0.2 0.25 0.3 0.35 0.4 0.45 0.5 0.55 0.8 0.85 0.7 0.75 0.8 0.05 0.8 0.95 1 1.05
Index of forward movement (*IFM*)
(h)
0 5 10 15 20 25
0.25 0.75 1.25 1.75 2.25 2.75 3.25 3.75 4.25 4.75 5.25 5.75 6.25 6.75
Index of horizontal swimming (*IHS*)

FIG. 5. (a-h).

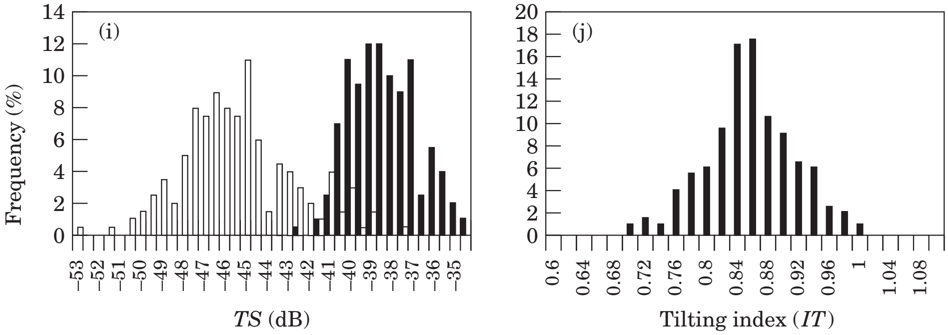

FIG. 5. (i-j).

FIG. 5. Frequency distribution of parameters: (a) average amplitude; (b) frequency of cycling; (c) range of sinusoidal cycle; (d) duration of single sinusoidal cycle; (e) swimming speed; (f) horizontal (■) and vertical indicies (□); (g) index of forward movement; (h) index of horizontal swimming; (i) maximum (■) and descending and ascending (□) target strengths; (j) tilting index, describing the sinusoidal movement of fishes recorded by a surface-facing transducer in the open water of the Rimov Reservoir during the summer 1998.

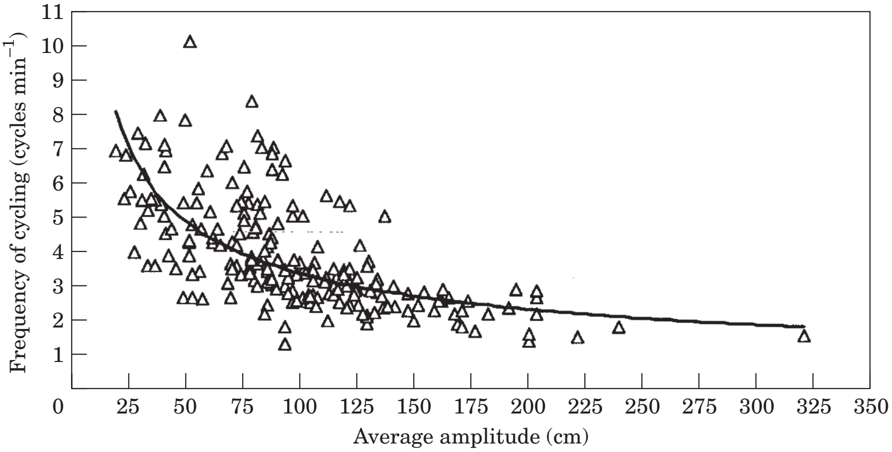

FIG. 6. The relationship between frequency of cycling (*FC*) and average amplitude (A_{aver}) of the sinusoidal cycle during up-and-down movement of open water fishes in the Rimov Reservoir. $y=38{\cdot}07 \,.\, x^{-0{\cdot}528}$, $r^2<0{\cdot}4556$, $F_{1,199}=166{\cdot}54$, $P<0{\cdot}001$.

The average value of the index of forward movement (*IFM*) was 0·55 (over half of the fish swimming trajectory represents forward swimming) [Fig. 5(g)]. *IFM* ranged from 0·10 (90% of trajectory was not necessary for direct crossing of the beam and other components of moving, especially up-and-down movement prevailed) to 0·95 (illustrates the dominant role of *EHR* compared to *HR* or *VR*). Increase of the *IFM* value was closely connected with the increase of swimming speed (regression analysis; $F_{1,199}=27{\cdot}18$, $P<0{\cdot}01$) and increase of fish length (regression analysis; $F_{1,199}=34{\cdot}78$, $P<0{\cdot}01$).

The average value of index of horizontal swimming (*IHS*) was 1·45 and ranged from 0·34 (extensive movement mainly in the vertical plane) to 5·71 (extensive movement mainly in the horizontal plane) [Fig. 5(h)]. The modal group was

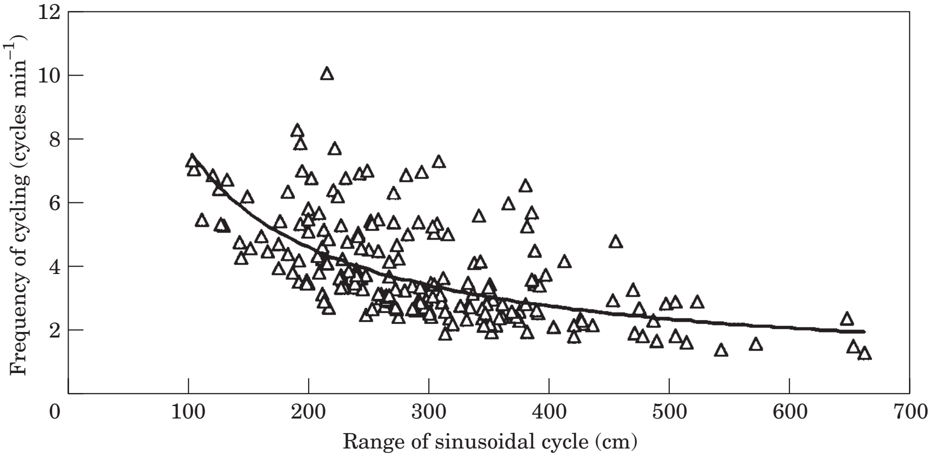

FIG. 7. The relationship between range of sinusoidal cycle (*RSC*) and frequency of cycling (*FC*) of open water fishes in the Rimov Reservoir. $y=234{\cdot}4\,.\,x^{-0{\cdot}741}$, $r^2=0{\cdot}4349$, $F_{1,199}=153{\cdot}15$, $P<0{\cdot}001$.

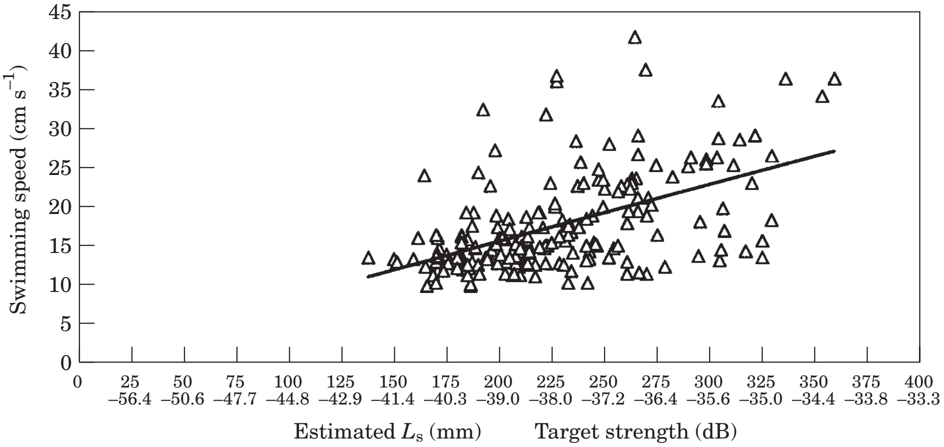

FIG. 8. The relationship between swimming speed (*SS*) and TS and estimated length (L_S, converted according to Love, 1971) of sinusoidally swimming open water fishes in the Rimov Reservoir. $y=0{\cdot}0723\,.\,x+1{\cdot}2599$, $r^2=0{\cdot}2697$, $F_{1,199}=73{\cdot}48$, $P<0{\cdot}01$.

IHS=1, which means that the horizontal and vertical components of fish movement were equal. The increase of *IHS* was significantly correlated with decrease of average amplitude (Fig. 9). Faster sinusoidal swimming was observed (regression analysis; $F_{1,199}=14{\cdot}70$, $P<0{\cdot}01$) and larger up-and-down swimming fishes were recorded (regression analysis; $F_{1,199}=49{\cdot}88$, $P<0{\cdot}01$) with increase of the *IHS* value.

TS during the sinusoidal cycle provide important information about changes in fish body orientation. The highest *TS* values were recorded at the turning points and TS_{upper} and TS_{lower} are identical (Table I). *TS* in transient phases of the cycle (TS_{desc} and TS_{asc}) were significantly lower [$t=34{\cdot}16$, d.f.$=200$, $P<10^{-6}$; Fig. 5(i)].

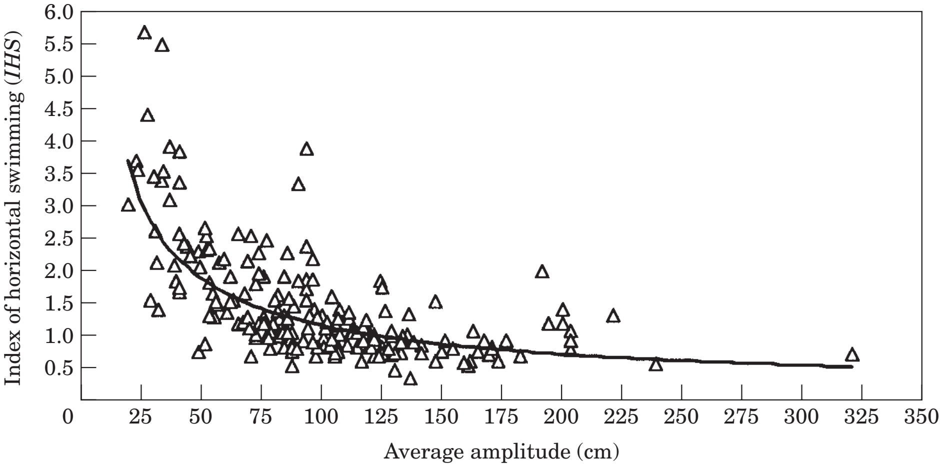

FIG. 9. The relationship between index of horizontal swimming (*IHS*) and average amplitude (A_{aver}) of up-and-down movement of open water fishes in the Rimov Reservoir. $y=29{\cdot}227 \,.\, x^{-0{\cdot}7029}$, $r^2=0{\cdot}4979$, $F_{1,199}=197{\cdot}31$, $P<0{\cdot}001$.

TABLE II. Number of fishes >1+ years with and without sinusoid cycling swimming pattern during day and night in three periods of study (summer 1998, November 1998, May 1999)

	Summer (July and August)		November		May	
	Day	Night	Day	Night	Day	Night
Hours of record processed	30	18	15	21	16	8
Cycling fishes	325	0	0	0	25	0
Non-cycling fishes	67	123	36	57	39	16

The average value of the tilting index (*IT*) was 0·85. The *IT* values ranged from 0·69 to 1·00 [Fig. 5(j)]. A value of *IT*=1·00 indicates perpendicular orientation of the fish to the cone of emitted ultrasound in each part of the sinusoidal cycle and no change in swim bladder volume. *TS* had thus the same value in all parts of the sinusoidal cycle (uppermost, descending, lowermost, ascending). An *IT* value of 0·69 shows that the reflection in the transient phases was weaker than in the top positions of the sinusoidal cycle (i.e. at turning points) and suggests in the transient phases an inclination of the fish body. The distribution of *IT* given in Fig. 5(j) was symmetrical showing that most fishes were tilted in a way that *TS* decreased by 15% from the maximum value.

The sinusoidal movement of pelagic fishes was closely dependent on time. It was never observed during the night (Table II, sinusoidal cycling swimming started after sunrise and was replaced by direct swimming before sunset). Up-and-down swimming was detected during all observations from June to August 1998. During the observations in mid-November 1998, sinusoidal movement of pelagic fishes was absent. A smaller data set from May 1999 showed less intense occurrence of sinusoidal cycling swimming in the open water, mainly because of the coincidence with the spawning period of part of the bream and bleak populations.

DISCUSSION

A majority of fishes >1+ years in the open water of the Rimov Reservoir seem to spend most of their summer days performing peculiar cycling movements instead of ' normal ' swimming. What can be the causes for this behaviour?

Simultaneous studies of cyprinid fish gut content (M. Vasek, J. Peterka, J. Matena, J. Kubečka, M. Čech, M. Prchalova, V. Drastik & M. Hladik, unpubl. data) showed that the period of sinusoidal swimming coincided with the period of intensive feeding on larger zooplankton, mainly *Daphnia* and *Leptodora*, which were highly preferred in the diet (Ivlev electivity indices $E_{Daphnia}=0{\cdot}68$, $E_{Leptodora}=0{\cdot}95$). Adult fishes (common bream, bleak and roach, together represent *c.* 90% of the fish stock of the Rimov Reservoir) of size structure similar to cycling fishes (Fig. 4) are clearly the main predators of zooplankton in the open water at these periods. Juveniles (fishes <100 mm) seem to avoid this area during the day and to stay in the littoral (Gliwicz & Jachner, 1992) or in shoals in upper layers of the hypolimnion (M. Čech, unpubl. data). Large, predatory fishes (Fig. 4) are present in the epilimnion, but do not perform sinusoidal movement.

The up-and-down movements probably relate to planktivory. Thetmeyer & Kils (1995) showed that transparency of zooplankton is an excellent strategy for staying invisible to horizontally scanning eyes. Planktonic prey might appear more visible against the bright light of the sky (darker due to absorbance at opaque parts of the body) or dark depths (brighter due to light scattered in their tissue) compared with the less contrasting background directly in front of straight swimming fishes (Janssen, 1981, 1982; Lazzaro, 1987; Thetmeyer & Kils, 1995). The up-and-down swimming may be a way the planktivorous fishes search for patches of planktonic food or larger zooplankton. Janssen (1982) assumed swim-search feeding behaviour for continually feeding, obligatory planktivores and hover-search for facultative planktivores. Omnivorous cyprinid fishes of the Rimov Reservoir are, because of their riverine origin (Fernando & Holčik, 1991; Holčik, 1998), clearly facultative planktivores. The continuous sinusoidal cyclic swimming during foraging on zooplankton, however, resembles the swim-search strategy of obligatory planktivores which can be (as shown in this study) adopted also by the facultative planktivores in the open water, when zooplankton represents their main feeding source.

When the sinusoidal swimming pattern was first observed, it was questioned whether it is caused by active up-and-down swimming or just by changes in swim bladder volume during the vertical movement (Videler, 1993; Webb, 1993*a*,*b*). Gliding up and down could theoretically be more advantageous for inspecting of large volumes of epilimnetic water with less expenditure on active metabolism (Weihs, 1973, 1974). Gliding pattern is an unlikely explanation, because the up-and-down swimming pattern is symmetric with respect to the cycle time. The role of the swim bladder seems to be rather limited. If a change of swim bladder volume determines the up-and-down movement, the *TS* in the descending phase should be smaller than in the ascending phase (fishes with reduced swim bladder volume would sink and vice versa). But this was not the case. Moreover, *TS* in the descending phase of the sinusoidal cycle was significantly higher than *TS* in the ascending phase of the sinusoidal cycle (t=4·72, d.f.=200, P<0·01). This is likely to be caused by a stronger echo in head aspect in comparison with the echo in tail aspect (Love, 1977). These results suggest that the up-and-down fish movement is an active mechanism with changes in body tilt in the direction of swimming. The values of *IT* even suggest the geometric tilt of the fish body during oscillations. The average decrease of 15% maximum *TS* in dB falls within the range of a 13–16% decrease of *TS*. For this range, it is possible to calculate an average body tilt angle during the ascending and descending phase of the cycle of *c.* 30° (Love, 1977). This is not far from optimal attack angles when the prey is visible for the predator but the predator is nearly invisible to the prey (Thetmeyer & Kils, 1995).

There is very little information on sinusoidal cyclic swimming patterns observed *in situ* in the literature. A rather similar pattern of swimming was briefly reported from a small section of a backwater locality in the Danube floodplain (Haberlehner, 1988). Diving observations there revealed up-and-down swimming by roach consuming plankton. Janssen (1981) noted up-and-down cycling for blueback herring *Alosa aestivalis* (Mitchill), when the fish fed only during the ascending phase of the cycle. With an experimental arrangement similar to the present observations (up-looking split beam sonar), Arrhenius *et al.* (2000) did not observe cyclical movement for juvenile brook trout *Salvelinus fontinalis* (Mitchill), alewife *Alosa pseudoharengus* (Wilson) and fry of yellow perch *Perca flavescens* (Mitchill). The results of their study, however, concentrated on measuring the swimming speeds of fishes, were similar to the values estimated in present study.

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APPENDIX. PARAMETERS DESCRIBING THE SINUSOIDAL MOVEMENT OF FISHES

[1] Average target strength of sinusoidally swimming fish (dB) (TS_{aver}) is calculated from all recorded target strength values of analysed sinusoidal trajectories.

[2] Average fish depth in sampled water column (m) (D_{aver}) is calculated as an average fish distance from the transducer and taken off from the distance between transducer and waveless water surface.

[3] Recorded time of the day (min) (*RT*) is the time period of the day when the sinusoidally swimming fish was recorded.

[4] Crossing time (s) (*CT*) is the time spent by a sinusoidally swimming fish in between the borders of emitted ultrasound cone.

[5] Number of recorded pings (echoes) (E_{no}) is the number of acoustic emissions reflected from each sinusoidally swimming fish.

[6] Number of recorded sinusoidal cycles (RC_{no}).

[7] Maximal amplitude of sinusoidal trajectory (cm) ($A_{\max}$).

[8] Minimal amplitude of sinusoidal trajectory (cm) ($A_{\min}$).

[9] Average amplitude of sinusoidal trajectory (cm) (A_{aver}) (all the amplitudes, $A_{\max}$, $A_{\min}$, A_{aver}, were measured in the vertical plane).

[10] Vertical range (cm) (*VR*) is defined as a total swimming range in the vertical plane of the sinusoidal movement [$VR = \mathrm{A}\rightarrow\mathrm{A}_1 + \mathrm{B}\rightarrow\mathrm{B}_1 \ldots + \mathrm{I}\rightarrow\mathrm{I}_1$, Fig. 2(a)].

[11] Horizontal range (cm) (*HR*) is defined as a total swimming range in the horizontal plane of the sinusoidal movement [$HR = \mathrm{A}\rightarrow\mathrm{A}_\mathrm{A} + \mathrm{A}_\mathrm{A}\rightarrow\mathrm{A}_\mathrm{B} \ldots + \mathrm{A}_\mathrm{D}\rightarrow\mathrm{J}$, Fig. 2(b)].

[12] Effective horizontal range (cm) (*EHR*) is defined as a value of the vector joining the first and the last recorded echo of a sinusoidally swimming fish in the horizontal plane [$EHR = \mathrm{A}\rightarrow\mathrm{J}$, Fig. 2(b)].

[13] Total recorded swimming distance (cm) (*TSD*), $TSD = \sqrt{[(VR)^2 + (HR)^2]}$, (Arrhenius *et al.*, 2000).

[14] Swimming speed (cm s^{-1}) (*SS*), $SS = (TSD)\,(CT)^{-1}$ (Arrhenius *et al.*, 2000).

[15] Frequency of cycling (cycles min^{-1}) (*FC*), $FC = (RC_{\text{no}})\,(CT)^{-1}$.

[16] Range of sinusoidal cycle (cm) (*RSC*), $RSC = (TSD)\,(RC_{\text{no}})^{-1}$.

[17] Duration of sinusoidal cycle (s) (*DSC*), $DSC = (CT)\,(RC_{\text{no}})^{-1}$.

[18] Horizontal index (*IH*), $IH = (HR)\,(EHR)^{-1}$ [represents in the horizontal plane the deviation value of the sinusoidal trajectory from the effective horizontal range (*EHR*)].

[19] Vertical index (*IV*), $IV = (VR)\,(EHR)^{-1}$ [represents in the vertical plane the deviation value of the sinusoidal trajectory from the effective horizontal range (*EHR*)].

[20] Index of forward movement (IFM), $IFM = (EHR)\ (TSD)^{-1}$ [in the vertical and in the horizontal level both displays the deviation value of the sinusoidal trajectory from the effective horizontal range (EHR)].

[21] Index of horizontal swimming (IHS), $IHS = (HR)\ (VR)^{-1}$ represents the share of horizontal components of movement of the sinusoidal swimming pattern.

[22] Average TS in uppermost position of sinusoidal cycle (dB) (TS_{upper}) is calculated from all recorded target strength values in uppermost position of each cycle of the analysed sinusoidal trajectory [turning point C, E, G, I, Fig. 2(a)].

[23] Average TS in lowermost position of sinusoidal cycle (dB) (TS_{lower}) is calculated from all recorded target strength values in lowermost position of each cycle of the analysed sinusoidal trajectory [turning point B, D, F, H, Fig. 2(a)].

[24] Average TS in descending phase of sinusoidal cycle (dB) (TS_{desc}) is calculated from all recorded target strength values in the descending phase of each cycle of the analysed sinusoidal trajectory [from turning point A→B, C→D, E→F, G→H, Fig. 2(a), turning points are not included in the calculation].

[25] Average TS in ascending phase of sinusoidal cycle (dB) (TS_{asc}) is calculated from all recorded target strength values in the ascending phase of each cycle of the analysed sinusoidal trajectory [from turning point B→C, D→E, F→G, H→I, Fig. 2(a), turning points are not included in the calculation].

[26] Average TS in top (uppermost and lowermost) positions of the sinusoidal cycle (dB) (TS_{max}), $TS_{\mathrm{max}} = 0{\cdot}5\ (TS_{\mathrm{upper}} + TS_{\mathrm{lower}})$ is assumed to be maximal fish TS. Straight ‘ normal ’ swimming position of fish at turning points was assumed.

[27] Average TS in transient (descending and ascending) phase of sinusoidal cycle (dB) ($TS_{\mathrm{desc\ \&\ asc}}$), $TS_{\mathrm{desc\ \&\ asc}} = 0{\cdot}5\ (TS_{\mathrm{desc}} + TS_{\mathrm{asc}})$ is calculated as an average from target strength values in both descending and ascending phases of the analysed sinusoidal trajectory.

[28] Tilting index (IT), $IT = (TS_{\mathrm{max}})\ (TS_{\mathrm{desc\ \&\ asc}})^{-1}$ is introduced to document the decrease of TS in descending and ascending phases of the cycle compared to TS_{max} in turning points.

[29] Estimated fish length (mm) (L_{S}), $L_{\mathrm{S}} = 10(10^{(0{\cdot}0524\ TS_{\mathrm{max\text{-}eb}})})$, where $eb = 0{\cdot}9 \log F\text{-}62$ (F − frequency of 120 KHz) is calculated using Love’s (1971) equation for vertical beaming at 120 KHz.