

Acoustic study of fish and invertebrate behavior in a tropical reservoir

Marie Prchalová ^{a,*}, Vladislav Draščík ^{a,b}, Jan Kubečka ^a, Boonsong Sricharoendham ^c,
Fritz Schiemer ^d, Jacobus Vijverberg ^e

^a Hydrobiological Institute AS CR, Na Sádkach 7, 370 05 České Budějovice, Czech Republic

^b Faculty of Biological Sciences, University of South Bohemia, 370 05 České Budějovice, Czech Republic

^c National Inland Fisheries Institute, Bangkok, Thailand

^d Department of Limnology, University of Vienna, Austria

^e NIOO–KNAW Centre for Limnology, The Netherlands

Accepted 11 March 2003

Abstract

The fish and invertebrate behavior of the Ubol Ratana Reservoir, Thailand, were monitored using up- and downlooking split beam sonar located at a fixed location. In the same area and period, ichthyoplankton nets and multimesh gillnets were used. The bulk of targets, recorded by acoustics and direct capture, consisted both of fish 3–4 cm long and insect larvae 0.2–1 cm long. Diurnal patterns of behavior were very distinct: during the daytime, invertebrates were hidden in the bottom and most fish stayed in compact shoals. Time course of acoustic fish biomass and abundance was very variable due to shoaling. Only the largest fish were recorded as solitary targets. At night, the whole acoustic range was filled with targets and the time course of fish biomass (5–15 kg ha⁻¹) and abundance (20–45 thousand individuals ha⁻¹) were more constant. The biomass increased mostly at surface layers. Fish appeared in the evening in the water column 1 h earlier and stayed there in the morning 1 h longer than invertebrates. Dawn and dusk are good periods for studying fish before invertebrates outnumber them. Apart from fish, according to the target strength, swimming speed and depth distribution, at least four groups of water invertebrates were distinguished acoustically, some with extremely fast vertical movement (7–9 cm s⁻¹ vertical speed). Comparison of up- and downlooking observations gave comparable results in midwater layer outside the near-field of the transducer. The uplooking approach can be more suitable for night records; downlooking for the day.

© 2003 Éditions scientifiques et médicales Elsevier SAS and Ifremer/IRD/Inra/Cemagref. All rights reserved.

Keywords: Acoustics; Echospecies; Target strength; Acoustic tracking and identification; Behavioral pattern

1. Introduction

Acoustic surveys of tropical lakes and reservoirs are much less numerous than similar surveys of temperate waters (Guillard, 1998; Schiemer et al., 2001; Tumwebaze et al., 2002). The main reason is smaller research intensity in developing countries. Another important reason may be the much more complex animal community, which is less known and may complicate interpretation of echosounder records. This paper represents a part of an attempt to estimate fish community of a large and relatively shallow reservoir in Thailand. The aim of this study was to establish acoustic conditions,

potential limitations, fish size distribution and diurnal cycle of animal behavior in the reservoir.

2. Materials and methods

2.1. Study area

The reservoir Ubol Ratana (16° 30'–16° 55' N; 102° 20'–102° 40' E) in Thailand, Khon-Kaen Province, belongs to the belt of tropical monsoon climate. The year of impoundment was 1965. The water surface area is 410 km², maximal depth is 19.5 m and average depth is 6.2 m (Pholprasith and Virapat, 1995; Simon et al., 2001). In 2000, ichthyofauna consisted of 67 species from 18 families. Most species are from families Cyprinidae, Cobitidae and Bargidae. Majority of

* Corresponding author. Fax: +420-38-5300248.

E-mail address: marie.prchalova@bf.jcu.cz (M. Prchalová).

Table 1
Parameters of sonar system

<i>Simrad EY 500—split beam echosounder</i>	
Operating frequency	120 kHz
Transmission power	63 W
<i>Simrad ES 20-7 G—circular beam transducer</i>	
Nominal 3 dB beam angle	7°
Face diameter	11 cm
<i>Transceiver</i>	
Pulse duration	0.1 ms
Frequency bandwidth	12 kHz
Pulse repetition rate	10 Hz
<i>Single echo detector</i>	
Min. and max. returned pulse width	0.6- to 1.8-fold transmitted pulse duration
Max. off axis distance	6 dB
Max. phase deviation	10 phase steps
TS threshold for 40 log R TVG	-79 dB
S_V threshold for 20 log R TVG	-65 dB

total fish biomass is represented by family Cyprinidae—90%, and then Clupeidae—5–10% (Pholprasith and Sirimongkonthaworn, 1999). Small clupeids are very abundant in the open water. The fixed location acoustic study was done at the sampling station 5 (Simon et al., 2001), which is located in the dam region with depth of 10 m. The distance from the shore was more than 3 km, the Secchi-disc transparency 1 m, dissolved oxygen concentration 7.1 mg l^{-1} , temperature $23.5 \text{ }^\circ\text{C}$ (no thermal stratification). The station was chosen due to good representativeness for the lacustrine part of the reservoir and good access.

2.2. Field survey

The Ubol Ratana Reservoir was studied during 9–11 February 2000 by the sonar system set as described in Table 1. According to the manufacturer, the safe start of the far-field is located 1 m from the transducer. This was verified by the in situ experiments with the standard target insonified at 10 cm distances from the transducer. From the distance of 90 cm onwards, the echo intensity from the standard target remained constant (40 log R time-varied-gain, TVG). The sonar system was calibrated with a tungsten-carbide standard target (32 mm; MacLennan and Simmonds, 1992). The echosounder was driven by a personal computer and all data were immediately stored on the hard disc of the PC. An accumulator 12 V battery powered whole sonar system and the computer.

The first 24 h run of records (12:30 9 February–2:30 10 February) was recorded with the uplooking position of the beam with the transducer mounted on the bottom facing vertically to the surface. Upward-looking vertical position was ensured by the heavy counterbalancing weight mounted to the cable socket of loosely held transducer. The second

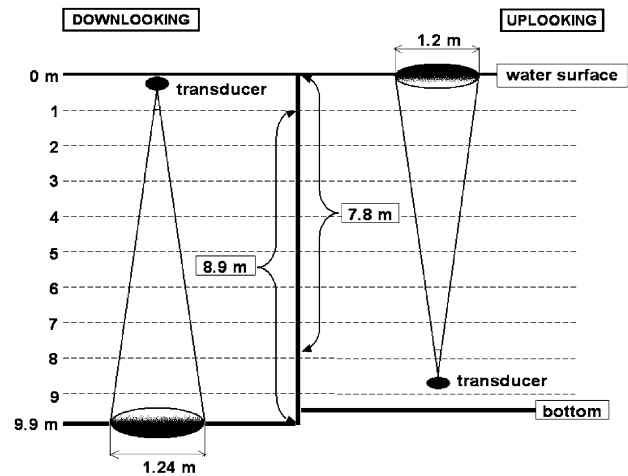


Fig. 1. Designs of up- and downlooking surveys with dividing of water column into depth layers and with diameters of acoustic beams in the furthest distance from the transducer. Uplooking transducer had slightly shorter range due to the holding frame and shallower site.

24 h run (13:15 10 February–12:00 11 February) was recorded with downlooking vertical beaming with the transducer mounted closely to the rectangle float. During calm weather of our survey, this setup ensured vertical orientation of the acoustic beam. Recording sites for two approaches were nearly the same, but due to some microhabitat differences, the uplooking site was slightly shallower than the downlooking site (Fig. 1). Recording range was also shortened due to the height of transducer holding frame (60 cm). The transducer had 130 m long cable and the sonar system was placed on anchored floating platform 100 m away from the transducer. Blind zone by the phase boundaries was about 15 cm thick.

The open water of the reservoir near the acoustic station was sampled by 5 min tows by an ichthyoplankton tow-net and multimesh gillnets. The parameters for the ichthyoplankton net were 1 m in diameter, mesh size 1.5 mm and design was similar as described in Wanzenböck et al. (1997). Gillnets were of bar mesh sizes 5, 6.25, 8, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm set for whole 24 h period, emptied every 4 h. Total length (mm) of all captured animals was measured.

2.3. Post processing

Sizes of all acoustically detected single targets were identified using Love's equation (Love, 1977) for 120 kHz for simplicity. Majority of fish have swimbladder and many of the invertebrates have gas inclusions. There is no direct information on target strength TS of local animals available. The biomass of fish was calculated with the length–weight relationship for Sri Lankan fish provided by Dr. U. Amarasinghe from the Kelaniya University, Sri Lanka. The marginal length for distinguishing between two main categories of targets—'fish' and 'invertebrates'—was set at average TS value -60.5 dB , which corresponds approximately to 15 mm (Love, 1977). This threshold corresponds to low frequency groups of both targets and captured animals as shown at

Table 2
Four diurnal periods in up looking and downlooking

Period	Uplooking	Downlooking
Daytime	12:30–17:30 7:00–12:30	13:15–17:45 6:45–11:45
Dusk	17:30–18:45	17:45–19:00
Night	18:45–5:45	19:00–5:45
Dawn	5:45–7:00	5:45–6:45

Fig. 5. ‘Large fish’ were defined as longer than 270 mm (~–36.5 dB in TS). Simrad EP 500 post-processing software was used for biomass and abundance estimation. The elementary sampling unit for this analysis was recording of one 5 MB*.dg* file (Simrad EY 500 software), which took 16–18 min. The records were processed by scaling total integrated volume backscattering coefficient S_v by average backscattering cross-section ζ_{bs} (MacLennan et al., 2002) of a particular layer producing this volume density. This abundance was then proportionally distributed into 3 dB TS frequency groups according to TS frequency distribution. For fish and invertebrate tracking (connecting neighboring hits into one animal record), we used Sonar 5 software (Balk and Lindem, 2002; mostly manual tracking with maximum ping gap of 1 ping and minimum 5 echoes in a track). Attention was paid to tortuosity of the targets, only targets with the smooth trajectory through the beam were accepted.

Uplooking records were divided into seven depth layers from the surface (0–7.8 m). Downlooking records were divided into nine depth layers from 1 to 9.9 m. The data from the first 1 m from the transducer were not used due to the near-field. Each layer was 1 m thick except the shallowest one, which was in uplooking 1.8 m and the deepest one in downlooking 0.9 m thick (Fig. 1). In presentation of results, the layers are given from the true surface of the reservoir for both up- and downlooking. The records were divided into four diurnal periods—daytime, night, dusk and dawn (Table 2).

3. Results

3.1. Comparison of up looking and downlooking approaches

The values of total fish biomass, abundance and average weight attained comparable levels in most time intervals

Table 3

Difference in total average fish biomass (B) and abundance (A) between uplooking (Up) and downlooking (Down) from the same depth layers (1–8 m); one way ANOVA, P -level of 0.001. Average weight was calculated as B/A

Period	Biomass (kg ha^{-1})				P	Abundance (individuals ha^{-1})				P	Average weight (g)	
	Up		Down			Up		Down			Up	Down
	Mean	S.D.	Mean	S.D.		Mean	S.D.	Mean	S.D.		Mean	Mean
Daytime	2.3	6.3	7.8	18.9	0.145	5 800	19 400	34 400	86 400	0.087	0.40	0.23
Dusk	15.4	9.8	10.5	8.6	0.478	20 000	12 200	23 700	20 300	0.765	0.77	0.44
Night	6.4	2.8	6.7	3.3	0.687	26 500	7 600	34 700	9 100	<0.001	0.24	0.19
Dawn	2.5	1.4	6.8	3.6	0.519	16 800	5 100	29 300	16 200	0.189	0.32	0.23
24 h	5.2	5.8	7.3	11.8	0.175	17 100	16 700	33 700	52 500	0.012	0.30	0.22

(Table 3). Fish recorded by uplooking had usually larger average weight and non-significantly smaller abundance. The only significant difference was found for night, when the layer 1–2 m contained extremely abundant targets in downlooking. Daytime records showed the largest differences and variability because of very distinct aggregating behavior. Uplooking records contained significantly less dense shoals. Invertebrates dominated size distribution of both records, but the downlooking records had slightly larger proportion of fish with a smaller modal length (Fig. 5).

3.2. Diurnal development of fish and invertebrate communities

During the daytime, most fish followed general tendency for forming shoals or staying near the bottom. Single fish targets rarely appeared. Invertebrates were not visible acoustically and were most likely hidden in the bottom. For most of the time, the daytime echogram was empty. During early dusk (17:28), shoals disintegrated and single fish appeared mostly in deeper layers. Invertebrates started to rise from the bottom 1 h later than fish (18:30). At night, the entire water column was filled with organisms. Most fish moved then gradually to the upper part of the water column (0–5 m) and stayed there throughout the night. Dawn sequence of events was opposite to the dusk: invertebrates were disappearing approximately 1 h earlier than fish (6:15 ~ last recorded invertebrate targets). At about 5:50, single fish started to descend to deeper waters and gradually disappeared from most of echograms (at about 7:00).

The phenomenon of earlier fish rising from the bottom can be also shown on the diurnal development of the share of fish on total abundance of all targets (Fig. 2). Night pattern was characterized by lower share of fish (5–10%) within deeper layers (5–8 m) and higher fish proportion in the upper layers (0–5 m; 15–25%). Invertebrates represent the rest to 100%. During dusk and dawn, the fish showed two peaks in target composition in the open water. They stayed in the open water as single targets longer than invertebrates. During both day and night, invertebrate targets prevailed. During the daytime, the sizing of targets is much less reliable due to aggregation and the proportion of fish fluctuated vigorously. During the night, enormous amounts of invertebrates emerged from the bottom and outnumbered fish, which were present as single targets as well.

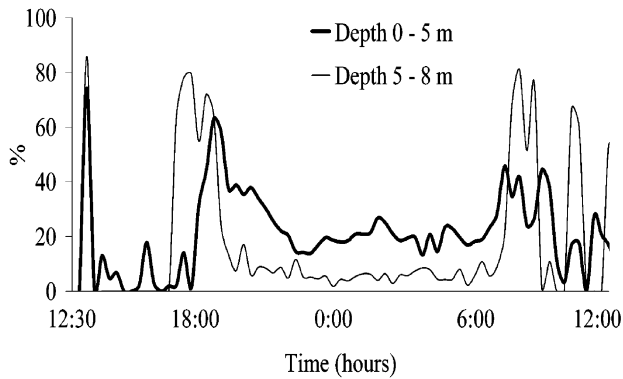


Fig. 2. Relative proportion of fish in total number of all recorded targets in two different parts of the water column; uplooking.

3.3. Biomass, abundance and average weight of fish

These three characteristics were calculated only for fish targets, $TS > -60.5$ dB. Biomass, abundance and average weight of fish followed a typical diurnal development. Appearance of fish shoals during the daytime caused extensive variation of fish biomass (Fig. 3, Table 3). During the night, the biomass stabilized on the level of $5\text{--}10\text{ kg ha}^{-1}$ and the hectaric abundance ranged between 20 and 45 thousand individuals, both showed less fluctuations and probably are more representative than the variable daytime data. The smallest average weight of fish was recorded at night. Slightly larger fish dominated single target population during the dusk while tiny fish were still in numerous small shoals.

Vertical distribution of fish biomass changed during the diurnal cycle (Fig. 4). During the day, the bottom layer (9–9.9 m) in downlooking contained high values of biomass. This peak consisted of bigger fish (average weight of 1.76 g, ~ 50 mm, ~ 50.5 dB), which did not seem to join the shoals. These fish seem to belong to the genus *Puntioplites* according to gillnets sampling. Another peak in daytime vertical distribution of fish biomass was recorded in upper layers especially by downlooking. Shoaling fish mostly composed this biomass. Night distribution of fish biomass was more even and more similar when recorded by different transducer deployments. The biomass was higher in upper layers; near-bottom peak of biomass was missing.

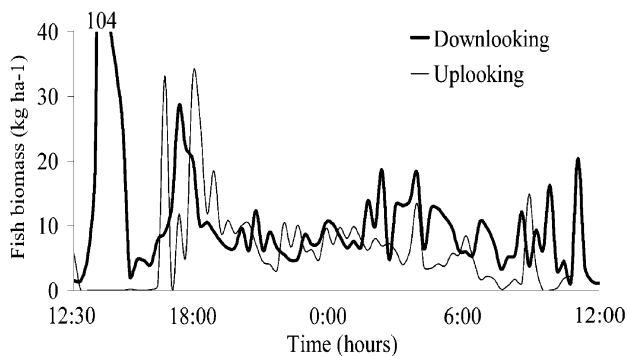


Fig. 3. The development of total fish biomass at all depth layers from up- and downlooking.

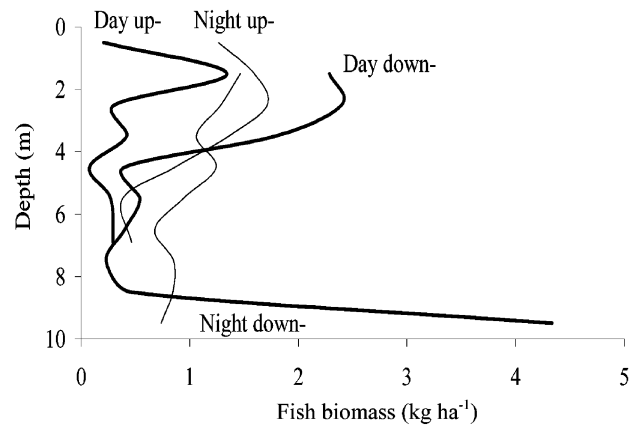


Fig. 4. Comparison of the vertical development of fish biomass during the daytime and the night in up- and downlooking. Thick line—day, thin line—night.

Occurrence of larger fish (≥ 27 cm, ~ 275 g, ~ 36.5 dB) was extremely sporadic. The longest detected target corresponded to 37 cm. The greatest frequency of larger fish was in the bottom layer in downlooking, but only with a density of 0.5 individual ha^{-1} . Low density of larger fish could be influenced by relatively small sampling volume.

3.4. Categories of acoustic targets

Fig. 5 gives the comparison between reconstructed target size by up- and downlooking acoustics with the direct capture by ichthyoplankton nets (the same depth layers, nighttime). Both approaches showed two peaks of two main groups of organisms: the first peak belongs to invertebrates with modal values from 3.5 to 5.1 mm (~ 72.5 to -69.5 dB). The second peak belongs to fish with values from 31 to 44 mm (~ 54.5 to -51.5 dB). After recalculating the acoustic length-frequency structure only for fish (>15 mm), the majority of fish individuals (70% in uplooking, 75% in downlooking, the same depth layers, nighttime) was represented by targets 22–44 mm long. According to direct catches, this peak consisted mostly of genus *Clupeichthys*, which was the most abundant fish from ichthyoplankton nets and also from gillnets. This genus covered length range from 22 to 44 mm of total length in catches from ichthyoplankton nets and range 30–58 mm from gillnets, with the most abundant size class 35–37 mm. In both acoustic and direct capture results, the invertebrate peak outnumbered the fish peak. The only exception was the bottom layer in downlooking, where frequencies in peaks were nearly equal. Modal length of small fish observed by the uplooking appeared slightly longer compared to downlooking. According to target strength, swimming and vertical speed, we were able to distinguish at least six categories of acoustic targets (acoustic species, echospecies), which are presented in Table 4 and are shown on echogram (Fig. 6). The pattern of echogram appearance (TS, duration-in-beam and change-in-range) was the initial criterion for discrimination of individual tracks into groups. Acoustic targets were analyzed from dusk and dawn in up- and downlooking. These

Table 4

Definition of categories of acoustic targets analyzed from dusk and dawn in uplooking and downlooking. The total length was calculated according to Love's general equation (1977)

Category of acoustic targets (number of tested targets)	Total length (mm)				Swimming speed (cm s ⁻¹)			Vertical speed (cm s ⁻¹)		
	Mean	Mean	S.D.	*	Mean	S.D.	*	Mean	S.D.	*
Fish (160)	42	-52.1	1.96	a	10.5	0.8	k	1.7	0.2	x
Slow targets (80)	3	-72.3	0.45	b	1.6	0.3	l	0.1	0.0	y
Ascending targets (40)	15	-60.5	0.71	c	2.4	0.1	l	1.6	0.2	x
Extreme targets (71)	10	-64.4	0.73	d	7.5	1.4	m	6.9	1.3	z
Standing targets (20)	13	-61.8	2.27	c	2.5	1.0	l	0.2	0.3	y
Subsurface liv. particles	<1.6	<-79	-	-	-	-	-	-	-	-

$$swim.speed = \sqrt{V_x^2 + V_y^2 + V_z^2} \cdot Vi, \text{ velocity in } x, y \text{ and } z \text{ direction, respectively, between first and last echo; } V_z, \text{ vertical speed (all speed calculations done according to Balk and Lindem, 2002).}$$

periods were appropriate for this kind of observation due to presence of single fish and invertebrates, which were spreading to the water column from the bottom. One way ANOVA rejected the hypothesis of homogeneity of parameters (TS, swimming and vertical speed) of echospecies (P -level < 0.001). Echospecies labeled with different letters in column* of Table 4 were found significantly different in selected parameters (P -level < 0.05; Tukey HSD test).

4. Discussion

4.1. Patterns of open water community

Short survey of a relatively shallow reservoir revealed the potential of vertical acoustic application in a complex system. Up- and downlooking approach usually provided comparable results. Uplooking can be more suitable for night recording, because more fish were in the upper part of the water column where there is the largest sampling volume. On the other hand, downlooking was more effective in recording

fish during daytime, when single larger fish tended to stay at the bottom layer. Both approaches have shown very distinct diurnal patterns of behavior like shoaling (Fréon et al., 1996; Helfman, 1993; MacLennan and Simmonds, 1992; Schiemer et al., 2001) during the day and shoal disintegration during the night and invertebrate emergence during the night. Acoustic study and direct sampling (Sricharoendham, personal communication) confirmed previous findings (Schiemer et al., 2001) that the fish community of a tropical reservoir is usually represented by huge numbers of tiny forage fish (average weight less than 1 g). This is very different compared to similar studies of temperate lakes and reservoirs where the weight of fish is 1–2 orders higher (Arrhenius et al., 2000; Čech and Kubečka, 2002).

4.2. Interpretation of echospecies

If we combine results from direct catch (Fig. 5) with categories of acoustic targets (Table 4), we can attempt to interpret some echospecies as reservoir animals. The combination is based on comparison of reconstructed total length

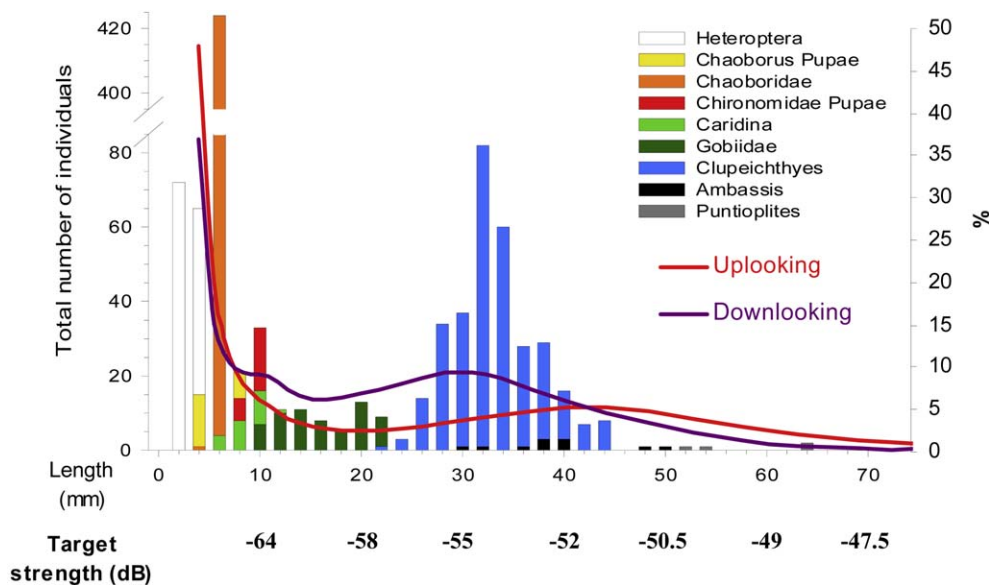


Fig. 5. Illustrative figure of size structure of invertebrates, ichthyoplankton and fish from night direct catch of ichthyoplankton nets (left x-axis with total number of individuals) and night acoustic length frequency structure in up- and downlooking (right y-axis with %). Values of TS corresponding to the length classes are given below x-axis.

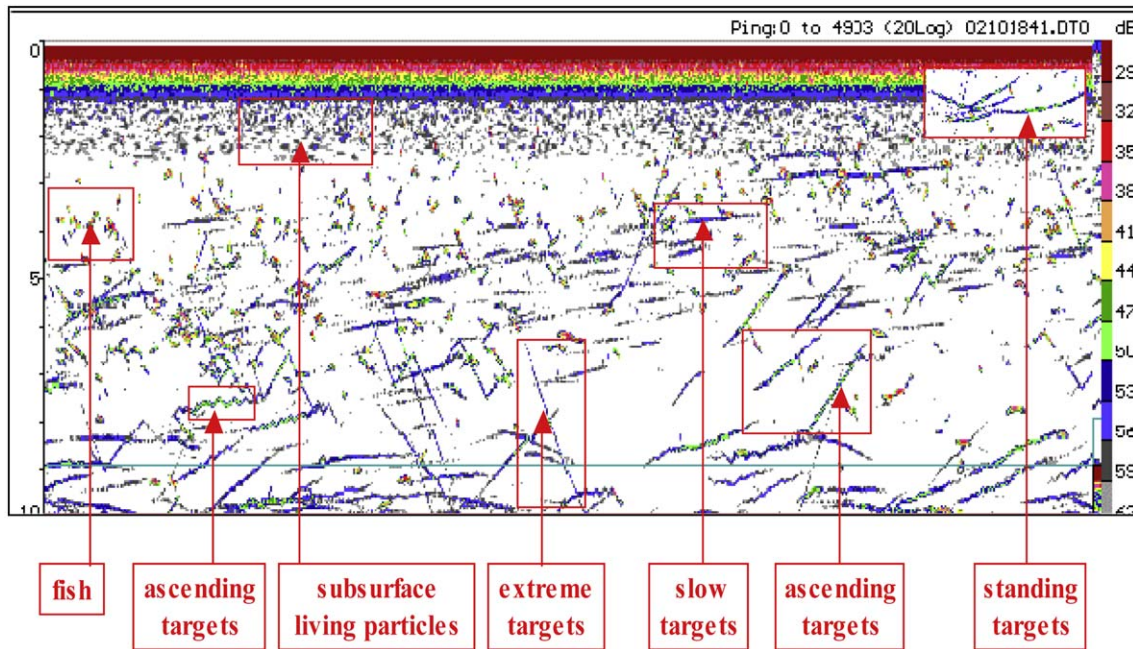


Fig. 6. Echogram image of six categories of echospecies—all categories are shown on this echogram were recorded during the dusk by downlooking transducer except category of standing targets, which was pasted from dawn record by uplooking transducer. Numbers of acoustic targets correspond to numbers in Table 4. X-axis corresponds to time (approximately 16 min) and y-axis is depth.

and swimming speed of organisms and one has to be aware that much more information about a complex system would be necessary for sound comparison. Also the application of general relationship of Love (1977) to all targets may be a big approximation, but it gives at least some idea about animal physical sizes when direct observations are absent. The latest larval fish studies (Rudstam et al., 2002) show that Love's equations (1977) are suitable for early juveniles (7–40 mm).

The first category is undoubtedly fish. They were swimming actively through whole acoustic beam. With average reconstructed total length of 42 mm, they were likely to belong to the genus *Clupeichthys*, which represented most fish in the catch of ichthyoplankton nets and smallmesh gillnets.

The second category (slow targets, reconstructed length of about 3 mm) is likely to consist of *Chaoborus* larvae and pupae. This echospecies represented the majority of invertebrate targets recorded in the open water and most of the catch of towed ichthyoplankton nets. They were present in all layers without any apparent swimming. This rather planktonic behavior distinguishes them from more nektonic echospecies of categories 3 and 4.

The third category (ascending targets, reconstructed length of about 15 mm) contained relatively fast rising organisms but with slow horizontal moving. They occurred during dusk and mainly in the lower part of the water column. Rarely they were also swimming down. Many of these targets exhibited fine oscillating movement while rising as shown in Fig. 6. With their average length, they match only to fish from family Gobiidae, but this is unlikely due to their patterns of movement. This pattern could correspond with behavior of pupae or maybe shrimps of genus *Caridina*.

The fourth category (extreme targets, reconstructed length of about 10 mm) had very expressive patterns of fast vertical movement, which does not agree with any pattern of movement of other organisms, shown in Fig. 6. The range of vertical speed was from 6 to 9 cm s⁻¹. Their movement was both ascending and descending. They appeared on records relatively scarcely (one individual per 2–4 min of record), but were present during all night and twilight observations. The patterns could represent some water Coleoptera or Heteroptera. Small Heteroptera have similar TS in temperate waters (Kubečka et al., 2000).

The fifth category of standing targets with average reconstructed length of about 13 mm appeared only during dawn in uplooking for a relatively short time (20 min) and only under the surface (up to 2 m). According to reconstructed length, they correspond to Gobiidae or *Caridina* but the swimming pattern does not resemble nekton. These targets created very long subsurface tracks while standing in a beam for a long time. Their temporal occurrence under the surface with nearly no moving in horizontal direction could indicate their affiliation with pupae of Chironomidae (10 mm; Fig. 5).

The last group was subsurface living particles present all night and during the twilight. These targets were too small for single target analysis with respect to the recording threshold. The size was smaller than -79 dB and they can only be observed in lower threshold echograms. They formed relatively compact belt under the surface down to 2 m of depth. They could be formed by the aggregations of zooplankton or algae. Dominant phytoplankton species, filamentous blue-green alga *Cylindrospermopsis raciborski* (Cyanophyta/Cyanobacteria), contained aerotopes, gas-filled vesicles, which allow floatation (Rott et al., 2002).

5. Conclusion

Open water of a tropical reservoir was found to be a comfortable environment for acoustic study of animal behavior. Both approaches of fixed location acoustic study—up- and downlooking—of the Ubol Ratana gave comparable results in all main characteristics of observed community.

Apparent circadian pattern of community behavior was found. Daytime records fluctuated significantly due to occurrence of fish shoals. Shoals varied in size and appeared with no apparent regularity. Single fish were during daytime mostly close to the bottom. Night records showed many hours of relatively stable behavioral pattern with much more equal dispersion of single targets. During dark, we also observed invertebrates, which were rising from the bottom during dusk. At dawn, fish and invertebrates were going down to the bottom and disappeared from the water column as single targets. Both small fish and invertebrates seemed to rely on darkness as a protective period for colonizing open water, this period started 1 h earlier and lasted 1 h longer for the fish. In most depth layers, except the deepest, invertebrates outnumbered the fish.

Due to more stable dispersion of community during night, the time course of biomass, abundance and average weight of fish was relatively regular. Vertical development of fish biomass showed that fish were at daytime on the bottom and surface layers and over night they were mainly in the upper part of the water column. Vertical development of abundance and average weight indicated that larger fish were in the bottom layer.

According to target strength, speed pattern of moving, depth and diurnal distribution, we are able to distinguish six acoustic species. The results show the potential of acoustic tracking for non-intrusive observation of behavior of individual echospecies even in a complex and diverse tropical ecosystem.

Acknowledgements

This study was supported by FISHSTRAT Project funded by European Commission and by Grant Agency of the Czech Academy of Sciences (project no. A 601 72 01 and program K 600 51 14). We thank anonymous referees and the editor for their constructive comments on this manuscript. We are also beholden to Gregory P. Setliff for revision of English.

References

Arrhenius, F., Benneheij, B.J.A.M., Rudstam, L.G., Boisclair, D., 2000. Can stationary bottom split-beam hydroacoustics be used to measure fish swimming speed in situ? *Fish. Res.* 45, 31–41.

- Balk, H., Lindem, T., 2002. Sonar4 and Sonar5-Pro Post Processing Systems. Lindem Data acquisition, Norway, pp. 155–189.
- Čech, M., Kubečka, J., 2002. Sinusoidal cycling swimming pattern of reservoir fishes. *J. Fish Biol.* 61, 456–471.
- Fréon, P., Gerlotto, F., Soria, M., 1996. Diel variability of school structure with special reference to transition periods. *ICES J. Mar. Sci.* 53, 459–464.
- Guillard, J., 1998. Daily migration cycles of fish populations in a tropical estuary (Sine-Saloum, Senegal) using a horizontal-directed split-beam transducer and multibeam sonar. *Fish. Res.* 35, 23–31.
- Helfman, G.S., 1993. Fish behaviour by day, night and twilight. In: Pitcher, T.J. (Ed.), *Behaviour of Teleost Fishes*. Chapman & Hall, London, pp. 479–512.
- Kubečka, J., Frouzová, J., Čech, M., Peterka, J., Ketelaars, H.A.M., Wagenvoort, A.J., Papáček, M., 2000. Hydroacoustic assessment of pelagic stages of freshwater insects. *Aquat. Living Resour.* 13, 361–366.
- Love, R.H., 1977. Target strength of an individual fish at any aspect. *J. Acoust. Soc. Am.* 62, 1397–1403.
- MacLennan, D.N., Fernandes, P.G., Dalen, J., 2002. A consistent approach to definitions and symbols in fisheries acoustics. *ICES J. Mar. Sci.* 59, 365–369.
- MacLennan, D.N., Simmonds, E.J., 1992. *Fisheries Acoustics*. Chapman & Hall, London, pp. 68–88.
- Pholprasith, S., Virapat, C., 1995. The management of fisheries in the Ubolratana Reservoir for a sustainable fishery. In: Petr, T., Morris, M. (Eds.), *Regional Symposium on Sustainable Development of Inland Fisheries Under Environmental Constraints*, Bangkok, Thailand, FAO Fish. Rep. No. 512, pp. 177–184.
- Pholprasith, S., Sirimongkonthaworn, R., 1999. The fish community of the Ubolratana Reservoir, Thailand. In: van Densen, W.L.T., Morris, M.J. (Eds.), *Fish and Fisheries of Lakes and Reservoirs in Southeast Asia and Africa*. Westbury Publishing, Otley, pp. 103–115.
- Rott, E., Peerapornpisal, Y., Ingthamjitr, S., Silva, E.I.L., 2002. Phytoplankton seasonality in reservoirs under monsoon climate in Sri Lanka and Thailand. 4th International Conference on Reservoir Limnology and Water Quality. České Budějovice, Czech Republic, pp. 290–291.
- Rudstam, L.G., VanDe Valk, A.J., Scheuerell, M.D., 2002. Comparison of acoustic and Miller high-speed sampler estimates of larval fish abundance in Oneida Lake, New York. *Fish. Res.* 57, 145–154.
- Schiemer, F., Amarasinghe, U., Frouzova, J., Sricharoendham, B., Silva, E.I.L., 2001. Ecosystem structure and dynamics—a management basis for Asian reservoirs and lakes. In: De Silva, S.S. (Ed.), *Reservoir and Culture-based Fisheries: Biology and Management*. Australian Centre for International Agricultural Research, Canberra, pp. 215–226.
- Simon, D., de Jesus, C., Boonchuwong, P., Mohottala, K., 2001. The role of reservoir and lacustrine fisheries in rural development: comparative evidence from Sri Lanka, Thailand and the Philippines. In: De Silva, S.S. (Ed.), *Reservoir and Culture-based Fisheries: Biology and Management*. Australian Centre for International Agricultural Research, Canberra, pp. 56–65.
- Tumwebaze, R., Getabu, A., Bayona, J., MacLennan, D.N., Cowx, I.G., 2002. Fisheries of Lake Victoria: an underwater perspective. In: Cowx, I.G. (Ed.), *Management and Ecology of Lake and Reservoir Fisheries*. Fishing News Books, Blackwell Science, Oxford, pp. 70–83.
- Wanzenböck, J., Matěna, J., Kubečka, J., 1997. Comparison of two methods to quantify pelagic early life stages of fish. *Arch. Hydrobiol. Spec. Issues Adv. Limnol.* 49, 117–124.