Aquat. Living Resour. 22, 69–77 (2009) © EDP Sciences, IFREMER, IRD 2009 DOI: 10.1051/alr/2009013

DOI: 10.1051/alr/2009013 www.alr-journal.org

Hydroacoustic estimates of fish stocks in temperate reservoirs: day or night surveys?

Vladislav Draštík^{1,2,a}, Jan Kubečka^{1,2}, Martin Čech¹, Jaroslava Frouzová¹, Milan Říha^{1,2}, Tomáš Jůza^{1,2}, Michal Tušer^{1,2}, Oldřich Jarolím^{1,2}, Marie Prchalová^{1,2}, Jiří Peterka¹, Mojmír Vašek¹, Michal Kratochvíl^{1,2}, Josef Matěna¹ and Tomáš Mrkvička^{1,2}

Received 1st April 2008; Accepted 9 March 2009

Abstract – Day and night acoustic surveys were used to compare fish stock estimates at eight European reservoirs and one flooded mining pit. During both photoperiods of summer, higher fish biomass was observed in the uppermost 4 m of the water column by horizontal beaming than in deeper water by vertical beaming. Comparisons of volume backscattering coefficient (s_v), fish biomass (kg ha⁻¹), abundance (ind. ha⁻¹) and average fish weight (g) did not show a common pattern among the reservoirs but were found to vary significantly across photoperiods. At most reservoirs, the night surveys had higher estimates than day surveys. However, at several reservoirs the opposite pattern was observed. These patterns could not be explained by the species composition of the fish stocks. Fish size distributions were found to be different between day and night. A higher proportion of 1+ and older fish were found during the night at two of three studied waterbodies. In general, it was not possible to decide whether day or night acoustic surveys gave more reliable fish stock assessments. We advise performing both day and night transects on a given water body before deciding when to conduct the full survey. For a complete fish assessment it is very desirable to combine acoustic mobile surveys with active sampling gear.

Key words: Hydroacoustics / Fish biomass / Diel migration / Man-made lake

Résumé - Evaluation hydro-acoustique de stocks de poissons en lacs artificiels de la zone tempérée : de nuit ou de jour? Des campagnes acoustiques nocturnes et durant le jour ont été effectuées pour comparer les estimations de stock de poissons de 8 lacs artificiels et un puits de mine inondée d'Europe centrale. Durant l'été, de jour comme de nuit, des biomasses plus élevées de poissons ont été observées dans la partie haute (jusqu'à 4 m de profondeur) de la colonne d'eau, par sondage acoustique horizontal que dans la partie plus profonde par sondage vertical. Des comparaisons du coefficient de rétro-(réverbération) en fonction du volume d'eau (s_v) , de la biomasse de poissons (kg ha⁻¹), de leur abondance (ind. ha⁻¹) et du poids moyen des poissons (g) ne montrent pas de schémas communs entre ces réservoirs mais varient significativement en fonction de la période du jour ou de la nuit. Pour la plupart des réservoirs, les campagnes nocturnes présentent des estimations plus importantes que celles effectuées de jour. Cependant, le contraire est aussi observé pour certains réservoirs. Ces différences ne peuvent s'expliquer par la composition en espèces des stocks de poissons. La répartition en tailles des poissons est différente entre la nuit et le jour. Une plus grande proportion de plus gros poissons (1+) est trouvée durant la nuit pour deux des trois lacs réservoirs et du lac minier. En général, il n'est pas possible de décider si des campagnes de jour ou de nuit fournissent des estimations plus fiables des stocks de poissons. Nous conseillons d'effectuer des transects de nuit et de jour avant de décider de la période d'évaluation. Pour une estimation complète, il est souhaitable de combiner des campagnes acoustiques mobiles avec un échantillonnage au moyen d'un engin de pêche.

1 Introduction

Hydroacoustic is a proven method for estimating fish abundance and biomass, and for enumerating population

trends (Horppila et al. 1996; Mehner and Schulz 2002; Wanzenböck et al. 2003; Mueller and Horn 2004; Simmonds and MacLennan 2005). The reliability and accuracy of acoustic estimates depend on many factors related to hydroacoustic equipment, environmental conditions and fish behaviour.

¹ Biology Centre of the AS CR, Institute of Hydrobiology, Na Sádkách 7, 370 05 České Budějovice, Czech Republic

² Faculty of Science, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic

^a Corresponding author: v.drastik@gmail.com

Reservoir	Year of	Area	Volume	Max. depth	Sampled vol.	Survey date
	filling	(ha)	(10^6 m^3)	(m)	D/N (%)	
Švihov	1976	1432	246	55.7	11/4	June 1997
Lučina	1975	73.5	4.6	21.9	8/16	June/July 1998
Chabařovice	2001	180	14.0	18.4	41/28	September 2006
Slapy	1957	1392	263.9	62	2/2	September 2004
Staviště	1959	12.7	0.4	9	75/25	July 1999
Římov	1978	210	34.5	43.9	17/20	August 2004
Žlutice	1968	141	11.5	21	15/20	June/July 1998
Vrchlice	1970	102.8	9.8	34	24/7	August 1996
Nýrsko	1969	141.6	20.8	32	26/22	May 1997

Table 1. Basic characteristics of studied reservoirs and the flooded mining pit (Chabařovice) and dates that acoustic surveys were carried out. Sampled volume represents a percentage of acoustically surveyed volume of reservoir volume (D/N, at day and at night).

Usually, fish are not distributed randomly in reservoirs. Reports of longitudinal (tributary-dam) and vertical gradients of fish abundance and biomass have been made for many European and American reservoirs (Aglen et al. 1999; Vašek et al. 2003; Matthews et al. 2004; Vašek et al. 2004; Draštík et al. 2008; Prchalová et al. 2008). Also the horizontal pattern (offshore-inshore) in fish distribution is nonrandom and could be species specific (Gauthier and Boisclair 1997; Jeppesen et al. 2006).

Fish distributions in the open water are known to change between day and night. During the day fish usually form schools making measurement of individual target strength (TS) difficult. Further, some species that stay closer to the bottom during daylight can go undetected by hydroacoustics (Axenrot et al. 2004; Guillard et al. 2004; Simmonds and MacLennan 2005). During the night fish schools disaggregate and measurements of individual TS are more reliable (Fréon et al. 1993; Fréon et al. 1996; Guillard et al. 2004). Also inshore-offshore migrations of juvenile and adult fish strongly influence hydroacoustic estimates and these migrations are species specific. Adult bream (Abramis brama), roach (Rutilus rutilus) and sander (Sander lucioperca) have been reported to perform partial movements from the pelagic zone to the littoral at night (Kubečka 1993; Jacobsen et al. 2004; Wolter and Freyhof 2004).

Recently, a significant effort has been made to unify acoustic methodology by American (Parker-Stetter et al. 2009; Rudstam et al. 2009) and European (CEN/TC 230/WG 2/TG 4 N 60¹) scientists. The need for such standard was highlighted at the international symposium of the Fish Stock Assessment Methods for Lakes and Reservoirs (Kubečka et al. 2009). So far there is a lack of clear guidance for deciding between day and night surveys.

In this study, we chose to study how the diel aspect of fish behaviour affects hydroacoustic assessment of fish stock in reservoirs. The aim of this work was to compare day and night estimates of volume backscattering coefficient (s_v), fish biomass and abundance and average fish weight obtained by routine acoustic surveys. Fish size distributions were com-

pared to determine if there were any differences between day and night populations of fish in the open water.

2 Material and methods

2.1 Study sites

Eight canyon-shaped reservoirs and one flooded mining pit were investigated (Table 1). Most reservoirs (Římov, Švihov, Nýrsko, Vrchlice, Žlutice, Lučina, Staviště, Slapy) serve as drinking water supplies and Chabařovice is a flooded mining pit. Most reservoirs had a meso- to eutrophic status with retention times longer than 100 days – Římov, Švihov, Žlutice, Lučina, Vrchlice and Staviště. Slapy Reservoir, situated in the reservoir cascade of the Vltava River, was a meso- to eutrophic reservoir with a relatively short retention time (less than 40 days). Littoral zones in all eight reservoirs were poorly developed. The Chabařovice flooded mining pit is oligo- to mesotrophic with a long retention time (no outflow so far, just evaporation). The littoral zone of the mine pit was much more developed with submerged plants present.

Species composition was obtained using a beach seine measuring 50-m long by 4-m high with mesh size (knot-to-knot) of 10 mm. Seining was performed during the same time-frames as the acoustic surveys (Table 1). Six to twelve hauls at each reservoir were done during the night by setting the net 30-40 m out from the shore at a depth of 4 m and subsequent dragging towards the shore (Říha et al. 2008). Each haul represented approximately $1500 \, \mathrm{m}^2$ of the netted area.

2.2 Acoustic surveys

Simrad EK60 and EY500 split-beam scientific echosounders operating at a frequency of 120 kHz with elliptical (ES 120_4, nominal beam angles 9.1 × 4.3°, beaming horizontally) and circular (ES 120_7C, nominal beam angles 7 × 7°, beaming vertically) transducers were used on Dory 13 boat (Staviště, Žlutice, Lučina, Vrchlice, Nýrsko, Švihov and Slapy) and Ota Oliva research vessel (Římov and Chabařovice). The whole system was calibrated by copper calibration sphere of 23 mm in diameter and TS estimated to –40.8 dB at each reservoir (Foote et al. 1987).

¹ CEN (The European Committee for Standardization or *Comité Européen de Normalisation*) CEN/TC 230/WG 2/TG 4 N 60, Water Quality – Guidance on the estimation of fish abundance with mobile hydroacoustic methods. A revised working draft for consideration by TG 4 Fish Monitoring (http://www.cen.eu).

A zig-zag trajectory was used as sampling design where the width of reservoir allowed. Acoustic surveys were divided into transects with different lengths at different reservoirs. At least 15 transects (15–75) with independent estimates of $s_{\rm v}$ (m² m⁻³), biomass (kg ha⁻¹), fish abundance (ind. ha⁻¹) and average fish weight (g) were available for both horizontal and vertical surveys. Each transect was cleared of noise (bubbles, debris, bottom structures etc.) by setting appropriate threshold and manual deletion, so only fish echoes remained for further analyses. For most surveys, the TS thresholds were set at –65 dB for horizontal beaming and –70 dB for vertical beaming. In noisier situations, the TS threshold was increased to –60 dB. The $S_{\rm v}$ threshold was set to have the same restriction (analyzing the same target population on the screen).

Raw acoustic data were analyzed with EP500 and Sonar5 (Balk and Lindem 2005) post-processing software. For calculating abundance (ind. m^{-3}) the " s_v/ts scaling" (s_v/ts is a term used in Sonar 5; in fact, s_v is scaled by the average backscattering cross section (σ_{bs}) derived from mean TS) approach was used with TS as a scaling factor derived from single echo detections or manually tracked fish (Slapy, Římov and Chabařovice). Average fish weight (g) was calculated by dividing the total weight of fish in each size group by the number of fish in that group. Fish biomass (kg ha⁻¹) was determined by multiplying average fish weight and fish abundance (ind. ha⁻¹). Acoustic data within 4 m of the horizontal and vertical transducers were excluded owing to the transducers nearfields. Data were processed out to 30 m range for the horizontal beaming to avoid beam bending which can occur at the thermocline. For the vertically-aimed transducer, we processed data to within 0.5 m of the bottom. For vertical beaming, fish lengths were estimated from TS using Love's (1971) equation. Horizontal records were first corrected for target directivity using a deconvolution procedure (Kubečka et al. 1994) and the targets of known aspects were sized by the regressions of Frouzová et al. (2005). Temperature and oxygen vertical profiles were measured using a calibrated YSI 556 MPS probe (Slapy, Římov, Chabařovice) or obtained from regular monitoring by Vltava River Authority.

2.3 Statistical analyses

The analysis of covariance test using reservoirs and photoperiods as covariables was used to compare the fish biomass in horizontal and vertical surveys (Statistica 7.1 (Statsoft Inc. 2006)). A nonparametric test for comparing two dependent samples was used for statistical comparison of s_v , fish biomass and abundance and average fish weight at day and night. Correlation between the s_v and fish biomass was computed using Statistica 7.1 (Statsoft Inc. 2006). Contingency tables were used to compare the size distributions derived from TS of the fish tracks collected during day and night (Slapy, Římov, Chabařovice). Fish lengths were divided into several groups and the counts of all groups compared. Yarnold's condition was used to identify if there were enough fish tracks in each group (Yarnold 1970). The groups were as follows: 0–5 cm, 5–10 cm, 10–15 cm, 15–20 cm, 20–25 cm, 25–30 cm, 30–35 cm,

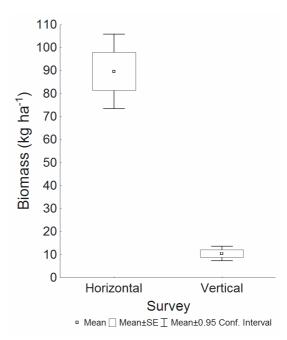


Fig. 1. The comparison of fish biomass in the horizontal and vertical surveys. Significantly higher fish biomass was observed by the horizontal beaming than vertical.

Table 2. Ratio between day and night volume backscattering cofficient (s_v), biomass, abundance and average fish weight from horizontal surveys (D/N – day to night ratio, * statistically significant, p < 0.05).

Reservoir	$s_{\rm v}$	Biomass	Abundance	Avg. weight
	D/N	D/N	D/N	D/N
Švihov	0.3*	0.2	0.3*	0.6*
Lučina	0.2*	0.3*	0.6	0.7*
Chabařovice	0.4*	0.4*	0.4*	0.6
Slapy	0.3*	0.4*	1.2	0.5
Staviště	0.2	0.5	0.1	5.3*
Římov	1.2	1.4	1.8*	1.5*
Žlutice	1.7*	3.7*	0.9	3.9*
Vrchlice	1.1	4.2*	0.3	0.8*
Nýrsko	26.8*	114.3*	6.3*	4.6*

35–40 cm, 40–45 cm, 50 cm and more. In all cases, Yarnold's condition was satisfied.

3 Results

Significantly greater fish biomass was observed by horizontal beaming than vertical beaming in the waters we studied $(F_{(1,1299)}=119.5,\ p<10^{-6};\ {\rm Fig.\ 1})$. Vertical fish distributions corresponded with well-established temperature and oxygen stratification in most reservoirs during summer (Fig. 2). The thermocline was at the depths of 3 to 8 m below the surface, and fish were very rarely observed below the thermocline. Therefore, we focused subsequent analyses using results from horizontal surveys.

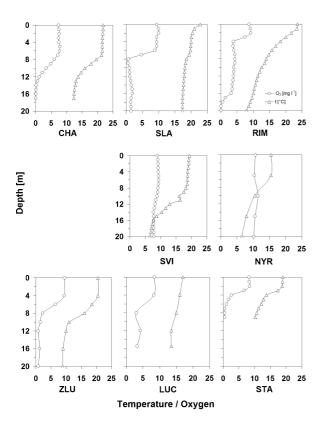


Fig. 2. Temperature and oxygen vertical profiles in studied reservoirs during time of surveying. Data for Vrchlice Reservoir (VRC) was not available. CHA: Chabařovice, SLA: Slapy, RIM: Římov, SVI: Švihov, NYR: Nýrsko, ZLU: Žlutice, LUC: Lučina, STA: Staviště.

Acoustic estimates from horizontal surveys differed during day and night (Table 2). All reservoirs were sorted by day-to-night ratios of s_v , biomass, abundance and average fish weight. Values above 1 coincide with higher daytime estimates, while values below 1 coincide with higher nighttime estimates.

Comparisons of s_v and fish biomass from day and night acoustic surveys (horizontal beaming) gave very similar results (Figs. 3, 4). Fish biomass was positively correlated with volume backscattering coefficients; biomass (kg ha⁻¹) = $(4.4 \times 10^7) \times s_v - 19.7, r = 0.90; F_{(1,16)} = 71.5, p < 10^{-6}.$ Comparison of fish abundances showed less similarity with s_v or fish biomass (Fig. 5). Generally higher estimates of acoustic biomass (s_v) were found in four reservoirs during the night (Chabařovice, Slapy, Švihov and Lučina) and in three during the day (Římov, Žlutice and Nýrsko). Stavište and Vrchlice showed no pattern between day and night surveys. Beach seining showed that cyprinids (roach, bream and rudd) were predominant at most reservoirs, except at Staviště and Nýrsko where perch were predominant (Table 3). Having higher acoustic estimates during the day or night was not related to differences in fish communities as measured by the beach seine.

Higher fish biomass estimates during the day corresponded well with higher average fish weight (e.g., Římov, Žlutice and

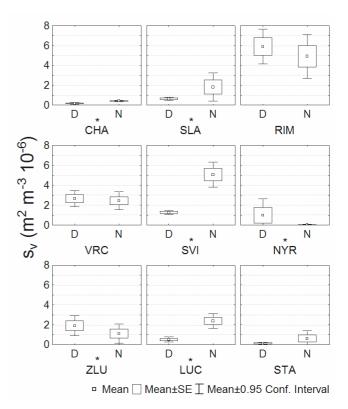


Fig. 3. The volume backscattering coefficients (s_v , m⁻² m⁻³) surveyed during the day and night by horizontal beaming in the studied reservoirs. Significant differences (* p < 0.05) were found between the day and night at some reservoirs. Mean, standard error of mean and 95% confidential intervals are presented.

Nýrsko, Fig. 6). This was only partially correct during the night (Slapy and Lučina). Comparison of predicted length distributions from TS by photoperiod were developed for select reservoirs: Chabařovice (Fig. 7a), Slapy (Fig. 7b) and Římov (Fig. 7c). In all cases, these distributions varied significantly [Chabařovice ($\chi^2 = 116.3$, $p < 10^{-6}$), Slapy ($\chi^2 = 466.6$, $p < 10^{-6}$), and Římov ($\chi^2 = 954.3$, $p < 10^{-6}$)]. Size classes that contributed to the significant results were 5–20 cm and 25–30 cm at Chabařovice, 5–10 cm and 20–25 cm at Slapy, and 10–25 cm at Římov. Generally, a higher proportion of fish in these size classes were found at night in Chabařovice and Slapy waterbodies, and during the day at Římov Reservoir.

4 Discussion

Good fish stock estimate provide data on both fish abundance and biomass (Kubečka et al. 2009). In relatively noisy horizontal beaming data, the possibility to discriminate small fish from non-fish targets is difficult (see below); what can substantially influence abundance results in situations when small fish are numerous. On the other hand, large fish are well recorded even in low signal-to-noise ratio and they usually compose the bulk of fish biomass. We consider biomass results to be much more robust and informative but we present also the abundance results to be comparable with a number of

Table 3. Fish species composition (% abundance, beach seine catches) in selected reservoirs. Roach (*Rutilus rutilus*), bream (*Abramis brama*), bleak (*Alburnus alburnus*), perch (*Perca fluviatilis*), sander (*Sander lucioperca*), pike (*Esox lucius*), rudd (*Scardinius erythrophtalmus*), ruffe (*Gymnocephalus cernuus*), tench (*Tinca tinca*). * Slapy from Hanel, 1988.

Reservoir	roach	bream	bleak	perch	sander	pike	rudd	ruffe	tench	others
Švihov	55	28	11	3		2				1
Slapy*	38		5	25				29		3
Lučina	81			14	2.5	2.5				
Chabařovice	1			21		1	74			3
Staviště	3			96				1		
Římov	32	46	3	3.5				9		6.5
Žlutice	66			12		3.5	18			0.5
Vrchlice	39	48		5	5	1	1			1
Nýrsko	2			95		1			2	

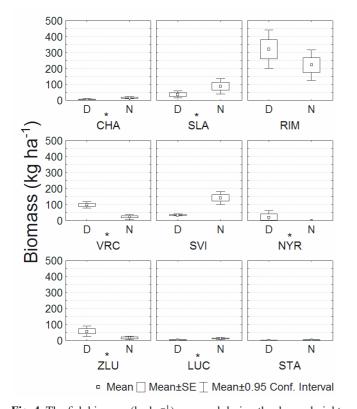


Fig. 4. The fish biomass (kg ha⁻¹) surveyed during the day and night by the horizontal acoustics in the studied reservoirs. Significant differences (* p < 0.05) were found between the day and night at some reservoirs. Mean, standard error of mean and 95% confidential intervals are presented.

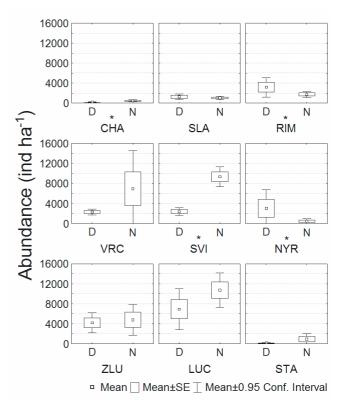


Fig. 5. The fish abundance (ind. ha^{-1}) surveyed during the day and night by the horizontal acoustics in the studied reservoirs. Significant differences (* p < 0.05) were found between the day and night at some reservoirs. Mean, standard error of mean and 95% confidential intervals are presented.

earlier studies dealing with abundance only (Wanzenböck et al. 2003; Godlewska et al. 2009; Yule et al. 2009).

Hydroacoustic surveys did not reveal a consistent diel pattern among the reservoirs in this study. In general we assumed that the higher estimate was the better stock assessment (i.e., we managed to survey a higher proportion of fish present in the reservoir). Night acoustic surveys gave higher results in four reservoirs (Švihov, Lučina, Chabařovice and Slapy) while daytime estimates were found to be higher in three reservoirs (Nýrsko, Žlutice and Římov). Two reservoirs (Staviště and Vrchlice) gave comparable results for day and night surveys.

Vertical survey estimates were small in general, and at some reservoirs nearly negligible. Fish species in manmade reservoirs have rarely been observed below the thermocline during summer thermal stratification (Kubečka and Wittingerová 1998; Matthews et al. 2004; Vašek et al. 2004; Järvalt et al. 2005), except for larval and juvenile perch (Čech et al. 2005). Diel vertical migration was not observed at the studied reservoirs, most likely because strict temperature and oxygen stratification of the water column prevent fish from swimming to deeper layers.

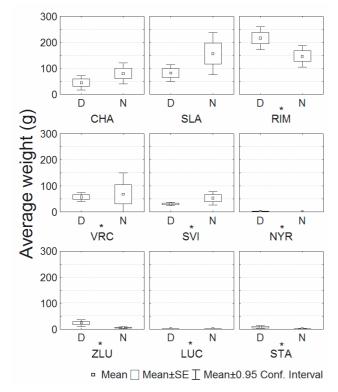


Fig. 6. The predicted average fish weight (g) surveyed during the day and night by the horizontal acoustics in the studied reservoirs. Significant differences (* p < 0.05) were found between the day and night at some reservoirs. Mean, standard error of mean and 95% confidential intervals are presented.

Diel horizontal migrations could explain some of the fish distribution patterns in pelagic and littoral zones during day and night. Higher fish estimates at night were in agreement with studies from other European and American reservoirs and lakes. In most studies, reported fish abundance in the epilimnions of pelagic zones has generally been low during daylight, increased at dusk and peaked at night (Bohl 1980; Gliwicz and Jachner 1992; Comeau and Boisclair 1998; Gaudreau and Boisclair 2000; Lewin et al. 2004; Gliwicz et al. 2006). The migration of small fish at dusk from littoral refuge to open water could explain a higher abundance of small fish at night in Lučina, Švihov, Slapy reservoirs. Unfortunately, detection of small fish by the horizontal beaming is a difficult challenge because signal-to-noise ratios are usually lower when horizontal beaming compared to vertical beaming (Simmonds and MacLennan 2005) and the deconvolution procedure (Kubečka et al. 1994) of randomly oriented fish provides the least reliable sizing of small fish. For example, it is virtually impossible to distinguish the least reflective (near tail- and head-) aspects of small fish from non-fish targets (Kubečka et al. 2000), which may cause suspiciously small fish size estimates (<1 cm) like those shown in Figs. 7b,c. For small fish, application of night trawling (Juza and Kubečka 2007) achieves much better accuracy than horizontal beaming. Another factor complicating detection of single targets of small fish during the day is shoaling (Bohl 1980; Gliwicz and

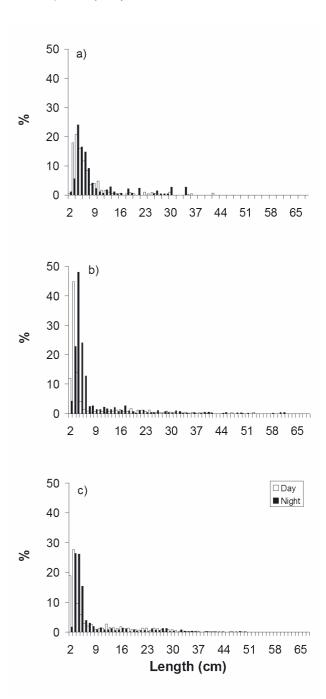


Fig. 7. The predicted size distribution of tracked fish (standard length) at the Chabařovice flooded mining pit (a), Slapy Reservoir (b) and Římov Reservoir (c). Significant differences were found between the day and night.

Jachner 1992; Axenrot et al. 2004; Gerlotto et al. 2004; Gliwicz et al. 2006; Guillard et al. 2006).

Night inshore migration of adult fish was reported as another general mechanism of fish horizontal movements (Schulz and Berg 1987; Kubečka 1993; Zamora and Moreno-Amich 2002; Yule et al. 2008; Godlewska et al. 2009). It is performed by larger fish and in the opposite direction of small fish (from open water to littoral). Migration of adult fish

to the littoral at night (Říha et al. 2008) might have caused the higher day estimates of fish in the open water observed at Římov and Žlutice reservoirs. The seasonal aspect of acoustic stock assessment in reservoirs and lakes is little known (Mehner and Schulz 2002; Yule et al. 2008). Our priority was to carry out the surveys in warm part of year when the fish distribute relatively evenly along the reservoir in order to exploit all available food resources. Except the Nýrsko survey, which was carried out immediately after perch spawning, all other surveys were carried out well outside the spawning season.

Diurnal changes of fish biomass and abundance are clearly a crucial question of stock assessment in reservoirs. Results of this study show that there is no simple pattern of diurnal spatial distributions. The distributional changes likely depend on age (size) and species composition of the fish stock which can vary across reservoirs and across time in a single reservoir. Acoustic estimates are complicated by a very shallow distribution of fish (epilimnion) and the need for horizontal beaming which has a number of inherent problems (reviewed by Simmonds and MacLennan 2005). Therefore, it is critical to complement the acoustic surveys by using groundtruth methods (trawling, gillnets, seining, etc.; for a review see McClatchie et al. 2000). In the present study, nine detailed acoustic surveys did not provide a clear pattern between day and night results, meaning some other factors that were not monitored were important. Possible explanations include presence or absence of fish predators (Schulze et al. 2006; Hölker et al. 2007; Horký et al. 2008), seasonal affects on distributions (Borcherding et al. 2002; Jacobsen et al. 2004; Yule et al. 2009), age composition and habitat preferences (Schulze et al. 2006; Dörner et al. 2007; Prchalová et al. 2008), moon phase (Gaudreau and Boisclair 2000; Horký et al. 2006) and food supply (Hölker et al. 2002; Wojtal et al. 2003).

5 Conclusion

We have not observed a consistent pattern of fish distributions during the day and night at all reservoirs. Horizontal surveying offers superior estimates than vertical surveying in the stratified reservoirs we studied. Acoustic estimates of s_v , fish biomass and abundance and average fish weight were higher at night than during day at four studied reservoirs, while results from three reservoirs were higher during daytime. Estimated size distributions of tracked fish were different between day and night. No general rule for deciding between day or night acoustic surveying was established and performing preliminary transects during both photoperiods before conducting a full survey is recommended. We highly recommend complementing acoustic surveys with direct methods of fish assessment (e.g., trawls, gillnets, beach and purse seine nets).

Acknowledgements. The authors would like to thank Zdeněk Prachař, Monika Wittingerová, Martina Vožechová and Milan Hladík and employees of Vltava River Authority for help in data collection, Brian Tlougan for correcting English. We are very are grateful to D. Yule and two anonymous referees for their helpful comments which considerably improved the manuscript. The study was supported by the

Grant Agency of the Czech Republic, project no. 206/06/1371 and 206/07/1392 and the Academy of Sciences of the Czech Republic, project no. 1QS600170504.

References

- Aglen A., Engas A., Huse I., Michalsen K., Stensholt B.K., 1999, How vertical fish distribution may affect survey results. ICES J. Mar. Sci. 56, 345–360.
- Axenrot T., Didrikas T., Danielsson C., Hansson S., 2004, Diel patterns in pelagic fish behaviour and distribution observed from a stationary, bottom-mounted, and upward-facing transducer. ICES J. Mar. Sci. 61, 1100–1104.
- Balk H., Lindem T., 2005, Sonar4 and Sonar5-Pro post processing systems (operating manual). Lindem Data Acquisition, Oslo.
- Bohl E., 1980, Diel pattern of pelagic distribution and feeding in planktivorous fish. Oecologia 44, 368–375.
- Borcherding J., Bauerfeld M., Hintzen D., Neumann S., 2002, Lateral migrations of fishes between floodplain lakes and their drainage channels at the Lower Rhine: diel and seasonal aspects. J. Fish Biol. 61, 1154–1170.
- Čech M., Kratochvíl M., Kubečka J., Draštík V., Matìna J., 2005, Diel vertical migrations of bathypelagic perch fry. J. Fish Biol. 66, 685–702.
- CEN (The European Committee for Standardization or *Comité Européen de Normalisation*) CEN/TC 230/WG 2/TG 4 N 60, Water Quality Guidance on the estimation of fish abundance with mobile hydroacoustic methods. A revised working draft for consideration by TG 4 Fish Monitoring (http://www.cen.eu).
- Comeau S., Boisclair D., 1998, Day-to-day variation in fish horizontal migration and its potential consequence on estimates of trophic interactions in lakes. Fish. Res. 35, 75–81.
- Dörner H., Hülsmann S., Hölker F., Skov C., Wagner A. 2007, Size-dependent predator-prey relationships between pikeperch and their prey fish. Ecol. Freshw. Fish. 16, 307–314.
- Draštík V., Kubečka J., Tušer M., Čech M., Frouzová J., Jarolím O., Prchalová M., 2008, The effect of hydropower on fish stocks: comparison between cascade and non-cascade reservoirs. Hydrobiologia 609, 25–36.
- Foote K.G., Knudsen H.P., Vestnes G., MacLennan D.N., Simmonds E.J., 1987, Calibration of acoustic instruments for fish density estimation. ICES Coop. Rep. 144, 1–70.
- Fréon P., Gerlotto F., Soria M., 1996, Diel variability of school structure with special reference to transient periods. ICES J. Mar. Sci. 53, 459–464.
- Fréon P., Soria M., Mullon C., Gerlotto F., 1993, Diurnal variation in fish density estimate during acoustic survey in relation to spatial distribution and avoidance reaction. Aquat. Living Resour. 6, 221–234.
- Frouzová J., Kubečka J., Balk H., Frouz J., 2005, Target strength of some European fish species and its dependence on fish body parameters. Fish. Res. 75, 86–96.
- Gaudreau N., Boisclair D., 2000, Influence of moon phase on acoustic estimates of the abundance of fish performing daily horizontal migration in a small oligotrophic lake. Can. J. Fish. Aquat. Sci. 57, 581–590.

- Gauthier S., Boisclair D., 1997, The energetic implications of diel onshore-offshore migration by dace (*Phoxinus eos* × *P. neogaeus*) in a small oligotrophic lake. Can. J. Fish. Aquat. Sci. 54, 1996–2006
- Gerlotto F., Castillo J., Saavedra A., Barbieri M. A., Espejo M., Cotel P., 2004, Three-dimensional structure and avoidance behaviour of anchovy and common sardine schools in central southern Chile. ICES J. Mar. Sci. 61, 1120–1126.
- Gliwicz M.Z., Jachner A., 1992, Diel migrations of juvenile fish: a ghost of predation past or present? Arch. Hydrobiol. 124, 385– 410.
- Gliwicz M.Z., Slon J., Szynkarczyk I., 2006, Trading safety for food: evidence from gut contents in roach and bleak captured at different distances offshore from their daytime littoral refuge. Freshw. Biol. 51, 823–839.
- Godlewska M., Długoszewski B., Doroszczyk L., Jóźwik A., 2009, The relationship between sampling intensity and sampling error empirical results from acoustic surveys in Polish vendace lakes. Fish. Res. 96, 17–22.
- Guillard J., Brehmer P., Colon M., Guennégan Y., 2006, Three dimensional characteristics of young–of–year pelagic fish schools in lake. Aquat. Living Resour. 19, 115–122.
- Guillard J., Lebourges-Dhaussy A., Brehmer P., 2004, Simultaneous Sv and TS measurements on Young-of-the-Year (YOY) freshwater fish using three frequencies. ICES J. Mar. Sci. 61, 267–273.
- Hanel, L. 1988, Another contribution to the knowledge of fish of Slapy Reservoir. Sborník vlastivědných prací z Podblanicka 24, 41–62 (in Czech).
- Hölker F., Dörner H., Schulze T., Haertel-Borer S.S., Peacor S.D., Mehner T. 2007, Fresh. Biol. 52, 1793–1806.
- Hölker F., Haertel-Borer S.S., Steiner S., Mehner T., 2002, Effects of piscivore-mediated habitat use on growth, diet and zooplankton consumption of roach: an individual-based modelling approach. Freshw. Biol. 47, 2345–2358.
- Horký P., Slavík O., Bartoš L., 2008, A telemetry study on the diurnal distribution and activity of adult pikeperch, *Sander lucioperca* (L.), in a riverine environment. Hydrobiologia 614, 151–157.
- Horký P., Slavík O., Bartoš L., Kolářová J., Randák T., 2006, The effect of the moon phase on the behaviour of pikeperch in the Elbe River. Folia Zool. 55, 411–417.
- Horppila J., Malinen T., Peltonen H., 1996, Density and habitat shifts of a roach (*Rutilus rutilus*) stock assessed within one season by cohort analysis, depletion methods and echosounding. Fish. Res. 28, 151–161.
- Jacobsen L., Berg S., Jepsen N., Skov C., 2004, Does roach behaviour differ between shallow lakes of different environmental state? J. Fish Biol. 65, 135–147.
- Järvalt A., Krause T., Palm A., 2005, Diel migration and spatial distribution of fish in a small stratified lake. Hydrobiologia 547, 197–203
- Jeppesen E., Pekcan-Hekim Z., Lauridsen T.L., Sondergaard M., Jensen J.P., 2006, Habitat distribution of fish in late summer: changes along a nutrient gradient in Danish lakes. Ecol. Freshw. Fish 15, 180–190.
- Juza T., Kubečka J., 2007, The efficiency of three fry trawls for sampling the freshwater pelagic fry community. Fish. Res. 85, 285–290.
- Kubečka J., 1993, Night inshore migration and capture of adult fish by shore seining. Aquac. Fish. Manage. 24, 685–689.

- Kubečka J., Duncan A., Duncan W.M., Sinclair D., Butterworth A.J., 1994, Brown trout populations of 3 Scottish lochs estimated by horizontal sonar and multimesh gill nets. Fish. Res. 20, 29–48.
- Kubečka J., Frouzová J., Čech M., Peterka J., Ketelaars H.A.M., Wagenwoort A.J., Papáček M., 2000, Hydroacoustis assessment of pelagic stages of freshwater insects. Aquat. Living Resour. 13, 361–366.
- Kubečka J., Hohausová E., Matina J., Peterka J., Amarasinghe U.S., Bonar S.A., Hateley J., Hickley P., Suuronen P., Tereschenko V., Welcomme R., Winfield I.J., 2009, The true picture of a lake or reservoir fish stock: A review of needs and progress. Fish. Res. 96, 1–5.
- Kubečka J., Wittingerová M., 1998, Horizontal beaming as crucial component of acoustic fish stock assessment in freshwater reservoirs. Fish. Res. 35, 99–106.
- Lewin W.-C., Okun N., Mehner T., 2004, Determinants of the distribution of juvenile fish in the littoral area of a shallow lake. Freshw. Biol. 49, 410–424.
- Love R.H., 1971, Dorsal aspect of an individual fish. J. Acoust. Soc. Am. 49, 816–823.
- Matthews W.J., Gido K.B., Gelwick F.P., 2004, Fish assemblages of reservoirs, illustrated by Lake Texoma (Oklahoma Texas, USA) as a representative system. Lake Reserv. Manage. 20, 219–239.
- McClatchie S., Thorne R.E., Grimes P., Hanchet S., 2000, Ground truth and target identification for fisheries acoustic. Fish. Res. 47, 173–191.
- Mehner T., Schulz M., 2002, Monthly variability of hydroacoustic fish stock estimates in a deep lake and its correlation to gillnet catches. J. Fish Biol. 61, 1109–1121.
- Mueller G., Horn M., 2004, Distribution and abundance of pelagic fish in Lake Powell, Utah, and Lake Mead, Arizona-Nevada. West. N. Am. Naturalist 64, 306–311.
- Parker-Stetter, S.L., Rudstam, L.G., Sullivan, P.J., and Warner, D.M., 2009, Standard operating procedures for fisheries acoustics in the Great Lakes. Great Lakes Fisheries Commission Special Publication, 09–01.
- Prchalová M., Kubečka J., Vašek M., Peterka J., Seďa J., Jůza T., Říha M., Jarolím O., Tušer M., Kratochvíl M., Čech M., Draštík V., Frouzová J., Hohausová E., 2008, Distribution patterns of fishes in a canyon-shaped reservoir. J. Fish Biol. 73, 54–78.
- Říha M., Kubečka J., Mrkvička T., Prchalová M., Čech M., Draštík V., Frouzová J., Hladík M., Hohausová E., Jarolím O., Jůza T., Kratochvíl M., Peterka J., Tušer M., Vašek M., 2008, Dependence of beach seine net efficiency on net length and diel period. Aquat. Living Resour. 21, 411–418.
- Rudstam L.G., Sullivan P.J., Parker-Stetter S.L., Warner D.M., 2009, Towards a standard operating procedure for fisheries acoustic surveys in the Laurentian Great Lakes, North America. ICES J. Mar. Sci. 66, in press.
- Schulz U., Berg R., 1987, The migration of ultrasonic-tagged bream, *Abramis brama* (L), in Lake Constance (Bodensee-Untersee). J. Fish Biol. 31, 409–414.
- Schulze T., Dörner H., Hölker F., Mehner T., 2006, Determinants of habitat use in large roach. J. Fish Biol. 69, 1136–1150.
- Simmonds E.J., MacLennan D.N., 2005, Fisheries Acoustics. Wiley-Blackwell, 2nd edition, Oxford.
- StatSoft Inc., 2006, STATISTICA (data analysis software system), version 7.1. http://www.statsoft.com.
- Vašek M., Kubečka J., Peterka J., Čech M., Draštík V., Hladík M., Prchalová M., Frouzová J., 2004, Longitudinal and vertical

- spatial gradients in the distribution of fish within a canyon-shaped reservoir. Int. Rev. Hydrobiol. 89, 352–362.
- Vašek M., Kubečka J., Sed'a J., 2003, Cyprinid predation on zooplankton along the longitudinal profile of a canyon-shaped reservoir. Arch. Hydrobiol. 156, 535–550.
- Wanzenböck J., Mehner T., Schulz M., Gassner H., Winfield I.J., 2003, Quality assurance of hydroacoustic surveys: the repeatability of fish-abundance and biomass estimates in lakes within and between hydroacoustic systems. ICES J. Mar. Sci. 60, 486–492.
- Wojtal A., Frankiewicz P., Izydorczyk K., Zalewski M., 2003, Horizontal migration of zooplankton in a littoral zone of the lowland Sulejow Reservoir (Central Poland). Hydrobiologia 506-509, 339–346.
- Wolter C., Freyhof J., 2004, Diel distribution patterns of fishes in a temperate large lowland river. J. Fish Biol. 64, 632–642.

- Yarnold J.K., 1970, The minimum expectation in χ^2 goodness of fit test and the accuracy of approximations for the null distribution. J. Am. Stat. Assoc. 65, 864–886.
- Yule D.L., Adams J.V., Stockwell J.D., Gormen O.T., 2008, Factors affecting bottom trawl catches: Implication for monitoring the fishes of Lake Superior. N. Am. J. Fish. Manage. 28, 109–122.
- Yule D.L., Stockwell J.D., Schreiner D.R., Evrard L.M., Balge M., Hrabik T.R., 2009, Can pelagic forage fish and spawning cisco (*Coregonus artedi*) biomass in the western arm of Lake Superior be assessed with a single summer survey? Fish. Res. 96, 39–50.
- Zamora L., Moreno-Amich R., 2002, Quantifying the activity and movement of perch in a temperate lake by integrating acoustic telemetry and a geographic information system. Hydrobiologia 483, 209–218.