

# To migrate, or not to migrate: partial diel horizontal migration of fish in a temperate freshwater reservoir

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**Abstract** The diel horizontal migration (DHM) of fish between the inshore and offshore zones of the Římov Reservoir (Czech Republic, deep, stratified, meso-eutrophic) was investigated by a combination of horizontal and vertical hydroacoustic surveys at 3-h intervals over 48 h and day/night purse seining in August 2007. An overwhelming majority of fish were aggregated within the epilimnetic layer. Considering only the horizontal surveys, cyclic diel fish movements between inshore and offshore habitats were apparent, while the total fish biomass remained constant between day and night. A higher fish biomass was detected in the offshore zone during daytime by both hydroacoustics and purse seining. In contrast, a

higher fish biomass was recorded at night in the inshore zone. Bream *Abramis brama*, roach *Rutilus rutilus*, and perch *Perca fluviatilis* dominated the daytime offshore fish assemblage whereas bleak *Alburnus alburnus* prevailed at night. Bream and roach decreased in abundance at night while perch completely disappeared from the offshore habitat. The diel differences in size distributions and direct catches suggested the population-wide horizontal offshore migration of bleak and inshore migration of all perch during dusk. On the other hand, partial inshore migration of bream and roach adults was observed during dusk (52 and 80%, respectively). The different proportions of offshore residents among species and size classes suggested that differences in size, and, therefore, predation vulnerability, contributed to the observed migration patterns.

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## Introduction

Diel habitat shifts are widespread phenomena observed in marine and freshwater ecosystems (Hasler & Villemonte, 1953; Zaret & Suffern, 1976; Axenrot et al., 2004; Mehner et al., 2007). The diel vertical migrations have received more attention even though diel horizontal migrations (DHM) represent the

principal component of fish spatiotemporal relationships in water bodies where the vertical movements are restricted by depth and other physical factors, such as anoxic and cold hypolimnion (Comeau & Boisclair, 1998; Gaudreau & Boisclair, 1998). DHM is frequently invoked to explain diel changes of fish assemblage structure in either inshore or offshore habitats (Gliwicz et al., 2006; Vašek et al., 2009; Říha et al., 2011), but only few studies have examined changes in both habitats simultaneously (Järvalt et al., 2005). Furthermore, DHM was frequently studied only in juvenile fish but there is a paucity of studies focused on the migration of adults.

The estimation of the fish population and trophic dynamics between inshore and offshore habitats requires an adequate quantitative description of DHM. Horizontal hydroacoustic methods provide the high spatiotemporal resolution and quantitative observation of undisturbed fish populations (Kubečka & Wittingerová, 1998; Drašík & Kubečka, 2005) even in shallow habitats (Thorne, 1998; Tátrai et al., 2008). This technique allowed us to monitor both offshore and inshore (depth >1.5 m, according to beam width) zones with high spatial coverage and continuously over long periods of time.

In freshwater fish, DHM is considered as a general phenomenon affecting the whole assemblage; yet adults and juveniles usually migrate in opposite direction (Schulz and Berg, 1987; Bohl, 1980; Gliwicz & Jachner, 1992; Wolter & Freyhof, 2004). The widely accepted hypothesis to explain this migratory behavior is a diurnal variation in habitat specific trade-offs between predation risk and growth rate. In this context, it has often been assumed that the inshore habitat offers lower predation pressure while the offshore zone presents a better growth opportunity (Gliwicz et al., 2006). Such a hypothesis may predict why and when a population migrates (Garner et al., 1998; Hölker et al., 2002), but it does not explain why some individuals migrate and others do not. Furthermore, the DHM has been shown to be variable according to the species in question (Järvalt et al., 2005), under different environmental conditions (Jeppesen et al., 2006), over a given season (Imbrock et al., 1996; Vašek et al., 2008), and during ontogeny (Werner & Hall, 1988).

Recently, the partial migration theory has come into prominence in fish ecology (Chapman et al., 2011a). At first, partial migration was described among

seasonally migrating fish species (Kerr et al., 2009; Brodersen et al., 2011) and later also among diel vertical migrants (Mehner & Kasprzak, 2011). This theory, which is based on individual behavioral decisions, is defined as a migration in which less than 100% of the population participates (Chapman et al., 2011b). As such, partial migration can be maintained in a population only as frequency-dependent evolutionary strategy, with an equal fitness outcome at equilibrium or when the optimum outcome for an individual is dependent upon its phenotype (Chapman et al., 2011b). Since a genetic basis of partial migration has not been demonstrated (Skov et al., 2010), the resident and migratory strategies are considered to arise from density-dependent phenotypic plasticity induced by environmental or endogenous cues (Brodersen et al., 2008).

This study aimed to address the spatiotemporal niche changes of freshwater fish in an offshore-inshore system. We described i) the extent, stability, and time course of DHM and we tested ii) whether DHM of the most common species is a case of the partial migration with a mixture of migrants and residents. We analyzed data from a continuous 48 h detailed hydroacoustic survey supplemented with simultaneous purse seining.

## Materials and methods

### Study site

The study was conducted at the Římov Reservoir (48°50' N, 14°30' E; South Bohemia, Czech Republic; Fig. 1A) during 7–9 August 2007. This reservoir was built in 1978 by damming the River Malše to create a water supply. The maximum and mean depth of the reservoir was 39 and 12 m, respectively, length 10 km, area 162 ha, and volume  $22.6 \times 10^6 \text{ m}^3$  at the water level (465.5 m a.s.l.) during the experiment. The study area covered 42 ha in the central part of the Římov Reservoir. The reservoir is dimictic, summer stratification occurs usually from April to October, with anoxic zone below 6 m depth. The average retention time of the water body is approximately 91 days and the trophic status is meso-eutrophic (Horňák et al., 2010). The fish assemblage in the Římov Reservoir is characterized as a stable cyprinid community (dominant species: roach, *Rutilus rutilus* (L.); bream, *Abramis brama* (L.); and bleak, *Alburnus alburnus* (L.)) with an

additional proportion of perch, *Perca fluviatilis* L. (Říha et al., 2009). Predatory fish (asp, *Leuciscus aspius* (L.); pikeperch, *Sander lucioperca* (L.); pike, *Esox lucius* L.; and European catfish, *Silurus glanis* (L.)) constitute an important proportion (14.5% of the biomass catch of the pelagic gillnets) of offshore assemblage (Prchalová et al., 2009).

### Acoustic equipment

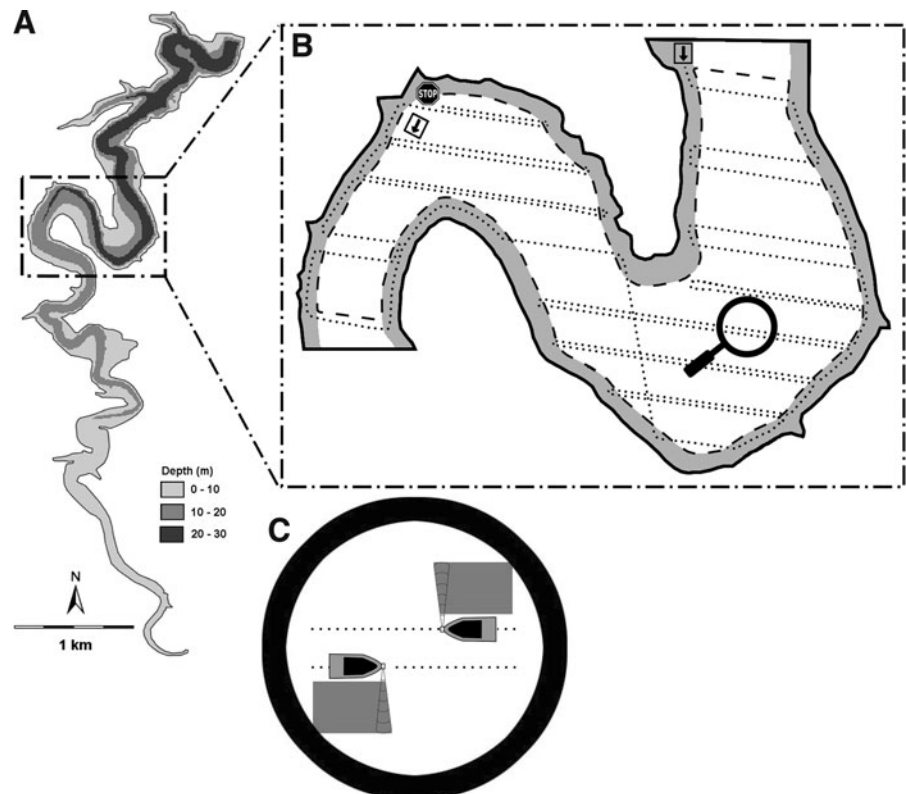
The acoustic study was made by a combination of a horizontally orientated elliptical transducer (ES120\_4; nominal beam angles  $9.2^\circ \times 4.3^\circ$ ) and a circular transducer (ES120\_7C; nominal angle  $6.4^\circ$ ) aimed vertically. Both transducers were operated by a SIMRAD EK 60 split-beam echosounder at the frequency of 120 kHz via a multiplexer. Transducers were installed at the front of the research vessel Ota Oliva on a special frame; the elliptical transducer was orientated starboard and tilted  $4^\circ$  downwards. The echosounder was driven by the SIMRAD ER 60 software (version 2.2.0), a pulse duration of 128  $\mu$ s was

constantly kept during the study period and the ping rate was set at the maximum (mostly around 5 pings  $s^{-1}$ ). Before the survey, the whole system was calibrated using a 23 mm diameter copper calibration sphere (target strength (TS)  $-40.8$  dB) according to Foote et al. (1987).

### Survey design

The acoustic survey was performed along a pre-designed dense parallel grid (Fig. 1B) with a constant speed of  $1.5$  m  $s^{-1}$ . The survey was divided into two parts (i) offshore part—which was 8 km long with a maximum trajectory in the open water and (ii) inshore part—3.5 km long with most of the trajectory passing near the banks with a horizontally orientated beam aimed toward the shore. The offshore transects located near the shore, mainly turnabouts, were excluded from analyses. The studied inshore part was limited to depths  $>1.5$  m. At this point, depending on the slope of inshore zone, the recording was filled with bottom echoes. The position of the survey boat was measured

**Fig. 1** Bathymetric map of the Římov Reservoir with study area highlighted by dot-dash rectangle (A). The pre-designed hydroacoustic survey design in detail (B). Dotted line represents the offshore part of the survey, the dashed line the inshore part. Gray color demarks the inshore zone. Arrows indicate the starting points of particular parts of the survey and the STOP sign indicates ending points of both parts of the survey. The radiating conic sections indicate the orientation of the transducer and surveyed area relative to the boat trajectory in magnification (C)



using a Garmin GPSMAP 60CSx GPS receiver with an external antenna attached to transducer's frame and the obtained geographic coordinates were embedded into the acoustic data files. Both offshore and inshore surveys were repeated every 3 h during 48-h cycle. A total number of 16 hydroacoustic surveys comprising both offshore and inshore parts were performed. Three surveys (0600–0900 and 1800–2100 during the first day and 0300–0600 on the second day) were not processed because of the very noisy data in combination with technical problems.

Vertical temperature and oxygen levels were measured using a calibrated YSI 556 MPS probe during the survey. The intensity of visible light was measured (in lux) 1 m under the water surface, using the LI-1400 datalogger with LI-193 sensor (LI-COR Biosciences). Sunset and sunrise were at 2030 and 0530, respectively (calculated using the spectral calculator [http://www.spectralcalc.com/solar\\_calculator/solar\\_position.php](http://www.spectralcalc.com/solar_calculator/solar_position.php)).

#### Data processing

Raw acoustic data were converted and analyzed with the Sonar5 Pro post-processing software (version 5.9.1, Balk & Lindem, 2009). The horizontal recordings were bound by setting the upper and lower limit of the pelagic layer at 4 and 20 m from the transducer, respectively. These limits were set to avoid a bias caused by the transducer near-field (2.29 m) or far-field non-spherical spreading induced by ray distortion at the thermocline or surface layers. A manually defined bottom line was used in order to exclude noisy parts in a record, or bank echoes occurring within the pelagic layer. In addition, Cross Filter Detector (Balk & Lindem, 2000) was used to eliminate noise in the horizontal data with the following parameters: foreground filter: height 5 and width 1, background filter: height 55 and width 1, offset + 6 dB, perimeter length: 10–10,000 (Number of samples around the detected region), ratio: min 1–max 270 (track length/mean echo length), max intensity: (–60 to –10 dB).

For the vertical data, a surface line was set at the distance 4 m from the transducer and an automatic algorithm was used to define the bottom line 0.3 m above the detected bottom. Only data within the pelagic layer or between these defined surface and bottom lines were processed. The whole horizontal survey was divided into 15 m long transects. Such a

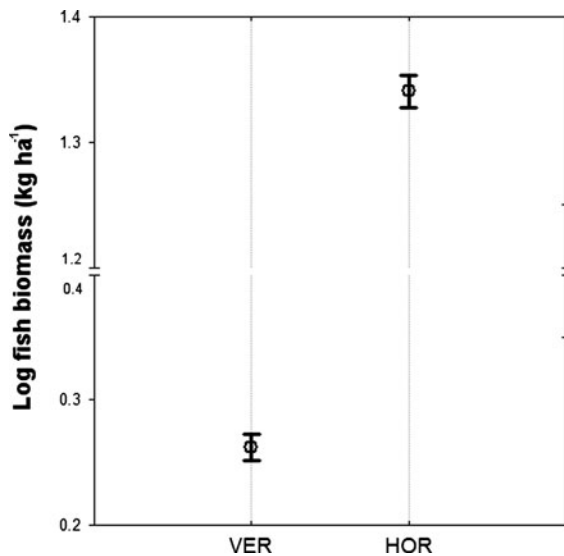
short length was chosen in order to reveal spatial distribution changes on this scale. The vertical recordings were divided into 6-m deep layers. Non-fish echoes were eliminated by setting a –65 dB and –67 dB minimum TS threshold for horizontal and vertical data, respectively. The analysis was not aimed at 0+ fish, and, therefore, the TS threshold of –57 dB for target size distribution was set to exclude the fish <6 cm and the fish abundance was calculated only for those >6 cm by multiplying the total fish abundance by the proportion of this group in the tracked targets.

All targets exceeding the threshold were echo-integrated for obtaining the volume backscattering strength coefficient  $s_v$ . Fish abundance was calculated by scaling the  $s_v$  by the average backscattering cross section ( $\sigma_{bs}$ ) derived from mean TS in the linear domain (“ $s_v$ /TS scaling”; Balk and Lindem 2009). Fish standard lengths (SL) were estimated from TS by applying the aspect deconvolution procedure (Kubečka et al., 1994) and the common European species TS/length regression described by Frouzová et al. (2005). Fish weight for each 1-cm length class was calculated from the length/weight relationship determined according to pelagic multimesh gillnet catches performed at the same location the next day after the acoustic survey. The average weight of the recorded acoustic population was calculated by dividing the total weight by the number of observed individuals. The biomass ( $\text{kg ha}^{-1}$ ) was then calculated by multiplying the abundance estimate ( $\text{inds. ha}^{-1}$ ) and the average weight.

The results of vertical surveys were not considered further, because an overwhelming majority of fish were gathered within the surface layer (significant difference between fish biomass in the horizontal and vertical surveys [ANOVA;  $F(1, 20560) = 16127$ ,  $P < 0.001$ ; Fig. 2]), which corresponded well with the warm and richly oxygenated epilimnion established in the reservoir.

#### Direct catches

The fish community was simultaneously sampled in adjacent offshore areas using a purse seine (Tischler et al., 2000; 120 m long, 12 m deep, and 6/8/10 mm mesh size front/mid/rear, respectively). Thirteen purse seine hauls (7 day, 6 night) were performed and 343 fish were caught in total. Caught fish were measured to the nearest 5 mm and released back to the reservoir.



**Fig. 2** Comparison of mean fish biomass estimates ( $\pm$ SE) during all the horizontal and vertical surveys. Both days were pooled

### Statistical analyses

Statistical analyses were carried out in the STATISTICA software package ver. 9.1. (StatSoft, Inc., 2010). Surveys between 0600 and 2100 (i.e., survey number 5, 6, 7, 12, 13, 14, 15, and 16) were merged and termed as day, surveys from 2100 till 0600 (i.e., survey number 1, 2, 3, 9, and 10) were combined as night. The data were log (+1) transformed prior to analyses.

Only odd transects were included in the dataset to avoid autocorrelation. The diel changes in acoustic fish biomass and abundance were evaluated by factorial analyses of variance (ANOVA) with daytime and habitat (offshore and inshore zones) as covariates. The difference between day and night purse seine catches was tested with *t* test.

For comparison of size-frequency distributions, all tracked and caught fish were grouped into three size classes (TS  $-57$  to  $-46$  dB, equivalent SL 6–18 cm;  $-46$  to  $-36$  dB or 18–50 cm and  $>-36$  dB or  $>50$  cm), termed small-, mid-, and large-sized fish, respectively. The Generalized linear model (GLZ) was used for the comparison of day and night size distributions. The size of the fish was modeled by multinomial distribution with three possible results (small, mid, large). The day time effect was chosen as a covariate in GLZ. The logit link function was used in GLZ.

### Results

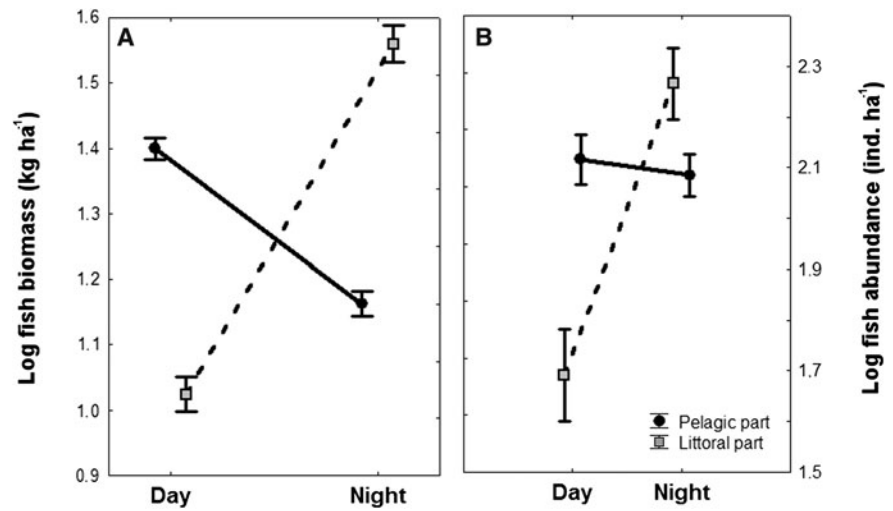
The horizontal fish distribution was not homogenous in any of the 13 analyzed hydroacoustic surveys. The mean fish biomass significantly differed in both types of habitats between day and night [ANOVA;  $F(1, 3674) = 147.5$ ;  $P < 0.001$ ; interaction effect of Habitat \* Time of a Day; Fig. 3A]. It was higher during day than during night in the offshore zone ( $165.49$  and  $110.53$  kg ha<sup>-1</sup>, respectively) and higher during night than day in the inshore zone ( $111.67$  and  $189.83$  kg ha<sup>-1</sup>, respectively). This pattern was consistent during both days of investigation [Day1: ANOVA;  $F(1, 1945) = 74.65$ ;  $P < 0.001$ ; Day2: ANOVA;  $F(1, 1729) = 52.58$ ;  $P < 0.001$ ]. No difference was found between fish biomass in the inshore and offshore zones when the daytime factor was not included during both days [ANOVA;  $F(1, 3674) = 0.02$ ,  $P = 0.88$ ].

The diel changes in the offshore fish assemblage were simultaneously investigated by purse seining. The average fish biomass in the offshore zone was assessed at  $78$  and  $38$  kg ha<sup>-1</sup> during day and night, respectively, but these values were not significantly different [ $t(11) = 0.58$ ,  $P = 0.57$ ; Fig. 4]. The daytime offshore assemblage was composed of bream, roach, and perch ( $51.4$ ;  $19.1$ ; and  $3.5$  kg ha<sup>-1</sup>, respectively), whereas the assemblage consisted of bream, bleak, and roach at night ( $27.4$ ;  $6.9$ ; and  $3.6$  kg ha<sup>-1</sup>, respectively).

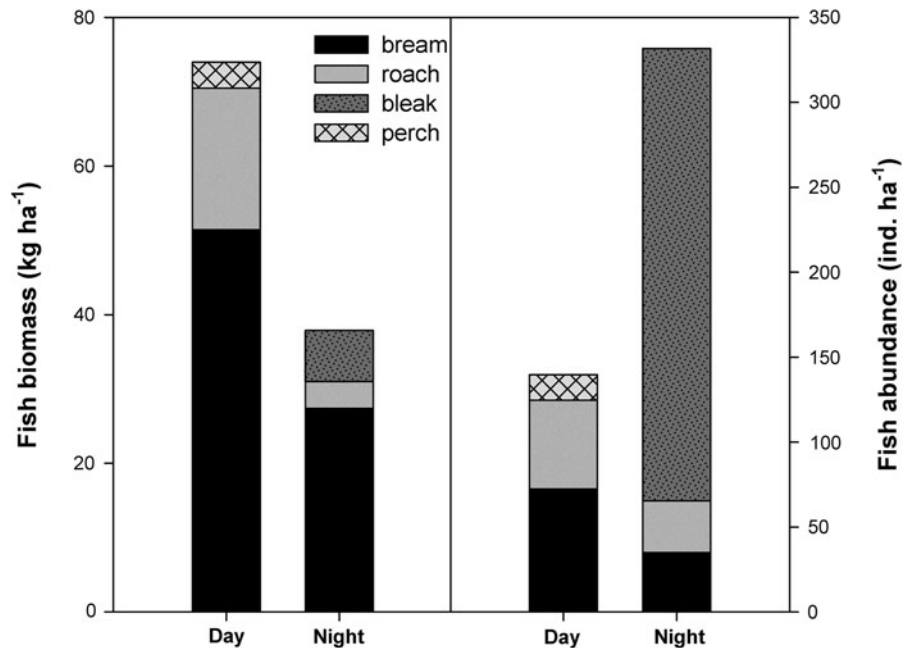
The mean acoustic fish biomass went through synchronic diel changes in the offshore and inshore zones and this pattern was identical during both days. In the offshore zone, the fish biomass continuously increased during the day, reaching its maximum in the afternoon (1500). Subsequently, fish biomass decreased with decreasing light intensity, reaching its minimum at 0300 (Fig. 5). Opposite to this, in the inshore zone, fish biomass was always higher at night than during day (Fig. 5).

The average fish abundance also differed between day and night in the inshore and offshore zones [ANOVA;  $F(1, 3674) = 77.039$ ,  $P < 0.001$ ; interaction effect of Habitat \* Time of a Day; Fig. 3B]. The abundance did not differ in the offshore zone [one way ANOVA,  $F(1, 2332) = 0.01685$ ,  $P = 0.9$ ] reaching  $616$  ind ha<sup>-1</sup> during daytime and  $600$  ind ha<sup>-1</sup> at night, whereas in the inshore zone exhibited a significantly higher fish abundance at night than during the day [one way ANOVA,  $F(1, 1342) = 1$ .

**Fig. 3** Mean fish biomass (A) and abundance (B) ( $\pm$ SE) acquired from the offshore (solid line) and inshore surveys (dashed line). Data from both days of investigation are grouped together



**Fig. 4** Biomass and abundance of fish caught by purse seine during day and night hauls with dominant species composition



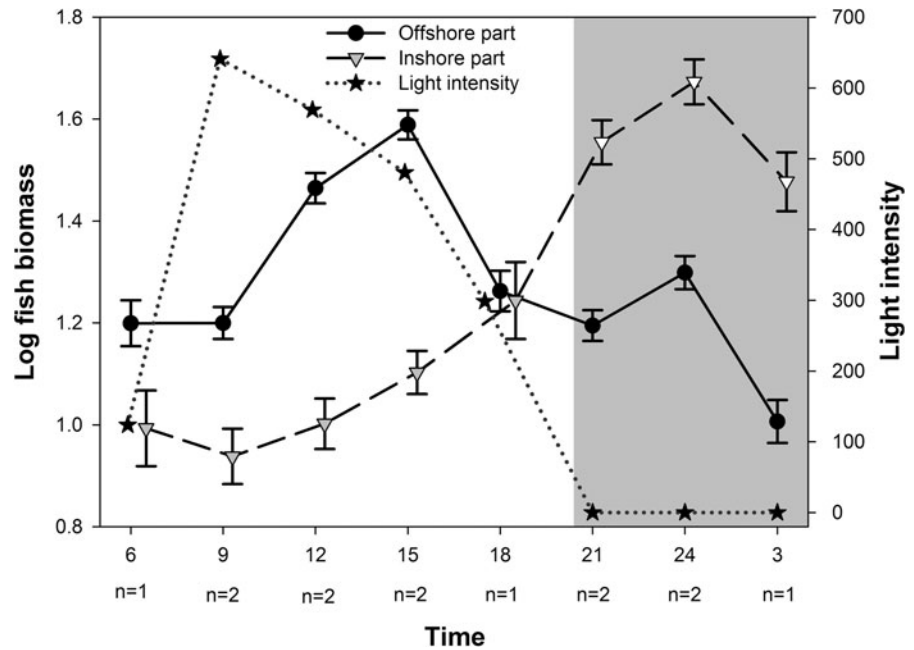
29,  $P < 0.001$ ], with mean values of 612 and 394 ind ha<sup>-1</sup>, respectively.

The three size classes of fish did not show the same pattern of diel abundance variation in the offshore zone (Fig. 6). The abundance of small fish fluctuated around 150 ind ha<sup>-1</sup> in the day and rapidly increased during the first part of the night (to 241 ind ha<sup>-1</sup>). The abundance of large-sized fish attained its highest values during the day (225 ind ha<sup>-1</sup>) and decreased constantly during the evening and night

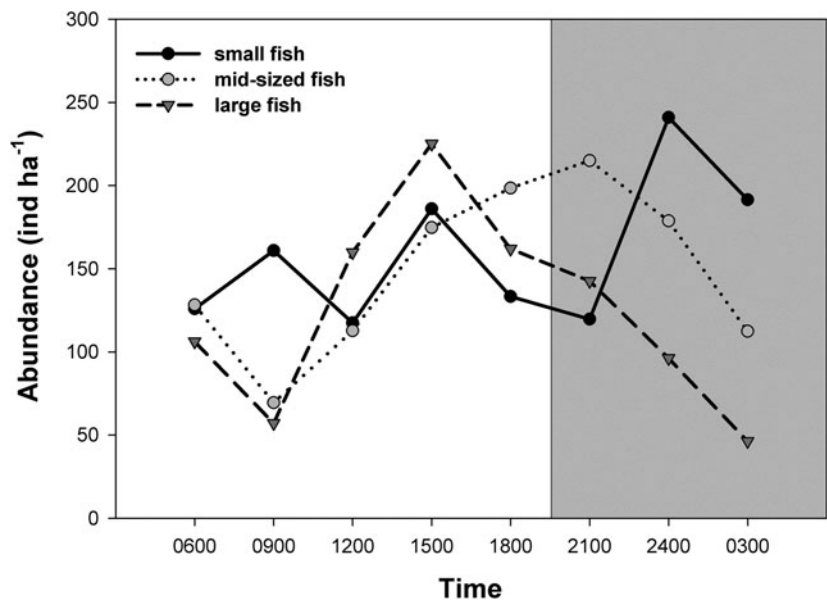
(to 46 ind ha<sup>-1</sup>). The mid-sized fish showed a mixed pattern in this respect.

The difference between day and night fish abundance assessed by purse seine was nearly significant [ $t(11) = -2.11$ ;  $P = 0.058$ ]. The average daytime abundance reached 140 ind ha<sup>-1</sup> (Fig. 4;  $n = 112$ ). Bream was found to be the dominant species in the epilimnion (72.3 ind. ha<sup>-1</sup>), followed by roach (52.4 ind ha<sup>-1</sup>) and perch (15 ind ha<sup>-1</sup>). The average fish abundance increased to 336 ind ha<sup>-1</sup> at night

**Fig. 5** Diel changes of mean acoustic fish biomass ( $\pm$ SE) in the offshore (solid line) and inshore parts (dashed line) and under water light intensity (dotted line) detected in the studied area of the Římov Reservoir. The data from two consecutive days were pooled; “*n*” indicates the number of surveys included



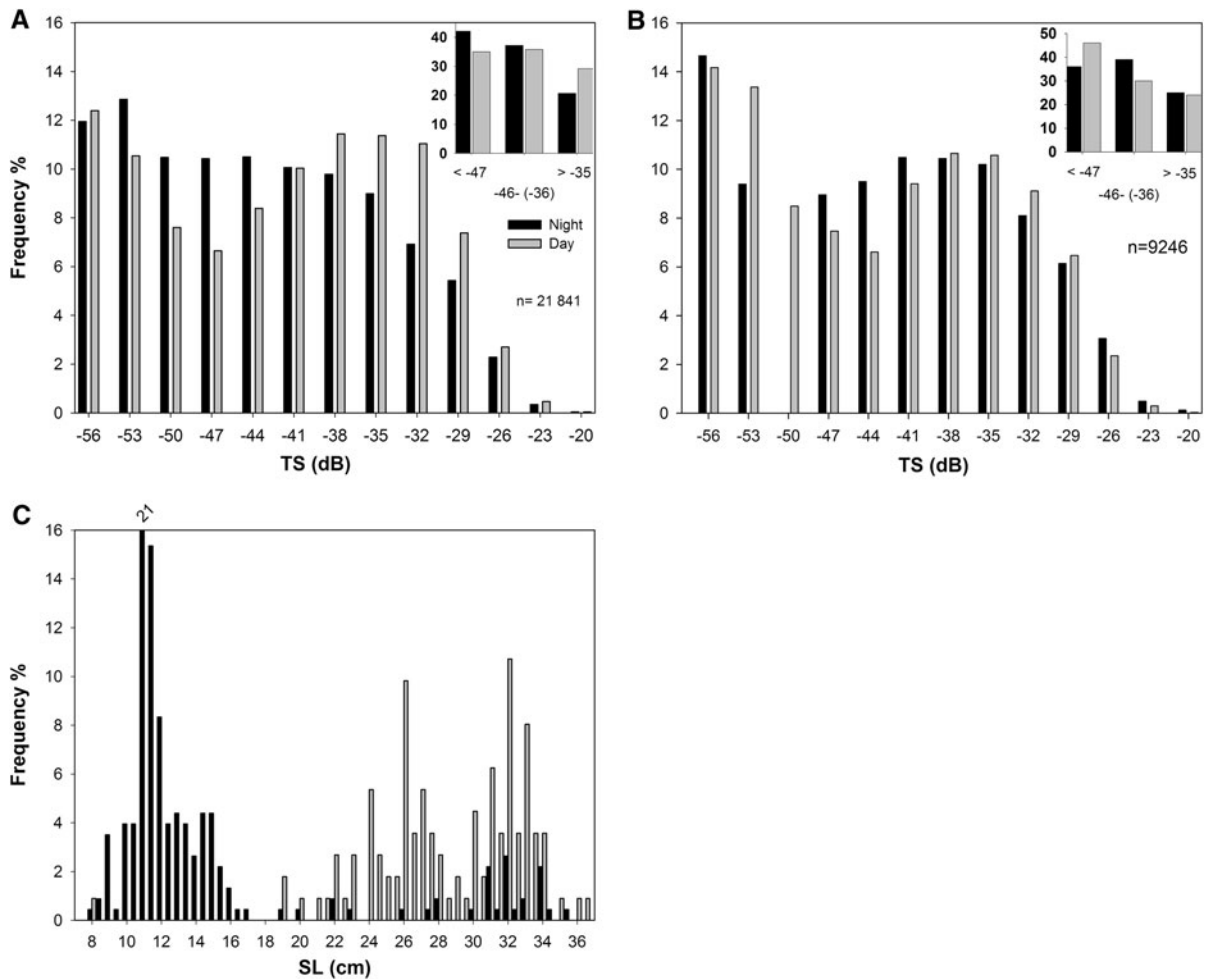
**Fig. 6** Fish densities of small-, mid-, and large-sized fish groups recorded at 3-h intervals in the offshore zone. Data from both investigated days are pooled



(Fig. 4;  $n = 228$ ), with bleak being the most abundant species ( $270 \text{ ind ha}^{-1}$ ). Bream and roach reached 35 and 31  $\text{ind ha}^{-1}$ , respectively, while perch was completely absent from the night offshore fish assemblage. Two-thirds of the night population of roach were subadults.

The size distributions of acoustic targets in the offshore zone differed significantly between day and

night [ANOVA;  $F(2, \text{Ln-likelihood } -23718.6; P < 0.01)$ ; Fig. 7A]. The proportion of large fish ( $\text{TS} > -35 \text{ dB}$ ) decreased at night, whereas that of small fish ( $\text{TS} < -46 \text{ dB}$ ) increased. The size distribution of fish caught by the purse seine also differed significantly between day and night [ANOVA;  $F(2, \text{Ln-likelihood } -158.5; P < 0.01)$ ; Fig. 7C]. The day assemblage was dominated by large-sized fish,



**Fig. 7** The day and night target strength distributions of acoustic targets into offshore (A) and inshore zones (B) and the length frequency of fish caught into the purse seine (C)

whereas small-sized fish clearly dominated at night. Also in the inshore part, the day and night size distributions differed [ANOVA;  $F(2; Ln\text{-likelihood} - 9903.2)$ ;  $P < 0.01$ ; Fig. 7B]. In contrast to the offshore zone at night, the proportion of small-sized fish declined in inshore zone and the mid-sized group of fish (TS  $-46$  to  $-36$  dB) increased.

## Discussion

The present study has shown that adult fish DHM is the main reason for the significant variation of fish biomass in the offshore and inshore zones during the diel cycle in the Římov Reservoir. However, the decreases of only 33 or 52% of biomass in offshore

zone at night, according to hydroacoustic and direct catch estimates, respectively, suggest that the night inshore migration does not encompass the entire day assemblage. The diel changes of fish biomass demonstrated that a substantial part of the day offshore assemblage exhibit a resident strategy at night, which resembles the pattern of diel partial vertical migration in coregonids described by Mehner & Kasprzak (2011). Partial migration was confirmed in populations of bream and roach, while perch and bleak seem to act via population-wide horizontal migration.

The vertical component of the observed fish movements can be excluded according to nearly deserted layers deeper than four meters, similar to the results in other studies in stratified reservoirs and lakes (Kubečka & Wittingerová, 1998; Brosse et al.,



1999; Čech & Kubečka, 2002; Knudsen & Sægrov, 2002; Draščík et al., 2009). In deep eutrophic water bodies, thermal and oxygen stratification exclude fish from deeper layers, so that no or only a very few fish occur under the thermocline in such systems (Järvalt et al., 2005; Prchalová et al., 2008; Prchalová et al., 2009; Jarolím et al., 2010).

The overall fish biomass recorded in the offshore and inshore zones were precisely inverse to each other during the diel cycle, which together with size distribution changes illustrates the process of DHM. The comparable fish biomass in offshore and inshore zones during 48-h period further suggest a relatively high site fidelity for a specific part of the reservoir observed also by Zamora & Moreno-Amich (2002) and Gaudreau & Boisclair (1998). Similar to our results, Draščík et al. (2009) recorded a higher fish biomass, with the significant contribution of large fish, in the offshore areas of several reservoirs during the day acoustic surveys. The exploitation of offshore zone as a daytime habitat was recorded also in telemetry studies for bream, roach, and perch adults (Schulz & Berg, 1987; Zamora & Moreno-Amich, 2002; Jacobsen et al., 2004). Furthermore, Vašek et al. (2009) also observed a higher proportion of large individuals during the day in a gillnetting study. In the littoral zone, an accumulation of higher fish biomass at night is in accordance with previous results obtained by beach seining in many reservoirs, including Římov, and lakes (Kubečka, 1993; Blackwell & Brown, 2005; Říha et al., 2008, 2011).

The dominant species occurring in the offshore zone of the Římov Reservoir (bream, perch, and roach) have been demonstrated to be horizontal migrants in lakes and rivers (Schulz & Berg, 1987; Imbrock et al., 1996; Zamora & Moreno-Amich, 2002; Jacobsen et al., 2004). Since bream, roach, and perch are predominantly zooplanktivorous and diurnal feeders during the summer and the inshore zone is usually undeveloped in canyon-shaped reservoirs like that of Římov (Vašek & Kubečka, 2004; Vašek et al., 2008), the inshore migration of these species is unlikely to be associated with intensive feeding on benthic organisms as described in lakes (Schulz & Berg, 1987).

In the case of perch, an exclusively visual forager, we observed population-wide inshore migration, suggested as an energy saving strategy under low light intensities when foraging is inefficient (Hasler & Villemonte, 1953; Imbrock et al., 1996; Čech et al.,

2009). The DHM was also mentioned as an advantageous strategy for potamal fishes in respect to saving the energetic costs of swimming by use of the inshore with slower water flows (Wolter & Freyhof, 2004).

Contrary to the situation in rivers, under lentic reservoir conditions the night inshore migration seems to represent an extra cost for the migrating part of bream and roach populations compared to their offshore resident conspecifics. This migrating behavior appears not to be of any evident advantage and seems to be, therefore, maladaptive. Individual phenotypic plasticity in the tendency to rest near structures, or a behavioral syndrome related to inshore migration of originally riverine populations (Fernando & Holčík, 1991; Sih et al., 2004) may probably explain the maintenance of partial migration of adults.

Additionally, the observed interspecific differences in the proportion of residents in the dominant species seem to be related to species-specific predation vulnerability. Nilsson & Brönmark (2000) demonstrated less predation vulnerability for bream in comparison with roach according to its higher body depth in the specific length in gape size limited predator's environment. Furthermore, Skov et al. (2011) revealed that individual predation risk is an important factor in the decision of an individual to migrate or not. This idea explains the highest proportion of bream among the offshore zone residents and the inshore displacement of all bleak and the juvenile roach during dawn. Fish in the offshore zone are probably able to assess the predation risks and perform a size-dependent migration strategy in a similar manner as the vertically diel migrating zooplankton (Hansson & Hylander, 2009).

The observed apparent increase of small fish abundance in the offshore zone at night, together with a coincident decrease of small fish representation in the inshore zone, corroborate the model of juvenile DHM, with an extension for bleak adults, where predation also plays an important role (Bohl, 1980; Gliwicz & Jachner, 1992). The offshore zone represents a risky place for small fish during daylight, because piscivorous fish (pikeperch, asp, and large perch) are abundant in this habitat (Vašek et al., 2008; Prchalová et al., 2009). Furthermore, even a few predator individuals in a lake were sufficiently frightening for subadults and induced offshore avoidance behavior (Brabrand & Faafeng, 1993; Gliwicz et al., 2006).

On the other hand, in the safer inshore zone with high small fish densities and low food abundance, the growth of fish can be reduced (Eklöv et al., 1994; Diehl & Eklöv, 1995). Juvenile and small-sized fish, therefore, avoid the offshore zone with a higher occurrence of predatory fish until dusk and move back to inshore at dawn. This strategy allows them to utilize the abundant zooplankton in the offshore zone during twilight, when they are still able to visually detect their prey, and still to minimize the chance of predator encounter (De Robertis et al., 2003).

The effect of juveniles and small-sized fish DHM on the offshore assemblage composition is probably slightly underestimated in the acoustic results because of a higher signal-to-noise ratio and the inherent difficulties of horizontal beaming. Under such conditions, the weak aspects (head and tail) of small fish could not be distinguished from the noise, thus distorting density and size distribution estimates, especially in situations in which small fish dominate the population (compare night size distributions in Fig. 7A, C). Despite this limitation, the increase of small fish abundance in the night offshore assemblage was apparent in acoustic results, although not at the same extent as by purse seining. A similar difference in size distributions derived from horizontal acoustics and purse seine catch were observed by Yule (2000) in North American lakes.

Our simultaneous detailed description of fish assemblage changes in inshore and offshore zones allows us to determine the approximate time periods when migration occurred. Morning DHM occurred most probably between 0500 and 0600 h while that in the evening took place between 1800 and 2100. This timing is congruent with the peaks of fish activity determined by Prchalová et al. (2010) from gillnet catches; it should be noted, however, that the evening part of the migration was recorded slightly earlier in this study.

Our results suggest predation risk as the main factor in the decision to migrate or not. However, other individual traits, such as body conditions (Brodersen et al., 2008), behavioral syndromes (Sih et al., 2004), or phenotypic polymorphism (Chapman et al., 2011a) may also be important drivers of partial DHM.

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