Mgr. Thesis

Faculty of Sciences, University of South Bohemia, České Budějovice

Pelagic behaviour of reservoir fishes: sinusoidal swimming and associated behaviour

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Anotace

Dlohodobá hydroakustická studie byla provedena v roce 2005 na údolní nádrži Římov v České republice. Zabývala se zejména chováním ryb ve volné vodě nádrže, se zvláštním zřetelem na sinusoidní plavání. Byl též zkoumán vliv podmínek prostření na chování pelagických ryb.

Annotation

Long-term fixed-location hydroacoustic study with uplooking transducer was performed during 2005 in Římov reservoir, Czech Republic. It dealt mainly with fish behaviour in the open water of reservoir, especially with sinusoidal swimming behaviour. The dependence of pelagic fish behaviour on environmental conditions was also studied.

Prohlášení

Prohlašuji, že svoji diplomovou práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své diplomové práce, a to v plném znění elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách.

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Oldřich Jarolím

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1 Introduction

1.1 Sinusoidal swimming

Haberlehner (1988) for the first time noticed up-and-down swimming of cyprinids in backwater of the Danube. Čech & Kubečka (2002) described the term 'sinusoidal swimming' on the basis of up-looking acoustic data. This term was implemented because trajectories of 'sinusoidally swimming' pelagic fish resembled sinusoid curve when displayed on the echogram. The patterns of TS change revealed that the sinusoidal swimming is an active swimming mechanism rather than mechanism based on swimbladder volume changes. Up-and-down swimming was detected during all observations from June to August 1998 and 83% of fish >100 mm exhibited this behaviour. This movement pattern was not observed in November. The rest of adult fish were either too close to the surface to be able to follow a sinusoidal trajectory or they swam straight just below the thermocline. Mean vertical distance between peak and trough (uppermost and lowermost positions of sinusoidal curve) ranged from 19 to 321 cm, average vertical range of the sinusoidal cycle was 98 cm and the duration of a sinusoidal cycle was 18 s on average. Generally, larger fish had higher frequency of cycling than smaller fish. A smaller data set from May 1999 showed less intense occurrence of sinusoidal cycling swimming in the open water, mainly because of the coincidence with the spawning period of part of the bream and bleak populations.

The most of planktivorous fish in the open water are visually oriented pump-filter feeders (Hairston, 1993, Vašek et al., 2003). Hence, the reason for sinusoidal swimming could be explained by the low contrast of zooplankton prey in case of head-on encounter. Optimal angle for the attack is 30-60° and attack outside Snell's window (less than 48.6 degrees to vertical plane) increases the visibility of prey (Thetmayer & Kils, 1995). Sinusoidal swimming in summer period is coincided probably with the foraging on larger zooplankton species (*Daphnia*, *Leptodora*) that are the most common prey of adult fish in summer (Vašek & Kubečka, 2004, Vašek et al., 2008).

1.2 Vertical fish distribution and migration

According to Prchalová et al. (2008) depth has the largest explanatory power for predicting fish community composition. Vertical fish distribution in open water of lakes and dimictic freshwater reservoirs is highly influenced by temperature and oxygen stratification. Fish are distributed mainly above thermocline due to the hypolimnetic oxygen depletion in spring and summer (Bohl, 1980, Hartmann & Löffler, 1989, Imbrock et al., 1996, Prchalová et al., 2008, Vašek et al., 2008) also the zooplankton populations predominantly occur in upper pelagic layers (Hudcovicová & Vranovsky, 2006, Ingeborg et al., 2007, Seďa, 2007).

The presence of adult fish in upper layers of pelagic zone during daytime was observed in many lakes and reservoirs with subsequent migration of adult fish into the littoral during the dusk (Schulz & Berg, 1987, Kubečka, 1993, Čech, 2001, Zamora & Moreno-Amich, 2002, Jacobsen et al., 2004, Peterka et al., 2007). Surface gill net catches in Římov reservoir, Czech Republic, were in 2000-2003 clearly dominated by three cyprinids: roach (*Rutilus rutilus*), bream (*Abramis brama*) and bleak (*Alburnus alburnus*). These species together accounted for 69–93% of total CPUE (*i.e.* catch per unit effort) by number and 66–96% of total CPUE by weight. Mid-water gill net CPUE was consistently lower than the surface gill net CPUE and the above-bottom CPUE was negligible or equal to zero (Vašek et al. 2004).

Diel vertical migration is a widespread behavioural pattern in populations of aquatic animals. Its adaptive value is explained by a trade-off between the protection against visually feeding predators in the dark hypolimnion during daytime and a higher food uptake in the upper food-rich layers during the night (Lampert, 1989, Dawidowicz et al., 1990, Guisande et al., 1991). However, foraging strategy seems to be the main reason for diel vertical migrations of freshwater fish (Eckmann & Imbrock 1996, Mehner 2006). All vertical migrations described in previously mentioned studies occurred in large scale (usually in order of tens of meters) between epilimnion and hypolimnion, while sinusoidal swimming proceeds only in epilimnion within few meters.

Behavioural changes within the diel cycle might be due to endogenous circadian rhythms as well as responses to environmental conditions like light-level, temperature, moon phase and piscivory (Thorpe & Rig, 1978, Peirson & Frear, 2003). The light intensity seems to be one of the most relevant factors that explain vertical distribution and migration of fish and their overall circadian activity (Černý, 1973, Helfman, 1981, Čech et al., 2005). Fish have an absolute preference for the light intensity values and react to the light intensity change, the higher is light intensity change the faster is vertical migration (Bohl, 1980). Appenzeller & Leggett (1995) observed a strong relationship between ambient light intensities and depth of fish layer in the water column. Järvalt et al (2005) described presence of fish between 2-3.5 m during the period of intensive solar radiation and their descent to deeper layers during sunrise and afternoon. Vertical distributions of zooplankton and fish are also affected by gradients in temperature, oxygen and food (Swierzowski et al., 2000, Järvalt et al., 2005).

Fixed location hydroacoustic (uplooking) has major advantages in studying open water ecosystem especially when most fish are distributed close to the surface. Uplooking vertical system has high signal-to-noise ratio compared to horizontal beaming and disturbance of fish is eliminated (Gjelland et al., 2004). The fish behaviour can be monitored for many days to view the effect of temporal and environmental changes. Stationary hydroacoustics was successfully used for understanding the distribution of fish in the lake (Stables & Thomas 1992) as well as for developing fish bypass systems (Johnson et al., 1992).

This study is meant as a completion of results of Čech & Kubečka (2002), who described sinusoidal swimming in Římov reservoir in summer 1998. Their study dealt mainly with general description of sinusoidal swimming pattern: range, peak-to-peak amplitude, target strength, cycling frequency etc. This recent study emphasizes more specific issues like changes in sinusoidal swimming pattern throughout the season, daily pattern of this behaviour and multidimensional analysis of features of all basic pelagic swimming patterns. The question of influence of environmental factors (weather conditions and temperature and oxygen stratification) is examined.

2 Methods

2.1 Study area

The study was carried out in Římov reservoir, Czech Republic, which spreads out in the altitude 471 m.s.l., having area 210 ha. The maximum depth is 45 m and the volume is 33.6 millions m^3 (Seďa et al., 2000). This dimictic reservoir is inhabited by 30 fish species of which five species have the highest ecologically relevant abundances: bream *Abramis brama*, roach *Rutilus rutilus*, bleak *Alburnus alburnus*, perch *Perca fluviatilis* and ruff *Gymnocephalus cernuus.* The reservoir has had stable fish composition with a relatively low proportion of predators since 1988-1989 when percid phase was replaced by cyprinid phase (Seďa & Kubečka, 1997, Říha et al., in press)

2.2 Data collection and evaluation

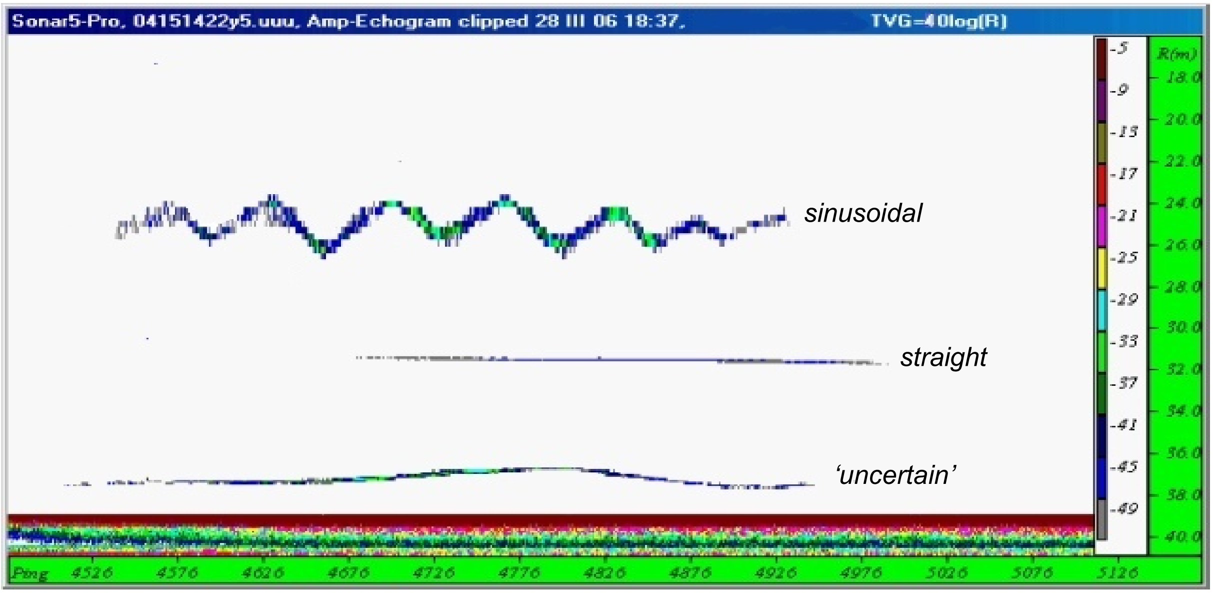
Scientific echosounder Simrad EY 500 together with ES 120-7G split beam transducer were used for obtaining the data. Signal frequency was 120 kHz, pulse length 0.1 ms, pulse interval 0.2 s and output power 63 W. The transducer was placed in the depth 38 m 1 m above the bottom in the lacustrine part of the reservoir near the old Malše rivercourse (see Vašek et al., 2008 for the location). Transceiver and PC were located 80 m away in the enclosed floating boat garage.

The echosounder was continually in operation from April to October 2005. Four limnologically distinctive periods were chosen for further analysis:

•beginning of spring stratification (14 - 16 April);
•clear water phase (30 May – 5 June);
•summer maximum of phytoplankton and zooplankton (9 - 12 August);
•beginning of autumn mixing (12 - 14 October).

Acoustic files were processed by software Sonar5 Pro. Total number of 5898 fish was manually tracked, *i.e.* echoes were combined into tracks and counted (Balk & Lindem, 2000). Manual tracking was prefered because automatic tracking was not able to distinguish individual fish when fish trajectories overlapped. The target strength (TS) thresholds (both Amp and SED) were set to value -56 dB. Time, depth, target strength, trajectory shape and change of range were recorded for individual fish. The most problematic part of the study was to determine whether the fish swims sinusoidally or straight. Sinusoidal swimming [Fig. 1] was defined as swimming along the trajectory that resembled sinusoid curve with at least one full cycle on the echogram (Čech & Kubečka, 2002). Straight trajectory [Fig 1] resembled straight line. Sometimes the fish trajectory was classified as ‘uncertain’ [Fig 1] in case it was not swimming sinusoidally but changes the range apparently.

Fig 1 Sinusoidal ,'uncertain' and straight trajectory as seen on the echogram



T-test were performed in Statistica (StatSoft), hierarchical ANOVA (factor date nested in factor month) was performed in R (language for statistical computing) as well as time series analysis. STL (*seasonal-trend loess,* nonparametric analogy of Fourier analysis) model (Becker et. al., 1988, Cleveland et al., 1990) was trying to distinguish daily changes (called 'seasonal component', S_v, in Cleveland et al., 1990), general trend (actual changes when daily changes were excluded ,'trend component', T_v) and unexplained residuals ('remainders', R_v). Raw data (Y_v) are equal to the sum of all components:

Eq. 1 $Y_v = T_v + S_v + R_v$

It worked on the basis of iterations, when significance of all fitted elements was compared with one another and with the variability of residuals. R functions *ts* and *plot.ts* were used to create and plot time series. Correspondence canonical analysis (CCA) was executed in CANOCO. All graphs were created in R, Sigma Plot and Statistica programs.

Standard length of fish was calculated by using formula:

Eq. 2 $L = 10^{(TS-m)/n}$

where n = 19.65, m = -92.8; ventral aspect (Frouzová et al. 2005). Only TS readings at peak or trough of sine curve when the fish are not tilted were considered (Čech & Kubečka, 2002). Weight of fish was calculated using length/weight relationship:

Eq. 3 $W = a \times L^b$

where a = 1,0943 x 10^{-5}, b = 3,1387. Parameters a and b were obtained from length/weight relationship for roach and bream caught in Římov reservoir in 2005. Those two cyprinids made up to majority of pelagic fish that year (Peterka et al., 2007). Biomass was calculated for each hour using formula:

Eq. 4 $$B = \overline{W} \times \frac{N \times t}{S} \times 10$$

where B is total biomass [kg.ha^{-1}], $\overline{W}$ is hourly averaged fish weight [g], N is number of observations per hour, S is water surface area covered by acoustic beam [m^2], t is average time spent in beam [s] and 10 is quotient for correction to [kg.ha^{-1}]. Abundance [ha^{-1}] was computed as:

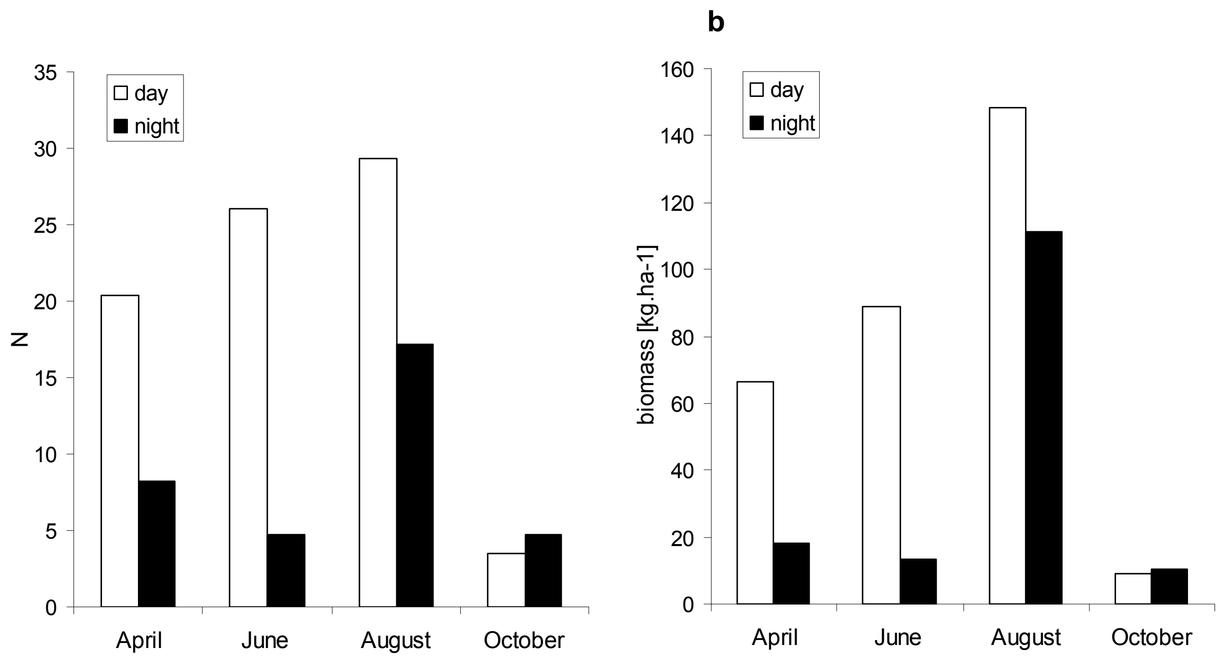
Eq. 5 $$A = \frac{B}{\overline{W}}$$

Vertical patterns in the temperature and dissolved oxygen were measured with calibrated OXI 196 probe (WTW, Germany). Meteorological data, were recorded by HBI meteorological probe MS16 (Fiedler-Mágr, Czech Republic), which comprises of global radiation probe GR01, temperature probe HST005 and rain gauge SR02. Global radiation (GR, [Wm^{-2}]) is made up of direct radiation, reflected radiation from the ground and diffuse radiation of visible spectrum (Gjelland et al. 2004). GR radiation data were used for definition of day and night: time interval when GR = 0 Wm^{-2} was defined as night. Complete extinction curve of GR in water column was recorded only for June data.

3 Results

Number of fish observations as well as average biomass were steadily rising from April to August [Fig. 2 (a) and (b)] The only exception is night in June, when very low numbers and biomass were observed. There were also very few fish in October in open water, especially the day biomass was very low. Temperature profiles [Fig. 3] showed sharp stratification in April, June and August and relatively loose temperature stratification in October. Lack of oxygen in deeper strata was recorded in all studied months except April. The water transparency [Tab. 1] was the highest during the clear-water phase at the beginning of June.

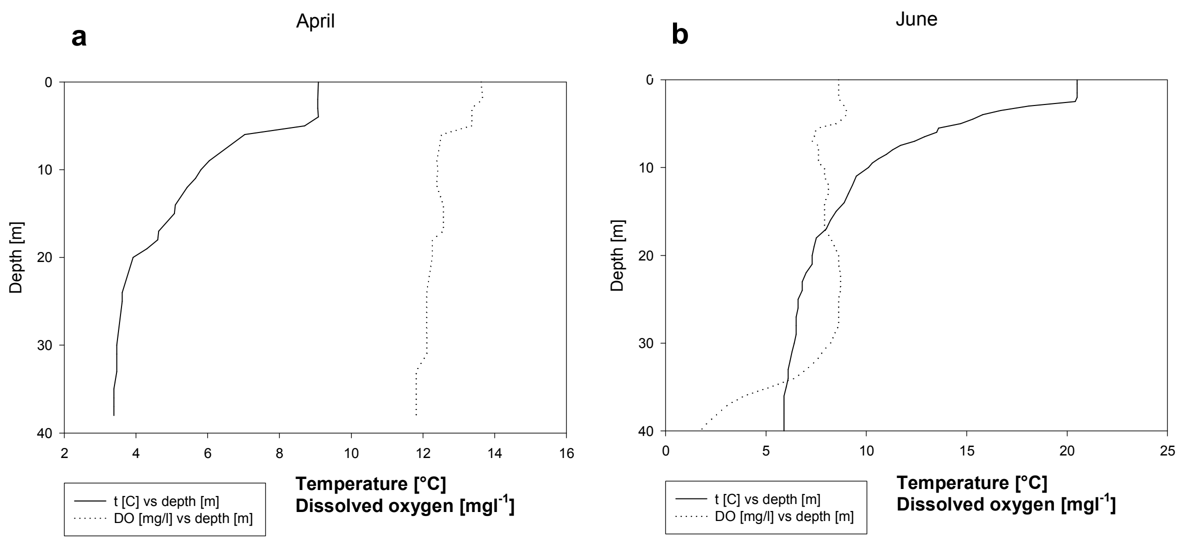
Fig. 2 a Number of observations of all fish per hour; **b** average biomass

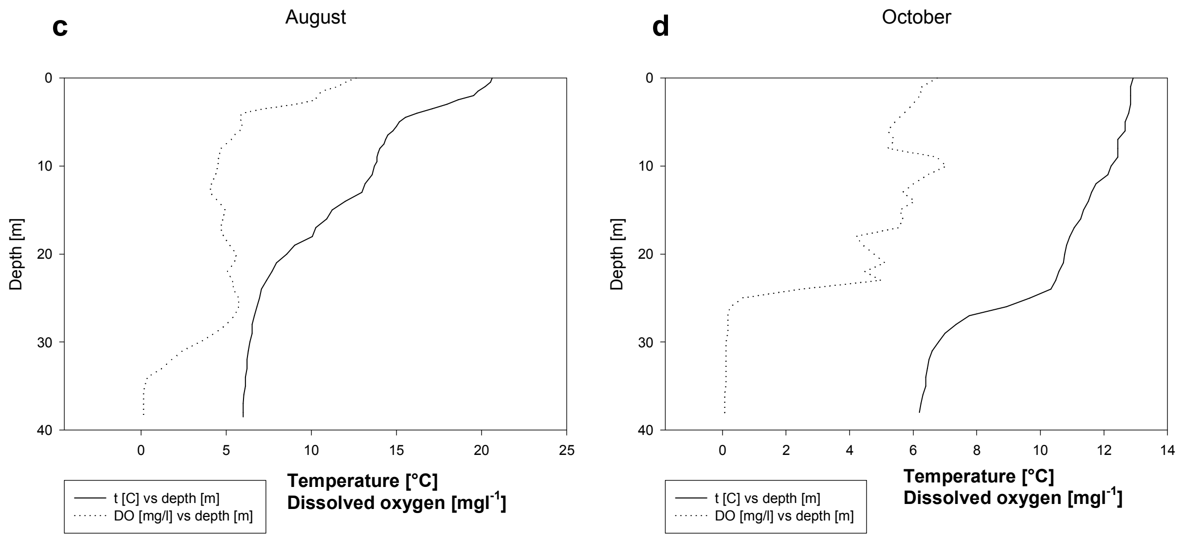


Tab. 1 Water transparency (as Secchi depth) in Římov reservoir in April, June, August and October 2005

date	transparency [cm]
20.4.2005	150
1.6.2005	500
3.8.2005	145
5.10.2005	310

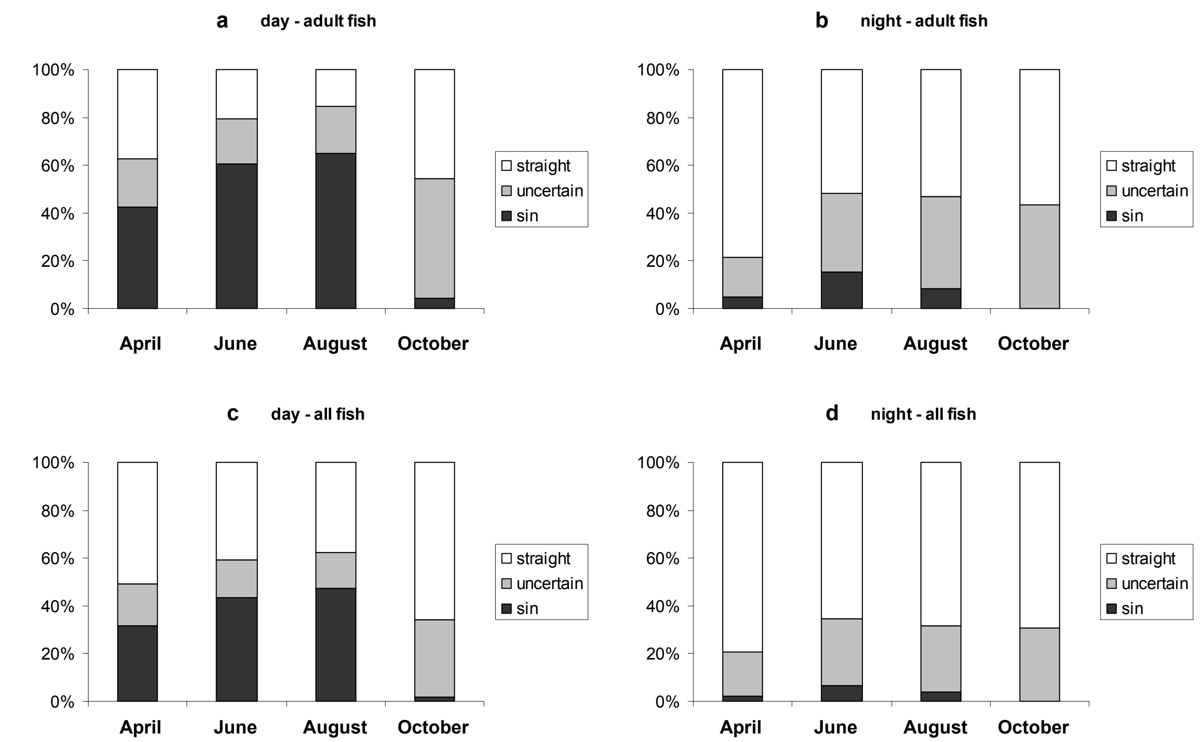
Fig. 3 Temperature (solid line) and oxygen concentration profiles (dotted line) in Římov reservoir in April, June, August and October 2005





Primary insight into data shows that proportion of sinusoidal fish was rising from April to August [Fig. 4 (a-d)]. The proportion of sinusoidal fish was negligible in October. Sinusoidal swimming pattern was observed nearly always during day.

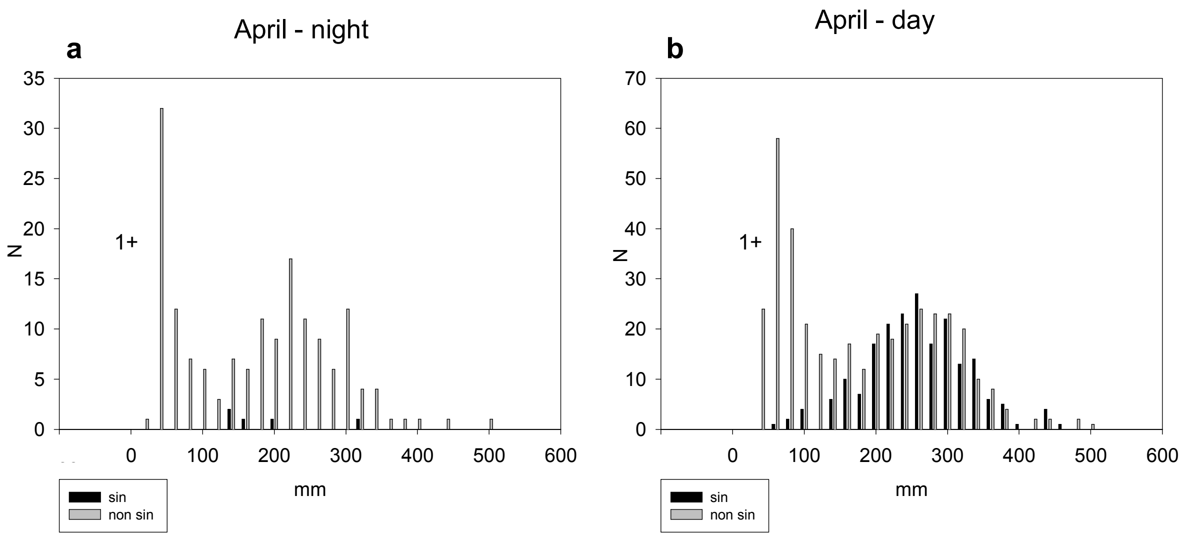
Fig. 4 Proportion of individual types of fish trajectory (sinusoidal, straight and uncertain). Figures **a** and **b** show percentage of observed trajectories of all adult (> 100 mm) fish, figures **c** and **d** deal with all fish. All fish trajectories shorter than 15 s (= average duration of sinusoidal cycle (Čech & Kubečka, 2002); 586 trajectories in total) were excluded in order to minimize the proportion of uncertain trajectories

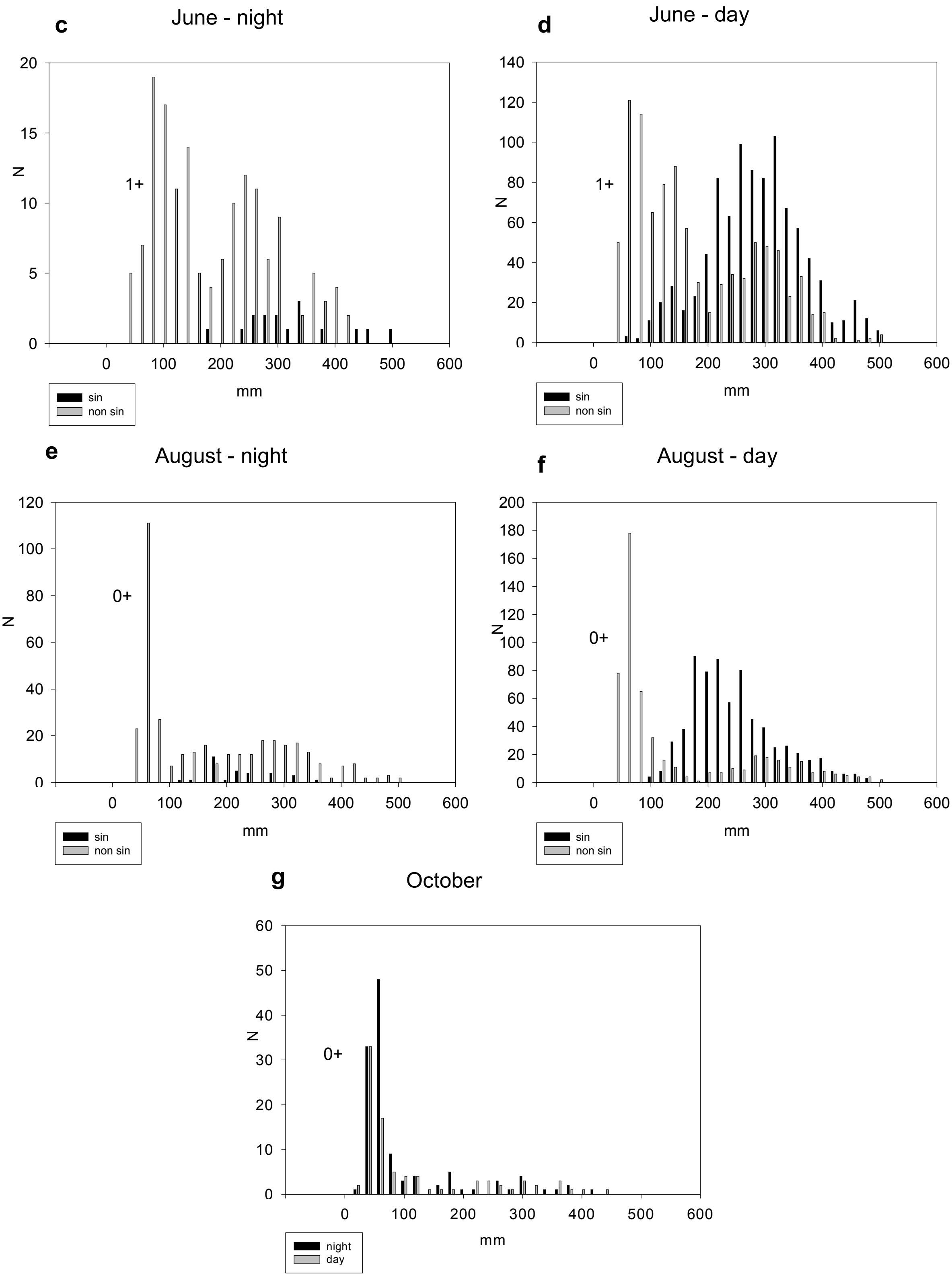


It is clear, that vast majority of sinusoidal trajectories sourced from adult fish and day records [see also Fig. 5]. Length frequency distributions in April showed distinct peak of 1+ fish (2004 year class, [Fig. 5]). Fish with sinusoidal swimming composed the majority of observations of individuals > 200 mm during the day. The situation is very similar in June records, while August records show the appearance of 0+ fish in the open water (2005 YC). The proportion of fish <200 mm with sinusoidal swimming mode increased in day records in August. 0+ fish dominated both day and night October records. Mean standard length of sinusoidal fish was 243 mm in April, 295 mm in June and 237 mm in August. Significant difference between length of sinusoidal fish was found for factor date ($F_{10,1875}$, ANOVA, $p<10^{-4}$) and for factor month ($F_{2,1875}$, ANOVA, $p<10^{-4}$). Size composition of sinusoidally swimming fish and straight swimming fish significantly differed in April ($t_{1,756}$, t-test, $p<10^{-4}$), in June ($t_{1,2061}$, t-test, $p< 10^{-4}$) and in August ($t_{1,1637}$, t-test, $p<10^{-4}$). October data were not tested because of the lack of sinusoidal trajectories.

The proportion of juvenile fish (smaller than 100 mm) steadily rose from April to October and was higher at night in comparison to day. No peak of 0+ fish was observed in April because there were no 0+ fish, while in June the reason for the lack of 0+ peak is the fact, that 0+ fish were probably too small that they fell bellow the threshold.

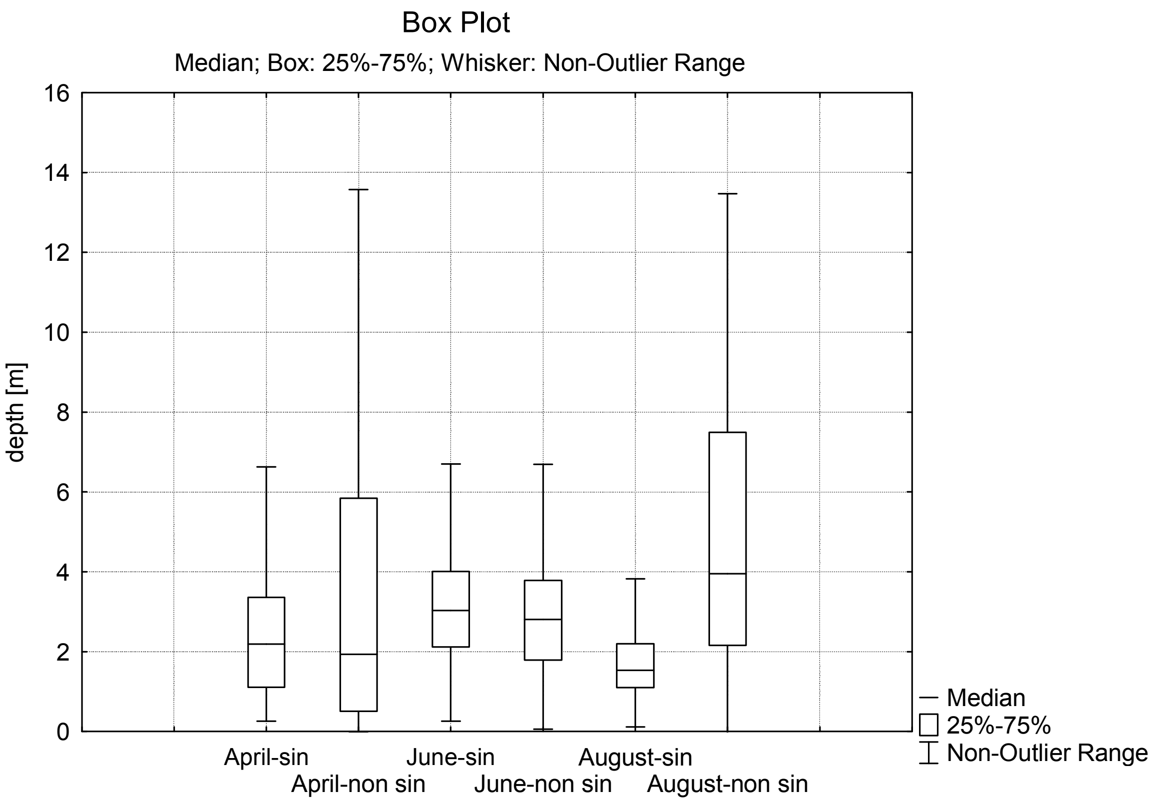
Fig. 5 Length-frequency distributions of fish with and without sinusoidal swimming pattern during day and night in April (**a**,**b**), June (**c**,**d**), August (**e**,**f**); **g** shows night and day length-frequency distributions of all fish in October (sinusoidal swimming was negligible in October – only 0.63 % of all fish performed this behaviour)





Mean depth of fish trajectories during both day and night [Fig. 6] also differed between both fish groups in April ($t_{1,756}$, t-test, p=0.0031) and in August ($t_{1,1637}$, t-test, $p<10^{-4}$), whereas was not significantly different in June ($t_{1,2061}$, t-test, p=0.8296).

Fig. 6 Mean depths of trajectories of all fish (both day and night). Plots the median, 25th and 75th quantiles as vertical boxes with error bars (non-outlier range)

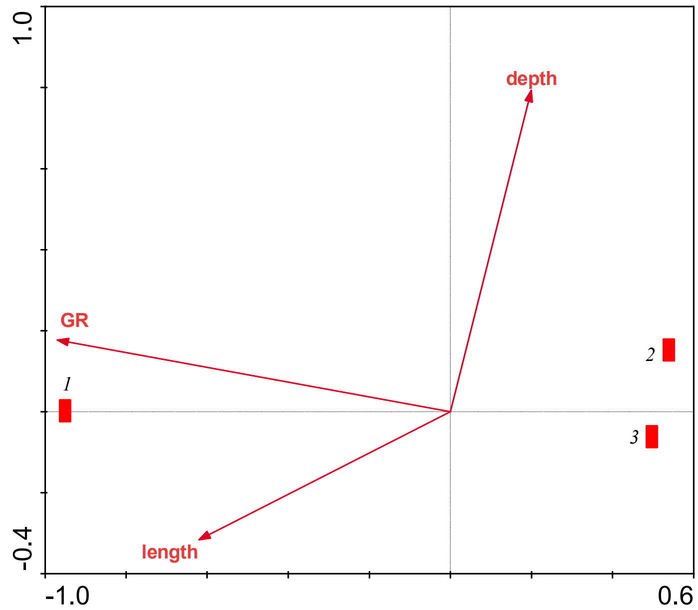


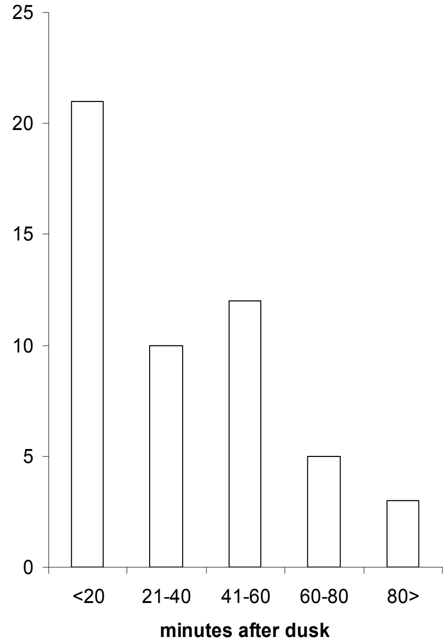
Number of sinusoidal fish is positively correlated with length and GR and weakly negatively correlated with depth, whereas number of straight and uncertain trajectories was negatively correlated with GR and length [Fig. 7].

Most fish performed sinusoidal swimming during the day, but some continued swimming sinusoidally also after the dusk [Fig. 8]. The number of such fish continually decreased after dusk and was nearly zero after 80 minutes. No such trajectory was observed before the dawn.

Fig. 7 Correspondence canonical analysis (CCA) using fish length, depth and GR as 'environmental factors' and type of trajectory (sinusoidal (1), uncertain (2) and straight (3)) as 'species'. First canonical axis explains 86.2 % of variability, Monte-Carlo test confirmed the significance of all canonical axes (F-ratio=9.13, p<0.01).

Fig. 8 Total number of observed sinusoidal trajectories after dusk (April - August)



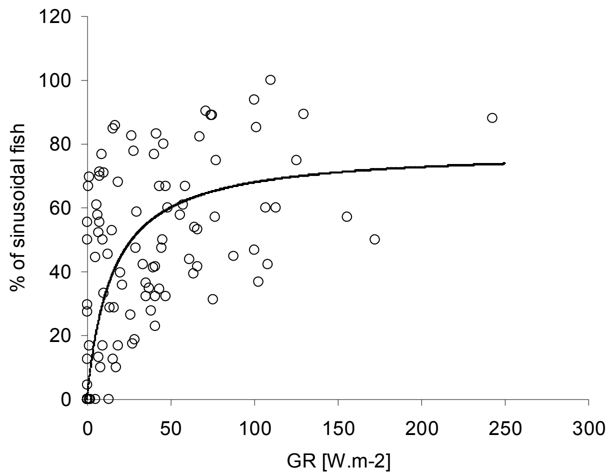


Relationship between percentage of fish (hourly value) with sinusoidal trajectories in June of all 'potentially sinusoidal' fish (length>100 mm, depth<4 m) and values of mean hour global radiation in depth, where fish occurred [Fig. 9], was found significant ($F_{1,12}$=98.4583, $p<10^{-4}$). Nonlinear saturation model [Eq. 6] was fitted: *sf* – percentage of sinusoidal fish trajectories, sf_{max} – maximum value of *sf* (sf_{max}=78.2%); *k* – empirical constant (k = 15.2 Wm^{-2}); R^2=0.4716.

Fig. 9 Relationship between percentage of sinusoidal trajectories and GR in June; nonlinear model [Eq. 6] was fitted

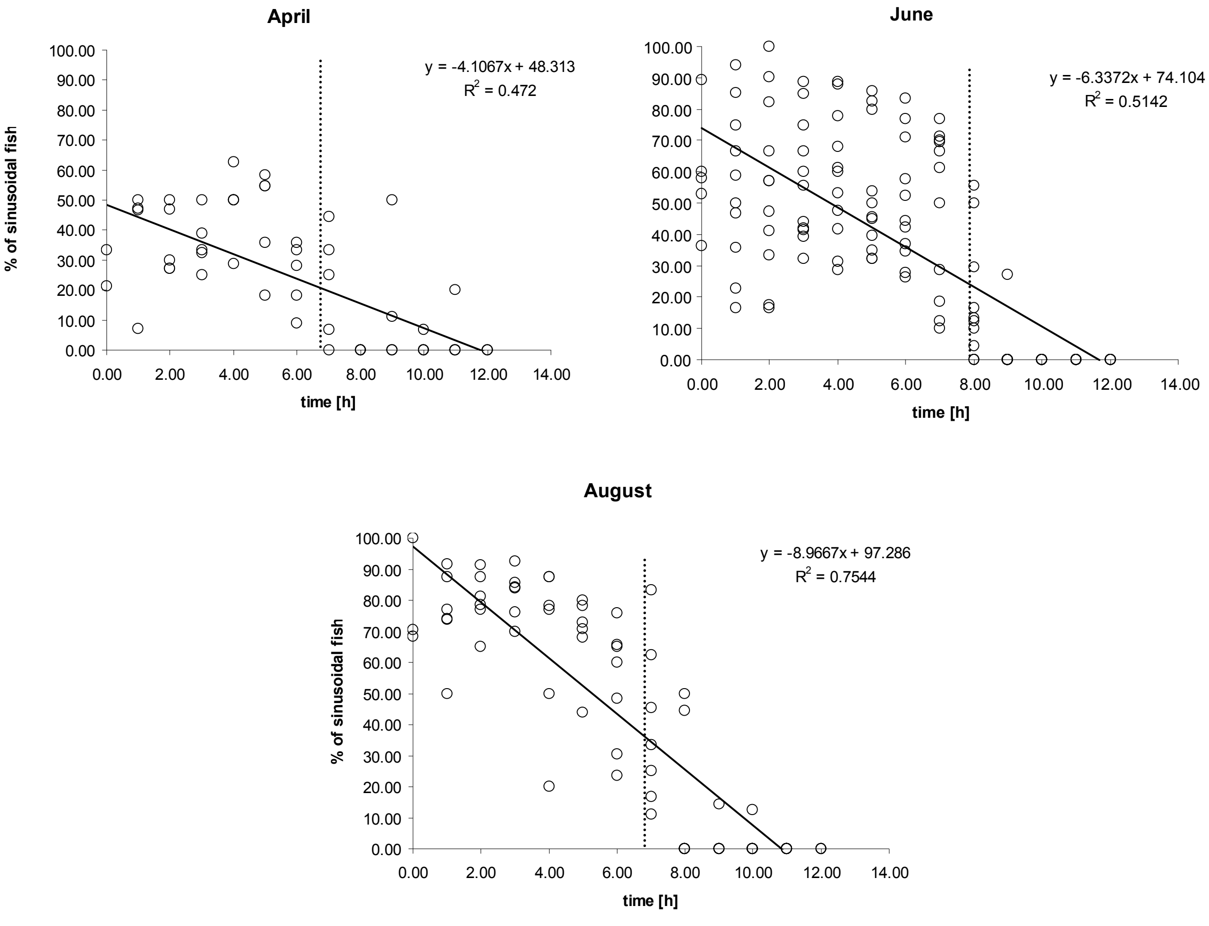
Eq. 6

$$sf = \frac{sf_{max} \times GR}{k + GR}$$



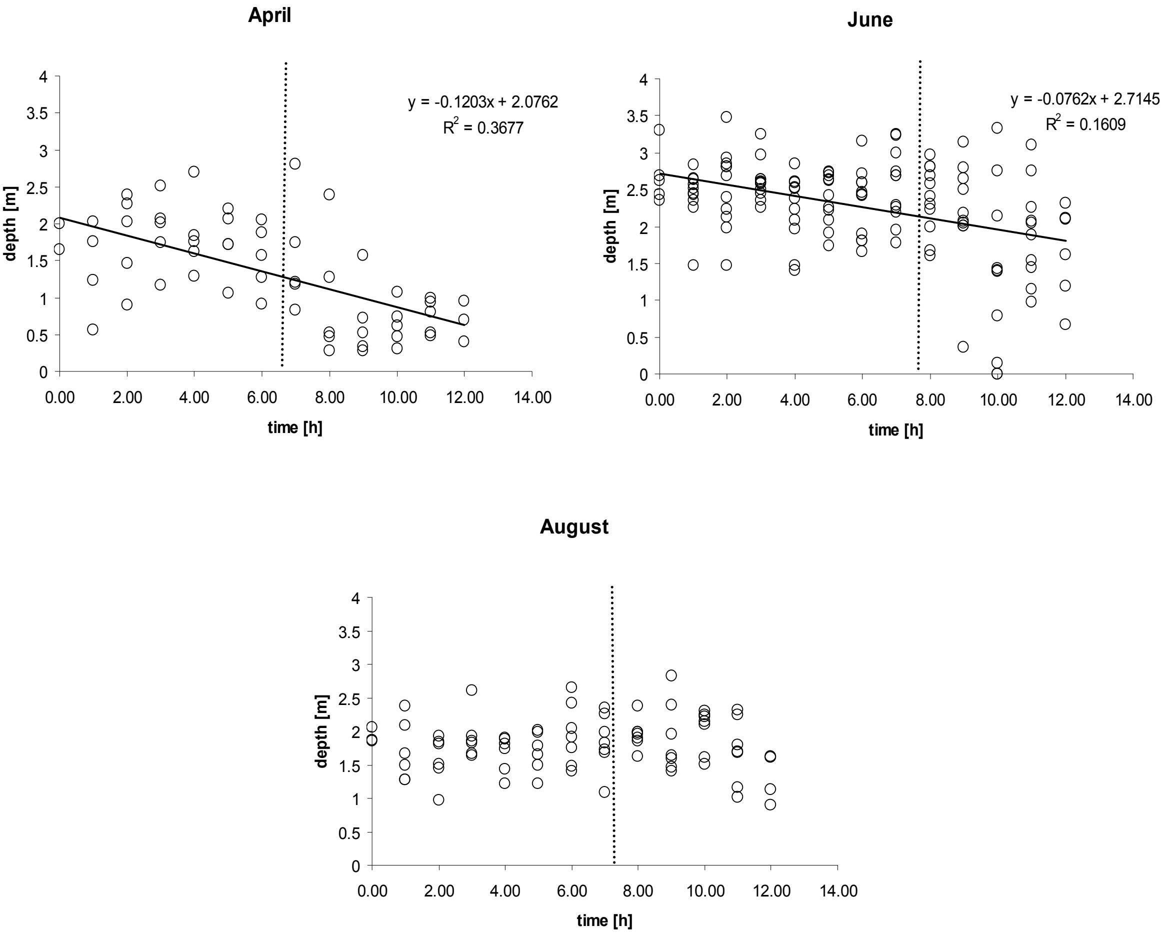
Hourly averaged proportion of trajectories of ‘potentially sinusoidal’ fish (length>100 mm, depth<4 m) also showed apparent pattern throughout the day in April ($F_{1,57}$=50.947, ANOVA, $p<10^{-4}$), June ($F_{1,126}$=133.38, ANOVA, $p<10^{-4}$) and August ($F_{1,77}$=236.54, ANOVA, $p<10^{-4}$) [Fig. 10]; it decreased with time difference from solar noon. Coefficients of determination were relatively high in all cases; linear models always explained more than 47.2% of variability.

Fig. 10 Percentage of sinusoidal fish vs. time difference from solar noon (noon: 0 hours). Each point represents hourly average of every processed day. Vertical dotted line marks the difference between solar noon and sunrise and sunset



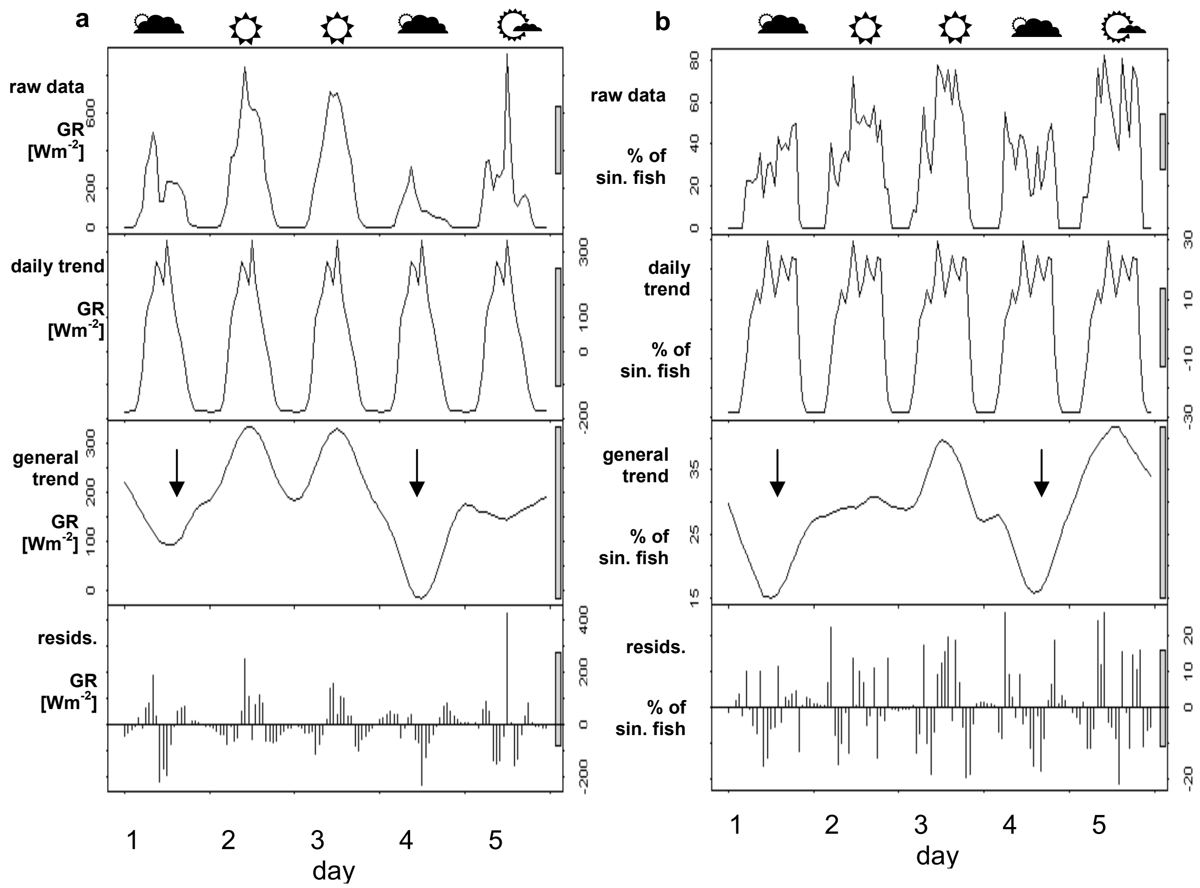
Mean depth of trajectories of ‘potentially sinusoidal’ fish (length>100 mm, depth< 4 m) showed clear pattern throughout the day in April ($F_{1,57}$=33.145, ANOVA, $p<10^{-4}$) [Fig. 11], when fish inhabited the deepest strata around the noon and the depth linearly decreased with the time difference from solar noon. Similar pattern was weaker in June ($F_{1,126}$=22.073, ANOVA, $p<10^{-4}$) and was not observed in August ($F_{1,77}$=0.0227, ANOVA, p=0.8807) [Fig. 11] when fish inhabited upper layers all the time.

Fig. 11 Mean depth of fish vs. time difference from solar noon (noon: 0 hours). Each point represents hourly average of every processed day. Vertical dotted line marks the difference between solar noon and sunrise and sunset



Percentage of sinusoidal fish during day seemed to be dependent on weather conditions (amount of clouds, surface global radiation). Fish performed sinusoidal swimming preferentially during sunny days (62% of fish swam sinusoidally) rather than during cloudy days (30% of fish swam sinusoidally) [Fig. 12]. Note the similarity between daily trends and the general trend of GR and % of sinusoidal fish. There was a decline of both GR and % of sinusoidal fish during the cloudy days.

Fig.12 Time series analysis of surface global radiation (**a**) and percentage of sinusoidal fish trajectories (**b**) in five sequential days in June revealed apparent relationship between sinusoidal swimming and global radiation. Percentage of sinusoidal fish was relatively low in the first and fourth day; those days were very cloudy (see arrows in trend component of both time series). Curves describing general trends of GR and percentage of sinusoidal fish are very similar. Weather icons are used to simplify the day values of global radiation. Thick grey lines on the right side of the plots give the same interval of GR (300 W.m^{-2}) or % of sinusoidal fish (22 %) for all panels



4 Discussion

Most fish in European reservoirs are of riverine origin and are not fully adapted to lacustrine environment (Fernando & Holčík, 1991). However, they seem to be able to exploit large part of the planktonic production (Seďa et. al, 2000). Our observations show, that the exploitation of open water resources is not the same throughout time and space. Fish presence in the open water is generally highest during the daytime and warm period of the year. Annual course of fish density in the open water coincides with the trend of pelagic gillnet CPUE (Vašek et. al., 2008). Lower fish densities recorded at night is not a usual hydroacoustic phenomenon (Freon et al., 1993, Comeau & Boisclair, 1998, Rakowitz & Zweimüller, 2000, Vehanen et al., 2005) and may have coincided with night inshore migration - adult fish had decreased efficiency of feeding on zooplankton during the night and may have migrated inshore (Brabrand & Faafeng, 1993, Evans, 1993, Čech, 2001). Most fish vanished from the open water in October, what corresponds with findings of Čech & Kubečka (2002) from November 1998. Lower fish abundance in June night may have coincided with spawning of bream.

Sinusoidal cycling swimming started after sunrise and was replaced by direct swimming just before the sunset (Čech & Kubečka, 2002), but was also sometimes observed at night, especially during first 80 minutes after dusk. The effect of high moon light could be condemned in this case, since moon phases ranged from new moon up to 7 days difference from new moon in all analyzed days and the moon was in the sky during first 80 minutes after dusk only in April. These facts denote some kind of inertia in sinusoidal swimming pattern.

Distinguishing between straight and sinusoidal swimming pattern was not easy (Čech & Kubečka, 2002), therefore hybrid category 'uncertain' for fish trajectories was implemented. Part of trajectories in 'uncertain' category was made of trajectories too short to determine clearly their pattern, these trajectories (duration in beam shorter than 15 s) made 23.5% of 'uncertain' on day and 18.6% at night. The rest of 'uncertain' trajectories in this category was closer to straight trajectories than to sinusoidal.

The proportion of sinusoidal trajectories during the day increased from April (42%) to August (63%) as well as number and total biomass of pelagic fish. The number of sinusoidal trajectories observed in October was negligible, what coincided with the low planktonic production (Seďa et al, 2007). Number of results confirmed relationship between sinusoidal swimming and global radiation. However at the highest radiation during the noon, sinusoidal fish tended to be slightly deeper than during morning and evening possibly avoiding the highest light intensities. Depth distribution of 'potentially sinusoidal' fish was not dependent on diurnal time in August (this corresponds with results of Čech & Kubečka, 2002 and low transparency).

Sinusoidal fish had narrower size range and were on average larger than non-sinusoidal, which consisted mostly of 0+, 1+ and large predatory fish. It can be hypothesized from the report of Peterka et al. (2007) and gillnet catches of Vašek et. al. (2008), that large sinusoidal fish of the length 150-450 mm are adult roach (*Rutilus rutilus*) and bream (*Abramis brama*). These larger cyprinids performing sinusoidal swimming appear closer to the surface than non-sinusoidal in April and August. No apparent difference between depths of sinusoidal and straight trajectories in June may be caused by the general development of fish community: 1+ fish behaved like 0+ fish in April (they were hidden in higher depths during the day) and took over the behaviour of adult fish in June at a time when new year class of 0+ fish emerged (Kubečka, 1985, Kubečka & Švátora, 1993). Another explanation could be the steep thermal stratification in June and thus concentration of fish near the surface. The presence of 0+ fish in August (they were deeper during the day and their size and behaviour corresponded to migrating bathypelagic perch juveniles, Čech et al., 2005) caused the difference in distributions of sinusoidally and straight swimming fish in this month.

Pattern of presence of sinusoidal fish trajectories in open water of reservoir during the day and season and dependence on weather conditions denotes that sinusoidal swimming is a feeding mechanism of some planktivorous fish. Hypothesis of feeding origin of sinusoidal swimming is supported by findings of Vašek & Kubečka (2004), who described circadian feeding activity of adult roach and bream with afternoon peaks and distinct night-time declines in gut fullness.

5 Conclusions

Our results confirmed the strong connection between the light and the percentage of fish using sinusoidal swimming. Average maximum proportions reached 78.2% of sinusoidal fish in total, the largest percentages were recorded in August. Sinusoidal swimming was nearly stopped after dusk (except for some fish performing sinusoidal swimming closely after dusk as kind of residual behaviour). This proportion also decreased with the time difference from solar noon. Generally, fish favoured sinusoidal swimming in sunny days. Size distribution of sinusoidal pelagic fish was changing during the season and mean size of fish with sinusoidal and straight swimming differed in all months. Mean depth of ‘potentially sinusoidal’ fish decreased accordingly to the time difference from solar noon except for August. Mean depth of fish with sinusoidal and straight swimming differed in April and August and was the same in June.

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