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RESEARCH PAPER

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Diel changeover of fish assemblages in shallow sandy habitats of lowland rivers of different sizes

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Abstract – Diel dynamics of species richness and fish abundance were studied in three lowland rivers that differed significantly in size (discharge) in to the upper Vistula River drainage system (Poland). Shallow sandy habitats at point bars were repeatedly sampled with beach seining over 24-h periods. Species richness peaked at dusk and then decreased throughout the 24-h period in all the rivers. Overall fish abundance changed similarly in the smallest and the largest river, whereas in the mid-sized river it increased in the late afternoon hours. Some species (three gudgeon species, golden loach, and chub) were persistently nocturnal, whereas others (dace, bleak, and roach) shifted to diurnal activity in the mid-sized and large rivers. These differences in diel changes in the abundance of certain species might be explained in the context of variation in availability (*i.e.*, proximity) of other, more heterogeneous habitats.

Keywords: 24-h cycle / lotic ecosystems / sandbars / riverine fishes / spatio-temporal variation

Résumé – **Changement circadien des assemblages de poissons dans les habitats sablonneux peu profonds des cours d'eau de plaine de différentes tailles.** La dynamique de la diversité des espèces et de l'abondance des poissons a été étudiée dans trois rivières de plaine de tailles (débits) très différentes, appartenant au bassin hydrographique de la Haute Vistule (Pologne). Des habitats sablonneux peu profonds ont été échantillonnés à plusieurs reprises au moyen d'une pêche à la senne de plage sur une période de 24 heures. Dans les trois rivières, la richesse en espèces a atteint son maximum au crépuscule, puis a diminué pendant toute la période de 24 heures. Dans l'ensemble, l'abondance du poisson a changé de façon similaire dans la plus petite et la plus grande rivière, alors qu'elle a augmenté dans la rivière de taille moyenne en fin d'après-midi. Certaines espèces (trois goujons, la loche « dorée » et le chevesne) étaient constamment nocturnes, tandis que d'autres (la vandoise, l'ablette et le gardon) sont passées à une activité diurne dans la rivière de taille moyenne et grande. Ces différences dans les changements circadiens d'abondance de certaines espèces pourraient s'expliquer dans le contexte des variations dans la disponibilité (c.-à-d. la proximité) d'autres habitats plus hétérogènes.

Mots-clés : Cycle de 24 heures / écosystèmes lotiques / habitat sableux / poissons de rivière / variation spatio-temporelle

1 Introduction

Temporal variation in riverine fish assemblages have been known and exploited by fishers for centuries. The seasonal migrations of anadromous or potamodromous species have been particularly thoroughly documented and studied (*e.g.*, Lucas *et al.*, 2001 and references therein). Fine-scale variation, however, has received far less attention. Nevertheless, diel differences in abundance and species richness in shallow inshore habitats are observed in various rivers in all climate zones (*e.g.*, Copp, 2010 and references therein). In most cases, an increase in fish abundance and species richness is observed at dusk and in subsequent night hours. However, inconsistencies in published results lead to two mutually exclusive hypotheses: (i) fish generally arrive in shallow inshore habitats

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Table 1. Sampling site characteristics.

River	Site	Latitude (°N)	Longitude (°E)	Elevation (m a.s.l.)	Discharge ($m^3 s^{-1}$)	River width (m)	Water depth (cm)	No. of sampling events	Water temperature (°C)			
									Spring	Summer	Autumn	Winter
Vistula	Łęka	50.2827	20.8498	168	230.0	181	45–65	7	16.1	21.5	7.8	5.1
Nida	Stara Rudawa	50.4131	20.5792	174	22.0	28	30–80	8	12.5	19.2	7.8	5.9
Czarna Nida	Gaj	50.7572	20.5052	211	6.5	15	30–95	8	11.3	21.4	4.8	4.2

at dusk mainly in small rivers whereas in large ones they occupy this type of habitat during the daytime (Copp, 2010) or (ii) nocturnal increase in abundance and species richness is more conspicuous in large rivers whereas in small ones fish occupy inshore habitats throughout 24-h periods (Janáč and Jurajda, 2013).

The validity of these hypotheses was verified by conducting a study on three rivers within a single watershed (the Vistula River drainage basin within the Baltic Sea catchment) that are direct tributaries of one another but that differ by an order of magnitude in terms of mean annual discharge.

2 Materials and methods

2.1 Study area

This study was performed in the upper Vistula River basin in Poland. With a length of 1047 km and a mean annual discharge at its mouth of approximately 1046 $m^3 s^{-1}$, the Vistula River is the longest river draining into the Baltic Sea. The first sampling site was located 766 km upstream from the river mouth in the upper course of the river. The mean annual discharge at the closest hydrological station is approximately 230 $m^3 s^{-1}$. The second sampling site was located in the Nida River, which is a left-bank tributary to the Vistula. It is a mid-sized lowland river 151 km in length with a mean annual discharge at its mouth of approximately 22 $m^3 s^{-1}$. The last sampling site was located in the Czarna Nida River, a tributary of the Nida River, which is 64-km long, and its mean annual discharge at the confluence with the Nida is 6.5 $m^3 s^{-1}$. The three rivers differ in mean annual discharge by an order of magnitude. Basic habitat characteristics, including elevation a.s.l., mean annual discharge at the closest hydrological station, mean riverbed width, minimum and maximum water depth recorded at the sampling site, water current velocity, number of sampling events, and seasonal variation in water temperature (daily minima and maxima) are summarized in Table 1. All three sampling sites were sandy point bars formed at inner bends of river meanders (Kellerhals and Church, 1989). The sites at the Czarna Nida and the Nida rivers were in semi-natural states as these river sections have never been channelized or modified in any way. Within the stretch studied, the Vistula River was modified to accommodate navigation, which included reinforcing the outer right river bank with boulders and modifying the inner left bank with stony dikes. This was done mostly in the 1970s, and over the interceding decades, the dike basins have completely filled in with mainly sandy sediment to form a new, close-to-natural sandy shoreline.

2.2 Fish sampling

Samples were taken every 3 h over a 24-h period. A total of 23 sampling events took place from August 2014 to March 2016 (Tab. 1). In the Czarna Nida and Nida rivers fish were collected with a 6 × 3 m seine net made of knotless nylon netting with a 6 mm mesh bar. In the Vistula River a 15-m-long bag seine net with two 6-m wings (8 mm mesh bar) and central bag 3 × 3 m (6 mm mesh bar) was used to increase sampling efficiency in the much larger, shallow habitats. The seine net was dredged by two operators approximately parallel to the shoreline and then beached at each site. The area sampled was approximately 180 m^2 in the Czarna Nida, 420 m^2 in the Nida, and 1200 m^2 in the Vistula. The catch per unit of effort (CPUE) was the raw number of fish caught in each haul. Since the main goal of the study was to investigate diel dynamics (and not total abundance), this approach was chosen as the most robust. Sampling started 3 or 6 h before sunset and continued for 24 h. All fish were identified to the species when they were held in net bags in the water close to the shore to prevent mortality. Identifications were based on the author's experience, available keys (*e.g.*, Kottelat and Freyhof, 2007), and a reference collection held at the Department of Ichthyobiology, University of Agriculture in Kraków.

2.3 Statistical analyses

Diel differences in species richness and abundance of the most dominant fish species (>100 specimens) were analyzed with generalized linear mixed-effects models (GLMM), with raw CPUE data and Poisson error distribution. This technique is suitable for analyzing non-normal data with random effects. Two explanatory variables were tested: time after dusk (continuous) and river (three levels: Czarna Nida, Nida, and Vistula; except for Kessler's gudgeon and golden loach,[1] which were analyzed only in the Vistula River) that was a fixed effect. Season (four levels: spring, summer, fall, and winter) was set as a random effect to account for pseudoreplications. In each case, four alternative models were fitted and compared according to their AIC values: (i) null model; (ii) a single fixed effect (time after dusk); (ii) two fixed effects (time after dusk and river) without interaction; and (iv) two fixed effects (time after dusk and river) with interaction. GLMM parameters were

[1] Vernacular and scientific names of all species were listed in Table 2.

Table 2. Total abundance of fish species in the Czarna Nida, Nida, and Vistula rivers.

Species	River		
	Czarna Nida	Nida	Vistula
Dace *Leuciscus leuciscus* (Linnaeus, 1758)	627	327	515
Common gudgeon *Gobio gobio* (Linnaeus, 1758)	839	114	89
Blake *Alburnus alburnus* (Linnaeus, 1758)	198	243	425
Roach *Rutilus rutilus* (Linnaeus, 1758)	401	257	6
Chub *Squalius cephalus* (Linnaeus, 1758)	333	26	51
Whitefin gudgeon *Romanogobio belingi* (Slastenenko, 1934)	0	63	238
Kessler's gudgeon *Romanogobio kesslerii* (Dybowski, 1862)	0	0	174
Baltic golden loach *Sabanejewia baltica* (Witkowski, 1994)	4	10	96
Spined loach (*Cobitis* sp.)	49	12	0
Barbel *Barbus barbus* (Linnaeus, 1758)	27	3	30
Nase *Chondrostoma nasus* (Linnaeus, 1758)	1	2	48
Vimba bream *Vimba vimba* (Linnaeus, 1758)	1	1	45
Pikeperch *Sander lucioperca* (Linnaeus, 1758)	2	2	37
White bream *Blicca bjoerkna* (Linnaeus, 1758)	0	14	16
Perch *Perca fluviatilis* (Linnaeus, 1758)	13	8	2
Spirlin *Alburnoides bipunctatus* (Linnaeus, 1758)	1	18	2
Cyprinidae larvae	3	0	14
Baltic bullhead *Cottus microstomu* (Heckel, 1837)	11	2	1
Asp *Leuciscus aspius* (Linnaeus, 1758)	3	0	7
Ide *Leuciscus idus* (Linnaeus, 1758)	7	0	2
Stone loach *Barbatula barbatula* (Linnaeus, 1758)	1	2	1
Giebel carp *Carassius gibelio* (Bloch, 1782)	1	1	2
Ruffe *Gymnocephalus cernua* (Linnaeus, 1758)	2	0	2
Rud *Scardinius erythrophthalmus* (Linnaeus, 1758)	2	1	1
Topmouth gudgeon *Pseudorasbora parva* (Temminck and Schlegel, 1846)	0	0	3
Welsh *Silurus glanis* (Linnaeus, 1758)	1	2	0
Pike *Esox lucius* (Linnaeus, 1758)	1	1	0
Burbot *Lota lota* (Linnaeus, 1758)	0	0	2
Ukrainian brook lamprey *Eudontomyzon mariae* (Berg, 1931)	1	0	0
Total fish catch	**2529**	**1109**	**1809**
Overal species richness	**24**	**21**	**25**

estimated using Laplace estimation. All calculations were performed with R software version 3.6.0 (R Core Team, 2019) using packages *lme4* (Bates *et al.*, 2015) and *ggeffects* (Lüdecke, 2018).

3 Results

A total of 5447 fish belonging to 29 species were caught. The fish assemblages in all three rivers were dominated by small-sized cyprinids. In the Czarna Nida River, common gudgeon predominated (33.2% of the total fish catch) over dace (24.8%), roach (15.9%), chub (13.2%), and bleak (7.8%). Another 19 species were noted to be far less abundant. In the Nida River, dace (29.5%), roach (23.2%), bleak (21.9%), and common gudgeon (10.3%) predominated decidedly over another 17 species. In the Vistula River, dace (28.5%) was followed by bleak (23.5%), whitefin gudgeon (13.2%), and Kessler's gudgeon (9.7%), while a small number of another 20 species was also noted (Tab. 2).

Species richness peaked at dusk and then gradually decreased during the night and the following day in all three rivers (Fig. 1a). The model with two fixed effects (time after dusk and river) without any interaction between them tended to be superior to the others (Tab. 3). Not surprisingly, the amplitude of differences between the maximum species richness at sunset and the daytime minimum varied among the rivers (on average, 6.25 *vs.* 2.60 in the Czarna Nida, 4.87 *vs.* 1.67 in the Nida, and 9.29 *vs.* 3.86 in the Vistula) as did their overall species diversity (24, 21, and 25 species, respectively).

Total fish abundance was highest at dusk, and then it decreased continually in both the smallest and the largest rivers, whereas the pattern was reversed in the mid-sized river. Fish abundance was generally much lower in the mid-sized Nida River than in either the Czarna Nida or Vistula rivers, and it increased subtly toward the late afternoon hours (Fig. 1b). This was indicated by the lowest AIC value of the model including the interaction of both fixed effects (Tab. 3).

Only eight species occurred frequently and numerously enough to allow comparative analyses of their diel dynamics among the rivers. All other species were noted either sporadically or in very low numbers, which rendered any modeling inconclusive.

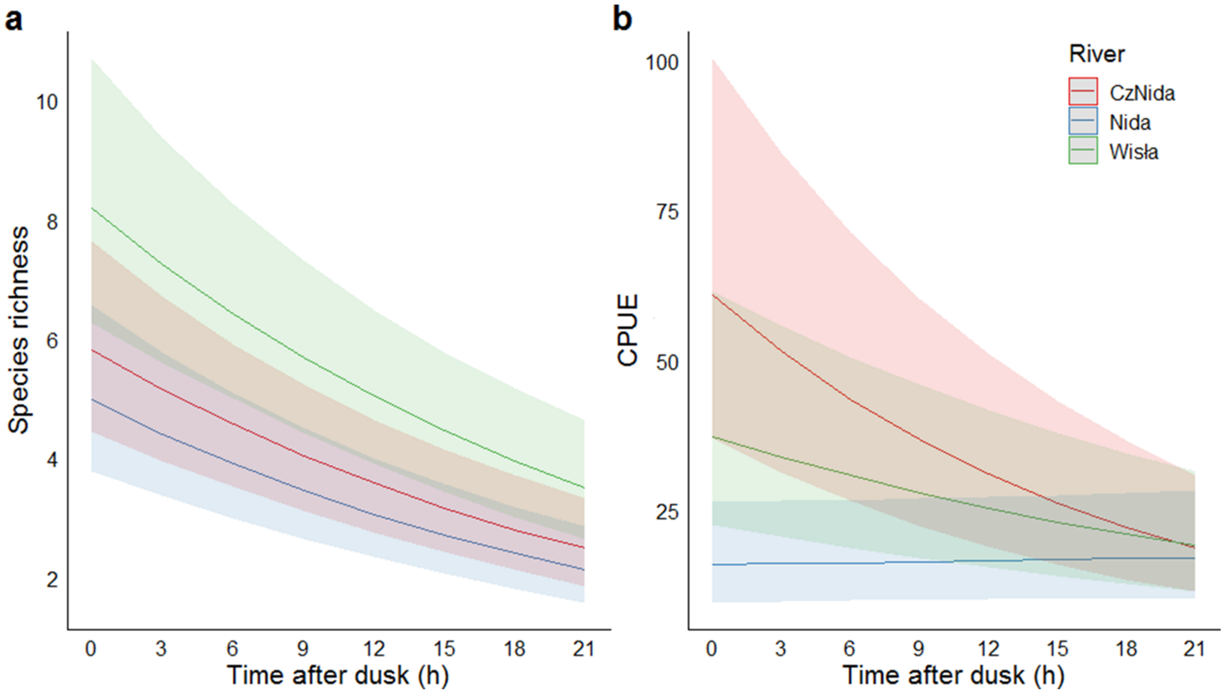

Fig. 1. GLMM plots with 95% confidence intervals (shaded area) of (a) species richness and (b) CPUE change over time in the Czarna Nida, Nida, and Vistula rivers.

Table 3. AIC values of the GLMM models analyzed.

Variable or species	Model			
	Null (intercept)	Time	Time + River	Time × River
Species richness	749.6	696.2	**666.4**	669.8
Total CPUE	5313.8	4996.2	4449.1	**4325.5**
Dace	2468.2	2470.1	2378.0	**2359.0**
Common gudgeon	2643.3	2487.4	1591.6	**1585.9**
Bleak	2003.6	1982.2	1880.3	**1758.3**
Roach	2705.4	2606.6	2114.0	**1971.8**
Chub	1407.6	1342.0	947.6	**946.9**
Whitefin gudgeon	809.6	650.2	552.1	**546.4**
Kessler's gudgeon	686.5	599.6	–	–
Golden loach	379.9	314.0	–	–

Dace, the most abundant species, exhibited conspicuous variation in diel dynamics of occurrence (in the model with two fixed factors, and their interaction had the lowest AIC value; Tab. 3). In the smallest stream its abundance peaked at dusk and decreased throughout the night and the next day. In the mid-sized river dace abundance remained at a relatively constant level throughout the 24-h period. On the other hand, in the largest river its abundance increased gradually toward sunset (Fig. 2a). Similarly to dace, bleak and roach tended to be nocturnal with peak abundances at dusk in the smallest Czarna Nida River, but their abundances were diurnal with the highest concentrations in the late afternoon in both of the larger rivers (Fig. 2c and d, respectively). The abundance of roach in the Vistula River was very low. The model with interaction was superior to all the others for both of these fish species (Tab. 3).

With all three gudgeon species, *i.e.*, the common gudgeon, whitefin gudgeon, and Kesssler's gudgeon, the pattern of diel dynamics was clear and consistent in all three rivers. Their abundance peaked at dusk and then gradually decreased over the subsequent 24-h period (Fig. 2b, f, g). In both common and whitefin gudgeons GLMM indicated significant interaction between both factors of time after dusk and river (Tab. 3) that resulted mainly from differences in CPUE values among the streams. Kessler's gudgeon occurred only in the Vistula River so analyses of its abundance were restricted to the null (intercept-only) model and the model including one fixed factor (time after dusk). The latter fit far better than the former

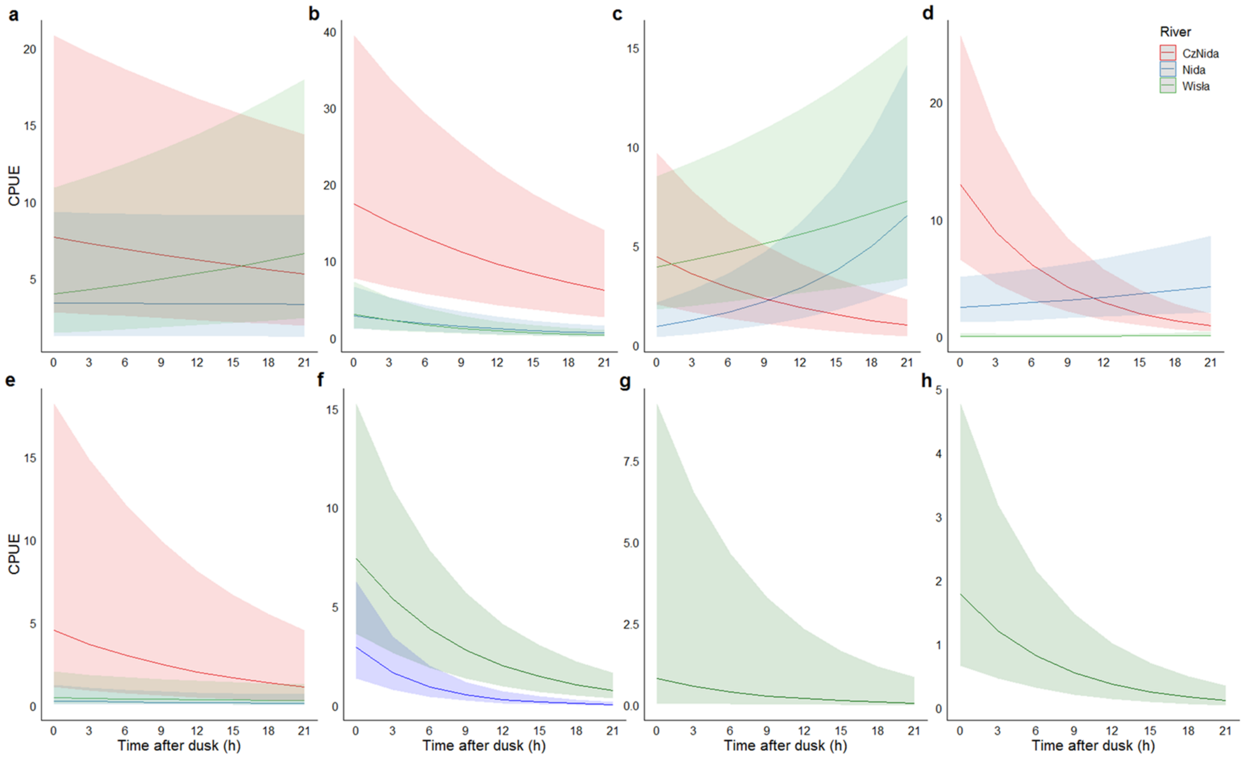

Fig. 2. GLMM plots with 95% confidence intervals (shaded area) of CPUE of fish species in the Czarna Nida, Nida and Vistula: (a) dace; (b) common gudgeon; (c) bleak; (d) roach; (e) chub; (f) whitefin gudgeon; (g) Kessler's gudgeon; (h) golden loach.

(Tab. 3). Similarly to Kessler's gudgeon, golden loach also exhibited a typically nocturnal pattern of occurrence, with abundance peaking at dusk and then decreasing sharply (Fig. 2h). This species was recorded in all three rivers; however, only in the Vistula River was its abundance high enough to permit any statistical analyses (Tab. 2). Nocturnal patterns of abundance were also noted for chub (Fig. 2e). The model with interaction between time after dusk and river had the lowest AIC (Tab. 3) that resulted from the low abundances of this species in the Nida and Vistula rivers compared to the Czarna Nida River (Tab. 2).

4 Discussion

Diel changeovers of fish assemblages in shallow riverine habitats are observed worldwide (*e.g.*, Copp and Jurajda, 1993, 1999; Arrington and Winemiller, 2003; Baumgartner *et al.*, 2008; Koščo *et al.*, 2008; Copp, 2010; Roach and Winemiller, 2011; Janáč and Jurajda, 2013) and studies that document no differences between day and night assemblages are scarce (Czeglédi *et al.*, 2016). This is why diel changeover is presumed to be of adaptive significance (Gliwicz and Jachner, 1992; Roach and Winemiller, 2011). Differences in the exploitation of various habitats are usually explained as trade-offs between predator (mainly piscivorous birds) avoidance and foraging. The existence of diel dynamics, even when there are no avian predators, points to the very deep evolutionary past of this phenomenon (Gliwicz and Jachner, 1992; Mehner, 2012). Alternatively, small-sized fishes occupying shallow inshore habitats nocturnally is interpreted as avoidance of large-bodied predatory fish (Helfman, 1993; Copp and Jurajda, 1999). The dynamic trade-off between predator (either birds or fish) avoidance and foraging in shallow habitats by using subtle differences in vision in various levels of illumination between prey and predators is referred to as the "antipredator window" (Clark and Levy, 1988; Scheuerell and Schindler, 2003). According to this concept, smaller-sized fishes use the dynamic twilight zone to move inshore and offshore to negotiate predators and to reach food items.

In most cases worldwide, twilight or nocturnal increases in both abundance and species richness are recorded (*e.g.*, Copp and Jurajda, 1993, 1999; Arrington and Winemiller, 2003; Baumgartner *et al.*, 2008; Koščo *et al.*, 2008; Copp, 2010; Roach and Winemiller, 2011), although some authors report the opposite scenario (Copp *et al.*, 2005; Mastrorillo and Copp, 2005). After an extensive review of the literature, including his own numerous studies, Copp (2010) concluded that nocturnal increases in abundance and species richness occur in small rivers, whereas the pattern is reversed in large rivers. On the other hand, Janáč and Jurajda (2013) came to the opposite conclusion that fish abundance and diversity increase at night in larger rather than smaller rivers. These authors point out the importance of habitat complexity in shaping the diel dynamics of fish assemblages. Similarly to Willis *et al.* (2005), they contend that more structured, complex habitats might provide richer, evenly-distributed resources, which makes diel differences in fish abundance less conspicuous. On the other hand, in unstructured habitats, like sandbars in lowland rivers, resources are more scarce, which forces fish to engage in changeovers of occurrence or behavior over 24-h periods.

The results of the present study indicate that in all three rivers, ranging from a stream to a large lowland river, notably more species are found in shallow sandy habitats at dusk and during the first few hours of night. However, the dynamics of fish abundance are more complex. In the smallest Czarna Nida River, the pattern of fish abundance followed that of species richness, peaking at dusk and rapidly decreasing thereafter. In the largest river, the Vistula, abundance dynamics were similar but were characterized by a lower amplitude. In the mid-sized Nida River, however, there were afternoon increases in fish abundance. These results led to the conclusion that there is no cline in diel variation of fish assemblages with regard to river size (discharge). Instead, there is an interesting shift from nocturnal to diurnal behavior in several species (dace, bleak, and roach). Five of the eight species analyzed in this study revealed similar patterns of diel changes in occurrence, which might be described as constantly nocturnal. These species (three gudgeon species, golden loach, and chub) always appeared in highest numbers at dusk and within the first few hours of darkness, after which their abundance decreased consecutively. The second group of species (dace, bleak, and roach) were nocturnal in the smallest stream, whereas in the two larger rivers their abundance either increased during the day to reach its maximum in the late afternoon, or it remained relatively constant throughout the 24-h period.

Sampling was performed in all three rivers in the similar habitats of sandy point bars (Kellerhals and Church, 1989). These are unstructured habitats with shallow waters (depths of usually <100 cm) and plain sandy bottoms. Structural objects, such as wood debris or macrophytes, are only found in these habitats sporadically. Thus, the one different pattern of fish abundance over a 24-h period that was found in this study cannot be explained by variations in habitat heterogeneity (Willis *et al.*, 2005; Janáč and Jurajda, 2013), but the sandbars sampled obviously differed in size. The sandy beaches in the Czarna Nida River had an area of only approximately 200 m^2. Just a few meters from the sandbar there was a deep (>150 cm) pool with overhanging riparian vegetation. The sandbar in the Nida River was much larger at approximately 650 m^2, and there was much more distance between the sandy beach and other microhabitats. The sandbar area in the Vistula River was the largest (>10,000 m^2) and many more heterogeneous habitats were remote (>50 m). According to the “inshore habitat retention” concept, such sandbars are very rich in phyto- and zooplankton (Schiemer *et al.*, 2001), especially at night (Jack *et al.*, 2006). Most probably in small streams, where various habitats and resources are in close proximity, most species utilize the “antipredator window” and immediately after sunset they arrive in shallow, inshore retention zones for extensive dusk feeding. In larger rivers, however, fish need to negotiate quite long distances to reach sandbars, which makes resources more scattered and competition for them more intense. This could explain why several species were preferably nocturnal in small streams whereas they switched to late afternoon hours of activity in larger rivers. If they could not reach a desired habitat fast enough at dusk, some species (especially those with better vision, like column feeders, *e.g.*, dace or bleak) could have decided to move into it earlier as a trade-off between avian predator avoidance and foraging. Typical bottom feeders, like gudgeons or golden loach, needed to wait longer, when lower illumination allowed them to avoid predation.

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