Structural and Physical Factors as Predictors of the Species Distribution and Diversity of Dragonflies and Damselflies (Odonata) in an Upland Storage Reservoir

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Accepted May 11, 2022 Published online June 02, 2022 Issue online June 30, 2022 Original article BUCZYŃSKI P., WALCZYK K., TAŃCZUK A., BUCZYŃSKA E., BOJAR P., GÓRAL N. 2022. Structural and physical factors as predictors of the species distribution and diversity of dragonflies and damselflies (Odonata) in an upland storage reservoir. Folia Biologica (Kraków) 70: 67-78. The negative impact of storage reservoirs on the environment has been well documented, but it appears that under certain circumstances these reservoirs can also help to protect biodiversity. The distribution of adult dragonflies and damselflies was studied in relation to eight environmental variables, in an upland storage reservoir and its feeder rivers located in South-East Poland (East-Central Europe). A total of 25 species were recorded, including 22 in the reservoir. Submerged and floating plants, width of the shallow littoral zone and the water movement/current were found to be the key drivers of the species distribution (pCCA, NMDS). Five species (Ischnura elegans, Sympetrum sanguineum, Platycnemis pennipes, Calopteryx splendens and Erythromma viridulum) were responsible for over 70% of the dissimilarities between the riverine and reservoir sites (SIMPER). In addition, Ischnura elegans, Orthetrum albistylum and Calopteryx virgo were distinguished as the indicator species (IndVal analysis) for the upland river-reservoir hydrological system. Our results highlight some design features of reservoirs that may help to maintain the diversity of odonates, as well as many other groups of aquatic organisms, as the former are well-known indicators of general biodiversity. Key words: biodiversity, environment, protection, anthropogenic waters, Poland. Paweł BUCZYŃSKI, Agnieszka TAŃCZUK[⊠], Department of Zoology and Nature Protection, Institute of Biological Sciences, Maria Curie-Skłodowska University, Akademicka 19, 20-033 Lublin, Poland. E-mail: pawbucz@gmail.com (P.Bu.), atanczuk@gmail.com (A.T.) Katarzyna WALCZYK, Maksymilianów 26B, 27-423 Maksymilianów, Poland. E-mail: kat.walczyk@wp.pl (K.W.) Edyta BUCZYŃSKA, Department of Zoology and Animal Ecology, University of Life Sciences in Lublin, Akademicka 13, 20-033 Lublin, Poland. E-mail: edyta.buczynska@gmail.com (E.B.) Paweł BOJAR, Prząśniczki 2/40, 20-838 Lublin, Poland. E-mail: pawel_bojar@interia.pl (P.Bo.) Nikola GÓRAL, Szarych Szeregów 1/17, 20-047 Lublin, Poland. E-mail: goral.nikola@gmail.com (N.G.)

Biodiversity loss is one of the most serious threats to the environment (WILSON 1985; SINGH 2002), and freshwater habitats are considered to be at the greatest risk of such losses (HARRISON *et al.* 2018). One of the main reasons for this is the degradation or disappearance of natural waters, as a result of direct or indirect human impacts on the environment (DUDGEON *et al.* 2006). Hence, there is an urgent need to seek ways of protecting freshwater habitats and their biodiversity, especially as they provide essential ecosystem services of benefit to mankind (HARRISON *et al.* 2010; CARPENTER *et al.* 2011). In this context, the significance of artificial water bodies is ambiguous. This ambiguity applies, for example, to the majority of the existing storage reservoirs, even if the strategy of their construction is usually a good illustration of the opinion that the 'management of freshwater resources is often focused on human water security rather than on the natural ecosystem's integrity' (HARRISON *et al.* 2018). These reservoirs are a component of an area's

© Institute of Systematics and Evolution of Animals, PAS, Kraków, 2022 Open Access article distributed under the terms of the Creative Commons Attribution License (CC-BY) <u>http://creativecommons.org/licences/by/4.0</u> hydrographic network, possibly even forming a substantial part of it (e.g. DONG *et al.* 2019), and therefore constitute an important habitat for wildlife. It is known that reservoirs may degrade rivers and adversely affect their biodiversity (KORNIJÓW 2009; BUCZYŃSKI 2015); but there is data indicating that, if appropriately designed and then properly managed, such reservoirs can also be beneficial (KORNIJÓW 2009; BUCZYŃSKI 2015; WU *et al.* 2019). This suggests that existing facilities may need to be modified. For this reason, analyses of biodiversity are very important in the case of reservoirs with different designs and methods of utilisation, functioning in different catchment areas and landscape types.

In the present paper, the dragonfly and damselfly assemblages of an upland water storage reservoir in East-Central Europe are analysed, along with stretches of the feeder rivers immediately above the reservoir. We focused on the structural features of the habitat and the immediate surroundings of the reservoir/rivers, as well as on certain physical factors, e.g. water movement, since these can easily be altered during the design of a reservoir or its possible modifications, in order to protect biodiversity. The object of the study-Wióry Storage Reservoir-was chosen because of its considerable habitat diversity. It is a water body that is typical in the uplands of Central and East-Central Europe. Dragonflies and damselflies (Odonata) were chosen as the research objects because they are good indicators of both the environmental quality and biodiversity (BULÁNKOVÁ 1997; GERLACH et al. 2013; KIETZKA 2019). Our aims were to determine: (1) the species richness and composition of the odonate fauna in the whole hydrological system, i.e. the reservoir itself and the stretches of the feeder rivers immediately above it; (2) the most significant habitat drivers of the species distribution; (3) indicator species characteristic of this type of hydrological system; and (4) the function of the storage reservoir in the conservation of the odonate species richness.

Material and Methods

Study area

Wióry Storage Reservoir (50°57′04.2″N, 21°10′27.2″E) is situated in Southern Poland, 145 km south of Warsaw and 37 km north-east of Kielce. It is located in the centre of the Kielce Upland, at the foot of the highest part of the Świętokrzyskie Mountains, which is an isolated, low-altitude mountain range. This area lies within the Tertiary tectonic uplift, with outcrops of Early Triassic to Late Cretaceous folded structures. Differences in resistance to weathering of the rocks have led to the formation of numerous hills, depressions and flat-bottomed river valleys (KONDRACKI 2011; SOLON *et al.* 2018).

The soil in the study area includes loess, brown soil and chernozems; there are also deposits of quartzite, while the lower-lying ground is overlain with sand and Quaternary, mostly red, clay (MARCINEK *et al.* 2011). The climate resembles a submontane one, being cooler and more humid when compared to nearby regions (KONDRACKI 2011). The average air temperatures during the period of 1990-2010 were as follows: annual: 6°C; February: -3°C; July: 17°C. In addition, the annual average precipitation was in excess of 600 mm (INSTYTUT METEOROLOGII I GOSPO-DARKI WODNEJ 2020).

Wióry Reservoir is situated in the lower course of the Świślina, a right-bank tributary of the Kamienna River, while its southern part is fed by the Pokrzywianka. It was built in 1980-2005 and became operational in 2007 (GŁÓWNY URZĄD STATYSTYCZNY 2020). The reservoir is almost completely surrounded by highly fertile arable land, with small areas of fallow land and extensively managed meadows. The only woodlands situated along the reservoir's 40 km long shoreline are small ones located near the dam and below the mouth of the Pokrzywianka, covering a distance of around 3 km (GEOPORTAL 2020; GMINA PAWŁÓW 2020).

The research was conducted at seven sites: four by the reservoir itself and three by the feeder rivers (Fig. 1). Sites 3 and 4 were representative of riverine habitats beyond the maximum extent of backflow from the reservoir. The Świślina and Pokrzywianka are both small upland-submontane rivers, with alternating dammed and naturally-flowing stretches and with quite strong currents. Site 5 lay in the backflow area of the Pokrzywianka, where the current was very slow, and the emergent and floating vegetation in the littoral zone were typical of lentic waters. The other study sites were situated by the reservoir itself. Sites 1 and 7 were in small bays with diverse emergent, floating and submerged vegetation. The shallow littoral zone was wide at Site 7 but narrow at Site 1, which meant it was almost totally exposed in summer when the water level was low. Site 2 lay in a stretch of straight shoreline with well-developed vegetation of a similar structure as that in Site 7. Site 6 was also in a section of straight shore, where there was strong water movement and sparse, periodically occurring submerged plants.

Field sampling

Sampling was carried out once a month at each site by 4-5 observers, from May to September 2020. Observations of the adult dragonflies and damselflies were conducted between 10:00 and 16:00 hrs on sunny days, with little if any wind. Species were identified with the naked eye or by using 10x binoculars. In the case of any doubt, an individual was caught



Fig. 1. Location of the study sites around Wióry Storage Reservoir and on its feeder rivers (https://geoportal.gov.pl). Inset: location of the research area in Poland. 1-7 – sampling sites, numbered as in the text.

with an entomological net for a closer examination. Once the species was identified, it was released back into the environment. The sampling sites encompassed shore sections 100 m long or longer, but the number of individuals were always calculated per 100 m. The species recorded were assigned to one of six categories: 1 - 1 individual per 100 m; 2 - 2 - 10; 3 - 11 - 20; 4 - 21 - 50; 5 - 51 - 100; and 6 - > 100 individuals per 100 m. Metamorphosis, tenerals, reproductive behaviour and feeding patterns were also recorded.

The following structural and physical habitat parameters were measured or defined at each study site: water movement (current or standing water) (code for the further analyses: WM), percentage of woodland within a 100 m radius of the site (For), cover of submerged and floating plants (SFP), cover of emergent vegetation (RB – reed beds), width of the shallow littoral zone (SLZ), degree of siltation (Silt), distance from the dam to the site (Dist), and the degree of shade (Shad). Each factor was measured or coded on a scale from 0 (absence / undeveloped) to 4 (complete cover / strongly developed). The scores were assigned on the basis of field observations and by the analysis of aerial photographs (GEOPORTAL 2020).

Biocoenotic and statistical analyses

All of the species were classified as 'autochthonous' if tenerals or intensive reproductive behaviour were observed; as 'probably autochthonous' if the reproductive behaviour was occasional (1-3 encounters) or numerous individuals were observed in a suitable habitat; and as 'recorded' in all other cases.

The division of the recorded species into ecological groups was adopted after BERNARD *et al.* (2009): rheobionts – *Calopteryx splendens*, *C. virgo*, *Ophiogomphus cecilia*; rheophiles – *Platycnemis pennipes*, *Gomphus vulgatissimus*; limnophiles – *Anax parthenope*; and eurytopes – other species.

Non-metric multidimensional scaling (NMDS) with a minimum spanning tree was used to discover the faunistic similarities between the sites. Calculations were based on the Bray-Curtis index. The similarity percentage method (SIMPER) was employed to identify the species responsible for assemblage discrimination between the riverine and reservoir sites. In addition, by applying an indicator species analysis IndVal (DUFRENE & LEGENDRE 1997), we were able to determine and graphically visualise the indicator species in both groups of sites. In the IndVal analysis, the statistical significances (p<0.05) were estimated by 9999 random reassignments (permutations) of sites across the groups. The analyses were performed in the PAST 4.09 program (HAMMER *et al.* 2001).

partial canonical correspondence analysis (pCCA) was used to display the effects of environmental variables on the species compositions of the dragonflies and damselflies. To eliminate the influence of time, we used a 'month' as a covariate. A forward selection of explanatory variables with 999 test permutations was undertaken in order to filter the significant (p<0.05) parameters primarily responsible for species variation. Significance tests of the first canonical axis and of all the axes were also performed. Since a collinearity was detected when fitting the variables, the variable 'distance from the dam (Dist)' was excluded from the analysis. On this basis, a pCCA biplot was generated showing the preferences of particular species for particular plants and substrata (marked with different colours). The analysis was performed in Canoco 5.0 (TER BRAAK & SMI-LAUER 2012).

Basic statistical analyses (tests) were done with the Statistica 13.0 software. GUILFORD's (1973) interpretation of the magnitude of significant correlations was adopted.

The following abbreviations for the species names of dragonflies and damselflies are used in Figs 5 and 6: Aes_aff – Aeshna affinis, Aes_cya – Aeshna cyanea, Aes_gra – Aeshna grandis, Aes_mix – Aeshna mixta, Ana_imp – Anax imperator, Ana_par – Anax parthenope, Cal_spl – Calopteryx splendens, Cal_vir – Calopteryx virgo, Cha_vir – Chalcolestes viridis, Coe_pue – Coenagrion puella, Cro_ery – Crocothemis erythraea, Ena_cyt – Enallagma cyathigerum, Ery_vir – Erythromma viridulum, Gom_vul – Gomphus vulgatissimus, Isc_ele – Ischnura elegans, Lib_dep – Libellula depressa, Lib_qua – Libellula quadrimaculata, Oph_cec – Ophiogomphus cecilia, Ort_alb – Orthetrum albistylum, Ort_can – Orthetrum cancellatum, Pla_pen – Platycnemis pennipes, Som_met – Somatochlora metallica, Sym_san – Sympetrum sanguineum, Sym_str – Sympetrum striolatum, Sym_vul – Sympetrum vulgatum.

Results

A total of 25 species of dragonflies and damselflies were recorded, 22 of which occurred in the basin of the storage reservoir. All but one of these 22 species were autochthonous or probably autochthonous. Only two species were recorded at all the sites – *Ischnura elegans* and *Sympetrum sanguineum*. The other species were found mainly by the rivers or the reservoir (Table 1).

The arrangement of the study sites on the NMDS plot (Fig. 2) showed that the riverine Sites 3 and 4 exhibited the greatest faunistic similarity (85%) and occupied the opposite end of Coordinate Axis 1 to the reservoir sites. The fauna of the riverine Site 5 displayed the strongest similarity to the fauna of the reservoir sites (especially Site 2-67%), while Coordinate Axis 1 indicated the gradient associated with the water movement/flow (from lotic to lentic habitats). In turn, Coordinate Axis 2 differentiated the sites in terms of the aquatic vegetation and shoreline type, i.e. small bays with the lushest vegetation (Sites 1 and 7 – negative axis values) vs. sites with a straight shoreline and less abundant vegetation (Sites 2 and 6 – positive axis values).

The evident diversity of the overall species richness and a strong differentiation of their numbers was apparent (Fig. 3), but these results were statistically insignificant (ANOVA p=0.28 and Kruskal-Wallis test p=0.20, respectively). Nonetheless, the values of both these factors were strongly correlated: Spearman's rank correlation R_s =0.82 (p<0.05). Within the storage reservoir and inflow section, Site 7 stood out in both respects, as the other sites were nearly as species-rich in dragonflies and damselflies but differed in their numbers. A comparison of particular sites and their habitat conditions indicated that the key factors were probably the quantitative richness of plants (favouring high densities of odonates) and water movement in the littoral zone (limiting the number of odonates).

The differences between the species richness and the abundance of odonates at the study sites, analysed with respect to sub-orders, turned out to be statistically highly non-significant: number of dragonfly species – Kruskal-Wallis test p=0.45; abundance of dragonflies – Kruskal-Wallis test p=0.52; number of damselfly species – Kruskal-Wallis test p=0.45; and abundance of damselflies – Kruskal-Wallis test p=0.35.

The following ecological groupings were recorded: rheobionts (3 species), rheophiles (2), limnophiles (1) and eurytopes (19). Their presence at the study sites is illustrated in Fig. 4. Rheobionts were present almost everywhere, but their large populations, as well as reproduction activities and development stages were re-

Table 1

Dragonflies recorded at the study sites: • – autochthonous species, \odot – probably autochthonous species, \bigcirc – recorded species, FR – feeder river, RI – river (inflow section), SR – storage reservoir. Maximum density: 1 –1 ind./100 m, 2 – 2-10, 3 – 11-20, 4 – 21-50, 5 – 51-100, 6 – >100

Species	Species' status							Maximum density						
	FR		RI	SR				FR		RI	SR			
	3	4	5	1	2	6	7	3	4	5	1	2	6	7
Calopteryx splendens (Harr.)	•	•		\odot	0	0	0	6	6		1	1	1	2
Calopteryx virgo (L.)	•	\odot						4	3					
Chalcolestes viridis (Vander L.)	0	\odot						2	2					
Platycnemis pennipes (Pall.)	•	•	•	•	•		0	5	5	5	6	4		2
Ischnura elegans (Pall.)	0	\odot	•	•	•	•	•	2	3	5	5	4	3	6
Enallagma cyathigerum (Charp.)		\odot					\odot		1					1
Coenagrion puella (L.)	0	•	\odot			0	\odot	1	1	3			1	5
Erythromma viridulum (Charp.)			\odot		0	•	•			2		3	4	6
Aeshna affinis Vander L.		\odot	\odot				\odot		2	2				2
Aeshna cyanea (O.F. Müll.)	0	\odot		0			\odot	2	1		1			2
Aeshna grandis (L.)	0							1						
Aeshna mixta Latr.	0	0	\odot		•	0	\odot	2	1	2		3	1	2
Anax imperator Leach				\odot			•				1			2
Anax parthenope (Sel.)					\odot		\odot					1		2
Gomphus vulgatissimus (L.)	\odot					•	0	2					1	1
Ophiogomphus cecilia (Fourcr.)							0							1
Somatochlora metallica (Vander L.)		\odot		\odot	0		\odot		2		1	1		2
Libellula depressa L.			\odot							2				
Libellula quadrimaculata L.				0							1			
Orthetrum albistylum (Sel.)			\odot	•	\odot	0	•			2	1	2	1	5
Orthetrum cancellatum (L.)		\odot	•	•	•	•	•		2	3	3	3	3	4
Crocothemis erythraea Brullé							•							4
Sympetrum sanguineum (O.F. Müll.)	•	•	•	\odot	•	O	•	3	3	5	2	4	2	6
Sympetrum striolatum (Charp.)		0		\odot			0		1		1			1
Sympetrum vulgatum (L.)		\odot	0	0	•	0			3	1	1	4	1	



Fig. 2. Two-dimensional non-metric multidimensional scaling (NMDS) plot of the study sites (grey dots – riverine sites, black dots – reservoir sites) based on dissimilarities between the dragonfly assemblages (Bray-Curtis distance matrix). Stress value = 0.09.



Fig. 3. General odonate species richness at the study sites (bars, Ns) and total number of odonates at the study sites (red line with nodes, Ni). A – autochthonous species, B – probably autochthonous species, C – recorded species, FR – feeder river, RI – river (inflow section), SR – storage reservoir.



Fig. 4. The proportions of ecological groups of the odonate fauna at the study sites. Upper diagram: qualitative data, lower diagram: quantitative data. A – rheobionts, B – rheophiles, C – limnophiles, D – eurytopes, FR – feeder river, RI – river (inflow section), SR – storage reservoir. Sites are numbered as in the text.

corded only along the rivers. By contrast, rheophiles were numerous and autochthonous in the reservoir, with their success probably owing to water movement in the shallow littoral zone at a given site, so long as it was not too strong or where the movement was moderated by littoral plants. This fact is best illustrated by the small number of rheophiles at Site 6, where the water movement was distinctive: the larvae were probably not able to survive on the mineral bottoms and littoral plants were practically absent. The only limnophile (Anax parthenope) was recorded solely at the sites with well-developed vegetation, with a spatial structure resembling the phytolittoral of a eutrophic lake (with zones consisting of amphiphytes, helophytes, nymphaeids and elodeids). Eurytopes were both species-rich and abundant at the majority of sites. Their species richness was low only in at the river sites.

A similarity percentage analysis (SIMPER) showed that just five odonate species were responsible for the differences between the riverine and reservoir sites, contributing 72% to the total dissimilarity. The overall average dissimilarity of the entire river-reservoir system was 87.4%. However, those species represented different ecological groups: the eurytope Ischnura elegans with the highest percentage (24.4%), followed by the eurytope Sympetrum sanguineum (18.2%), the rheophile *Platycnemis pennipes* (15.8%), the rheobionts Calopteryx splendens (8.2%) and the thermophilous eurytope *Erythromma viridulum* (5.6%). It is worth mentioning that, except for Sympetrum sanguineum, all of these species were strongly associated with the presence of plants. An indicator species analysis (IndVal - Fig. 5) - as an alternative to the SIMPER – showed that *Ischnura elegans* (67%), *Orthetrum albistylum* (33%), *O. cancellatum* (31%) and Sympetrum sanguineum (25%) had the highest in-



Fig. 5. Indicator species analysis (IndVal) for odonate species at both types of sites (1 – reservoir, 2 – river). The indicator value of the species is given on a scale from 0 to 100%.

dicator values for the reservoir sites. The key species for the riverine sites were *Calopteryx virgo* (47%), *C. splendens* (26%) and *Platycnemis pennipes* (21%). *Ischnura elegans, Orthetrum albistylum* and *Calopteryx virgo* were determined to be the best candidates as indicators for this upland river-reservoir hydrological system; this result was also confirmed by the statistical significances (p<0.005).

A partial CCA for all the sites (river – inflow section – storage reservoir) explained 34.2% of the variability in the dragonfly occurrence. The permutation test results for the first axis and all the axes were significant: pseudo-F=4.02, p=0.001; pseudo-F=1.8, p=0.002, respectively. Three of the predictors were statistically significant: submerged and floating plants (SFP), which explained 13% of the variability, and which in turn made a 38% contribution to the whole of the variation (p=0.001); width of the shallow littoral zone (6.3%, 18.5%, p=0.005); and water movement (4.7%,

13.6%, p=0.05) (Fig. 6). The first axis was defined by SFP (r=-0.83) and the second by SLZ (r=-0.6). Species including Calopteryx splendens, C. virgo, Gomphus vulgatissimus, Chalcolestes viridis and Aeshna cvanea exhibited a positive coordinate on Axis 1 and were closely associated with the fastest current/water movements. The same applied to the number of rheobionts. Erythromma viridulum, Anax imperator, A. parthenope, Orthetrum albistylum and O. cancellatum were strongly associated with the presence of submerged and floating plants. Meanwhile, Enallagma cyathigerum, Coenagrion puella and Somatochlora metallica were associated with the widest shallow littoral zone, whereas Aeshna affinis and A. mixta had intermediate values for this factor, in contrast to the libellulid species (e.g. Sympetrum spp. and pioneering Libellula depressa).

No statistically significant Spearman rank correlations (R_s) were found between the variables and the



Fig.e 6. pCCA ordination biplot showing the distribution of Odonata at all the study sites vs. the variables analysed. Statistically significant variables are underlined. The abbreviations for the habitat variables and of the species names of the dragonflies (black) and damselflies (red) are as in the text. N_spec – number of species, N_indiv – number of individuals, No_rhph – number of rheophile individuals, No_rhbio – number of rheobiont individuals, No_lm – number of limnophile individuals. Triangles: green – species closely associated with aquatic plants, blue – species associated with shrubs, orange – species associated with dead organic matter, brown – species associated with the muddy substratum.

species richness and abundance of the two odonate sub-orders. The only exceptions were moderate correlations between the cover of emergent vegetation on the one hand, and the anisopteran species richness (R_s =0.46) and abundance (R_s =0.48) on the other. In the pCCA (Fig. 6), the anisopteran and zygopteran species were similarly arranged around the vectors of statistically significant factors. Only the cover of submerged and floating plants was associated with distinctly more anisopteran species, which tallied with the Spearman rank correlations, as described above.

Discussion

General remarks on the dragonfly fauna

The species richness of dragonflies and damselflies varies greatly according to the geographic region (BERNARD et al. 2009; BOUDOT & KALKMAN 2015; KALKMAN et al. 2018), which is why the odonates from the Wióry Storage Reservoir are best compared with the data from Poland as a whole, as well as the physiographical macroregion in which the reservoir is situated. A total of 25 species were recorded in the study area (34% of the 74 species hitherto recorded in Poland) (BERNARD et al. 2009; BUCZYŃSKI et al. 2019), with 22 of them in the storage reservoir (30%). This comprised 40% and 35%, respectively, of the 63 species already recorded in the Kielce Upland (BERNARD et al. 2009; GRZEDZICKA 2010; STAŚKOWIAK 2014; GWARDJAN et al. 2015; STAŚKOWIAK 2015; 2017; STAŚKOWIAK & SOWA 2018; GWARDJAN 2020; BUCZYŃSKI & BIE-LAK-BIELECKI 2021). These numbers are significant.

The species richness of dragonflies and damselflies at the Wióry Reservoir site was significant in the context of the data gathered at similar sites elsewhere in Poland. The upland areas of the country form quite a compact latitudinal belt, and since they are of a very similar latitude and altitude (KONDRACKI 2011), they are comparable. From 9 to 37 species have been recorded (av. = 19.5±8.6) in those Polish upland reservoirs for which extensive data is available (BUCZYŃSKI 2001; BUCZYŃSKI & TOŃCZYK 2004; BUCZYŃSKI 2008; CUBER 2008; TOŃCZYK & STANKIEWICZ 2008; ŻURAWLEW 2013; BUCZYŃSKI 2015; BUCZYŃSKI *et al.* 2020). Thus, the number of species recorded at the Wióry Reservoir was well above the average for comparable reservoirs.

Data from some other reservoirs indicates how important the spatial structure of a habitat may be for odonate diversity. For example, the shore of the Zemborzyce Reservoir (near Lublin, SE Poland) is partly concreted and not greatly diversified; only a small part has a shallow bay with a natural shore and shallow littoral, where the vegetation and structure are similar to that of eutrophic lakes. 28 dragonfly and damselfly species were recorded at this particular place (82% of the total), but no more than 12 species (35%) were found elsewhere in that reservoir. Moreover, the density of imagines was 5-11 times greater in the shallow bay (BUCZYŃSKI 2015). The key factors in relation to the total odonate richness in another small water body, located in Pietermaritzburg (RSA), were determined to be the areas of shallow water, and the gain and loss of various odonate species with the advancing succession of vegetation and changes in its spatial composition (SUH & SAMWAYS 2005).

Environmental drivers and species distribution patterns

Based on the faunistic similarity (NMDS) or pCCA, the dragonfly and damselfly distribution patterns at the study sites revealed the significance of the predictors of structural and physical habitat characteristics. The structural predictors were interconnected: a shallow littoral zone was beneficial for the development of a dense cover of submerged and floating vegetation. The crucial function of such plants has been highlighted in the results of many papers (e.g. REMSBURG & TURNER 2009; BUCZYŃSKI 2015; NAGY et al. 2019; PERRON et al. 2021). The pCCA showed not only which elements of the habitat structure are important, but also that structural factors may predominate over those associated with the physical and chemical properties of the water or with the landscape. Similar results, especially regarding the key role of the littoral vegetation cover, were obtained by PETROVIČOVÁ et al. (2021), who analysed the occurrence of dragonflies and damselflies in other kinds of artificial lentic waters. HALL et al. (2015) found structural and landscape parameters to be the most crucial factors for the presence of adult odonates; moreover, the percentage of species variation explained in their RDA was very similar to the results that we obtained. Such conclusions have also been drawn from studies focused on the occurrence of caddisflies (Trichoptera) in storage reservoirs (e.g. BUCZYŃSKA et al. 2016; BUCZYŃSKA 2019). Our inferences could thus relate to all kinds of aquatic invertebrates, as regards maintaining the high biodiversity of their habitats.

It was expected that the third key driver of odonate distribution would relate to the physical factors, especially water movement, in the hydrological system studied here. Since it has a considerable influence on both biotic components, such as the composition of the vegetation, and abiotic factors like the pH and oxygen content of the water, water movement is regarded as the most important factor in structuring the assemblages of aquatic environments (DEL-CLARO & GUILLERMO 2019). Moreover, while many insect taxa are amphibiotic, it is the water movement that primarily determines the ecological distribution of species, especially in relation to morphological and behavioural adaptations (DEL-CLARO & GUILLERMO 2019). Although rheobionts and rheophiles were relatively few in number compared with eurytopes within the whole river-reservoir system, they played a crucial part in the faunistic diversity and the odonate assemblages. Moreover, this group was significant in terms of distinguishing the indicators of the habitat differentiation (lentic vs. lotic waters). The SIMPER and IndVal analyses showed that dragonflies are not only good indicators of the habitat quality or general habitat richness (SAHLÉN & EKESTUBBE 2001; MARTIN & MAYNOU 2016), but are also well suited to a biotope characterisation (CLARK & SAMWAYS 1996).

The importance of storage reservoirs for odonate conservation

The data presented in this paper, as well as that published in the literature (MITRA 2000; SUH & SAMWAYS 2005; ANDREW et al. 2013; BARBOSA et al. 2019; BUCZYŃSKI et al. 2020), demonstrates that storage reservoirs may be important for the protection of dragonfly and damselfly diversity. The comparison made in the second paragraph of this section shows that in Poland, for example, an average of ca. 26% of the national odonate fauna can be recorded as present in a single upland reservoir. Their significance may be greater still on the scale of larger regions. BUCZYŃSKI (2015), for example, stated that more than 50 species were found in the storage reservoirs in East-Central Poland, i.e. 72% of the 69 species hitherto recorded in this region (BERNARD et al. 2009; BUCZYŃSKI et al. 2019). Such reservoirs may be valuable secondary habitats for stenotopic species, especially those preferring mesotrophic and eutrophic lakes (KOSKEN-NIEMI 1994; PETZOLD 2002; SHARMA & JOSHI 2007; CUBER 2008; FULAN et al. 2010; BUCZYŃSKI 2015). These inferences may be of great significance for biodiversity protection as a whole, as some studies have shown that odonates are useful bioindicators of general biodiversity (SAHLÉN & EKESTUBBE 2001; KIETZKA 2019).

Besides their economic function, storage reservoirs can play a highly beneficial role in nature conservation, especially if specific measures are taken to protect particular species and their assemblages, and to sustain the richest possible odonate fauna. In such cases, the spatial diversity of the reservoirs is crucial – especially the presence of more or less extensive shallow littoral zones and a rich, but not too dense, spatially-diverse vegetation (SUH & SAMWAYS 2005; data in this paper). Hence, new reservoirs should be designed in such a way that the water they contain should also permanently cover the shallower areas. The colonisation of the reservoirs by plants ought to proceed spontaneously and the subsequent succession should be monitored, since the odonate biodiversity and many other species benefit from the differentiation of successional stages, with the maximum biodiversity being achieved in the middle stages (BERNARD et al. 2002; SUH & SAMWAYS 2005; WILDERMUTH 2005; BUCZYŃSKI 2015). This may also make a reservoir attractive for angling and other forms of recreation. In this regard, the existing reservoirs should be appropriately modified. Storage reservoirs are among the most widespread anthropogenic waters (BIEMANS et al. 2011). Since they already exist and new ones are constantly being built, they can be utilised for the protection of odonates and other aquatic organisms, which should enhance the habitat resources and stabilise the populations of many species. Furthermore, with appropriate planning, such measures need not be costly.

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Author contributions

The authors declare no conflict of interest in relation to this study.

References

- ANDREW R.J., THAOKAR N., VERMA P. 2013. Odonate Diversity at Wena Dam of Nagpur District (Ms), India. Int. J. Sci. Res. 2: 1-3. https://www.doi.org/10.36106/ijsr
- BARBOSA M.S., BORGES L.R., VILELA D.S., VENÂNCIO H., SAN-TOS J.C. 2019. Odonate Communities of the Sucupira Reservoir, Rio Uberabinha, Minas Gerais, Brazil. Pap. Avulsos Zool. **59**: e20195922. https://doi.org/10.11606/1807-0205/2019.59.22
- BERNARD R., BUCZYŃSKI P., TOŃCZYK G. 2002. Present state, threats and conservation of dragonflies (Odonata) in Poland. Nat. Conserv. 59: 53-71.
- BERNARD R., BUCZYŃSKI P., TOŃCZYK G., WENDZONKA J. 2009. A distribution atlas of dragonflies (Odonata) in Poland. Bogucki Wydawnictwo Naukowe, Poznań, Pp. 256.
- BIEMANS H., HADDELAND I., KABAT P., LUDWIG F., HUTJES R.W.A., HEINKE J., VON BLOH W., GERTEN D. 2011. Impact of reservoirs on river discharge and irrigation water supply during the 20th century. Water Resour. Res. **47**: W03509. https://doi.org/10.1029/2009WR008929
- BOUDOT J.-P., KALKMAN V. (eds.) 2015. Atlas of the European dragonflies and damselflies. KNNV Publishing, The Netherlands. Pp. 380.

- BUCZYŃSKA E. 2019. Storage reservoirs beyond a lake district as secondary habitats for caddisflies (Insecta: Trichoptera) in an area of karst origin (SE Poland). Knowl. Manag. Aquat. Ecosyst. 420: 4. https://www.kmae-journal.org/10.1051/kmae/2019005
- BUCZYŃSKA E., BUCZYŃSKI P., ZAWAL A., STĘPIEŃ E. 2016. Environmental factors affecting micro-distribution of larval caddisflies (Trichoptera) in a small lowland reservoir under different types of watershed usage. Fundam. Appl. Limnol. 188: 157-170. https://doi.org/10.1127/fal/2016/0833
- BUCZYŃSKI P. 2001. Ważki (Insecta: Odonata) Krzczonowskiego Parku Krajobrazowego [Dragonflies (Insecta: Odonata) of the Krzczonowski Landscape Park]. Parki Nar. Rez. Przyr. **20**: 63-78. (In Polish with English abstract).
- BUCZYŃSKI P. 2008. Ważki (Odonata) Lasów Kozłowieckich [Dragonflies (Odonata) of the Kozłowieckie Forests]. Odonatrix
 4: 33-42. (in Polish with English abstract).
- BUCZYŃSKI P. 2015. Dragonflies (Odonata) of anthropogenic waters in middle-eastern Poland. Mantis, Olsztyn. Pp. 272.
- BUCZYŃSKI P., BIELAK-BIELECKI P. 2021. Dysjunktywne stanowisko szklarnika górskiego *Cordulegaster bidentata* Selys, 1843 (Odonata: Cordulegastridae) w Kotlinie Sandomierskiej [Disjunctive site of Sombre Goldenring *Cordulegaster bidentata* Selys, 1843 (Odonata: Cordulegastridae) in the Sandomierz Basin]. Odonatrix **17** (5): 1-9. (In Polish with English abstract).
- BUCZYŃSKI P., BUCZYŃSKA E., MICHALCZUK W. 2019. From Southern Balkans to Western Russia: Do First Polish Records of *Pantala flavescens* (Fabricius, 1798) (Odonata: Libellulidae) Indicate a Migration Route? J. Ent. Res. Soc. **21**: 11-16.
- BUCZYŃSKI P., TOŃCZYK G. 2004. Rola parków narodowych w ochronie ważek (Odonata) w Polsce [The importance of nationals parks for the protection of dragonflies (Odonata) in Poland]. Parki Nar. Rez. Przyr. 23: 357-380. (In Polish with English abstract).
- BUCZYŃSKI P., BUCZYŃSKA E., BARANOWSKA M., LEWNIEWSKI Ł., GÓRAL N., KOZAK J., TARKOWSKI A., SZYKUT K.A. 2020. Dragonflies (Odonata) of the city of Lublin (Eastern Poland). Pol. J. Entomol. **89**: 153-180.

https://doi.org/10.5604/01.3001.0014.4239

- BULÁNKOVÁ E. 1997. Dragonflies (Odonata) as bioindicators of environment quality. Biologia 52: 177-180.
- CARPENTER S.R., STANLEY E.H., VANDER ZANDEN M.J. 2011. State of the World's Freshwater Ecosystems: Physical, Chemical, and Biological Changes. Annu. Rev. Environ. Res. **36**: 75-99. https://doi.org/10.1146/annurev-environ-021810-094524
- CLARK T.E., SAMWAYS M.J. 1996. Dragonflies (Odonata) as indicators of biotope quality in the Kruger National Park, South Africa. J. Appl. Ecol. 33: 1001-1012.
- CUBER P. 2008. Biodiversity of Kozłowa Góra Reservoir, Upper Silesia, Poland. (In: P. KOČÁREK, V. PLÁŠEK, K. MALACHOVÁ eds. Environmental changes and biological assessment IV. Ostrava, Czech Republic, April 10-11th 2008. Book of Abstracts. Department of Biology and Ecology, University of Ostrava, Ostrava): 38.
- DEL-CLARO K., GUILLERMO R. 2019. Aquatic insects. Springer International Publishing, Cham. Pp. 737.
- DONG N., YU Z., YAN C., YAN M., WANG W. 2019. Hydrological impact of a reservoir network in the upper Gan River Basin, China. Hydrol. Process. **33**: 1709-1723. https://doi.org/10.1002/hyp.13433
- DUDGEON D., ARTHINGTON A.H., GESSNER M.O., KAWABATA Z.-I., KNOWLER D.J., LÉVÊQUE C., NAIMAN R.J., PRIEUR-RICHARD A.-H., SOTO D., STIASSNYAND M.L.J., SUL-LIVAN C.A. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biol. Rev. **81**: 163-182. http://dx.doi.org/10.1017/S1464793105006950
- DUFRENE M., LEGENDRE P. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecol. Monogr. **67**: 345-366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.

0.CO;2

- FULAN J.Â., RAIMUNDO R., FIGUEIREDO D., CORREIA M. 2010. Abundance and diversity of dragonflies four years after the construction of a reservoir. Limnetica **29**: 279-285. http://dx.doi.org/10.23818/limn.29.23
- GEOPORTAL [on line] 2020. Geoportal krajowy [National Geoportal]. https://mapy.geoportal.gov.pl (last access on 18 February 2022). (In Polish).
- GERLACH J., SAMWAYS M.J., PRYKE J. (2013) Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. J. Insect Conserv. **17**: 831-850. https://doi.org/10.1007/s10841-013-9565-9
- GMINA PAWŁÓW [online]. 2020. Oficjalna strona Gminy Pawłów [Official website of the Pawłów Commune]. https://pawlow.pl (last access on 24 December 2020). (In Polish).
- GRZEDZICKA E. 2010. Preferencje siedliskowe ważek na wybranym obszarze Gór Świętokrzyskich i Płaskowyżu Suchedniowskiego oraz możliwości ich ochrony [Habitat preferences of the dragonflies from chosen area of Świętokrzyskie Mountains and Suchedniów Plateau with its' conservation abilities]. Wiad. Entomol. **29** (Supl.): 123-128. (In Polish with English abstract).
- GŁÓWNY URZĄD STATYSTYCZNY. 2020. Rocznik Statystyczny Rzeczypospolitej Polskiej [Statistical Yearbook of the Republic of Poland]. Główny Urząd Statystyczny, Warszawa. Pp. 789. (In Polish).
- GUILFORD J.P. 1973. Fundamental statistics in psychology and education (5th ed.). McGraw-Hill, New York, NY. Pp. xii + 546.
- GWARDJAN M. 2020. Owady: Ważki Odonata [Insects: Dragonflies – Odonata). (In: L. BUCHHOLZ, M. JÓŹWIAK, J. REK-LEWSKI, P. SZCZEPANIAK eds. Świętokrzyski Park Narodowy. Przyroda i Człowiek [Świętokrzyski National Park. Nature and Humans]. Świętokrzyski Park Narodowy, Uniwersytet Jana Kochanowskiego, Bodzentyn – Kielce): 344-350. (In Polish).
- GWARDJAN M., PRZYBYLSKA J., MANIARSKI R. 2015. Ważki (Odonata) Kielc [Dragonflies (Odonata) od Kielce]. Naturalia 4: 90-107. (In Polish with English abstract).
- HALL A.M., MCCAULEY S.J., FORTIN M.-J. 2015. Recreational boating, landscape configuration, and local habitat structure as drivers of odonate community composition in an island setting. Insect Conserv. Divers. 8: 31-42. https://doi.org/10.1111/icad.12080
- HAMMER Ø., HARPER D.A.T., RYAN P.D. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4: 4.
- HARRISON I., ABELL R., DARWALL W., THIEME M.L., TICKNER D., TIMBOE I. 2018. The freshwater biodiversity crisis. Science **362**: 1369. https://doi.org/10.1126/science.aav9242
- HARRISON P.A., VANDEWALLE M., SYKES M.T., BERRY P.M., BUGTER R., DE BELLO F., FELD C.K., GRANDIN U., HARRING-TON R., HASLETT J.R., JONGMAN R.H.G., LUCK G.W., DA SILVA P.M., MOORA M., SETTELE J., SOUSA J.P., ZOBEL M. 2010. Identifying and prioritising services in European terrestrial and freshwater ecosystems. Biodiv. Conserv. 19: 2791-2821. https://doi.org/10.1007/s10531-010-9789-x
- INSTYTUT METEOROLOGII I GOSPODARKI WODNEJ [online]. 2020. Mapy klimatu Polski [Climate maps of Poland]. https://klimat.imgw.pl/pl/climate-maps (last access on 25 December 2020). (In Polish).
- KALKMAN V.J., BOUDOT J.-P., BERNARD R., DE KNIJF G., SUG-LING F., TERMAAT T. 2018. Diversity and conservation of European dragonflies and damselflies (Odonata). Hydrobiologia **811**: 269-282. https://doi.org/10.1007/s10750-017-3495-6
- KIETZKA G.J. 2019. Dragonflies as bioindicators and biodiversity surrogates for freshwater ecosystems. Unpublished doctoral thesis, Stellenbosch University, Department of Conservation Ecology and Entomology, Faculty of AgriSciences, Stellenbosch. Pp. 191.
- KONDRACKI J. 2011. Geografia regionalna Polski [Regional geography of Poland]. PWN, Warszawa. Pp. 468. (In Polish).

- KORNIJÓW R. 2009. Controversies around dam reservoirs: Benefits, costs and future. Ecohydrol. Hydrobiol. **9**:141-148. https://doi.org/10.2478/v10104-010-0001-4
- KOSKENNIEMI E. 1994. Colonization, Succession and Environmental Conditions of the Macrozoobenthos in a Regulated, Polyhumic Reservoir. Int. Rev. ges. Hydrobiol. Hydrogr. **79**: 521-555. https://doi.org/10.1002/iroh.19940790405
- MARCINEK J., KOMISAREK J., BEDNAREK R., MOCEK A., SKIBA S., WIATROWSKA K. 2011. Systematyka gleb Polski [Polish soil classification]. Roczn. Glebozn. **62**: 1-193. (In Polish with English abstract).
- MARTIN R., MAYNOU X. 2016. Dragonflies (Insecta: Odonata) as indicators of habitat quality in Mediterranean streams and rivers in the province of Barcelona (Catalonia, Iberian Peninsula). Int. J. Odonatol. **19**: 107-124.

https://doi.org/10.1080/13887890.2016.1172991

- MITRA A. 2000. Annotated Odonata inventory of the Asan Reservoir, Dehra Dun, India. Not. Odonatol. **5**: 57-60.
- NAGY H.B., LÁSZLÓ Z., SZABÓ F., SZŐCS L., DÉVAI G., TÓTHMÉRÉSZ B. 2019. Landscape-scale terrestrial factors are also vital in shaping Odonata assemblages of watercourses. Sci. Rep. 9: 18196. https://doi.org/10.1038/s41598-019-54628-7
- PERRON M.A.C., RICHMOND I.C., PICK F.R. 2021. Plants, water quality and land cover as drivers of Odonata assemblages in urban ponds. Sci. Total Environ. **773**: 145467. https://doi.org/10.1016/j.scitotenv.2021.145467
- PETROVIČOVÁ K., LANGRAF V., DAVID S., KRUMPALOVÁ Z., SCHLARMANNOVÁ J. 2021. Distinct Odonata assemblage variations in lentic reservoirs in Slovakia (Central Europe). Biologia **76**: 3727-3741. https://doi.org/10.1007/s11756-021-00864-0
- PETZOLD F. 2002. Erster Nachweis von *Leucorrhinia albifrons* in Thüringen (Odonata: Libellulidae). Libellula **21**: 37-39.
- REMSBURG A.J., TURNER M.G. 2009. Aquatic and terrestrial drivers of dragonfly (Odonata) assemblages within and among north-temperate lakes. J. North Am. Benthol. Soc. 28: 44-56. https://doi.org/10.1899/08-004.1
- SAHLÉN G., EKESTUBBE K. 2001. Identification of dragonflies (Odonata) as bioindicators of general species richness in boreal forest lakes. Biodiv. Conserv. 10: 673-690. https://doi.org/10.1023/A:1016681524097
- SHARMA G., JOSHI P.C. 2007. Diversity of Odonata (Insecta) from Dholbaha Dam (Distt. Hoshiarpur) in Punjab Shivalik, India. J. Asia Pac. Entomol. **10**: 177-180. https://doi.org/10.1016/S1226-8615(08)60350-7
- SINGH J.S. 2002. The biodiversity crisis: A mulifaceted review. Curr. Sci. 82: 638- 647.
- SOLON J., BORZYSZKOWSKI J., BIDŁASIK M., RICHLING A., BADORA K., BALON J., BRZEZIŃSKA-WÓJCIK T., CHABUDZIŃSKI Ł., DOBROWOLSKI R., GRZEGORCZYK I., JODŁOWSKI M., KIS-

TOWSKI M., KOT R., KRĄŻ P., LECHNIO J., MACIAS A., MAJCHROWSKA A., MALINOWSKA E., MIGOŃ P., MYGA-PIĄTEK U., NITA J., PAPIŃSKA E., RODZIK J., STRZYŻ M., TERPIŁOWSKI S., ZIAJA W. (2018) Physico-geographical mesoregions of Poland: Verification and adjustment of boundaries on the basis of contemporary spatial data. Geogr. Pol. **91**: 143-170. https://doi.org/10.7163/GP0I.0115

- STAŚKOWIAK A. 2014. Przyczynek do fauny ważek Skarżyska i okolic [Contribution to the fauna of dragonflies in Skarżysko and its vicinity]. Skarżyski Zesz. LOP **13**: 1-25. (In Polish).
- STAŚKOWIAK A. 2015. Suplement do fauny ważek okolic Skarżyska-Kamiennej [Supplement to the fauna of dragonflies in the vicinity of Skarżysko-Kamienna]. Skarżyski Zesz. LOP 14: 1-12.
- STAŚKOWIAK A. 2017. Suplement II do fauny ważek okolic Skarżyska-Kamiennej [Supplement II to the fauna of dragonflies in the vicinity of Skarżysko-Kamienna]. Skarżyski Zesz. LOP **15**: 1-5. (In Polish).
- STAŚKOWIAK A., SOWA R. 2018. Ważki Ziemi Skarżyskiej [Dragonflies of the Skarżysko Land]. PiS Agencja Wydawniczo-Poligraficzna, Skarżysko-Kamienna. Pp. 126. (In Polish).
- SUH A., SAMWAYS M.J. 2005. Significance of temporal changes when designing a reservoir for conservation of dragonfly diversity. Biodiv. Conserv. **14**: 165-178. http://dx.doi.org/10.1007/s10531-005-3652-5
- TER BRAAK C.J.F., ŠMILAUER P. 2012. Canoco reference manual and user's guide: software for ordination (version 5.0). Microcomputer Power, Ithaca, NY. Pp.496.
- TOŃCZYK G., STANKIEWICZ M. 2008. Ważki (Odonata) Parku Krajobrazowego Wzniesień Łódzkich [Dragonflies (Odonata) of the Lodz Hills Landscape Park]. Odonatrix **4**: 1-11. (In Polish with English abstract).
- WILDERMUTH H. 2005. Management of Small Waters to Promote Aquatic Biodiversity in Rural and Urban Nature Conservation Areas – Efficiency control using the example of dragonflies in the 'Schweizer Mittelland'. Nat.schutz Landsch.plan. 37: 193-201. (In German).
- WILSON E.O. 1985. The Biological Diversity Crisis. BioScience 35: 700-706. https://doi.org/10.2307/1310051
- WU H., CHEN J., XU J., ZENG G., SANG L., LIU Q., YIN Z., DAI J., YIN J., YE S. 2019. Effects of dam construction on biodiversity: a revew. J. Clean. Prod. **221**: 480-489. https://doi.org/10.1016/j.jclepro.2019.03.001
- ŻURAWLEW P. 2013. Ważki (Odonata) pogranicza Wysoczyzny Kaliskiej i Równiny Rychwalskiej (Wielkopolska) [Dragonflies (Odonata) of the borderland between the Kalisz High Plain and Rychwalska Plain (Great Poland)]. Odonatrix **9**: 33-54. (In Polish with English abstract).