

## In search of suitable habitats for water beetles (Insecta: Coleoptera) within a heavily transformed river system

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The Odra is a large, regulated river, along which many groynes have been built. There are few publications examining how groynes affect the functioning of a river. We investigated the effect of these hydro-engineering structures on the water beetle fauna of a river subject to strong human pressure. The species composition, assemblages, functional and ecological groups of these beetles in groyne fields were compared with those of oxbows in the Odra valley. We demonstrated that the groyne fields were highly beneficial for water beetle development, offering highly suitable alternative habitats to oxbows which, though natural, are sensitive and endangered habitats in river valleys. The numerically dominant species in the groyne fields were rheophiles, which are typical of weakly eutrophic, well-oxygenated oxbows. Species-wise, eurytopes were the most important beetle assemblage. Macrophytes and organic matter were the factors governing the occurrence of saprophages and polyphages, which provide plentiful food resources for the predominating predators in these habitats. Either the pH, visibility, temperature, hardness and O<sub>2</sub> both the vegetation, water depth, breadth of the littoral of the two habitat types were key to the beetles' distribution. The presence of groyne fields has rendered the species richness of the Odra's water beetles comparable with that of large, natural rivers, which amply demonstrates that not all anthropogenic transformations of habitats are inherently negative.

Key words: Odra, oxbows, groynes, species distribution, potential habitats.

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Over the centuries, nearly all the large rivers of Europe have become hydromorphologically transformed as a result of human activities (Brunke *et al.* 2002; Kleinwächter *et al.* 2003; Costea *et al.* 2013; Lewin 2014). However, the extensive hydrobiological literature is dominated by publications relating to smaller watercourses like streams. This is no doubt due to the very considerable difficulties of carrying out research on a large river draining an extensive catchment area. These two elements form a coherent

ecosystem in which strong interactions occur among its biotic and abiotic components that maintain the necessary dynamic equilibrium, as pointed out by Vannote *et al.* (1980) and Doretto *et al.* (2020), the authors of the River Continuum Concept (RCC). In recent years, attention has been drawn to the fact that this dynamic equilibrium can be disturbed by manifold human activities, for example, agriculture, forestry, urban expansion, industry and infrastructure construction (Allan 1995; Norris & Thoms 1999;

Doretto *et al.* 2020; Turič *et al.* 2021; Knehtl *et al.* 2021). The deterioration in water quality, the probable consequence of these activities, usually leads to a decline in the biodiversity of these environments (Vinson & Hawking 1998; Bates *et al.* 2007; Kennedy & Turner 2011).

In the last 300 years, the River Odra (Czech: Odra, German: Oder), the subject of this study, has had barrages constructed across it and, in some places, dykes built alongside. Moreover, short-cuts dug across the bases of the river's meanders have reduced its original length by 25% (Rast *et al.* 2000). This straightening out of the river's course has deprived it of the natural pools of still water, typical of large, natural rivers, which has impoverished the aquatic fauna and flora. In the 18th century, groynes began to be constructed along the river – these are extant along the 350-km stretch from Brzeg Dolny all the way to Czelin. Another type of water body that enriches the hydrographical network of the Odra valley are oxbows, remnants of the original course of the river. Even so, entry to them is very often merely screened by a groyne, so that in fact they are not completely cut off from the mainstream, thereby facilitating the free circulation of water and the migration of organisms. Both the groyne fields and the oxbows may be of great significance for the Odra's assemblage of invertebrates and the local biodiversity. These areas may also play an important part in the river's self-cleaning processes. In the context of the ecological disaster that befell the Odra in the summer of 2022 (Absalon *et al.* 2023; Free *et al.* 2023), they may act as refuges of fauna from which the mainstream can be recolonised, once the wave of contamination has passed (Allan 1998; Ward *et al.* 2002).

To date, these potential refuges have been little studied, however. Only a small number of detailed papers have been published on their zooplankton (Ławniczak *et al.* 2008), molluscs (Piechocki & Szlauer-Łukaszewska 2013), ostracods (Szlauer-Łukaszewska 2015), dragonflies (Buczyński *et al.* 2017), leeches (Jabłońska-Barna *et al.* 2017) and caddisflies (Buczyńska *et al.* 2018). Some relevant information is also given in the report by Schöll *et al.* (2003). The results of these studies are absolutely crucial and may offer points of reference as the river's renaturalisation is tracked.

An important and very numerous taxonomic group of organisms inhabiting river valleys are water beetles (Biesiadka & Pakulnicka 2004; Buczyński *et al.* 2011; Pakulnicka *et al.* 2012; Costea *et al.* 2013; Pakulnicka & Nowakowski, 2016; Turič *et al.* 2020). They are quite diverse in terms of species, trophic relationships and ecology (Gioria *et al.* 2010a, 2010b; Costea *et al.* 2013; Pakulnicka *et al.* 2015a, 2016).

Many such beetles also have considerable capacities to disperse and migrate, which are characteristics that affect the structures of beetle communities in the floodplains of rivers, both when these are swollen and when they are carrying optimal volumes of water. At the same time, the stenotopicity and demanding habitat requirements of some species imply that they are good bioindicators of the state of surface waters (Gioria *et al.* 2010a, 2010b; Pakulnicka *et al.* 2015a, 2015b; Turič *et al.* 2020). The growing significance of biomonitoring, in combination with the need for the permanent monitoring of the water's physical and chemical parameters, has taken on a new dimension in light of the recent environmental disaster on the Odra. This is also confirmed by the new challenges currently facing ecologists (Ziglio *et al.* 2006).

Knowledge of the beetle fauna of groyne fields and modified oxbows provides a foundation on which specific proposals for the planning and implementation of large-river restoration measures can be based. This is not only important in light of the EU recommendations for protecting biodiversity and improving the state of the waters, contained in the Natura 2000 programme and the Water Framework Directive, but also for sound economic reasons – making use of existing habitats is more expedient than, for example, undertaking a costly and often unworkable reconstruction of river meanders.

The aims of our study were: (i) to define the species, ecological and trophic structures of the beetle assemblages inhabiting the groyne fields and oxbows; (ii) to highlight factors exerting a significant influence on the structure of these assemblages and the trophic groups of beetles in both types of habitats; (iii) to try and find an answer to the question – Can groyne fields in a large, radically transformed river offer an alternative lentic habitat for water beetles, approximating that of near-natural oxbows?

## Material and Methods

### Study area

The study covered the middle and lower course of the River Odra over a distance of around 420 km, from Uraz (51°14'N, 16°51'E) to Ognica (53°04'N, 14°22'E). A series of groynes built from stone blocks have been constructed along the 350 km-long stretch of the river from Brzeg Dolny to Czelin. The spaces between them – the groyne fields – where the current is slower, are filled with sandy or muddy sediments and frequently support marshland vegetation with



Fig. 1. Study habitats: A – the River Odra, B – groynes and groyne fields, C – oxbow.

dominant *Phalaris arundinacea* L.; elodeids have also been recorded in this zone (Fig. 1). The central, deepest parts have sandy bottoms, upon which rest large boulders and huge amounts of shell debris. The sediments of the areas in front of the groynes, which are attacked by the oncoming, swirling waters of the river, are usually of sand and gravel. Apart from the pools that have formed between the groynes, the other lentic habitats found along this stretch of the Odra are oxbows, most of which have a permanent connection with the river. The oxbows we explored were from 520 to 5000 m long and from 20 to 630 m wide (Fig. 1). Their bottoms are covered by sandy and silty sediments with a considerable admixture of organic matter, sometimes forming a sapropel. The littoral zone is dominated by sedges *Carex* spp. with admixtures of other helophytes; elodeids and nymphaeids also occur. When the water levels are high, the meadow vegetation behind the banks is inundated (Piechocki & Szlauer-Lukaszewska 2013). Along the stretch of the Odra that we explored we

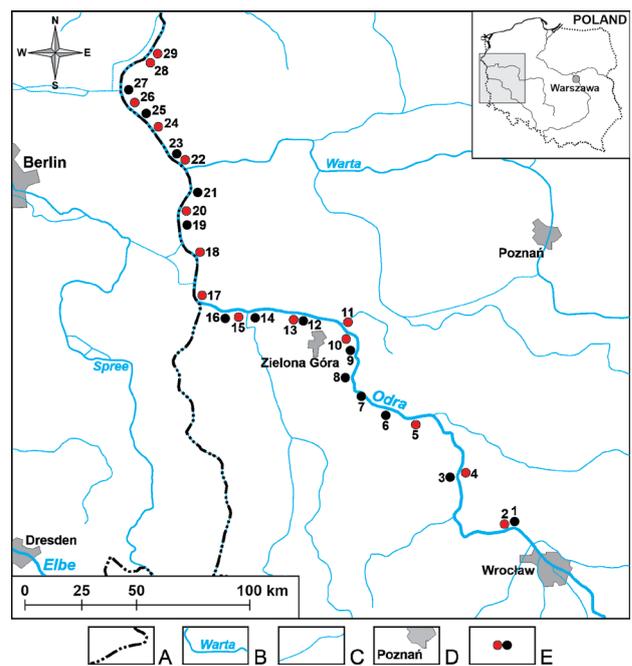


Fig. 2. Study area: A – Polish-German border, B – large rivers, C – tributaries, D – cities, E – research stations (groyne fields: red dots, oxbows: black dots).

set up a total of 27 research stations located in both environments: 15 in the groyne fields and 14 in the oxbows (Fig. 2). On the stretch below Czelin (3 stations where a total of 54 samples were collected) there are neither groynes nor groyne fields – the banks are reinforced with boulders, reedbeds emerge above the water surface – and no beetles were caught there. Therefore, those samples were not taken into consideration in the subsequent statistical analyses.

#### Sampling procedures

The water beetles were caught in spring, summer and autumn in both 2009 and 2010; some additional material was acquired in October 2012. A total of 539 faunistic samples were obtained. The insects were collected with a 25 cm wide handnet fitted with a 0.25 mm mesh netbag. In places where the bottom was even, the net was dragged for a specified distance to scoop up the surface layer of bottom sediment. Where the bottom was overgrown or uneven, stony or very hard, the sample was taken from a specified area by sweeping the net back and forth over it. The results were recalculated and expressed as the number of individuals per 1 m<sup>2</sup>. The research stations were selected so as to ensure the maximum possible coverage of all the habitats accessible during the various study periods. The adults collected (965) were identified to species level and the larvae (315) to generic level.

Twelve physical and chemical parameters of the water and seven structural parameters of the river or oxbows were measured at each station. The specific electrolytic conductivity (EC), total dissolved solids (TDS), salinity (SALIN), pH, dissolved oxygen content (O<sub>2</sub>) and temperature (TEMP) were measured using a multifunctional probe (Hach-Lange HQ40d). Visibility (VISIB) was assessed with a Secchi disc. Ammonium nitrogen (NH<sub>4</sub>), nitrites (NO<sub>2</sub>), nitrates (NO<sub>3</sub>), phosphates (PO<sub>4</sub>) and water hardness (HARD) were measured *in situ* with a Slandi LF 300 portable photometer for measuring contaminants in waters and effluents. At each station we measured the depth of the bottom (DEPTH), the breadth of the littoral (LITTOR), and the degree of plant cover (PLANTS) based on phytosociological relevés (Braun-Blanquet 1964). The substrate composition at each sampling site was estimated as the proportion of each of the following substrate particle size classes: mud (< 0.06 mm diameter – MUD), sand (0.06-2 – SAND), gravel (> 2-64 – GRAVEL) and rock (> 64 – STONES) (Gordon *et al.* 1992).

#### Biocoenotic indices and statistical analyses

The following indices were used for the species diversity analyses and comparisons: S – number of

species, N – number of individuals, D – dominance (% contribution of the taxa).

The beetle taxa were assigned to 6 functional feeding groups (FFG): FF – active filter feeders, GR-SC – grazers and scrapers, MIN – miners, PRE – predators, SHR – shredders, and POL – polyphages (Uwadia 2010; Ramírez & Gutiérrez-Fonseca 2014). In addition, 6 ecological groups were distinguished – rheobionts, rheophiles, tyrophiles, halophiles, argilophiles and eurytopes – in order to determine the holistic character of the fauna (Biesiadka 1980).

Because the samples of aquatic beetles were collected on several different dates (to take into account the phenological aspect) from the habitats distinguished in the river and oxbows, we used a GLM (Generalized Linear Model) for repeated measures ANOVA (Hocking 1996) to determine the significance of differences in the number of species and the abundance of beetles. First, we checked the assumptions of normality (Shapiro-Wilk test) and the homogeneity of variances (Levene's test). The GLM repeated measure models were calculated on the basis of Type III sums of squares so as to take the unbalanced design into account. Significant results were tested for pairwise comparisons using Tukey's HSD post-hoc tests. The dependent variables (abundance and number of species) were transformed where necessary to satisfy the requirements of parametric tests (Saint-Germain *et al.* 2007; Cremona *et al.* 2008). Correspondence analysis (CA) (Clausen 1998) was used to determine dependences between the abundance of water beetles within the ecological groups, the functional feeding groups (FFG) and the habitats. The analysis involved two dimensions: one explained the largest part of the general chi-squared statistics (% of inertia), the other dimension increased the percentage of the explained inertia. Relationships between the FFG of beetles (N – abundance, S – number of species) and the environmental parameters at the sampling sites were determined using principal components analysis (PCA). All the calculations were performed in Statistica, ver. 13.5 (StatSoft, Tulsa, USA).

To distinguish the key environmental drivers responsible for the variation among the beetle species we used Canonical Correspondence Analysis (CCA) for two sets of variables separately: the 12 physical and chemical parameters of the water, and the 7 features describing the structure of the sites. Matrices with no data transformation were used according to O'Hara & Kotze (2010). Stepwise selection with 999 test permutations was used to filter the significant variables ( $p < 0.05$ ) (Šmilauer & Lepš 2014). The computations were performed and plotted in CANOCO 5.0 statistical software (ter Braak & Šmilauer 2012).

## Results

### General comments on the beetle fauna

A total of 1280 beetles belonging to 66 taxa were collected, 280 from the river (40 taxa) and 1000 from the oxbows (57 taxa) (Table 1).

The most numerous species in the dominance structure were *Laccophilus hyalinus* (26.0%) and *Hygrotus versicolor* (9.4%), eudominants in both the groyne fields and the oxbows. *Haliplus fluviatilis*

(6.6%), a species particularly abundant in the oxbows, was of somewhat lesser importance in the entire material. The GLM Repeated Measure ANOVA indicated significant differences in both the numbers of species ( $F_{(1,27)} = 9.49906$ ,  $p = 0.005$ ) and the abundance of beetles ( $F_{(1,27)} = 9.88372$ ,  $p = 0.004$ ) in the two habitats (Table 2).

This analysis also showed up significant differences in the dependence on the phenological period, i.e. the month when sampling took place, of both the numbers of species ( $F_{(6,27)} = 4.31$ ,  $p = 0.00047$ ) and

Table 1

Water beetles inhabiting groyne fields (GF) and oxbows (OX) on the Odra River. FFG – functional feeding group (FF – active filter feeders, GR-SC – grazers and scrapers, MIN – miners, POL – polyphagous species, PRE – predators, SHR – shredders), ECG – ecological group (Rb – rheobionts, Re – rheophiles, T – tyrphophiles, Ha – halophiles, Arg – argilophiles, E – eurytopes), N – number of individuals, D [%] – dominance

Taxa	Code	FFG	ECG	Station No.	GF		OX	
					N	D	N	D
<b>Haliplidae</b>								
<i>Haliplus confinis</i> Steph.	Hal_con	POL	Arg	16	–	–	1	0.1
<i>Haliplus fluviatilis</i> Aubé	Hal_fluv	POL	Re	1, 3, 6, 8, 9, 12-14, 16, 17, 20, 21, 25-27	6	2.1	79	7.9
<i>Haliplus heydeni</i> Wehn.	Hal_hey	POL	E	15, 16, 21, 27	1	0.4	4	0.4
<i>Haliplus lineatocollis</i> (Marsh.)	Hal_lin	POL	Rb	15	1	0.4		
<i>Haliplus obliquus</i> (Fabr.)	Hal_obl	POL	Arg	14			1	0.1
<i>Haliplus</i> sp. (larvae)	Hal_sp	GR-SC	–	1, 3, 6, 8-10, 12, 15-17, 25, 27	12	4.3	49	4.9
<i>Peltodytes caesus</i> (Duft.)	Pel_cae	POL	E	1, 6, 16, 25	–	–	11	1.1
<b>Gyrinidae</b>								
<i>Gyrinus substriatus</i> Steph.	Gyr_sub	PRE	E	21	–	–	1	0.1
<b>Noteridae</b>								
<i>Noterus clavicornis</i> (De G.)	Not_cla	PRE	E	1, 2, 22	2	0.7	1	0.1
<i>Noterus crassicornis</i> (O.F. Müll.)	Not_cra	PRE	E	1	–	–	15	1.5
<b>Dytiscidae</b>								
<i>Agabus</i> sp. (larvae)	Aga_sp	PRE		1, 3, 22, 27	1	0.4	4	0.4
<i>Ilybius fenestratus</i> (Fabr.)	Ily_fen	PRE	Re	16, 19	1	0.4	3	0.3
<i>Ilybius</i> sp. (larvae)	Ily_sp	PRE	–	18, 20, 27	4	1.4	3	0.3
<i>Platambus maculatus</i> (L.)	Pla_mac	PRE	Re	16, 25	–	–	2	0.2
<i>Colymbetes fuscus</i> (L.)	Col_fus	PRE	E	8, 12, 15, 24, 25	4	1.4	8	0.8
<i>Colymbetes paykulli</i> (Er.)	Col_pay	PRE	T	13, 15, 18, 20, 22, 27	11	3.9	2	0.2
<i>Colymbetes striatus</i> (L.)	Col_str	PRE	T	19	–	–	1	0.1
<i>Rhantus consputus</i> (Sturm)	Rh_con	PRE	E	5, 8	1	0.4	1	0.1
<i>Rhantus latitans</i> Sharp	Rh_lat	PRE	E	11-18, 22, 25	11	3.9	5	0.5
<i>Rhantus suturalis</i> (W.S. MacL.)	Rh_sut	PRE	E	16, 21	1	0.4	1	0.1
<i>Rhantus</i> sp. (larvae)	Rh_sp.	PRE	–	3, 8, 12-16, 20, 27	16	5.7	20	2.0
<i>Cybister lateralimarginalis</i> (De G.)	Cyb_lat	PRE	E	19, 25	–	–	2	0.2
<i>Dytiscus</i> sp. (larvae)	Dyt_sp	PRE	–	20, 27	1	0.4	1	0.1
<i>Hydroglyphus pusillus</i> (Fabr.)	Hdg_pus	PRE	Arg	3	–	–	1	0.1
<i>Nebrioporus depressus</i> (Fabr.)	Neb_dep	PRE	Rb	3, 15	1	0.4	3	0.3
<i>Hydroporus angustatus</i> Sturm	Hyd_ang	PRE	T	9	–	–	1	0.1
<i>Hydroporus incognitus</i> Sharp	Hyd_inc	PRE	T	11, 16, 21, 25	1	0.4	3	0.3
<i>Hydroporus palustris</i> (L.)	Hyd_pal	PRE	E	3, 12, 17, 21, 25, 26	2	0.7	25	2.5

Table 1 cont.

Taxa	Code	FFG	ECG	Station No.	GF		OX	
					N	D	N	D
<i>Hydroporus (Hydroporus) sp.</i> (larvae)	Hyd_sp	PRE	–	3, 9, 12, 14, 16, 21, 25, 27	–	–	127	12.7
<i>Hydroporus (Suphrodytes) sp.</i> (larvae)	Sup_sp	PRE	–	12, 13, 16	12	4.3	1	0.1
<i>Graptodytes pictus</i> (Fabr.)	Gra_pic	PRE	E	3, 8, 12, 13, 16	1	0.4	7	0.7
<i>Porhydrus lineatus</i> (Fabr.)	Por_lin	PRE	Re	3, 16	–	–	2	0.2
<i>Hygrotus impressopunctatus</i> (Schall.)	Hyg_imp	PRE	E	22, 27	11	3.9	1	0.1
<i>Hygrotus inaequalis</i> (Fabr.)	Hyg_ina	PRE	E	16, 27	1	0.4	1	0.1
<i>Hygrotus versicolor</i> (Schall.)	Hyg_ver	PRE	Re	3, 4, 8, 9, 12, 14-17, 19, 21-23, 25, 27	20	7.1	100	10.0
<i>Hygrotus sp.</i> (larvae)	Hyg_sp	PRE	–	3, 5, 6, 8, 9, 12-17, 19, 20, 22, 27	30	10.7	86	8.6
<i>Hyphydrus ovatus</i> (L.)	Hyp_ova	PRE	E	8, 9, 12-14, 16, 19, 20, 21, 25	3	1.1	25	2.5
<i>Laccophilus hyalinus</i> (De G.)	Lac_hya	PRE	Re	1-3, 6-9, 11-17, 19-22, 25-27	77	27.5	256	25.6
<b>Dryopidae</b>								
<i>Dryops sp.</i> (larvae)	Dry_sp	GR-SC	–	13	1	0.4	–	–
<b>Elmidae</b>								
<i>Limnius volckmari</i> (Panz.)	Lmn_vol	GR-SC	Rb	16	1	0.4	–	–
<b>Heteroceridae</b>								
<i>Heterocerus fuscus</i> Kiesenw.	Het_fus	GR-SC	Re	4	1	0.4	–	–
<b>Helophoridae</b>								
<i>Helophorus griseus</i> Herbst	Hel_gri	SHR	Arg	8, 16, 21	–	–	4	0.4
<i>Helophorus minutus</i> Fabr.	Hel_min	SHR	Arg	13	1	0.4	–	–
<b>Hydrochidae</b>								
<i>Hydrochus brevis</i> (Herbst)	Hdr_bre	SHR	E	9, 14, 21	–	–	3	0.3
<i>Hydrochus crenatus</i> (Fabr.)	Hdr_cre	SHR	E	19	–	–	1	0.1
<b>Spercheidae</b>								
<i>Spercheus emarginatus</i> (Schall.)	Spe_ema	FF	E	3, 4, 9, 12, 15, 16, 21, 25	6	2.1	28	2.8
<b>Hydrophilidae</b>								
<i>Laccobius minutus</i> (L.)	Lcb_min	SHR	Arg	1, 12, 13, 15, 19, 21, 22, 25, 27	9	3.2	19	1.9
<i>Hydrobius fuscipes</i> (L.)	Hdb_fus	SHR	E	1, 14, 15, 18, 21, 25	3	1.1	5	0.5
<i>Hydrochara caraboides</i> (L.)	Hdr_car	SHR	E	9	–	–	1	0.1
<i>Hydrophilus piceus</i> (L.)	Hdp_pic	SHR	E	16	1	0.4	–	–
<i>Anacaena lutescens</i> (Steph.)	Ana_lut	SHR	T	25	–	–	1	0.1
<i>Chaetarthria seminulum</i> (Herbst)	Cha_sem	SHR	E	16	–	–	1	0.1
<i>Cymbiodyta marginella</i> (Fabr.)	Cym_mar	SHR	T	3	–	–	1	0.1
<i>Enochrus bicolor</i> (Fabr.)	Eno_bic	SHR	Ha	20	1	0.4	–	–
<i>Enochrus ochropterus</i> (Marsh.)	Eno_och	SHR	T	27	–	–	1	0.1
<i>Enochrus quadripunctatus</i> (Herbst)	Eno_qua	SHR	E	22	2	0.7	–	–
<i>Enochrus sp.</i> (larvae)	Eno_sp	PRE	–	27	–	–	1	0.1
<i>Helochaeres obscurus</i> (O.F. Müll.)	Hlc_obs	SHR	E	1, 9, 11-13, 16, 18, 21, 22, 25, 27	17	6.1	29	2.9
<i>Coelostoma orbiculare</i> (Fabr.)	Coe_orb	SHR	E	16, 22	2	0.7	–	–
<i>Cercyon convexiusculus</i> Steph.	Cer_con	SHR	E	27	–	–	1	0.1
<b>Hydraenidae</b>								
<i>Hydraena palustris</i> Er.	Hya_pal	GR-SC	T	9, 19, 27	–	–	5	0.5
<i>Limnebius atomus</i> (Duft.)	Lim_ato	GR-SC	E	16, 21, 25	–	–	5	0.5
<i>Limnebius truncatellus</i> (Thunb.)	Lmb_tru	GR-SC	Rb	1, 3, 9, 12	–	–	4	0.4
<i>Ochthebius minimus</i> (Fabr.)	Och_min	GR-SC	E	9, 12, 18, 19, 27	1	0.4	7	0.7
<b>Scirtidae</b>								
<i>Cyphon sp.</i> (larvae)	Cyp_sp	GR-SC	–	3, 7, 9, 15	2	0.7	23	2.3
<b>Curculionidae</b>								
<i>Tanysphyrus lemnae</i> (Payk.)	Tan_lem	MIN	E	9, 25, 27	–	–	6	0.6
N=	–	–	–	–	280	100.0	1000	100.0

Table 2

General linear model (GLM) for repeated measure Analysis of Variance (ANOVA) of water beetles in two types of habitats in the River Odra

Parameter	Effect	SS	df	MS	F	p
Number of species	intercept	8397.05	1	8397.054	27.69769	0.000015
	habitat	2879.81	1	2879.812	9.49906	0.004694
	Error	8185.54	27	303.168		
	Time	4016.95	6	669.491	4.30653	0.000467
	Time*habitat	1334.46	6	222.411	1.43066	0.025876
	Error	25184.46	162	155.460		
Abundance	intercept	1329.364	1	1329.364	68.86215	0.000000
	habitat	190.802	1	190.802	9.88372	0.004027
	Error	521.227	27	19.305		
	Time	236.094	6	39.349	6.77592	0.000002
	Time*habitat	48.035	6	8.006	1.37860	0.022618
	Error	940.763	162	5.807		

the abundance of beetles ( $F_{(6,27)} = 6.78$ ,  $p = 0.000002$ ). The GLM repeated measure ANOVA highlighted the significant synergistic effect between the habitat type and phenological period, with respect to both the number of species ( $F_{(6,162)} = 1.431$ ,  $p = 0.026$ ) and the number of beetles ( $F_{(6,162)} = 1.379$ ,  $p = 0.023$ ). The significant differences (Tukey's HSD post-hoc test) between the subclasses are illustrated in Fig. 3.

Particularly noteworthy are the statistically significant differences in the numbers of species found in both habitats in October ( $p = 0.008$ ) and in the abundance of beetles in May ( $p = 0.027$ ) and August ( $p = 0.049$ ).

Faunistic similarities, ecological elements and functional feeding groups

The species richness in the ecological structure of the entire material was the greatest among eurytopes (56.4% of all species), followed by rheophiles (14.1%) and tyrphophiles (12.8%). The ecological structure of the beetle fauna in the two habitats was much the same, albeit with more tyrphophiles and argilophiles in the oxbows and more rheobionts in the groyne fields (Fig. 4A).

However, the ecological structure differed where the abundances of the ecological groups were concerned: 61.5% of the individuals found were rheophiles, while 29.9% were eurytopes. The proportions of the other groups were not significant. Analysis of the beetle fauna in the two habitats showed that rheophiles were quantitatively more important in the oxbows, while eurybionts were likewise more important in the groyne fields (Fig. 4B).

As regards the trophic structure, the largest numbers of beetles in both habitats (Fig. 5) were preda-

tors (more than 70% of the total). In the river, detritivores, mainly shredders, were quite important; against that, there were considerable numbers of largely phytophagous beetles in the oxbows. Among the latter, grazer-scrappers and polyphages were present in abundance, along with a few miners. Filter feeders were few in number in both habitats. The qualitative trophic structure was similar: the principal element here consisted of predators, whereas the species diversities in the other FFGs resembled one another.

The trophic structures of the beetle assemblages in both habitats were phenologically diverse (Fig. 6). In spring, the largest numbers of beetles in both habitats were predators. In summer, the significance of this group decreased distinctly, making way for a clear increase in the proportion of detritus feeders (like shredders and active filter feeders), and phytophages (grazer-scrappers, miners and polyphages). Polyphages were particularly numerous in the oxbows.

Relationships between the ecological and functional feeding groups of Coleoptera in both types of habitats and with respect to the habitat conditions

CA analysis of the ecological structure of the beetles in both habitats revealed significant differences in the counts of beetles representing different ecological groups ( $\chi^2 = 441.41$ ,  $df = 130$ ;  $p = 0.00001$ ).

Together, the two dimensions explained 71.26 % of the total chi-squared statistic (total inertia). The most important relationship demonstrated was that rheophiles exhibited a clear preference for oxbows,

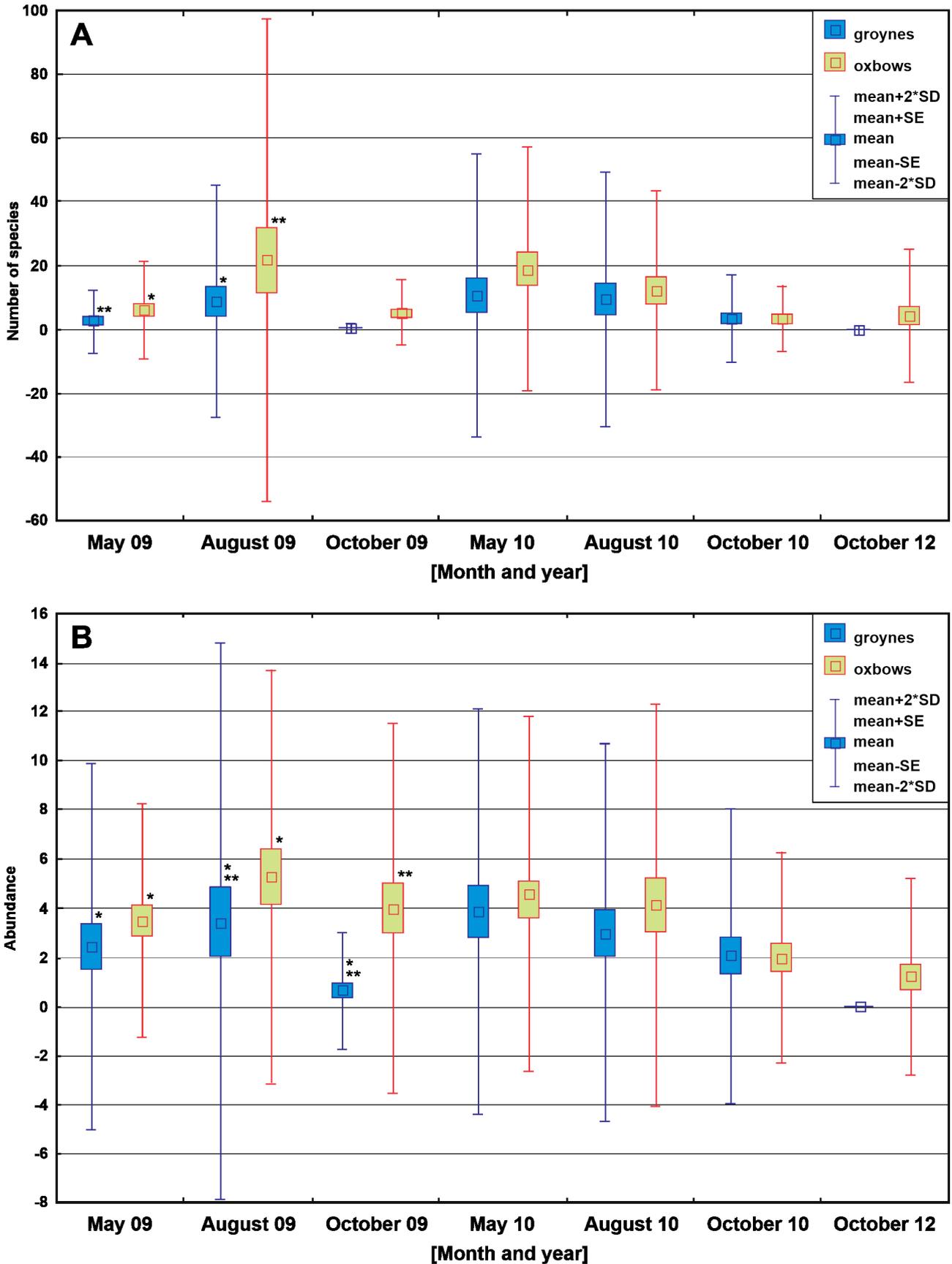


Fig. 3. Results of a Tukey *post-hoc* test for GLM repeated measure ANOVA. The diagram shows the statistically significant synergistic effect between habitats and seasons on: A – the number of species in the microhabitats distinguished at each research station, B – the abundance of beetles. \*  $p < 0.05$ ; \*\*  $p < 0.01$ .

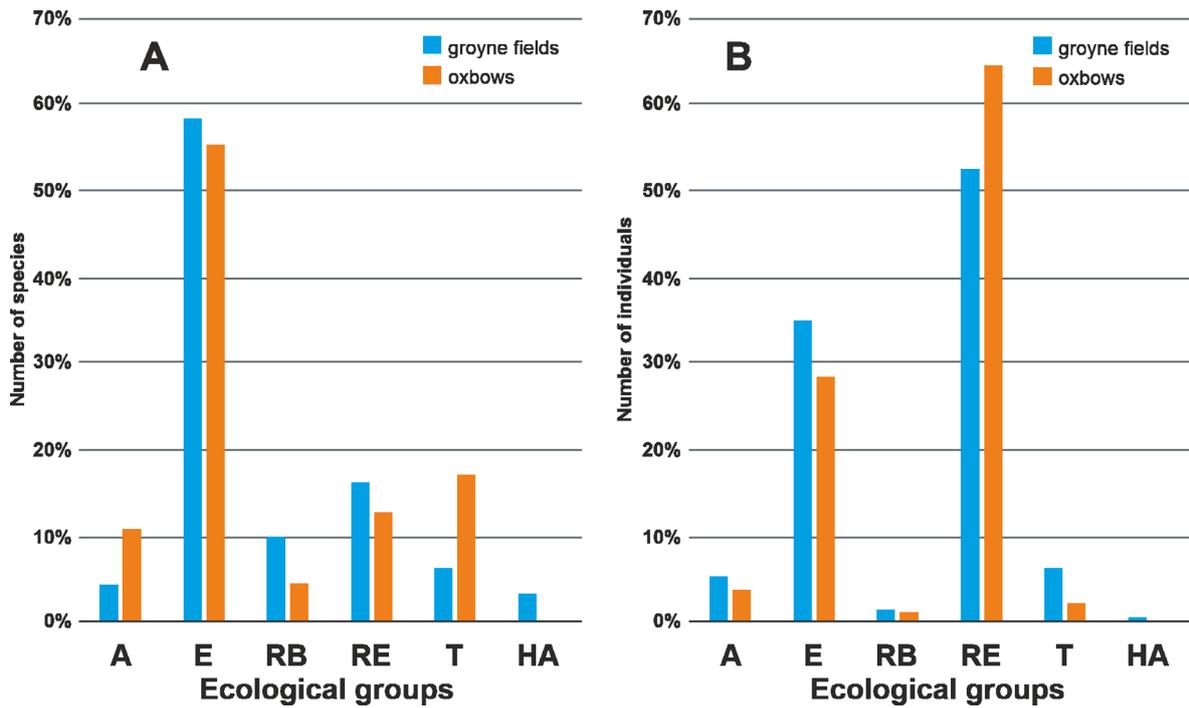


Fig. 4. The ecological structure of water beetles in both habitat types: A – number of species, B – number of individuals. Abbreviations as in Table 1.

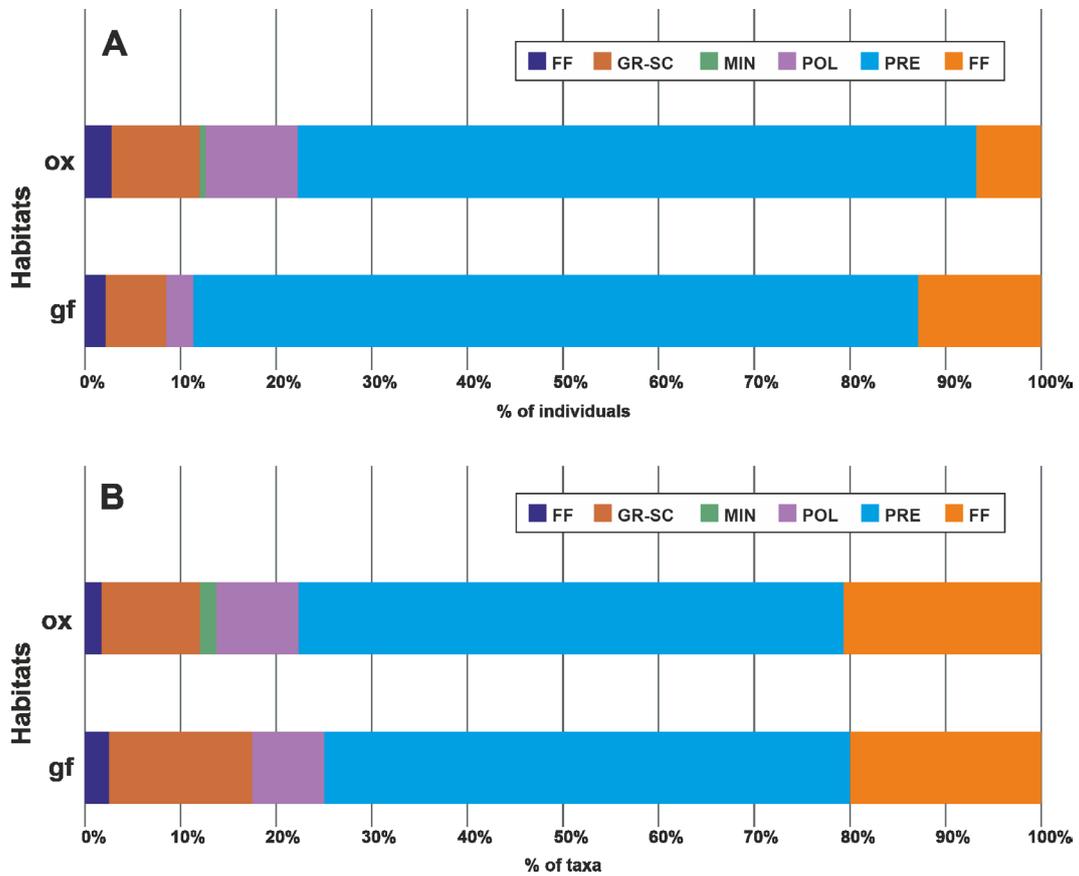


Fig. 5. Functional feeding groups of aquatic beetles in the groyne fields (gf) and oxbows (ox). A – percentages of individuals, B – percentages of taxa. Abbreviations as in Table 1.

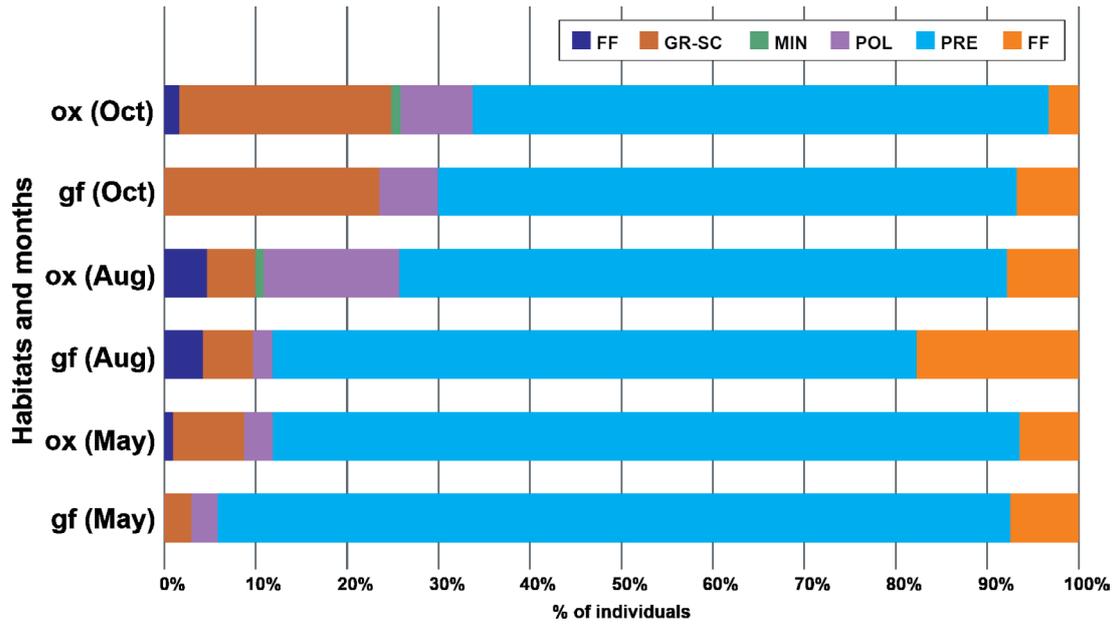


Fig. 6. Seasonal changes in the abundance of the functional feeding groups of water beetles in groyne fields (gf) and oxbows (ox). Abbreviations as in Table 1.

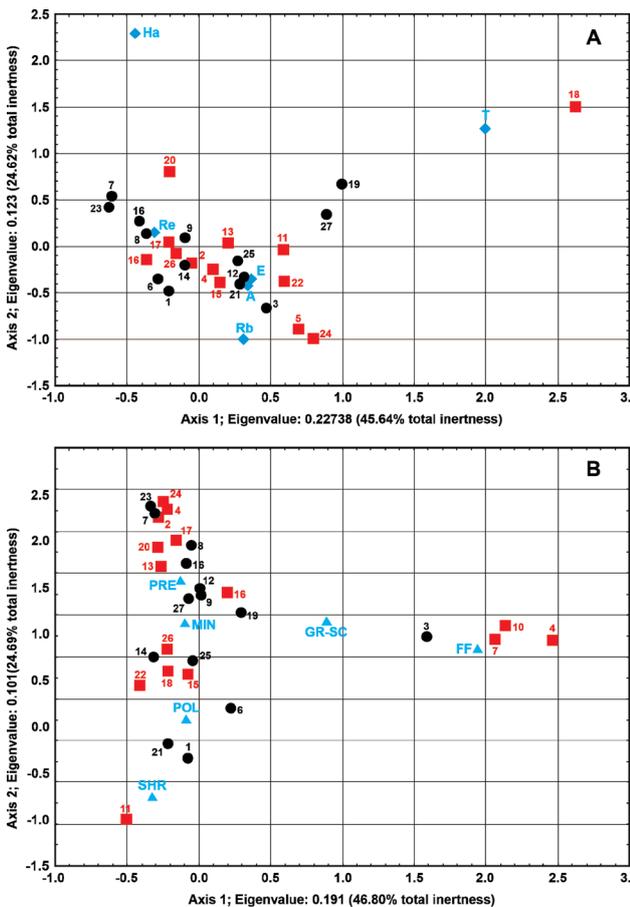


Fig. 7. Correspondence Analysis (CA) showing the relationships between the ecological groups (A) and functional feeding groups (B) of the beetle communities (blue diamonds) and the two habitats (groyne fields – red squares, oxbows – black dots) at the 27 research stations along the first and second axes. Abbreviations as in Table 1.

whereas rheobionts displayed a pronounced affinity for the groyne fields (Fig 7A).

Analysis of the beetles’ trophic structure also highlighted significant differences in the numbers of aquatic beetle FFGs ( $\chi^2 = 522.73$ ,  $df = 140$ ;  $p = 0.00031$ ). The two dimensions together explained 71.38% (b) of the total chi-squared statistic (total inertia). The analysis upheld the positive correlations between active filter feeders (FF) and shredders (SHR) with groyne fields. In turn, grazers and scrapers (GR-SC), miners (MIN) and polyphages (POL) were shown to have a strong relationship with oxbows. Predators were common in both habitats (Fig. 7B, Table 3).

Principal component analysis (PCA) of the variables representing the parameters of habitats and trophic groups distinguished in our study (Fig. 8) showed that the first axis, representing the highest eigenvalues, corresponded most strongly with the variables “polyphages”, “predators”, “plants”, “Cond”, “TDS” and “NO<sub>3</sub>”, and that the second axis showed the strongest correlations with the variables “miner”, “filter feeder” and “O<sub>2</sub>”.

Positive correlations were obtained between the “SHR (N)” and “NH<sub>4</sub>” ( $r_p = 0.37$ ), “polyphages” and “plants” ( $r_p = 0.25$ ), “predator” and “mud” ( $r_p = 0.17$ ), “grazer and scraper” and “sand” ( $r_p = 0.12$ ), “filter feeder” and “sand” ( $r_p = 0.06$ ), while the correlations were negative between “filter feeder” and “O<sub>2</sub>” ( $r_p = -0.33$ ), “predator” and “depth” ( $r_p = -0.33$ ), “polyphages” and “depth” ( $r_p = -0.21$ ), and “grazer and scraper” and “TDS” ( $r_p = -0.24$ ) (Table 3).

Table 3

Correlation matrix from the PCA panel between the various functional feeding groups and the habitat parameters

Variable	FF (S)	FF (N)	GR-SC (S)	GR-SC (N)	MIN (S)	MIN (N)	POL (S)	POL (N)	PRE (S)	PRE (N)	SHR (S)	SHR (N)
FF (S)	1.00	0.84	0.13	0.00	0.07	0.03	0.01	0.05	0.13	0.06	0.07	0.07
FF (N)	0.84	1.00	0.04	-0.03	0.01	0.00	0.00	0.03	0.05	0.03	0.01	0.04
GR-SC (S)	0.13	0.04	1.00	0.50	0.05	0.00	0.08	0.11	-0.07	0.04	-0.02	0.00
GR-SC (N)	0.00	-0.03	0.50	1.00	0.01	-0.01	0.26	0.18	0.15	0.25	-0.06	-0.05
MIN (S)	0.07	0.01	0.05	0.01	1.00	0.86	0.00	-0.01	0.02	0.00	0.14	0.04
MIN (N)	0.03	0.00	0.00	-0.01	0.86	1.00	-0.02	-0.02	0.03	0.01	0.06	0.01
POL (S)	0.01	0.00	0.08	0.26	0.00	-0.02	1.00	0.70	0.30	0.45	0.16	0.20
POL (N)	0.05	0.03	0.11	0.18	-0.01	-0.02	0.70	1.00	0.19	0.43	0.26	0.50
PRE (S)	0.13	0.05	-0.07	0.15	0.02	0.03	0.30	0.19	1.00	0.56	0.18	0.23
PRE (N)	0.06	0.03	0.04	0.25	0.00	0.01	0.45	0.43	0.56	1.00	0.13	0.21
SHR (S)	0.07	0.01	-0.02	-0.06	0.14	0.06	0.16	0.26	0.18	0.13	1.00	0.81
SHR (N)	0.07	0.04	0.00	-0.05	0.04	0.01	0.20	0.50	0.23	0.21	0.81	1.00
NH <sub>4</sub>	-0.01	-0.02	0.00	-0.01	-0.03	-0.02	0.02	0.28	-0.02	0.02	0.25	0.37
NO <sub>2</sub>	-0.02	-0.01	-0.05	-0.06	0.01	-0.01	-0.01	0.07	-0.12	-0.05	0.08	0.10
NO <sub>3</sub>	-0.19	-0.12	-0.08	-0.09	-0.02	0.04	-0.15	-0.18	-0.14	-0.14	0.00	-0.04
O <sub>2</sub>	-0.34	-0.36	0.04	-0.08	-0.09	-0.09	0.01	0.11	-0.04	-0.05	0.02	0.12
O <sub>2</sub> %	-0.26	-0.28	0.03	-0.07	-0.09	-0.07	0.03	0.15	0.01	0.01	0.06	0.18
pH	-0.05	-0.05	-0.04	-0.03	-0.02	-0.02	-0.04	-0.02	-0.09	-0.05	0.08	0.03
PO <sub>4</sub>	0.03	0.07	-0.05	-0.06	0.01	0.00	-0.05	-0.05	-0.06	-0.06	0.02	-0.02
cond	-0.19	-0.18	0.02	-0.07	-0.04	-0.02	-0.14	-0.14	-0.19	-0.17	-0.09	-0.09
TDS	-0.18	-0.17	0.02	-0.07	-0.04	-0.02	-0.17	-0.15	-0.24	-0.18	0.00	-0.05
temp	-0.01	0.00	-0.07	-0.04	-0.02	-0.01	-0.02	0.00	-0.08	-0.03	0.09	0.04
hardn	0.03	-0.09	-0.01	-0.12	0.19	0.18	0.01	0.02	0.06	0.01	0.15	0.14
visib	-0.11	-0.17	0.01	0.00	0.03	0.00	-0.04	-0.03	-0.06	-0.04	0.07	0.00
salin	0.10	0.09	0.00	-0.02	-0.02	-0.02	-0.07	-0.05	-0.08	-0.06	-0.07	-0.05
depth	0.12	0.10	0.06	-0.01	-0.03	0.00	-0.21	-0.09	-0.33	-0.16	-0.15	-0.10
stones	0.01	-0.03	0.00	-0.03	-0.04	-0.03	-0.01	-0.03	-0.13	-0.07	0.06	-0.01
gravel	-0.07	-0.06	-0.04	-0.04	-0.03	-0.03	-0.01	0.07	-0.11	-0.04	0.08	0.12
sand	-0.06	-0.10	0.13	0.05	0.04	0.01	-0.04	-0.01	-0.10	-0.09	-0.11	-0.10
mud	0.06	0.12	-0.10	-0.01	-0.01	0.01	0.04	-0.01	0.17	0.12	0.04	0.05
plants	0.00	-0.03	0.10	0.05	0.08	0.06	0.25	0.17	0.10	0.06	0.11	0.11
littoral	-0.04	-0.16	-0.13	-0.19	0.04	-0.01	0.02	0.04	0.06	0.04	0.23	0.18

FF – active filter feeders, GR-SC – grazers and scrapers, MIN – miners, POL – polyphagous species, PRE – predators, SHR – shredders, (N) – means abundance, (S) – means number of species

Environmental factors responsible for the distribution of beetles

CCA of the relationships between beetle occurrence and the physical and chemical parameters of the water in both habitats showed that both ordination axes together explained 36.3% of the overall variance. The following factors turned out to be statistically significant: “pH”, explaining 12.6% of the total variability, “Visib” (12.3%), “temp” (10.8%), “hard” (10.0%) and “O<sub>2</sub>” (10.0%). The plot indicates

that rheobionts, like *Haliphus lineatocollis*, *Limnebius truncatellus* and *Nebrioporus depressus* formed a fairly uniform group of beetles, as did rheophiles (*Hygrotus versicolor*, *Laccophilus hyalinus*, *Ilybius fenestratus*, *Platambus maculatus*, *Porhydrus lineatus*, *Rhantus latitans*). Both groups preferred clean, cooler, well-oxygenated water. In warmer water, we found species typical of small water bodies, eurytopes, and species preferring harder water such as *Laccobius minutus* (Fig. 9).

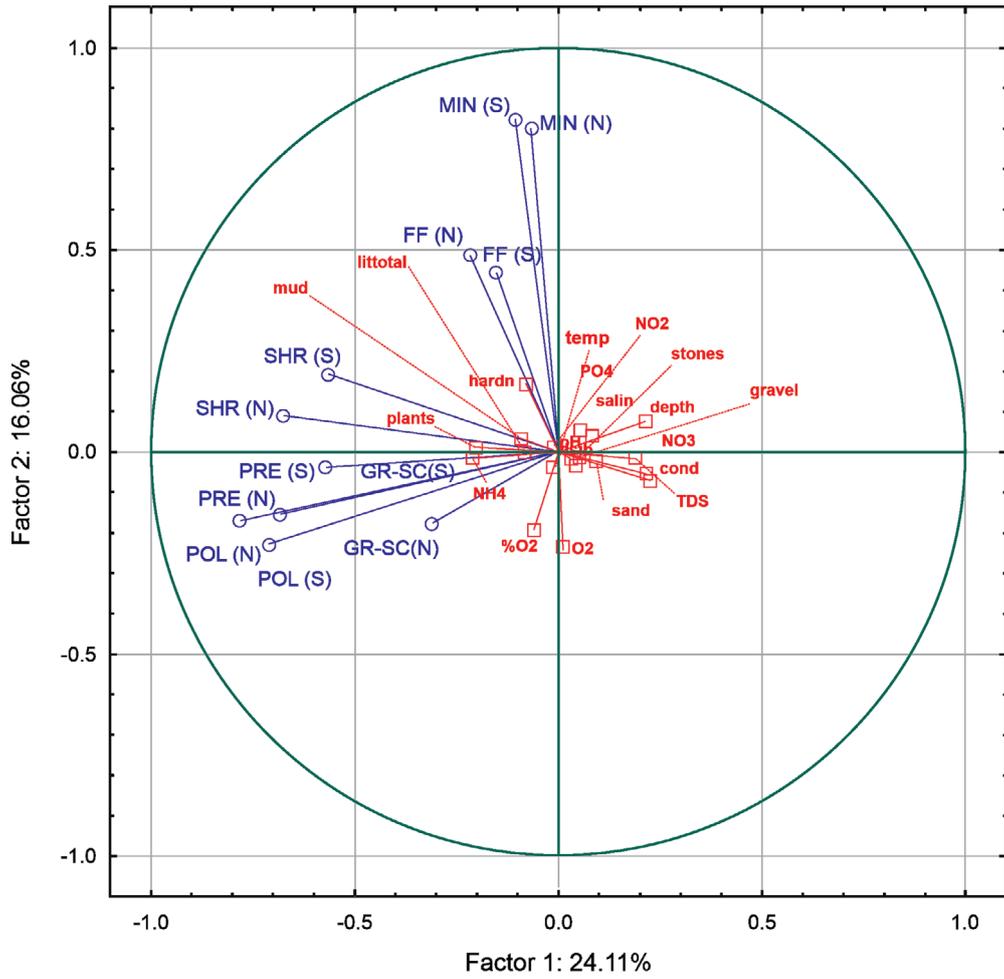


Fig. 8. Principal component analysis (PCA) of the variables representing the parameters of habitats and functional feeding groups of beetles distinguished in our study. Abbreviations as in Table 1.

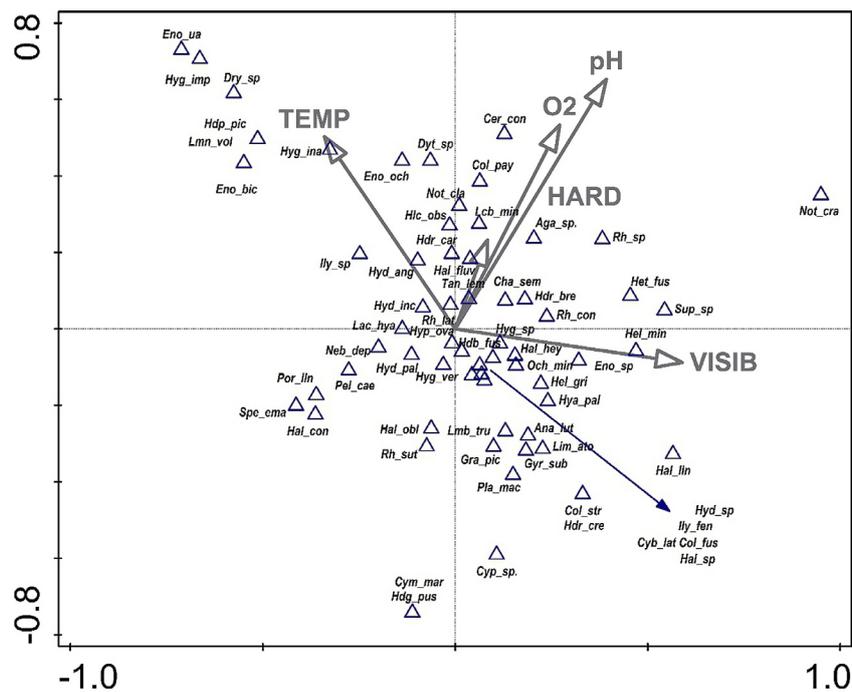


Fig. 9. CCA biplot showing beetle taxa in relation to the physical and chemical parameters of the oxbows and riverine sites (only significant parameters with  $p < 0.05$  are shown). The abbreviations of the variables and beetle taxa codes are given in the text and in Table 1.

CCA of the relationships between the beetle associations and structural factors indicated that the first and second ordination axes together explained 47.76% of the total variance. The statistically significant factors were “plants” (22.6% of the overall variability), “littor” (19.7%) and “depth” (14.9%) (Table 4). The plot shows that the deeper the water, the greater the proportion of “good swimming” species, primarily Dytiscidae, and of rheobionts

like *Limnius volckmari* and *Limnebius truncatellus*, which usually occurred in faster-flowing river water. There was a distinct positive correlation between “plants” and “littor”, and eurytopes. Less overgrown environments were preferred by rheophiles (*Porhydrus lineatus*, *Ilybius fenestratus*, *Laccophilus hyalinus*). Rheobionts like *Nebrioporus depressus* and *Haliphus lineatocollis* were negatively correlated with “plants” (Fig. 10).

Table 4

Basic statistics for significant ( $p < 0.05$ ) of the environmental variables obtained in the forward selection procedure in the Canonical Correspondence Analyses

Parameters	Explains [%]	Contribution [%]	Pseudo – F	P – value
Physical and chemical parameters				
pH	1.2	12.6	2.1	0.008
Visibility [m]	1.2	12.3	2.1	0.004
Temperature [°C]	1.0	10.8	1.8	0.004
Hardness [mg CaCO <sub>3</sub> ·dm <sup>-3</sup> ]	0.9	10.0	1.7	0.050
O <sub>2</sub> [mg·dm <sup>-3</sup> ]	0.9	10.0	1.7	0.026
Structural factors				
Plants (1-5)	1.5	22.6	2.6	0.004
Littoral [m]	1.3	19.7	2.3	0.002
Depth [m]	1.0	14.9	1.7	0.044

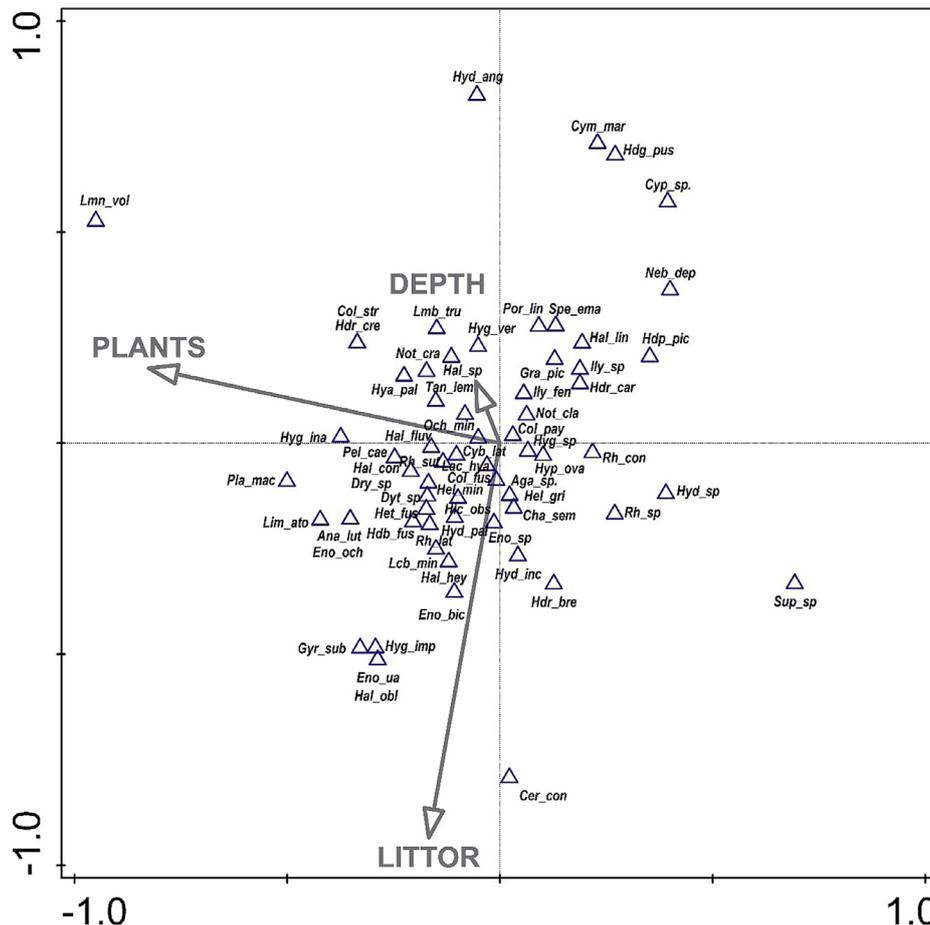


Fig. 10. CCA biplot showing beetle taxa in relation to the structural parameters of the oxbow and riverine sites (only significant parameters with  $p < 0.05$  are shown). The abbreviations of the variables and beetle taxa codes are given in the text and in Table 1.

## Discussion

General comments on the beetle fauna of the River Odra and its oxbows

Papers focusing on the ecology of invertebrates of flowing waters and their valleys have usually related to smaller streams. Large lowland rivers have seldom been explored in this respect, especially where their natural character has been artificially modified (Brunke *et al.* 2002; Kleinwächter *et al.* 2003; Lewin 2014). Allan (1998), who takes the RCC into consideration, maintains that analyses of ecological processes occurring in flowing waters should account for the heterogeneity of the environment, including factors that arise from human activities.

A good example is the radically transformed River Odra. Because there are insufficient relevant data (Piechocki & Szlauer-Łukaszewska 2013; Buczyński *et al.* 2017; Jabłońska-Barna *et al.* 2017), it is very difficult to establish the effect of these hydroengineering works on the animal and plant communities living there. The main source of data on the beetle fauna of the Odra in its entirety is the report by Schöll *et al.* (2003), which lists 18 taxa (species and genera) and states whether they do or do not inhabit three stretches of the river (upper, middle, lower), along with 5 others caught in its tributaries. Further fragmentary faunistic data can be found in three other papers (Roger 1856; Reitter 1870; Greń 2017). Nevertheless, it is worth attempting to evaluate the conditions offered by the Odra to the water beetles living there, and to compare them with those in other lowland rivers that have been explored in this respect to a greater or lesser extent (Biesiadka & Pakulnicka 2004; Persson Vinnersten *et al.* 2009; Buczyński *et al.* 2011; Pakulnicka & Nowakowski 2012; Turić *et al.* 2020). Characteristic of large lowland rivers are the various water bodies in their valleys: oxbows are of fundamental functional significance, as to a large extent they govern the biological communities of rivers, including those of beetles (Biesiadka & Pakulnicka 2004; Sanderson *et al.* 2005; Jurkiewicz-Karnkowska 2006; Piechocki & Szlauer-Łukaszewska 2013; Lewin 2014; Buczyński *et al.* 2011; da Conceição *et al.* 2017; Buczyńska *et al.* 2018).

The Odra is an example of a profoundly transformed river, the bank lines of which have been straightened. River regulation leads to a simplification of the bank line and the disappearance of important microhabitats, mostly lentic ones, and this impoverishes the species richness (Kleinwächter *et al.* 2003; Jurkiewicz-Karnkowska 2006; Buczyński

*et al.* 2017). However, the total of 40 water beetle taxa found in the Odra is comparable with the species richness of these insects found in natural lowland rivers in Poland, like the Narew (52 species), Neman (44) and Bug (44) (Biesiadka & Pakulnicka 2004; Buczyński *et al.* 2011; Pakulnicka & Nowakowski 2012). The key to explaining this richness appears to be the presence of groynes on the Odra, which have compensated for the loss of biodiversity caused by the realignment of the bank line. This was confirmed by earlier reports of other taxa occurring along the Odra, especially Odonata (Buczyński *et al.* 2017) and Trichoptera (Buczyńska *et al.* 2018), and by the results of zoobenthos studies in other rivers (Tockner 1996; Brunke *et al.* 2002). Buczyński *et al.* (2017) drew attention to the distinctly higher species richness of dragonfly assemblages on the sections of the Odra with groynes than along the groyne-free, regulated stretches, which provides further evidence of the significance of groynes for the local biodiversity. Our data corroborate these reports. Earlier papers also demonstrated that the canalisation of a river dramatically reduces the density and species richness of water beetles (Bates *et al.* 2007; Kennedy & Turner 2011). This is probably due to the lack of Coleoptera from the groyne-free reaches of the Odra: beetles may well have been present there, but in such small densities that none were caught, even though these stretches were regularly surveyed. In contrast, the material acquired from the reaches with groynes was relatively rich.

In north-central Europe water beetles are a group of organisms that display a high level of eurytopicity and have considerable dispersal abilities (Lundkvist *et al.* 2002). In accordance with the ecological and biogeographical theory, this results from a great many causes affecting the patterns of geographic variation of biological communities (Currie 1991; Krebs 2008). Nevertheless, there are few species among the beetles with special preferences restricting them to particular habitat types; but it is these stenotopes that are the best bioindicators, facilitating the evaluation of habitat conditions (Gioria *et al.* 2010a, 2010b; Pakulnicka *et al.* 2015a; Turić *et al.* 2020). This high level of eurytopicity among the Coleoptera is distinctive in most aquatic environments, in which it is eurytopes that manifest the greatest species differentiation (Biesiadka & Pakulnicka 2004; Buczyński *et al.* 2011; Pakulnicka & Nowakowski 2012; Pakulnicka *et al.* 2015a, 2015b). Our research has shown that the same applies to the Odra's groyne fields: this aspect is the faunistic foundation of the whole assemblage. The species richness among the rheophiles and tyrophiles is much smaller.

The close proximity of oxbows undoubtedly affects the ecological structure of the beetles in the groyne fields; various hydroengineering modifications have ensured that most of the oxbows have a permanent water connection with the river. This means that river water flows continuously through the oxbows, which substantially retards their eutrophication (Pakulnicka & Nowakowski 2012; Pakulnicka *et al.* 2016). The so-called ecological integrity of the river-floodplain system, expressed by e.g. the Floodplain Index (Chovanec *et al.* 2005; Waringer *et al.* 2005), is one of the most important elements in maintaining well functioning invertebrate fauna in specific reference conditions. In recent years, numerous authors have demonstrated the significant influence of catchment area factors (including the presence of other waters) on the fauna colonising a river (Pakulnicka *et al.* 2016; Zawal *et al.* 2016). Many hydrobiologists have drawn attention to the special importance of oxbows in the shaping of riverine communities (Biesiadka & Pakulnicka 2004; Jurkiewicz-Karnkowska 2006; Paula-Bueno & Fonseca-Gessner 2015; Obolewski *et al.* 2009; Pakulnicka & Nowakowski 2012; Lewin 2014; Pakulnicka *et al.* 2016). We collected 57 species of water beetles in the Odra's oxbows; this figure is only slightly smaller than that obtained for the oxbows of other lowland rivers (Biesiadka & Pakulnicka 2004; Buczyński *et al.* 2011; Pakulnicka & Nowakowski 2012).

Despite the qualitative dominance of eurytopes, we demonstrated a distinct quantitative predominance of rheophiles in the synecological structures of both habitat types. This has been confirmed by studies of other groups of organisms, like dragonflies and caddisflies, in the Odra valley (Buczyński *et al.* 2017; Buczyńska *et al.* 2018). The most numerous among them were *Laccophilus hyalinus*, *Hygrotus versicolor* and *Haliphus fluviatilis*. Furthermore, these species were usually the most abundant ones found in the studies of other lowland rivers (Biesiadka & Pakulnicka 2004; Buczyński *et al.* 2011; Pakulnicka & Nowakowski 2012). This ecological structure, especially in the groyne fields, testifies to their excellent ecological condition, since a predominance of eurytopes in biological communities is a response to unpropitious environmental conditions (Clausnitzer 2003; Šiling & Urbanič 2016). Therefore, the highest proportion of rheophiles in both the groyne fields and the oxbows of the Odra indicates not only a high level of faunistic similarity, but also the similar habitat conditions which they imply, an aspect that has been corroborated by earlier studies of macroinvertebrates in the Odra (Buczyński *et al.* 2017; Buczyńska *et al.* 2018).

Analysis of the trophic groups showed that most of the species in the beetle fauna of both habitats were predators, which at the same time were the most numerous. Less abundant in the groyne fields were saprophages, mainly shredders, whereas in the oxbows there were fewer phytophages and polyphages. We also noticed a phenological change in the trophic structure: the numerical preponderance of predators in spring diminished distinctly in successive months, with a concomitant rise in the abundance of the other trophic groups – saprophages, phytophages and polyphages. This is evidently associated with the new growing season, the appearance of young plants and the increasing supply of organic matter in the form of detritus (including FPOM, the presence of which is revealed by the autumn records of active filter feeders, especially in the groyne fields) and also confirmed by the results of PCA. This dependence between the characteristics of organism assemblages and the presence of plants and organic matter has been demonstrated by other authors, both from the Odra (Szlauer-Lukaszewska 2015; Buczyński *et al.* 2017; Buczyńska *et al.* 2018) and other rivers (e.g., Eggers 2006; Sanderson *et al.* 2005; Paula-Bueno & Fonseca-Gessner 2015). In addition, Biesiadka & Pakulnicka (2004) showed that the diminishing numbers of predators in oxbows combined with the simultaneous increase in the percentages of Hydrophilidae were a sign of their eutrophication. Hence, a greater richness of predators is indicative of the generally good ecological condition of the two habitat types we studied.

#### The effect of environmental parameters on the beetle assemblages

Our principal component analysis (PCA) of the variables representing the parameters of the habitats and trophic groups confirmed earlier data that the presence of vegetation in aquatic environments (both fresh biomass and decomposed in the form of detritus) have a positive influence on the occurrence and abundance of species representing lower trophic levels, especially polyphages and saprophages (Eggers 2006; Sanderson *et al.* 2005; Paula-Bueno & Fonseca-Gessner 2015). The plentiful food resources undoubtedly favour the occurrence of predators, which are predominant in both the groyne fields and the oxbows of the Odra, as regards both species richness and abundance. Our study confirmed that the degree of vegetation cover is key to the distribution of species (CCA), and that beetles prefer habitats supporting vegetation to habitats on the mineralised bottom. They provide not only foraging areas and concealment from potential predators (Eggers 2006;

Buczyński *et al.* 2017), but also sites for oviposition into plant tissues, e.g. for many predators, particularly Dytiscidae (Paula-Bueno & Fonseca-Gessner 2015).

In contrast, habitats devoid of vegetation, with a mineral substrate containing various size fractions (sand, gravel or stones), are where active filter feeders and rheobionts occur, e.g. *Nebrioporus depressus* and *Haliplus lineatocollis* (Galewski 1978; Friday 1988).

Depth is another important factor governing the occurrence of beetles (Pakulnicka *et al.* 2015b; Pakulnicka & Zawal 2018); we, too, were able to confirm this in the habitats we explored. We found only a very few species in deeper waters. Some of them, like *Limnius volckmari* and *Limnebius truncatellus*, breathe by means of a plastron, obtaining oxygen dissolved in the water; therefore, they do not have to rise to the surface at all to replenish their oxygen supplies (Heckmann 1983; Flynn & Bush 2008). Their typical habitat is the bottom of the lotic zone of the river. Besides these, we found haliplid and dytiscid species, all good swimmers, which have to renew the oxygen they carry under their elytra (Madsen 2012).

The nature of the faunal relationships in the individual habitats is likely to be influenced by both the physical and chemical properties of the water (Marchese *et al.* 1992; Sanderson *et al.* 2005; Costea *et al.* 2013; Pakulnicka *et al.* 2015b). Our CCA and PCA have shown that a higher temperature offers more propitious conditions for detritus consumers, both shredders and active filter feeders. These are mainly species preferring small water bodies, not only eurytopes, but also those that prefer harder water, e.g. the argilophiles *Laccobius minutus* and *Hygrotus impressopunctatus*, and tyrphophiles like *Colymbetes paykulli* (Galewski 1978; Savage & Gazey 1987; Friday 1988; Pakulnicka *et al.* 2015b). On the other hand, evidently clean, cooler and well-oxygenated waters are preferred by both the above-mentioned rheobionts as well as by rheophiles like *Hygrotus versicolor*, *Laccophilus hyalinus*, *Ilybius fenestratus*, *Platambus maculatus*, *Porhydrus lineatus* and *Rhantus latitans*. The influence of the oxygen content and water temperature on the aquatic invertebrate community has been highlighted by other researchers (Smith *et al.* 2003; Tara *et al.* 2011; Tichá *et al.* 2012; Buczyński *et al.* 2017; Buczyńska *et al.* 2018; Pakulnicka & Zawal 2018). Worth looking at are the following three species – *Porhydrus lineatus*, *Hygrotus versicolor* and *Colymbetes striatus* – all of which are closely associated with the waters of clean oxbows (Galewski 1978; Friday 1988; Biesiadka &

Pakulnicka 2004). River water regularly circulates through these oxbows, so their trophic development is limited and their ecological stability maintained. The presence of these species in groyne fields implies that, as in the oxbows, the water parameters in the former are optimal; in contrast, the presence of plants creates a stable living habitat, protected from river wave action (Tockner 1996; Brunke *et al.* 2002).

## Conclusions

Groyne fields restore the habitat heterogeneity on a regulated river, thus compensating for losses in its biodiversity. These habitats have fairly good water parameters and are structurally appropriate, so they are eminently suitable for the occurrence of water beetles, especially rheophiles, the most distinctive element among them. Because there is considerable faunistic similarity between the beetle assemblages of groyne fields and oxbows, the latter function in much the same way as the former and can act as an important refuge for many species that inhabit large lowland rivers. This is crucial for biodiversity conservation, particularly in view of anticipated, further hydro-engineering works on those rivers and in their valleys. This implies that groyne construction is advantageous, but solely on already regulated rivers. Our data by no means offer an argument in favour of river canalisation; conversely, they indicate that strongly transformed watercourses can benefit from the creation of these alternative lentic habitats, thereby enlarging their area along the entire river valley.

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## Author contributions

Study conception and design: A.S.Ł., P.B., J.P., E.B.; Material preparation, data collection and analysis A.S.Ł., P.B., J.P., E.B.; Writing the article: A.S.Ł., P.B., J.P., E.B.; Final approval of the article: A.S.Ł., P.B., J.P., E.B.

## Conflict of Interest

The authors declare no conflict of interest.

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