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The effect of hydrological connectivity on water beetles fauna in water bodies within the floodplain of a lowland river (Neman river, Belarus)

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Abstract

The middle course of the Neman River is the habitat of 120 water beetle species. Water beetles were most abundant in the Neman River, its major tributaries and oxbow lakes. They consisted of four synecological groups: rheobiontic and rheophilic organisms, type "a" and "b" stagnobionts. The diverse types of aquatic environments constitute faunal centers which, in addition to the specific and dominant Coleopteran populations, also feature migrational elements. The presence of close relations between the fauna of different environments indicates that they form a single, faunistically integrated hydrological system.

INTRODUCTION

Water beetles are the group of organisms, which constitute the main element of fauna settled in various aquatic environments, including the flowing water. Due to the fact that many of them are predators, they play a significant role in aquatic biocenoses as regulators of abundance of other taxa of organisms. The water beetle fauna of flowing waters has been thoroughly researched and documented by a vast body of literature. To date, less attention has been paid to the floodplains of large lowland rivers that have been slightly regulated and thus have remained in a relatively natural state. One of such rivers is the Neman River rising in Belarus. Although the coleopteran fauna of Belarus has been investigated by numerous authors (Biesiadka & Pakulnicka 2004; Moroz 1983, 1993, 1995, 2000; Moroz & Maksimienkov 2001; Moroz et al. 2004; Radkevich 1936; Ryndevich 1991, 1992a,b, 1995; Shaverdo 1995, 1997, 1998; Ryndevich & Moroz 2000; Zaharenko & Moroz 1988), and some of the above studies are devoted to water beetles inhabiting the rivers of the area, none of the reports offers a comprehensive analysis of the relationships between the coleopteran fauna of different water bodies, as part of a single, cohesive hydrological system.

The Neman River Valley is an area whose characteristic feature is a large diversity of the hydrographic network, which favors the occurrence of very rich and diverse fauna of aquatic beetles. At the same time, many elements making up this network, maintain constant or periodic hydrological connection. No doubt that this affects the nature of the fauna of beetles occurring here. Thus, the question arises, what factors influence the formation of beetle fauna in the river valley. This problem deserves attention and goes beyond the regional issues. All the more that these issues are mentioned

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not only by entomologists (Biesiadka & Kurzątkowska 2003, Biesiadka & Cichocka 2004, Biesiadka & Pakulnicka 2004, Czachorowski 2004, Przewoźny et al. 2006), but also by hydrobiologists, in relation to other groups of organisms (Castella et al. 1984, 1991; Castella & Amorós 1988; Jurkiewicz-Karnkowska 2006; Kajak 1959; Obolowski et al. 2009; Reckendorfer et al. 2006, Ward 1998, Ward et al. 2002).

The objective of the present study was to investigate the water beetle fauna in the middle course of the Neman River and in the water bodies situated in its floodplain terrace, and to determine factors which affect the faunistic relations in the studied area.

MATERIALS AND METHODS

The study covered the hydrographic system of the middle course of the Neman River, which is part of the Nemansko–Predpolesskij District in Belarus (Jurkiewicz et al. 1979 as cited in Alexandrovitch et al. 1996), from the town of Syalyets (53°53' N, 25°18' E) to the Lithuanian border. The investigated area covered the Neman River, tributary sections close to the river mouth and water bodies in the floodplain terrace, mostly oxbow lakes and intermittent water bodies. Samples were collected at 36 sampling sites (Fig. 1).

The Nemen River

The third largest lowland river in Belarus (937 km in length). In the studied area, the width of the river reaches 40–80 m with an average depth of around 1 m. The investigated area was characterized by an abundance of rush vegetation, represented by *Glyceria maxima*, *G. fluitans*, *Acorus calamus*, *Schoenoplectus lacustris*, *Butomus umbellatus*, *Equisetum limosum*, *Hydrocharis morsus-ranae*, and by *Potamogeton perfoliatus*, *P. pectinatus* and *Elodea canadensis* in the elodeid zone. The river bed is covered by sand and gravel with locally occurring silt. The stream environment features rocks covered by crustaceous lichens and *Hildenbrandia rivularis* (sites: 1, 5, 13, 14, 20, 31, 34, 36).

Large tributaries

The Neman River features many large tributaries with an average width of 5–30 m. They are: Svisloč, Kotra, Zelvianka, Ščara, Lepiada and Dzitva. Those

tributaries are characterized by a relatively slow current and highly diverse aquatic vegetation. The predominant type of substratum is sand or sand and gravel. Tributaries form oxbow lakes (sites 8, 10, 16, 17, 26, 33, 35).

Small tributaries

Small tributaries are abundant in the investigated area. They include minor tributaries of the Polnica River, Zarečanka, Puškarka, Jelnia, Turja and Zazulanka. All of those tributaries are mountain streams with a rapid current and a width of 1.5 – 4 m. Aquatic vegetation is poorly developed. Small tributaries have a rocky and gravelly bottom (sites 3, 4, 6, 19, 23, 24).

Oxbow lakes

There is a scant number of oxbow lakes in the floodplain terrace of the Neman River. Their surface area, depth and aquatic vegetation development are vastly differentiated. Some oxbow lakes are intermittent (sites 2, 9, 11, 12, 15, 18, 25, 27, 32).

Intermittent water bodies

Intermittent water bodies are weakly represented. Their surface area and depth vary. They are overgrown with different grass species, including *Equisetum* sp., *Glyceria maxima*, *Hottonia palustris* and *Hydrocharis morsus-ranae* (sites 21, 22, 28, 29, 30).

The water body in the quarry (site 7)

This water body covers an area of 200×80 m. Aquatic vegetation is represented by *Typha latifolia*, *Phragmites australis*, *Potamogeton filiformis* and *P. lucens*.

The substratum comprises lime deposits

The study was conducted in the spring, summer and autumn of 1997 and 1998. Faunal samples were collected with the use of a hydrobiological scoop and traps. Throughout the experimental period, a total of 270 samples were taken, and the collected material comprised 2635 water beetles of 120 species. The identified species were classified into four synecological groups: rheobiontic and rheophilic organisms, type "a" and "b" stagnobionts. The rheobiontic group of taxa comprises species found exclusively in flowing waters, which dwell in habitats

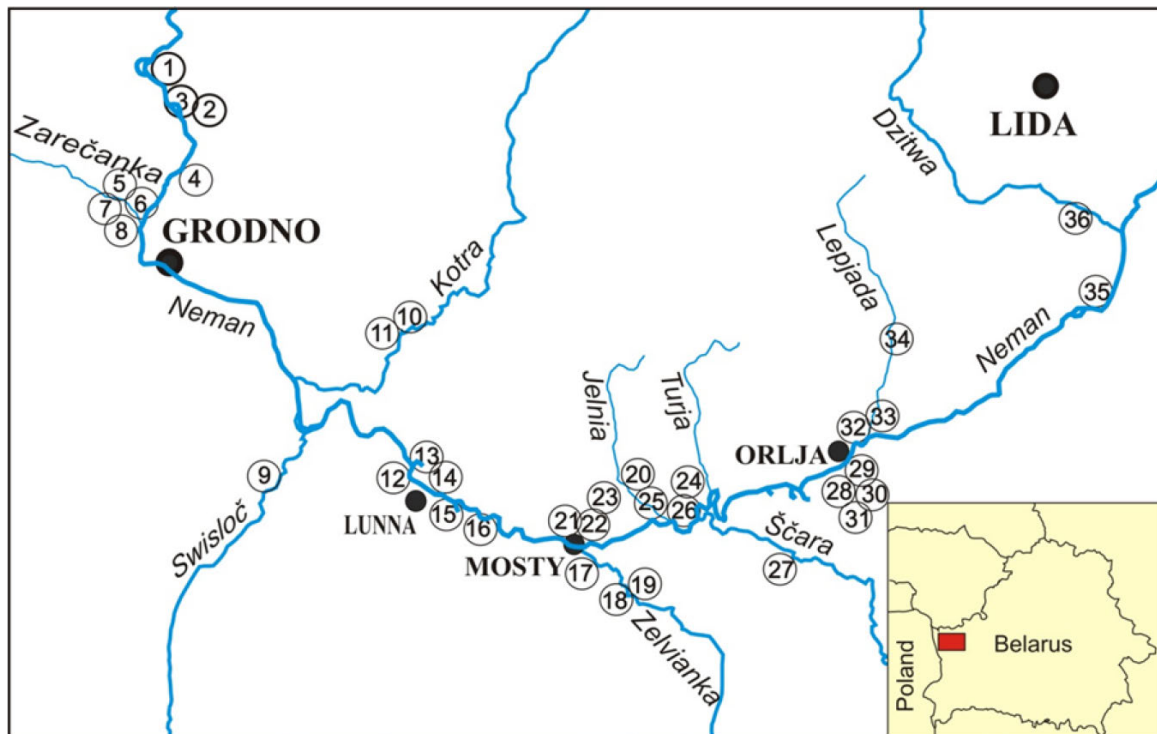


Fig. 1. Study area with sampling sites marked (1-36).

with a strong river current on a rocky or gravelly substratum. Those species have a low migration capacity and they are a characteristic feature of flowing waters. The rheophilic group consists of species characteristic of the overgrown zones of sluggish rivers and large, slightly eutrophicated lakes. This group of species is characterized by a high dispersion capacity, which explains their presence in other types of waters of "good ecological status". Type "a" stagnobionts comprise species which are found mostly in small, slightly eutrophicated water bodies. They are characteristic of dystrophic and argilotrophic waters, as well as oxbow lakes with clean water, which are periodically and regularly flushed by flowing waters. Type "b" stagnobionts include species typical of small, strongly eutrophicated water bodies, including intermittent ones. They are generally characterized by a high migration capacity, and they affect the formation of Coleopteran fauna in other types of water bodies.

The analysis of water beetle groups in the identified types of aquatic environments was performed with the application of the dominance index (Odum 1971). Faunal similarities between particular sites were also analyzed based on the Bray-Curtis formula (Bray and Curtis 1957) by the group-average link method for the hierarchical clustering of objects. The results are presented in the form of a

dendrogram of faunal similarities.

The authors also investigated the similarities between sites (objects) identified in view of the structure of their characteristic features, such as the intermittent nature, flow rate and size of a water body, substratum type and the abundance of macrophytic vegetation. The objects (sites) were grouped in accordance with the identified characteristics by a hierarchical cluster analysis with the use of the complete linkage method and the Euclidean metric measuring the distance between two points (Hartigan 1975). Since the sites exemplify the nominal variability type (river, oxbow lakes, small tributary, large tributary, intermittent water body), and their characteristic features (variables) reflect the variability resulting from the adopted scale of variation, cluster systems were also selected for the analysis of the structure of variability of the objects' specific properties with the use of the procedure for grouping the objects and properties. This procedure supports the identification of objects on the assumption that both incidents and variables simultaneously contribute to the creation of cluster systems (Hartigan 1975). The causes of variation in the investigated water bodies were also determined by correspondence analysis (Hoffman and Franke 1986). The affiliation of objects (sites) to the determined clusters, identified in view of the

quantitative structure of water beetle associations, as well as clusters identified based on the structure of the objects' characteristic features, was verified with the application of the sign test and McNemar's test (Sokal and Rohlf 1995). All calculations were performed in the *Statistica 7.0* application.

RESULTS

General description of the collected material

The following species were most abundant in the collected samples: *Laccobius minutus*, *Laccophilus hyalinus*, *Gyrinus aeratus* and *Haliphus fluvialilis*, accounting for 41.9% of the collected material (Table 1).

The water beetle fauna in the investigated area is ecologically diverse. Its main body comprises type "a" stagnobionts, which account for 37.8% of all collected beetles. Forty species were classified in this group, the most abundant being: *Laccobius minutus*, *Helophorus minutus*, *H. granularis*, *H. griseus*, *Anacaena lutescens* and *Porhydrus lineatus*. Rheophilic organisms, represented by 11 species, mostly *Laccophilus hyalinus*, *Gyrinus aeratus* and *Haliphus fluvialilis*, also had a high quantitative contribution (33.3% of the collected beetle samples). The most ecologically diverse group were type "b" stagnobionts comprising 57 species, which were mostly represented by *Limnebius crinifer*, *Gyrinus natator*, *Noterus crassicornis*, *Hyphydrus ovatus* and *Haliphus ruficollis*. Nevertheless, this group had a limited quantitative contribution of only 19.2% in the collected beetle population. A less populous group were the rheobiontic organisms, which accounted for 9.7% of the collected material and were represented by 12 species, mainly from the families *Elmidae* and *Hydraenidae*, with a clear dominance of *Oulimnius tuberculatus* and *Hydraena gracilis*.

Beetles occurrence in the identified types of water bodies

The Neman River

The collected samples consisted of 608 individuals (23.1% of the collected material) representing 44 species. The most abundant species were *Laccophilus hyalinus* (29.9%) and *Laccobius minutus* (26.5%) (Table 1). The main body of the fauna reported in this area were rheophilic organisms, represented by 5 species accounting for 53.1% of all collected beetles. Type "a" stagnobionts with 16

Table 1

Occurrence of water beetles in particular types of water bodies: E – synecological element: re – rheophils, rb – rheobionts, sa – type "a" stagnobionts a, sb – type "b" stagnobionts b, N – number of individuals, % – dominance

	species	E	Neman	Ox-bow lakes	Small tributaries	Large tributaries	Intermittent water bodies	other	N	%
1	<i>Gyrinus aeratus</i> Steph.	re	76	31		163			270	10.25
2	<i>Gyrinus marinus</i> Gyll.	re		1		3			4	0.15
3	<i>Gyrinus minutus</i> (Fabr.)	sb				2			2	0.08
4	<i>Gyrinus natator</i> (L.)	sb	4	12		35			51	1.94
5	<i>Gyrinus substriatus</i> Steph.	sb	1	2		18	4		25	0.95
6	<i>Orectochilus villosus</i> (O.F.Müll)	re	1		4	3			8	0.30
7	<i>Peltodytes caesus</i> (Duft.)	d	2	7		1		1	11	0.42
8	<i>Brychius elevatus</i> (Panz.)	rb				2			2	0.08
9	<i>Haliphus flavicollis</i> Sturm	re		3		1			4	0.15
10	<i>Haliphus fluvialilis</i> Aubé	re	62	24	10	99			195	7.40
11	<i>Haliphus fulvicollis</i> Er.	sa					1		1	0.04
12	<i>Haliphus fulvus</i> (Fabr.)	sa		1					1	0.04
13	<i>Haliphus heydeni</i> Wehncke	d	3	1		3			7	0.27
14	<i>Haliphus immaculatus</i> Gerh.	d		3	1				4	0.15
15	<i>Haliphus lineatocollis</i> (Marsh.)	rb			5				5	0.19
16	<i>Haliphus lineolatus</i> Marsh.	d		1		2			3	0.11
17	<i>Haliphus ruficollis</i> (Deg.)	d	8	11		17	8		44	1.67
18	<i>Haliphus wehncke</i> Gerh.	d	1	1		5			7	0.27
19	<i>Noterus clavicornis</i> (Deg.)	d		1		1			3	0.11
20	<i>Noterus crassicornis</i> (O.F.Müll)	d		14		1	13		28	1.06
21	<i>Hydroporus angustatus</i> Sturm	sa					1		1	0.04
22	<i>Hydroporus glabriusculus</i> Aubé	sa					1		1	0.04
23	<i>Hydroporus neglectus</i> Schaum	sa				2			2	0.08
24	<i>Hydroporus palustris</i> (L.)	sb		2			8		10	0.38
25	<i>Hydroporus tristis</i> (Payk.)	sa	1						1	0.04
26	<i>Hydroporus umbrinus</i> (Gyll.)	sa		1					1	0.04
27	<i>Graptodytes pictus</i> (Fabr.)	sb	3			12			15	0.57
28	<i>Porhydrus lineatus</i> (Fabr.)	sa	3	26		3	3		35	1.33
29	<i>Coelambus impressopunctatus</i> (Schall.)	sb		9			9	1	19	0.72
30	<i>Coelambus polonicus</i> (Aubé)	sa					9		9	0.34
31	<i>Hygrobia decoratus</i> (Gyll.)	sa		7			4		11	0.42
32	<i>Hygrobia inaequalis</i> (Fabr.)	sb		20					20	0.76
33	<i>Hygrobia versicolor</i> (Schall.)	re				1	1		2	0.08
34	<i>Potamonectes depressus</i> (Fabr.)	re				20			20	0.76
35	<i>Scoradites halensis</i> (Fabr.)	sa		1	9		1	1	12	0.46
36	<i>Hydroglyphus pusillus</i> (Fabr.)	sa		2		3	3		10	0.38
37	<i>Hyphydrus ovatus</i> (L.)	sb	11	12	1	5			29	1.10
38	<i>Laccophilus hyalinus</i> (Deg.)	re	182	15	6	110	2		315	11.95
39	<i>Laccophilus minutus</i> (L.)	sb	1	8		3	6		18	0.68
40	<i>Copelatus haemorrhoidalis</i> (Fabr.)	sa					2		2	0.08
41	<i>Platambus maculatus</i> (L.)	re		8	23	22	2		55	2.09
42	<i>Agabus bipustulatus</i> (L.)	sb					4		4	0.15
43	<i>Agabus congenens</i> (Thunb.)	sb					1		1	0.04
44	<i>Agabus fuscipennis</i> (Payk.)	sb			3				3	0.11
45	<i>Agabus sturmi</i> (Gyll.)	sb		1					1	0.04
46	<i>Agabus uliginosus</i> (L.)	sb					1		1	0.04
47	<i>Ilybius ater</i> (Deg.)	sa		1					1	0.04
48	<i>Ilybius fenestratus</i> (Fabr.)	re	2	1		1			4	0.15
49	<i>Ilybius fuliginosus</i> (Fabr.)	sb			3	2			5	0.19
50	<i>Ilybius guttiger</i> (Gyll.)	sa	1						1	0.04
51	<i>Ilybius obscurus</i> (Marsh.)	sa		1					1	0.04
52	<i>Ilybius similis</i> Thoms.	sa	1						1	0.04
53	<i>Rhantus exoletus</i> (Forst.)	sb		3		1	1		5	0.19
54	<i>Rhantus latitans</i> Sharp	sb					2		2	0.08
55	<i>Rhantus notaticollis</i> (Aubé)	sb		1					1	0.04
56	<i>Rhantus notatus</i> (Fabr.)	sb		1					1	0.04
57	<i>Rhantus pulverosus</i> (Steph.)	sb		4					4	0.15
58	<i>Hydaticus semingeri</i> (Deg.)	sb		3		2			5	0.19
59	<i>Hydaticus continentalis</i> Balf.-Browne	sb	1	1			1		3	0.11
60	<i>Hydaticus transversalis</i> (Pont.)	sb		1			2		3	0.11
61	<i>Dytiscus dimidiatus</i> Bergstr.	sb				1			1	0.04
62	<i>Dytiscus marginalis</i> (L.)	sa					1		1	0.04
63	<i>Acilius canaliculatus</i> (Nic.)	sa		2			2		4	0.15
64	<i>Acilius sulcatus</i> (L.)	sb		1		1			2	0.08
65	<i>Graphoderus cinereus</i> (L.)	sb		1					1	0.04
66	<i>Cybtister laterimarginalis</i> (Deg.)	sb		2					2	0.08
67	<i>Ochthebius minivius</i> d'Orychmont	sa		4		1	5		10	0.38
68	<i>Ochthebius minimus</i> (Fabr.)	sb		1	1	3	1		6	0.23
69	<i>Hydraena excisa</i> Kiew.	rb			20				20	0.76
70	<i>Hydraena emarginata</i> Rey	rb							1	0.04
71	<i>Hydraena gracilis</i> Germ.	rb		1	58				59	2.24
72	<i>Hydraena maria</i> Kiew.	rb			1				1	0.04
73	<i>Hydraena palustris</i> Er.	sa	1				1		3	0.11
74	<i>Hydraena pygmaea</i> Waterh.	rb			1				1	0.04
75	<i>Hydraena riparia</i> Kugel.	rb	2	2	31	6			41	1.56
76	<i>Limnebius aluta</i> (Bedel)	sb		1					1	0.04
77	<i>Limnebius atomus</i> (Duft.)	sb		1					1	0.04
78	<i>Limnebius crinifer</i> Rey	sb	22	1		1	40		64	2.43
79	<i>Limnebius papposus</i> Muls.	sb				1			1	0.04
80	<i>Limnebius truncatulus</i> Thoms.	sb	1	2	1	3	18		25	0.95
81	<i>Hydrachus brevis</i> (Herbst)	sb	1	1		1			3	0.11
82	<i>Hydrachus carinatus</i> Germ.	sb		5			1		6	0.23
83	<i>Hydrachus ignicollis</i> Motsch.	sb		2					2	0.08
84	<i>Helophorus aequalis</i> (Thoms.)	sa		1		1	3		5	0.19
85	<i>Helophorus aquaticus</i> L.	sa	1				6		7	0.27
86	<i>Helophorus flavipes</i> (Fabr.)	sa		3	1	1	9		14	0.53
87	<i>Helophorus fulgidicollis</i> Motsch.	sa	8	4			9		21	0.80
88	<i>Helophorus grandis</i> Ill.	sa					30		30	1.14
89	<i>Helophorus granularis</i> (L.)	sa	4	25		9	106		144	5.46
90	<i>Helophorus griseus</i> Herbst	sa	7	33		2	39		81	3.07
91	<i>Helophorus minutus</i> Fabr.	sa	4	4		3	146	1	158	6.00
92	<i>Helophorus nanus</i> (Sturm.)	sa		3		1	1		5	0.19
93	<i>Helophorus obscurus</i> Muls.	sa		1		2			3	0.11
94	<i>Helophorus strigifrons</i> Thoms.	sa					1		1	0.04
95	<i>Coelostoma articulata</i> (Fabr.)	sb		1		2			3	0.11
96	<i>Cercyon convexusculus</i> Steph.	sb	1	1	1	1	1		5	0.19
97	<i>Cercyon analis</i> (Payk.)	sb	2						2	0.08
98	<i>Hydrobius fuscipes</i> (L.)	sb	1	2	1	3	4		11	0.42
99	<i>Anacaena limbata</i> (Fabr.)	sb	2	1		2			5	0.19
100	<i>Anacaena lutescens</i> Steph.	sa	3	8	1	21	12		45	1.71
101	<i>Laccobius alutaceus</i> Thoms.	sa	6	2		12	2		22	0.83
102	<i>Laccobius minutus</i> (L.)	sa	161	97	4	36	9	17	324	12.30

	species	E	Neman	Ox-bow lakes	Small tributaries	Large tributaries	Intermittent water bodies	other	N	%
103	<i>Laccobius sinuatus</i> Motsch.	sa	4	1					5	0.19
104	<i>Laccobius striatulus</i> (Fabr.)	re		1					1	0.04
105	<i>Helophorus griseus</i> Müll.	sb	1	4		1	3	1	10	0.38
106	<i>Helophorus punctatus</i> (Forst.)	sb				1			1	0.04
107	<i>Enochrus affinis</i> (Thunb.)	sa		2		6	3		11	0.42
108	<i>Enochrus coarctatus</i> (Thunb.)	sa	3	2		3	1		9	0.34
109	<i>Enochrus isotae</i> Hebaud	sa				1			1	0.04
110	<i>Enochrus melanoscephalus</i> (Oliv.)	sa	1						1	0.04
111	<i>Enochrus quadripunctatus</i> (Herbst)	sb	3	1					4	0.15
112	<i>Cymbiodyta marginella</i> (Fabr.)	sa					2		2	0.08
113	<i>Hydraena caraboides</i> (L.)	sb	3	3			2		8	0.30
114	<i>Berosus luridus</i> (L.)	sb		2					2	0.08
115	<i>Berosus signatellus</i> (Charp.)	sb				1			1	0.04
116	<i>Berosus spinosus</i> (Stev.)	sb		2					2	0.08
117	<i>Elmis aenea</i> (Müll.)	rb			20	1			21	0.80
118	<i>Elmis maugetii</i> Latr.	rb	1		16				17	0.65
119	<i>Limnius volchmani</i> (Panz.)	rb			4				4	0.15
120	<i>Oulimnius tuberculatus</i> (Müll.)	rb			69	14			83	3.15
	Total		608	472	297	685	549	24	2635	100.00

species had a very high quantitative contribution of 34.4% in the total abundance. The greatest species diversity was observed in the group of type "b" stagnobionts, which were represented by 21 species with a collective 12.0% contribution in all the samples. The beetle group in the Neman River also comprised a rheobiontic component represented by two species, *Hydraena riparia* and *Elmis maugetii* which had a 0.5% contribution in the material collected in this area.

Large tributaries

The largest part of the experimental material, comprising 685 beetles represented by 61 species, was collected in this environment. In quantitative terms, the most important role was played by *Gyrinus aeratus* (23.8%), *Laccophilus hyalinus* (16.1%) and *Haliphus fluvialis* (14.5%). Rheophilic organisms proved to be the most significant component of this group, featuring 10 species with 61.8% contribution in the locally collected material. Type "b" stagnobionts were characterized by the greatest species diversity, featuring 30 species representing 19.3% of the total sample volume. Type "a" stagnobionts were represented by 17 species with a collective 15.3% contribution in the entire beetle material. Rheobiontic organisms had the smallest contribution (3.4%) in this group, with only 4 species represented.

Small tributaries

The experimental material comprised 297 beetles representing 28 species. The most abundant species in this group were *Oulimnius tuberculatus* (23.2%), *Hydraena gracilis* (19.5%) and *H. riparia* (10.4%). *Platambus maculatus*, *Elmis aenea* and *E. maugetii* were also relatively abundant. Rheobiontic organisms, represented by 12 species (76.1% of the collected material), had a predominant contribution in the local

fauna. The rheophilic group was also relatively well represented by 4 species with a combined 14.5% contribution of the total abundance. Type "a" stagnobionts (5.4%) and type "b" stagnobionts (4%) were also reported in this group. They were represented by 5 and 8 species, respectively.

Oxbow lakes

A total of 472 water beetles representing 76 species were collected. The most abundant oxbow lake species was *Laccobius minutus* (20.6% of the collected material). The following species were also relatively abundant: *Helophorus griseus* (7.0%), *Gyrinus aeratus* (6.6%), *Porhydrus lineatus* (5.5%), *Helophorus granularis* (5.3%) and *Haliphus fluvialis* (5.1%). Nearly half of the material collected in oxbow lakes (49.2%) comprised type "a" stagnobionts represented by 24 species. Greater species diversity was reported in the group of type "b" stagnobionts where 42 species were noted with the total 32.4% contribution in all locally collected beetles. Rheophilic organisms had a less pronounced contribution in this group (17.8%) and were represented by 8 species. Rheobiontic organisms were represented by two species – *Hydraena gracilis* and *H. riparia* – which made up 0.6% of the collected material.

Intermittent water bodies

The experimental material collected in intermittent water bodies comprised 549 individuals belonging to 54 species. The most populous group were type "a" stagnobionts which were represented by 28 species with a total 78% dominance of all collected beetles. The most abundant species were: *Helophorus minutus* (26.6%), *H. granularis* (19.3%), *H. griseus* (7.1%) and *H. grandis* (5.5%). Similarly high species diversity was reported in the group of type "b" stagnobionts where 23 species were classified. This group had only 24% contribution in the collected material. The remaining components were rheophilic organisms - *Hygrotus versicolor*, *Laccophilus hyalinus* and *Platambus maculatus* – which accounted for only 1.0% of all individuals.

Other

The material collected in a water body situated in the quarry comprised only 24 beetles representing 7 species. The dominant species was *Laccobius minutus*, which had 70.8% contribution in the collected

material. *Hydroglyphus pusillus*, *Scarodytes balensis* and *Helophorus minutus* were much less abundant. All of the above species belong to type "a" stagnobionts, which had a collective 87.5% contribution in the group. The remaining components were type "b" stagnobionts.

Analysis of faunal similarities between the sampling sites

A general analysis of faunal similarities between the sampling sites indicates that the minimum similarity value, from among the applied clustering values, was 0.72%, while the maximum value reached 74.8% (Fig. 2).

The identified habitats are clearly grouped in three clusters. Cluster 1 comprises mostly intermittent water bodies where the general faunal similarity value reaches 29%. The greatest faunal similarity of 37.6% was noted between sites 28 and 29. They featured a total of 38 species, where only 7 species were shared by both sites. The most abundant species in the entire group were type "a" stagnobionts: *Helophorus granularis*, *H. griseus* and *H. minutus*.

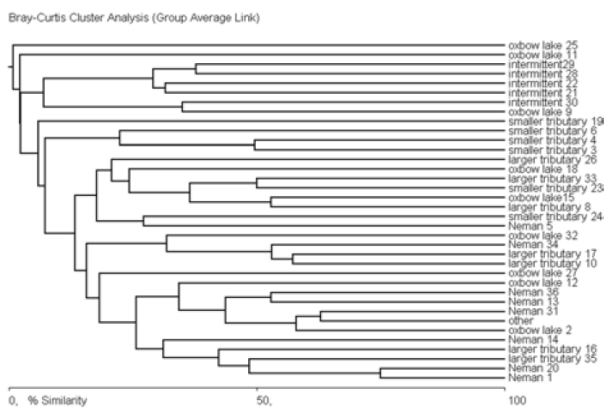


Fig. 2. Dendrogram of faunal similarities between the sampling sites.

Cluster 2 is more homogenous, grouping four small tributaries with a general faunal similarity of 22.4%. The greatest similarity (49.6%) was reported between sites 3 and 4. A total of 16 species were collected at both sites, including only 5 shared species belonging to the group of rheobiontic organisms, including the dominant species of *Hydraena excisa*, *H. gracilis* and *H. riparia*, as well as the less abundant *Elmís aenea* and *Limnius volchmari*.

Cluster 3 is the largest and features the greatest

species diversity. It covers the remaining sites in oxbow lakes, the Neman River and its large tributaries with a general faunal similarity of 13.2%. The greatest similarity (74.8%) was reported between two sites (1 and 20) on the Neman River. From among a total of 16 species, three were shared, including species which dominated at both sites – rheophilic *Laccophilus hyalinus* and *Laccobius minutus* representing type "a" stagnobionts. Lower faunal similarity values were noted between oxbow lakes and the Neman River (sites 1 and 31 – 58.8%), between oxbow lakes and large tributaries (sites 8 and 15 – 52.7%), between the Neman River and its large tributaries (sites 10, 17 and 34 – 52.9%), and between small and large tributaries (sites 23 and 33 – 49.9%).

Site grouping according to the identified characteristic features

The described characteristics of sampling sites (intermittent nature of a water body, substratum type, surface area, rate and pattern of overgrowing and water flow rate) supported the identification of three groups of sites, where each group is subject to further internal subdivision (Fig. 3). The process of classifying the sites into groups (clusters), as per their characteristic features, is consistent with the process of assigning the sites to clusters based on the results of grouping similarities in the quantitative species structure of the investigated beetle associations (sign test: $Z=2.041$, $p=0.041$). The analysis of assigning the sites to three main clusters, tested with the Wilcoxon matched pair test, indicates the consistency of divisions ($Z=2.201$, $p=0.028$). Only 6 out of 36 sites occupy a different place in the hierarchy. In accordance with the division based on the similarity between the characteristic features of different types of water bodies, sites 12, 15, 18, 27 and 32, which represent oxbow lakes, belong to the same category as two other oxbow lakes (sites 9 and 11) and intermittent water bodies (sites 21, 22, 25, 28, 29 and 30) (Fig. 3), while as regards faunal similarity, they were assigned to a different group comprising the Neman River and its large tributaries (Fig. 2). Based on the identified properties, site 23 (small tributary) is similar to another separate group of small tributaries (Fig. 3), while with respect to faunal similarity, the beetles of this tributary classify this site to a different group of objects covering the Neman River and its large tributaries (Fig. 2).

The results of grouping the sites and their

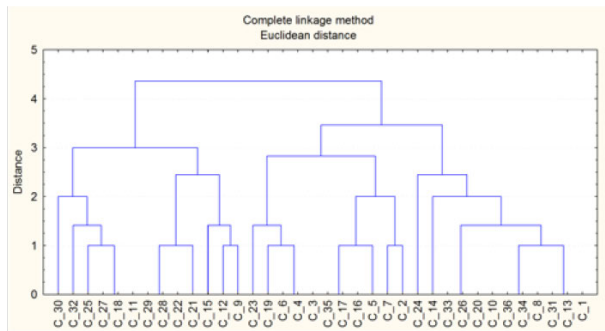


Fig. 3. Dendrogram of similarity between characteristics of positions.

characteristics according to the average measure of the identified qualities indicate that the seasonality and the pattern of overgrowing are the main factors which differentiate the structure of the investigated water bodies (Fig. 4). The factors which came next in the rank of importance were the water flow rate and the substratum type, while the size of a water body was the least influential factor.

Similar results were reported in the correspondence analysis of data structure (Fig. 5). The variability of individual features shows two dimensions of characteristic properties ($\chi^2=751.41$, $df=225$, $p<0.05$), and the main factors differentiating the sites were the intermittent nature of a water body, the flow rate and the abundance of macrophytic vegetation.

DISCUSSION

Recently there has been an increasing interest in the floodplains of large lowland rivers, in particular those which have remained in a relatively natural state. Researches focus on the relationships between the fauna inhabiting rivers and the fauna of other water bodies located within the rivers' floodplain terraces. The faunistic and ecological characteristics of hydrobiont communities, resulting from the hydrological connectivity of the system, have also been described (Castella et al. 1984, 1991; Castella & Amoros 1988; Jurkiewicz-Karnkowska 2006; Kajak 1959; Obolewski et al. 2009; Reckendorfer et al. 2006, Ward 1998, Ward et al. 2002). The above problems have also been addressed by coleopterologists. Since the available literature on the subject does not feature any studies investigating the ecological relationships between the water beetle fauna in rivers and other aquatic environments situated in river valleys, this discussion will make a minimal reference to literary sources.

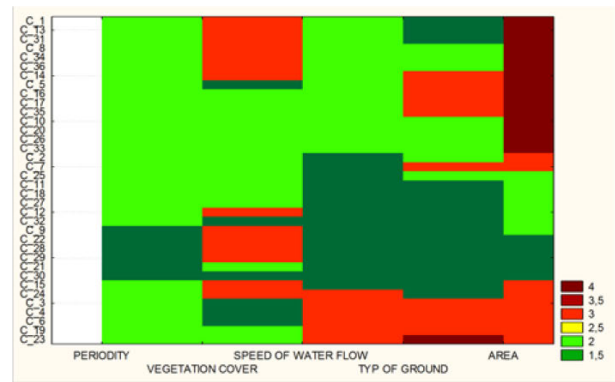


Fig. 4. Results of grouping the positions and its characteristics.

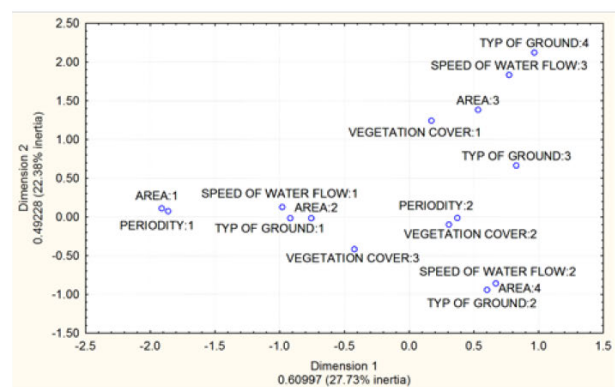


Fig. 5. Structure of variability in characteristics of positions singled out using the correspondence analysis.

The first study to tackle the subject is a paper by Kordylas (1990), which discusses the relationship between the water beetle fauna of the Pasłęka River and the rheolimnic Pierzchalski reservoir. Faunal relationships between the entomofauna of the river and the water bodies located in its valley were described by Czachorowski et al. (1993) and Mielewczyk (2003). Studies presenting a more detailed analysis of water beetles in the valleys of the Narew River (Biesiadka and Pakulnicka 2004) and the Bug River (Przewoźny et al. 2006) were published at a later date.

The hydrologic backbone of the studied valley is the Neman River with numerous large and small tributaries. Its floodplain terrace is also characterized by the presence of numerous stagnant water bodies, in particular oxbow lakes and intermittent water bodies. The above types of water bodies can be described with the use of characteristic features, such as seasonality, abundance of macrophytic vegetation,

a water flow rate, substratum type and surface area. Those factors, where seasonality and the abundance of macrophytic vegetation play the most important role, determine local habitat conditions. They are specific to a given group of aquatic environments and clearly differentiate various types of water habitats, as shown by the analysis of grouping the sites according to the identified properties. Those qualities are responsible for the characteristic features of the fauna inhabiting a given environment and they affect its specificity. For this reason, the diverse types of water habitats in the floodplain terrace of the Neman River create faunal centers dominated by a specific water beetle element (Fig. 6).

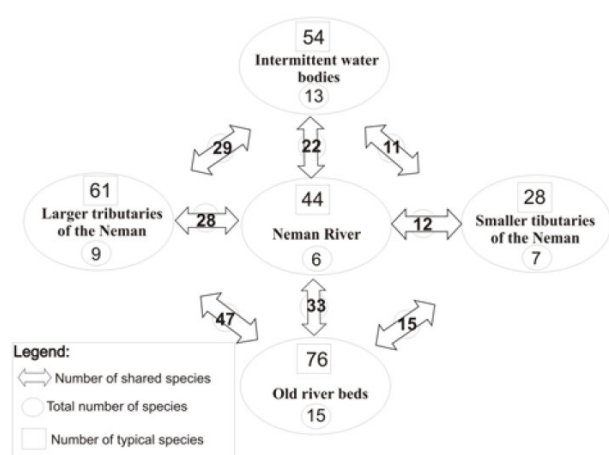


Fig. 6. General model of faunal dependencies between water beetles in the Neman River valley.

Flowing waters of the investigated valley are the faunal centers of two synecological groups. Both the Neman River and its large tributaries are the habitat of numerous rheophilic fauna, which shows a preference for localities with a weak current. Small tributaries with a strong current are the activity centers of specific rheobiontic fauna. Yet a different type of faunal center is offered by oxbow lakes where type "a" stagnobionts are the characteristic and predominant element, in particular species such as *Porhydrus lineatus*, which generally dwells in permanent, slightly eutrophicated water bodies. From among the identified synecological groups, only type "b" stagnobionts do not form their own faunal centers. They are generally dispersed across different types of aquatic habitats, and they migrate to intermittent water bodies only during the breeding season. Insolation takes place more rapidly in intermittent water bodies, which offer a more

favorable habitat than other aquatic environments.

An analysis of species diversity in various faunal centers points to differences in the total number of species, as well as in the number of species which are found exclusively in a single center. The smallest number of exclusive species were found in flowing waters, in particular in the Neman River (13.6% of all determined species), in large tributaries (14.7%) and in small tributaries (25%). The above faunal relations between flowing water bodies show that the degree of stability varies subject to the size of the water body and to the degree of resistance to faunal distortions caused by a high water level or flooding which are typical river valley phenomena.

A relatively small number of species, which are exclusive for a given type of water environment and high contribution of shared species offers a solid proof that synecological elements migrate between the analyzed habitats. The extensive ability of water beetles to actively spread between different environments was noted by, among others, Fernando (1959); Barnes (1983); Ward (1992) and Mielewczyk (1997). Those mutual faunal relations result in significant faunal similarities between different types of water bodies, and the relevant degree of similarity is much higher than could be expected based on the habitat characteristics alone. Special attention should be paid to oxbow lakes whose fauna is more similar to that of flowing water bodies than that of other oxbow lakes situated in the same valley. The above is confirmed by a certain dissonance between the analysis of site grouping based on faunal similarities and the analysis of grouping the same sites, which relies on their physical properties. Owing to the above, the investigated aquatic environments create a faunistically integrated system. This phenomenon was also observed in studies investigating other groups of aquatic invertebrates, including Heteroptera, Trichoptera and Hydrachnida (Biesiadka & Kurzątkowska 2003; Biesiadka & Cichocka 2004; Czachorowski 2004). A similar observation was made in reference to the water beetle fauna of other river valleys, including Narew (Biesiadka & Pakulnicka 2004) and Bug (Przewoźny et al. 2006).

In addition to the typical element, which determines faunal stability, the identified centers comprise a migrational element that spreads between the centers and affects total species diversity in the investigated beetle fauna. This faunal interchange results not only from active migration between individual centers, but it is also caused by high water-

level periods, which contribute to hydrological connections between the centers. This phenomenon was also observed in the Narew River valley (Biesiadka & Pakulnicka 2004).

The dominant group of beetles migrating between different types of water environments are rheophilic organisms which are accompanied by type "a" and "b" stagnobionts. Those elements generally support the faunal interchange between various water bodies. Rheobiontic taxa, the remaining beetle group determined in the analyzed environments, are characterized by a limited migrational capacity.

Faunal interchange between centers takes place in two directions. One of the most important faunal centers in the Neman River's floodplain valley are oxbow lakes, which are characterized by the greatest beetle species diversity. Only 15 out of the 76 determined species were specific to that environment. The remaining faunal elements were beetles which also inhabit large tributaries and the Neman River itself – the sources of rheophilic fauna interchange. Oxbow lakes are also an important source of fauna represented by type "a" stagnobionts for the above environments.

The Neman River is a faunal center with only 6 species exclusive to that environment. The remaining species inhabit also other environments, in particular oxbow lakes and large tributaries and, to a lesser extent, intermittent water bodies and small tributaries. Whereas the Neman River is a donor of rheophilic fauna for the former, it is also the recipient of stagnobionts from oxbow lakes and intermittent water bodies as well as, to a lesser degree, rheobiontic fauna from small tributaries.

Large tributaries are yet another faunal center with only 9 exclusive species. The observed faunal relations between that environment and the remaining centers indicate that the highest number of species shared with large tributaries inhabit oxbow lakes and the Neman River.

Small tributaries are the most specific centers distinguished by greatest stability. The local beetle fauna is characterized by a high degree of homogeneity and specificity. It is dominated by rheobiontic species which are found in every studied watercourse. The above observation was confirmed by studies on aquatic hemipterans (Biesiadka & Kurzątkowska 2003), Hydrachnida (Biesiadka & Cichocka 2004) and Trichoptera (Czachorowski 2004). Those beetles migrate to the Neman River and its large tributaries only to a limited extent. The low number of species shared with other aquatic

environments is indicative of a relatively weak faunal interchange between small tributaries and other types of water bodies.

Small intermittent water bodies whose fauna is dominated by type "b" stagnobionts have different faunal features. Type "b" stagnobionts and the accompanying scant synecological groups are found only during the breeding season, after which they migrate to all types of water bodies found in the Neman River valley, as demonstrated by the presence of shared species in those environments.

An analysis of faunal relations between different types of aquatic environments in the Neman River valley indicates that oxbow lakes and Neman's large tributaries play a key role in shaping the local faunal relations. The greatest species diversity of the water beetle fauna was observed in those environments. Although a slightly lower species diversity was reported in Neman, the highest number of beetles was collected in the river which also contributes significantly to faunal relations in the area. A similar distribution pattern was observed in respect of Hydrachnida (Biesiadka & Cichocka 2004) and Heteroptera (Biesiadka & Kurzątkowska 2003), which inhabit this part of the Neman River valley. A high number of species common to all three aquatic environments indicates that the most intense faunal interchange takes place between those water bodies. The above results not only from the high dispersion capacity of water beetles, but also from changes in hydrological conditions observed seasonally in the river valley, such as high water-level periods, during which the waters of the Neman River and its large tributaries come into contact with oxbow lakes, supplying those water bodies with beetle fauna. Oxbow lakes are also reservoirs of fauna which is restored after an intense high water-level period. The important role played by the studied water bodies, in particular oxbow lakes, in the process of shaping the faunal relations in river valleys was also confirmed by a study on beetles fauna in the valleys of Narew (Biesiadka & Pakulnicka 2004) and Bug (Przewoźny et al. 2006).

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