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The formation of water beetle fauna in anthropogenic water bodies

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Abstract

Studies on the fauna of water beetles inhabiting anthropogenic water bodies were conducted on 44 clay-pit and gravel-pit ponds. A total of 125 water beetle species were identified. The dominant species were *Scarodytes halensis* and *Laccobius minutus*, representing the argillophilous component. Eurytopic, lake and riverine, and peatland species were also identified. Among the environmental factors determining the diversity of the water beetle fauna in particular types of habitats, the most significant role was played by the substratum and succession stage.

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INTRODUCTION

Anthropogenic water bodies, formed as a result of mineral extraction, are an important element of a hydrographical network. However, they have not aroused much interest among hydrobiologists. Polish literature on aquatic Coleoptera provides scant information on artificial reservoirs, although the ecology of water beetles is relatively well-known. Noteworthy works devoted to this subject include those by Łęgosz-Owsianna (1955), Tranda (1959), Biesiadka (1977), Mielewczyk (1997, 1997a) as well as by Kowalik and Buczyński (2003). As regards foreign reference materials, some fragmentary data about water beetles can be found in papers by Stöckel (1983) and Spitzenberg (1988). Attention should be also paid to reports by Barnes (1983) and Carl (1997), which describe the colonization process of anthropogenic water bodies.

The aim of the present study was to describe changes in the water beetle fauna that take place during the succession of anthropogenic water bodies, as well as to determine the environmental factors that have the most significant effect on the development of water beetle communities. The general purpose was to define the role of anthropogenic water bodies in the ecological landscape, and to determine whether they provide habitats for specific fauna and to what degree they act as substitute habitats for other hydrobionts.

MATERIALS AND METHODS

Field investigations were carried out systematically from May 1997 to October 1999 on 44 water bodies located in the Mazurian Lake District. Samples were taken with a hand scoop net and trap nets. A total of 561 samples were collected.

The water bodies examined in the study differed in terms of the following four variables: type of substratum; type of aquatic vegetation; surface area; depth. Taking into account the type of substratum, the water bodies were divided into clay-pit ponds and gravel-pit ponds. The structure and stage of aquatic vegetation development, i.e., the main indicators of the succession process, enabled dividing the water bodies into three age groups, namely newly-formed, with no aquatic vegetation; older, gradually colonized by rush plants such as *Carex* sp., *Juncus* sp., *Heleocharis* sp., *Glyceria maxima*, *Scirpus silvaticus*, *Hydrocharis morsus-ranae*, *Alisma plantago-aquatica* and other, scattered bulrushes, mostly *Typha latifolia*, nymphs: *Lemna minor*, *L. trisulca*, *Potamogeton natans* and elodeids: *Elodea canadensis*, *Ceratophyllum demersum*, *P. perfoliatum*, *P. obtusifolius*, *P. lucens*; and old, overgrown with dense stands of *Phragmites australis*. According to their

permanence and size, the water bodies were divided into three categories: intermittent pools and small bodies of water covering an area of several square meters; medium-sized bodies of water that were not too deep covering an area of about 0.5; and large, deep bodies of water covering an area of over 0.5 ha. Samples were taken in three main zones of water beetle occurrence, i.e., in the ecotone zone, at a depth of around 20 to 30 cm, and at a depth of 50 to 70 cm (Table 1a).

Table 1

The characteristic of designated habitats (A) and their membership to 12 clusters (B). (Substratum: 1 – clay, 2 – gravel, Stage of succession: 1 – newly formed, 2 – older, 3 – old; surface area: 1 – small, 2 – medium, 3 – large; depth: 1 – ecotone zone, 2 – at a depth of around 20-30 cm, 3 – around 50 cm)

A					B
variable/habitat	substratum	stage of succession	surface area	depth	cluster
1	1	1	1	1	1
2	1	1	1	3	11
3	1	1	2	1	3
4	1	1	2	2	3
5	1	2	1	1	3
6	1	2	1	2	1
7	1	2	1	3	12
8	1	2	2	1	3
9	1	2	2	2	2
10	1	2	2	3	9
11	1	3	1	1	6
12	1	3	1	2	6
13	1	3	2	1	6
14	1	3	2	2	6
15	1	3	2	3	8
16	1	3	3	1	6
17	1	3	3	2	6
18	1	3	3	3	6
19	2	1	1	1	1
20	2	1	1	2	1
21	2	1	1	3	1
22	2	1	2	1	3
23	2	1	2	2	4
24	2	1	2	3	4
25	2	2	1	1	1
26	2	2	1	2	1
27	2	2	2	1	3
28	2	2	2	2	4
29	2	2	2	3	4
30	2	3	3	1	5
31	2	3	3	2	7
32	2	3	3	1	4
33	2	3	3	2	10

Taking into consideration all possible combinations of the above variables, 33 habitats were designated in the water bodies analyzed (Table 1a).

The faunal similarities between the designated habitats were determined using the Bray–Curtis formula (Bray and Curtis 1957). Multivariate discriminant analysis (Afifi and Clark 1996) was applied to specify the factors affecting the diversity of the water beetle fauna. The analysis was based on a dendrogram illustrating faunal similarities between habitats. Twelve clusters, at a similarity level of $\geq 40\%$, were determined on the basis of the species composition of water beetle communities. The values of Fisher's linear discriminant functions, standardized coefficients of canonical functions as well as the values of Wilks's lambda statistics were calculated for particular clusters. Discriminant analysis was performed to establish relationships between water beetles found in a given habitat and the characteristics of this habitat (type of substratum, stage of succession, surface area, depth at which a given species occurs).

RESULTS

The experimental materials comprised 8154 water beetles representing 125 species belonging to six families (Table 2). Dytiscidae made up the majority of the fauna collected. The water beetle fauna was ecologically differentiated and consisted of 8 synecological components, understood as groups of species sharing common habitat preferences (Table 2). The component typical of small, strongly eutrophic water bodies was characterized by the highest species diversity. It was composed of 63 species that accounted for 33.4% of the total collected material. In terms of quantity, the most important role was played by argillophilous beetles (54.6% of the total abundance). The other synecological components, i.e., peatland species and those associated with surface waters, were less diversified and their quantitative significance was low.

The detailed analysis of the experimental materials revealed considerable differences between the types of water bodies (Table 2). However, as many as 83 species were found in both types of waters. Twenty-five species occurred exclusively in clay-pit ponds, while 16 species were present only in gravel-pit ponds. In both types of water bodies the highest species diversity was observed within Dytiscidae, represented primarily by species associated with strongly eutrophic waters in clay-pit ponds, and by argillophilous species in gravel-pit ponds. There were also distinct differences in the densities of water beetles inhabiting both types of waters. The mean number of individuals per sample was 13.3 and 21.6 in clay-pit and gravel-pit ponds, respectively. The dominant species in clay-pit ponds were *Noterus crassicornis* (15.5%), *Scarodytes halensis* (9.8%), and *Laccobius minutus* (6.7%). The last two species also

Table 2

Occurrence of water beetles in the types of waters investigated. E – synecological element (1A - peatbog element connected with the ecotone zone, 1B - peatbog element connected with more depth, 2A - lake-river element, 3A - element associated with small, strongly eutrophic water bodies with the ecotone zone, 3B - element associated with small, strongly eutrophic water bodies with more depth, 4A - argillophilic element connected with the ecotone zone, 4B - element associated with small, strongly eutrophic water bodies connected with more depth, 5 - element associated with surface waters), N – number of individuals, G - I,II, III – stage of succession of clay pits, Z - I,II, III – stage of succession of gravel pits

Species / type of waters	E	Clay pits			Gravel pits			Total N	(%)
		G-I	G-II	G-III	Z-I	Z-II	Z-III		
GYRINIDAE								1.02	
<i>Gyrinus caspius</i> Ménetr.	5					1		1	0.01
<i>Gyrinus marinus</i> Gyll.	5		6	13	1	16	2	38	0.47
<i>Gyrinus minutus</i> Fabr.	5						4	4	0.05
<i>Gyrinus natator</i> (L.)	5					2		2	0.02
<i>Gyrinus substriatus</i> Steph.	5		3		19	7	8	37	0.45
<i>Gyrinus sufriani</i> Scriba	5						1	1	0.01
HALIPLIDAE								0	6.06
<i>Peltodytes caesus</i> (Duft.)	3B	58	31	14		2		105	1.29
<i>Halipilus confinis</i> Steph.	4B			3				3	0.04
<i>Halipilus flavicollis</i> Sturm	2A			34				34	0.42
<i>Halipilus fluviatilis</i> Aubé	2A	3	2	39		1	1	46	0.56
<i>Halipilus fulvicollis</i> Er.	1A		1	2	2			5	0.06
<i>Halipilus fulvus</i> (Fabr.)	2A			87		1	2	90	1.10
<i>Halipilus heydeni</i> Wehncke	3B		3	6	1	1		11	0.13
<i>Halipilus immaculatus</i> Gerh.	3B		4	40			1	45	0.55
<i>Halipilus lineolatus</i> Mann.	3B			37			1	38	0.47
<i>Halipilus obliquus</i> (Fabr.)	4B		1	20	1		3	25	0.31
<i>Halipilus ruficollis</i> (Deg.)	3B	1	4	41	2	3	12	63	0.77
<i>Halipilus wehncke</i> Gerh.	3B		1	28				29	0.36
NOTERIDAE								0	9.63
<i>Noterus clavicornis</i> (Deg.)	3A	1	3	192	2	7	5	210	2.58
<i>Noterus crassicornis</i> (O.F.Müll)	3A	3		565	2	3	2	575	7.05
DYTISCIDAE									48.09
<i>Hydroporus angustatus</i> Sturm	1A	1	2	16	1	1	6	27	0.33
<i>Hydroporus erythrocephalus</i> (L.)	1A			3			7	10	0.12
<i>Hydroporus fuscipennis</i> Schaum	3A						10	10	0.12
<i>Hydroporus incognitus</i> Sharp	1A			16	3	2	19	40	0.49
<i>Hydroporus neglectus</i> Schaum	1A			4		1	4	9	0.11
<i>Hydroporus nigrita</i> (Fabr.)	1A					1		1	0.01
<i>Hydroporus obscurus</i> Sturm	1A			1				1	0.01
<i>Hydroporus palustris</i> (L.)	3A		2	19	3	3	32	59	0.72

Species / type of waters	E	Clay pits			Gravel pits			Total N	(%)
		G-I	G-II	G-III	Z-I	Z-II	Z-III		
<i>Hydroporus planus</i> (Fabr.)	3A			3	4	3	43	53	0.65
<i>Hydroporus pubescens</i> (Gyll.)	1A						1	1	0.01
<i>Hydroporus striola</i> (Gyll.)	3A						8	8	0.10
<i>Hydroporus tristis</i> (Payk.)	1A			4		5	3	12	0.15
<i>Hydroporus umbrosus</i> (Gyll.)	1A			2			5	7	0.09
<i>Suphrodytes dorsalis</i> (Fabr.)	3B	1		1	1			3	0.04
<i>Graptodytes pictus</i> (Fabr.)	3B	3	10	204	1		8	226	2.77
<i>Porhydrus lineatus</i> (Fabr.)	2A	1	10	32	2			45	0.55
<i>Hygrotus confluens</i> (Fabr.)	4B				10			10	0.12
<i>Hygrotus impressopunctatus</i> (Schall.)	3B		2	40	6	6	58	112	1.37
<i>Hygrotus decoratus</i> (Gyll.)	1A		1	20	1	2	23	47	0.58
<i>Hygrotus inaequalis</i> (Fabr.)	3B	5	17	94	23	13	38	190	2.33
<i>Hygrotus versicolor</i> (Schall.)	2A			55		1		56	0.69
<i>Potamonectes canaliculatus</i> (Lacord.)	4B		1		43	6		50	0.61
<i>Scarodytes halensis</i> (Fabr.)	4B	137	205	17	1341	308		2008	24.63
<i>Hydroglyphus hamulatus</i> (Gyll.)	2A		1	85	1			87	1.07
<i>Hydroglyphus geminus</i> (Fabr.)	4B	15	6	7	169	5		202	2.48
<i>Hyphydrus ovatus</i> (L.)	3B	9	58	26	8	4		105	1.29
<i>Laccophilus hyalinus</i> (Deg.)	2A		1	28			2	31	0.38
<i>Laccophilus minutus</i> (L.)	3B	22	58	151	4	24	24	283	3.47
<i>Copelatus haemorrhoidalis</i> (Fabr.)	1B			3			1	4	0.05
<i>Agabus bipustulatus</i> (L.)	3B					1		1	0.01
<i>Agabus paludosus</i> (Fabr.)	2A						2	2	0.02
<i>Agabus sturmii</i> (Gyll.)	3B				1			1	0.01
<i>Agabus undulatus</i> (Schrank)	3B			13	1			14	0.17
<i>Ilybius ater</i> (Deg.)	1B			5				5	0.06
<i>Ilybius crassus</i> Thoms.	1B			3				3	0.04
<i>Ilybius fenestratus</i> (Fabr.)	2A			18				18	0.22
<i>Ilybius fuliginosus</i> (Fabr.)	3B	1	7		1			9	0.11
<i>Ilybius guttiger</i> (Gyll.)	1B			1				1	0.01
<i>Ilybius quadriguttatus</i> (Lacord.)	1B						1	1	0.01
<i>Ilybius similis</i> Thoms.	1B		1		1			2	0.02
<i>Rhantus bistriatus</i> (Bergstr.)	3B			1				1	0.01
<i>Rhantus exsoletus</i> (Forst.)	3B			2				2	0.02
<i>Rhantus grapii</i> (Gyll.)	3B			1				1	0.01
<i>Rhantus latitans</i> Sharp	3B			1				1	0.01
<i>Rhantus notaticollis</i> (Aubé)	3B			3	1		1	5	0.06
<i>Rhantus notatus</i> (Fabr.)	3B		6	4	2	2	2	16	0.20
<i>Rhantus suturalis</i> Macleay	3B	2	7	6	1	29	1	46	0.56
<i>Colymbetes fuscus</i> (L.)	3B			3				3	0.04
<i>Colymbetes payculli</i> Er.	1B			1			1	2	0.02

Species / type of waters	E	Clay pits			Gravel pits			Total N	(%)
		G-I	G-II	G-III	Z-I	Z-II	Z-III		
<i>Colymbetes striatus</i> (L.)	1B			1			1	2	0.02
<i>Hydaticus aruspex</i> Clark	1B			2		1		3	0.04
<i>Hydaticus seminiger</i> (Deg.)	3B	1	2	6	1	1		11	0.13
<i>Hydaticus continentalis</i> J.Balrour Browne	3B			4				4	0.05
<i>Hydaticus transversalis</i> (Pont.)	3B			8				8	0.10
<i>Dytiscus circumcinctus</i> (Ahr.)	3B		1				1	2	0.02
<i>Dytiscus dimidiatus</i> Bergstr.	3B			3		1		4	0.05
<i>Dytiscus marginalis</i> L.	3B			2	2	2		6	0.07
<i>Acilius canaliculatus</i> (Nic.)	1B	3	3	25	1	2	2	36	0.44
<i>Acilius sulcatus</i> (L.)	3B	1	1	1	2	2	1	8	0.10
<i>Graphoderus austriacus</i> (Sturm)	3B			1	1			2	0.02
<i>Graphoderus cinereus</i> (L.)	3B			3			1	4	0.05
HYDRAENIDAE								0	
<i>Ochthebius hungaricus</i> Eltrödy-Yonga	4A				2			2	0.02
<i>Ochthebius minimus</i> (Fabr.)	3A	1	2	2	2	8	1	16	0.20
<i>Hydraena palustris</i> Er.	1A			8	1			9	0.11
<i>Hydraena riparia</i> Kugel.	2A	1	6	9			1	17	0.21
<i>Limnebius aluta</i> (Bedel)	3A			8	1	8	2	19	0.23
<i>Limnebius atomus</i> (Duft.)	3A			7				7	0.09
<i>Limnebius crinifer</i> (Rey)	3A	2	2	6		3		13	0.16
<i>Limnebius papposus</i> Muls.	3A	4	2	1	2	4		13	0.16
<i>Limnebius parvulus</i> (Herbst)	3A	3	7	55	6	23	10	104	1.28
HYDROPHILIDAE								0	32.76
<i>Hydrochus angustatus</i> Germ.	3A		1		1		1	3	0.04
<i>Hydrochus brevis</i> (Herbst)	3A				1		1	2	0.02
<i>Hydrochus crenatus</i> (Fabr.)	3A			18			10	28	0.34
<i>Hydrochus elongatus</i> (Schall.)	3A			6			5	11	0.13
<i>Hydrochus ignicollis</i> Motsch.	3A		1	30	1	3	3	38	0.47
<i>Helophorus aequalis</i> (Thoms.)	4A		7	1	7	2		17	0.21
<i>Helophorus grandis</i> Ill.	4A		2	2	7			11	0.13
<i>Helophorus granularis</i> (L.)	4A			2	3	1		6	0.07
<i>Helophorus griseus</i> Herbst	4A	4	18	7	37	6	1	73	0.90
<i>Helophorus minutus</i> Fabr.	4A	13	7	46	59	9	4	138	1.69
<i>Helophorus nubilus</i> Fabr.	4A	1	2					3	0.04
<i>Coelostoma orbiculare</i> (Fabr.)	3A			3		2		5	0.06
<i>Cercyon marinus</i> Thoms.	3A			1				1	0.01
<i>Cercyon tristis</i> (Ill.)	3A			1				1	0.01
<i>Hydrobius fuscipes</i> (L.)	3B	1	2	18		1	9	31	0.38
<i>Anacaena lutescens</i> (Steph.)	1A	2	4	149	5	30	10	200	2.45
<i>Laccobius atrocephalus</i> (Reitt.)	4A		1		1	3		5	0.06
<i>Laccobius colon</i> (Steph.)	4A	1	2	3	1			7	0.09

Species / type of waters	E	Clay pits			Gravel pits			Total N	(%)
		G-I	G-II	G-III	Z-I	Z-II	Z-III		
<i>Laccobius bipunctatus</i> (Fabr.)	4A		3	3	1	2		9	0.11
<i>Laccobius minutus</i> (L.)	4A	79	32	133	1190	386	56	1876	23.01
<i>Laccobius sinuatus</i> Motsch.	4A				2	5		7	0.09
<i>Laccobius striatulus</i> (Fabr.)	2A	1			5	5	5	16	0.20
<i>Helochares griseus</i> Müll	3A	1	4	57	7	5	9	83	1.01
<i>Helochares punctatus</i> Sharp	3A			4				4	0.06
<i>Enochrus affinis</i> (Thunb.)	1A	1		2			8	11	0.13
<i>Enochrus coarctatus</i> (Gredl.)	1A			3			1	4	0.05
<i>Enochrus fuscipennis</i> (Thoms.)	3A			1				1	0.01
<i>Enochrus nigrinus</i> (Aharp)	3A			1				1	0.01
<i>Enochrus melanocephalus</i> (Oliv.)	1A	1		2				3	0.04
<i>Enochrus quadripunctatus</i> (Herbst)	3A		4	13	3		6	26	0.32
<i>Enochrus testaceus</i> (Fabr.)	3A			4				4	0.05
<i>Cymbiodyta marginella</i> (Fabr.)	1A			1	1		1	3	0.04
<i>Chaetarthria seminulum</i> (Herbst)	3A			9	2	2		13	0.16
<i>Hydrophara caraboides</i> (L.)	3B	1	3	15	2	4	4	29	0.36
<i>Hydrophilus aterrimus</i> Eschscholtz	3B			1				1	0.01
		385	573	2702	3016	982	496	8154	100.00

dominated in gravel-pit ponds accounting for 36.7% and 36.3% of all individuals, respectively.

The analysis of faunal similarities between the designated habitats provided an insight into the development of water beetle fauna (Fig. 1). Of the 12 clusters, the most developed is cluster 6, comprising habitats located in the oldest, medium-sized or large clay-pit ponds (Table 1a, b). The similarity

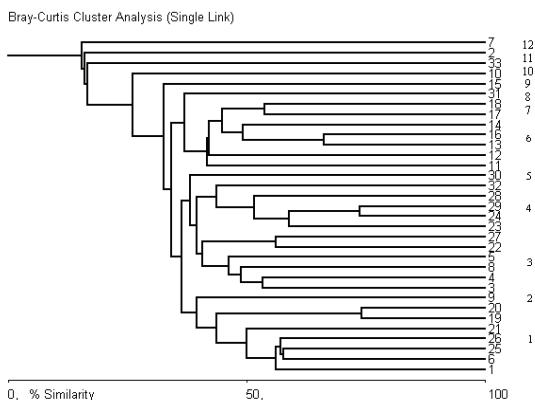


Fig. 1. Analysis of fauna similarities between the selected habitats.

between these habitats ranged from 66.3% to 41.7%. Among the synecological components, the most numerous group was formed by beetles associated with strongly eutrophic waters. Water beetles typical of weakly eutrophic lakes and rivers were represented by 10 species (15% of total abundance). Particular attention should be paid here to the presence of *Hydroglyphus hamulatus*, which is rare in Poland and prefers clean, well-oxygenated lakes, and to *Hydraena riparia*, typical of running waters. Cluster 4 is also relatively well-developed. This cluster includes habitats situated in medium-sized gravel-pit ponds, representing all stages of succession. The faunal similarity between them was 43.7% to 73.7%. argillophilous species, dominated by *Laccobius minutus* and *Potamonectes canaliculatus*, and species associated with strongly eutrophic waters accounted for 51.9% and 43.4% of the total abundance, respectively. Cluster 1 consists of quite uniform habitats, most of which are newly-formed bodies of water with no aquatic vegetation. These are small gravel-pit ponds for which faunal similarities range from 43.7% and 74.1%. The vast majority of the fauna (87.1%) are beetles associated with argillophilous waters.

Discriminant analysis revealed that among all variables that had a statistically significant effect on the formation of water beetle communities in particular types of habitats the most important role was played by succession stage and substratum since the values of canonical functions were the highest for these variables (Table 3).

Table 3

Statistical description of the discriminant analysis of 12 groups of habitats

cluster	Function			
	1	2	3	4
Value of canonical discriminant function at cluster 1	-1.912	-0.138	0.384	-0.64
Value of canonical discriminant function at cluster 2	0.463	-0.937	-0.45	0.697
Value of canonical discriminant function at cluster 3	-1.145	-9.97E-02	-1.282	0.372
Value of canonical discriminant function at cluster 4	-0.416	1.423	0.701	0.433
Value of canonical discriminant function at cluster 5	1.474	2.515	-0.797	-0.436
Value of canonical discriminant function at cluster 6	2.008	-0.697	-0.422	-0.343
Value of canonical discriminant function at cluster 7	1.979	2.218	0.492	2.81E-02
Value of canonical discriminant function at cluster 8	2.551	-1.204	1.333	7.65E-02
Value of canonical discriminant function at cluster 9	0.968	-1.234	0.839	1.161
Value of canonical discriminant function at cluster 10	1.979	2.218	0.492	2.81E-02
Value of canonical discriminant function at cluster 11	-1.361	-2.139	1.025	1.008
Value of canonical discriminant function at cluster 12	0.222	-2.11	1.519	-7.62E-02
Percentage of variance	52.9	27.6	14	5.5
Canonical correlation	0.892	0.819	0.713	5.37E-01
Wilks' Lambda function	0.023	0.115	0.349	0.712
Chi ² function	90.079	51.889	25.236	8.17E+00
Substrate	-0.295	0.816	0.409	-0.298
Stage of succession	0.847	0.016	0.264	-5.80E-01
Surface area	0.414	0.487	-0.378	0.688
depth	0.357	-0.21	0.911	3.28E-01
df	44	30	18	8
Significance	0	0.008	0.119	0.417

DISCUSSION

Anthropogenic water bodies should be perceived as dynamic systems performing a crucial role in the ecological landscape. It is interesting to observe the rate of colonization and stabilization as well as directions of succession taking place in these ecosystems. Such studies on water beetle fauna have been conducted by Tranda (1959) and Barnes (1983).

The type of substratum and the stage of succession corresponding to the age of a water body are particularly important for the development of coleopteran fauna in artificial reservoirs (Tranda 1959 and Barnes 1983). This is distinct for other groups of insects, e.g., dragon-flies (Buczyński 1999, Buczyński and Pakulnicka 2000). Newly-formed water bodies, not overgrown with aquatic vegetation, are usually characterized by low stability in both abiotic and biotic conditions, including variable thermal conditions, exposure to insolation, and insufficient food resources. It follows that the beetles which colonize such bodies of water must be well adapted to extreme living conditions. However, many of the species found in such water bodies exhibit wide ecological tolerance and their occurrence there may be considered accidental. Successful colonization of new water bodies by beetles is dependent on their mobility (Barnes 1983) as well as on physiological adaptation to selecting suitable habitats (Ward 1992). The species that are the first to colonize a newly-formed clay-pit or gravel-pit pond most often show strong flying ability (some of them have to cover a distance of at least 16 km) (Mielewczyk 1997), in contrast to the species that inhabit older and more stable ecosystems. The latter group also includes flightless beetles and beetles with poor flying ability. This fact contributed to the formation of a very similar species structure of coleopteran cenoses in many water bodies representing the same type. The beetles that are the first colonizers of newly-formed bodies of water are: *Haliplus obliquus*, *Potamonectes canaliculatus*, *Scarodytes halensis*, *Hydroglyphus geminus*, *Acilius canaliculatus*, *Hygrotus confluens*, *Limnebius papposus*, *Helophorus griseus*, *Laccobius sinuatus*, and *Enochrus melanocephalus*. These are thermophilous, predacious, southern European species. The presence of thermophilous species in clay-pit and gravel-pit ponds has also been observed among other systematic groups, e.g., dragon-flies (Stark 1978). The majority of thermophiles (representing the argillophilous component) are associated with waters with elevated mineralization levels, which indicates that the chemical properties of water, and especially the salinity level, are key factors affecting the colonization of newly-formed water bodies.

The growth of aquatic plants, observed already in the first year of the existence of a water body, the mosaic structure of habitats, shading of the substratum, and the development of the debris chain that is missing immediately

after water body formation (Barnes 1983) result in higher species diversity among beetles. This phenomenon, described by Tranda (1959) and Barnes (1983), is also common in other taxonomic groups (Stark 1978, Donath 1980, Lipsey and Malcolm 1981, Carl 1997). In such cases changes in the species composition are observed, including a substantial decrease in the contribution of pioneer species, especially in waters with increased mineralization levels.

Clay-pit and gravel-pit ponds develop along different lines. Transformations of gravel-pit ponds are directed towards eutrophic ecosystems, dominated by eurytopic species typical of small water bodies, accompanied by a peatland component. Clay-pit ponds, particularly large, deep ones, develop towards lake-like bodies of water, characterized by low trophy and dominated by species typical of small water bodies accompanied by species found in clean oligotrophic waters, e.g., *Hydroglyphus hamulatus* and *Haliphus fulvus*, as well as the less numerous *Haliphus confinis*, *H. flavicollis*, *H. fluviatilis*, *H. immaculatus*, *H. lineolatus*, *H. obliquus*, *Hygrotus versicolor*, *Ilybius fenestratus*, and *Agabus bipustulatus*.

Succession-related changes in the water beetle fauna indicate that the anthropogenic water bodies examined in the study have a fundamental influence on the functioning of the entire ecological landscape. These water bodies undergo naturalization and overtake the function of disappearing natural water bodies (inland brackish bodies of water, small tarns or lakes with low trophic levels) in the ecological landscape. Moreover, they contribute to maintaining the constancy of occurrence of rare and alien species, mostly Mediterranean, such as *Potamonectes canaliculatus*, *Hygrotus confluens*, and *Ochthebius hungaricus*. This not only enables increased species biodiversity in the region, but also preserves stability in faunal relationships.

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