

Reproduction of *Potamothrix hammoniensis* (Oligochaeta) in shallow eutrophic lakes

by

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DOI: [10.1515/ohs-2018-0017](https://doi.org/10.1515/ohs-2018-0017)

Category: **Original research paper**

Received: **September 06, 2017**

Accepted: **January 05, 2018**

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Abstract

The aim of the study was to indicate the abiotic parameters of water and bottom sediments, which significantly affect the reproduction of *Potamothrix hammoniensis* in 9 shallow eutrophic lakes, of which 5 were dominated by macrophytes and 4 – by phytoplankton. Samples were collected once a month from January to December 2012.

The percentage of *Potamothrix hammoniensis* individuals with a developed reproductive system varied in individual lakes and ranged from 14 to 72%. There was no correlation between the distinguished lake types and the proportion of sexually mature individuals. The reproductive activity was not observed in summer and early autumn. Among the measured parameters, the highest values of the Pearson correlation coefficient were found between the percentage of individuals with a developed reproductive system and the conductivity ($r = 0.69$; $p < 0.001$), pH ($r = 0.51$; $p = 0.002$) and the organic matter content in the sediments ($r = -0.42$; $p = 0.012$). It is worth noting that there was no correlation between the percentage of sexually mature specimens and the water temperature ($r = -0.22$, $p = 0.204$) and the oxygen concentration ($r = -0.08$; $p = 0.648$).

Key words: Oligochaeta, reproduction, shallow lakes, abiotic parameters

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Introduction

Potamothenis hammoniensis is one of the dominant species of Oligochaeta, abundantly inhabiting European waters up to Siberia (Grigelis 1990). The taxon is relatively rare in south-western France and in Spain (Martinez-Ansemil, Prat 1984). Although this typical pelophilous species prefers eutrophic waters, it is also found in oligotrophic lakes (Lang 1984). The high tolerance of this taxon in relation to habitat conditions is also evident in its frequent occurrence in lakes of various depths. According to Wiśniewski (1978), *P. hammoniensis* often dominates in all areas of the bottom in deep stratified lakes of central and northern Poland, being usually the only representative of this group of animals in the profundal zone, even at great depths. On the other hand, Żbikowski (2011) found overwhelming dominance of this species also in shallow eutrophic lakes.

The consequence of the mass occurrence of *Potamothenis hammoniensis* is the significant impact of the species on the functioning of aquatic ecosystems. It is an important element of the food base of predatory invertebrates and benthic fish (Jónasson, Thorhauge 1976). In addition, through bioturbation (Svensson et al. 1998), modification of oxygen conditions at the lake bottom and change in the structure of soft-bottom sediments (Ciutat et al. 2006), the species significantly affects the direction and intensity of substance exchange in the sediment/water interface (Rișnoveanu et al. 2004), which determines, among other things, the productivity of lakes. It is obvious that the role of *P. hammoniensis* in the environment largely depends on its abundance, which is strongly associated with the reproductive success. It seems, therefore, that the research aimed at identifying the factors that affect the reproductive activity of this important element of the biocoenosis of aquatic ecosystems is fully justified.

The results of previous studies indicate that the reproduction period of *Potamothenis hammoniensis* is definitely dependent on the temperature (Jónasson, Thorhauge 1972) and the oxygenation of the near-bottom water (Thorhauge 1975). According to Jónasson (1972) and Arkhipova (1980), the species breeds at low temperatures. On the other hand, the oxygen deficit, often occurring in early summer, ends the reproduction period irrespective of the thermal conditions (Thorhauge 1975). It can therefore be assumed that the reproductive activity of *P. hammoniensis* in deep lakes is more dependent on the oxygenation of the water above the bottom, because the water temperature in the deeper profundal of stratified lakes is usually within the limits

of reproduction throughout the year.

Most studies on reproductive activity of *Potamothenis hammoniensis* were conducted in deep stratified lakes, where the dynamics of thermal and aerobic conditions during the year is completely different compared to shallow water bodies. According to Żbikowski (2011), the oxygenation of the near-bottom water in shallow lakes is generally good, except for the ice cover period, while in the growing season the water temperature often exceeds 20°C.

Considering the above information, the aim of this study was to indicate the abiotic parameters of water and bottom sediments, which significantly affect the reproduction of *Potamothenis hammoniensis*.

It was hypothesized that, unlike in deep lakes, the reproduction period of this species is more dependent on the temperature of water above the bottom than the water oxygenation.

Materials and methods

Study area

The research was carried out in 9 lakes. Almost all of them (except Lake Głuchowskie) are located in north-eastern Poland (Fig. 1) in the Iława Lake District, which is the western part of the Masurian Lake District. Unlike other lake districts in Poland, small and shallow lakes are predominant here (surface area < 100 ha, maximum depth < 5 m). Polymictic lakes constitute as



Figure 1

Location of the studied lakes in Poland

much as 64% of all lakes in this region (Marszelewski 2005). The lakes under study (except Lake Głuchowskie) are located in a relatively short distance from the town of Ława. Whereas Lake Głuchowskie is situated about 30 km north of Toruń, near the village of Bielczyny. The studied lakes are shallow, polymictic and small (except Lake Jeziorak and Lake Karaś), and are characterized by a high trophic level (Table 1).

The studied lakes were divided into macrophyte-dominated (5) and phytoplankton-dominated (4) lakes (Table 1). The first group included lakes where, due to the high water transparency, submerged plants cover the lake bottom also in central parts. In addition to the depth, the lakes also vary in their exposure to wind, abundance and the taxonomic composition of submerged macrophytes. Almost all of them (except Lake Głuchowskie) are surrounded by forests. The lakes dominated by phytoplankton, on the other hand, included those where, due to the low water transparency, the presence of macrophytes was limited to a very narrow littoral zone. These lakes were divided into two groups: shallower and deeper lakes. The first group included lakes where the ratio of euphotic depth to the depth of a lake was higher than 1, so light reached the bottom of a lake, whereas in the deeper phytoplankton-dominated lakes the above ratio was less than 1, so it was dark at the bottom.

Collection of samples, parameters measured and statistical analysis

Samples were collected once a month from January to December 2012. Water transparency was measured using a Secchi disc. We used a luxometer Slandi LX204 to assess the light conditions. We also calculated the vertical attenuation coefficient of light under water (E) (Scheffer 1998: 22, Eq. 2). Furthermore, to estimate the amount of light reaching the bottom, we multiplied the E value by the lake depth (D). This index ($E \times D$) is related to the shade level at the lake bottom (the higher ED value, the less light reaches the bottom) (Scheffer 1998). Moreover, we calculated the euphotic depth (Scheffer 1998: 25, Eq. 7), i.e. the depth beyond which the light level falls below 1% of the surface irradiation and is considered too low to maintain positive net photosynthesis of algae.

We measured temperature, conductivity, pH and oxygen concentration of the near-bottom water layer with a core sampler and a MultiLine P4 (WTW) Universal Pocket Sized Meter.

The bottom sediments (0–5 cm top layer) were collected with the same core sampler. Water content was measured by oven-drying sediments to a constant weight at 104°C, and organic matter content (OC) was determined after igniting dried sediments at

Table 1

Basic characteristics of the studied lakes

Parameter	Macrophyte-dominated lakes					Phytoplankton-dominated lakes			
						shallower	deeper		
	Zielone	Karaś	Piotrkowskie	Głuchowskie	Ząbrowo	Jeziorak*	Stęgwica	Kolmowo	Silm
Surface (ha)	20.2	423.3	54.4	24.1	12.7	80.0	39.7	43.4	58.8
Maximum length (m)	1375	4100	1450	740	960	2800	1880	1050	1625
Maximum width (m)	240	2250	850	475	215	1000	290	550	800
Maximum depth (m)	2.4	2.8	2.5	4.5	1.6	2.0	1.4	5.7	3.8
Mean depth (m)	1.3	0.6	1.7	2.2	1.1	1.3	1.0	3.1	2.0
Number of sampling locations	6	2	2	2	2	7	7	4	3
Depth at sampling locations (m)	1.5–2.2	1.6; 2.0	1.5; 2.0	3.0; 4.0	1.2; 1.5	1.0–1.5	1.2–1.4	2.0–3.0	3.5
Catchment ¹	F	A/M	F	A	F/A	F/T	F	A	F
Wind exposure	low	high	medium	high	low	medium	medium	high	medium
Dominating elodeid species ²	E.c.	Ch.sp.	Ch.sp.	C.d.	C.d.				
Elodeid abundance ³	5	7	8	8	9	1	1	1	1

* – Lake Jeziorak is the longest lake in Poland (length: 27.4 km, surface: 3230 ha). The study in this lake was carried out in a shallow bay part (its morphometry is provided in Table 1) located in the oldest southern part of the lake.

1 - F – forest, A – agricultural, M – marsh, T – affected by tourism; 2 – E.c. – *Elodea canadensis*, Ch.sp. – *Chara* sp., C.d. – *Ceratophyllum demersum*; 3 – the abundance of elodeids refers to their density in the central part of the lake, assessed arbitrarily on a scale from 1 to 10, where 1 denotes the complete absence of plants, and 10 means that the macrophytes overgrow the entire water volume

550°C for 2 h. The latter parameter was expressed in two ways: (1) as a percentage of dry mass of the sediments and (2) in milligrams of dry mass per unit of fresh sediment volume (10 cm³). The former value is a standard method of presenting the OC of bottom sediments. However, in our opinion, the latter figure is a better predictor of the amount of organic matter at the bottom, potentially available to animals. Sediment oxygen demand (SOD) was estimated by adding 300 ml of 100% oxygen saturated tap water to a special dish containing 20 cm³ of fresh sediments. The oxygen uptake was measured after 1 h, at 20°C.

Samples of Oligochaeta in the macrophyte-dominated lakes were collected using a core sampler (catching area 40 cm², 7–10 replicate samples). In the phytoplankton-dominated lakes, we used an Ekman-Birge grab (catching area 225 cm², 2–4 replicate samples). The samples were rinsed using a 0.2 mm sieve and preserved in 4% formaldehyde.

An important aspect of the study was to indicate the relationship between the size of an individual and its ability to reproduce. Given that Oligochaeta – due to the pressure of predators – very often do not have the hind part of the body (Wiśniewski 1979), the size of individuals was determined based on the width of the 8th body segment. According to Jenderedjian & Unanian (1987), the diameter of the 8th segment (the widest part of the body) is the most commonly used and most practical parameter that characterizes the body size of Oligochaeta. The body width was measured using the IPS-512 Image Analyzer and then the individuals were divided into the following size classes:

class	width of the 8 th segment (mm)
I	< 0.20
II	0.21–0.30
III	0.31–0.40
IV	0.41–0.50
V	0.51–0.60
VI	0.61–0.70
VII	0.71–0.80
VIII	0.81–0.90
IX	0.91–1.00
X	1.01–1.10
XI	1.11–1.20
XII	1.21–1.30

Individuals at different stages of the reproductive system development (mainly those with the developing clitellum) were considered as capable of reproduction. The proportion of such individuals was not calculated as usual in the whole population, but only among those individuals whose size (in this

case, starting from class V) indicated the ability to reproduce. According to the authors of the presented paper, this approach allows for a more precise assessment of the reproductive activity of the species under study, because it does not take into account any individuals that are still too young to reproduce, and whose proportion in the total population may vary.

To indicate which of the measured abiotic parameters of the water and bottom sediments are correlated with the development of the reproductive system of *P. hammoniensis*, linear Pearson correlations between the percentage of sexually mature specimens and the environmental variables were calculated.

Results

Small oligochaetes classified into class II, III and IV were not considered in this paper, as no individuals with a developed reproductive system were found among them. Over 2700 individuals of *Potamothrix hammoniensis* were examined (Table 2). Most of the studied specimens were medium-sized individuals, included in classes from V to VII.

The percentage of individuals with a developed reproductive system among the individuals capable of reproduction (starting from class V) varied in particular lakes and ranged from 14 to 72% (Fig. 2). It should be noted that the highest value was found in Lake Głuchowskie, where the number of examined individuals was the smallest one – only 43. On the other hand, in lakes with the highest number of studied individuals (Lake Stęgwica – 973 and Lake Zielone – 678), the proportion of sexually mature individuals was relatively small, 15 and 17%, respectively. There was no correlation between the lake type and the proportion of individuals with a developed reproductive system.

Single individuals with a developed reproductive system were observed already in class V (Table 3). Lake Jeziorak is distinguished by the fact that the reproductive organs were found in as many as 12% of individuals included in this class. Even though a higher value (20%) was determined in Lake Głuchowskie, only 5 individuals were in this class, thus only 1 specimen was capable of reproduction. It should be noted, however, that the highest percentage of sexually mature individuals in the distinguished classes was determined in the latter lake.

Generally, the percentage of reproducing *Potamothrix hammoniensis* individuals increased with their size (Table 3). This pattern was very clear in the macrophyte-dominated lakes, while small exceptions to this rule were recorded in the

Table 2

Number of examined individuals of *Potamothenis hammoniensis* – the sum of all sampling sites and dates

Lakes	Macrophyte-dominated					Ph-D		Ph-S		Sum	Sum		
	Zielone	Ząbrowo	Karaś	Piotrkowskie	Gluchowskie	Kolmowo	Silm	Stęgwica	Jeziorak		M	Ph-D	Ph-S
V	163	18	31	33	5	68	11	270	95	694	250	79	365
VI	204	22	15	20	12	100	54	327	91	845	273	154	418
VII	161	17	15	19	18	57	34	230	69	620	230	91	299
VIII	109	20	13	1	6	37	18	92	37	333	149	55	129
IX	26	13	12	4	2	16	12	43	22	150	57	28	65
X	13	10	9	1		5	8	9	6	61	33	13	15
XI	2	2	1			2	5	2	1	15	5	7	3
XII						1				1		1	
Sum	678	102	96	78	43	286	142	973	321	2719	997	428	1294

M – macrophyte-dominated, Ph-D – deeper phytoplankton-dominated, Ph-S – shallower phytoplankton-dominated

Table 3

Percentage of sexually mature individuals of *Potamothenis hammoniensis* in the distinguished size classes

Lakes	Macrophyte-dominated					Ph-D		Ph-S		Average	Average		
	Zielone	Ząbrowo	Karaś	Piotrkowskie	Gluchowskie	Kolmowo	Silm	Stęgwica	Jeziorak		M	Ph-D	Ph-S
V	0	0	0	0	20	1	0	1	12	2	< 1	1	4
VI	3	18	0	0	67	10	24	7	19	10	7	15	10
VII	20	47	40	26	78	25	15	17	35	24	28	21	21
VIII	42	70	54	100	100	32	44	36	73	46	50	36	47
IX	62	85	83	100	100	75	92	84	82	80	75	82	83
X	85	100	100	100		80	100	67	100	90	94	92	80
XI	100	100	100			50	80	100	100	87	100	71	100
XII						100				100		100	

M – macrophyte-dominated, Ph-D – deeper phytoplankton-dominated, Ph-S – shallower phytoplankton-dominated

phytoplankton-dominated lakes. Most individuals in the largest-size classes have a developed reproductive system.

The percentage of individuals with a developed reproductive system varied in particular months (Fig. 3). The results do not allow to indicate a period in

which the percentage of sexually mature individuals would be only relatively high. There were also no regularities related to the distinguished types of lakes. Noteworthy is the lack of individuals reproducing in the summer months. On the other hand, only individuals with a developed reproductive system were recorded in the period from March to May and in November and December.

Physical and chemical parameters of water and bottom sediments (annual average values) of the studied lakes are presented in Table 4. Water transparency was higher in the macrophyte-dominated lakes (1.7–2.1 m) than in the phytoplankton-dominated ones (0.7–1.4 m). Water temperature ranged from 11.2 to 14.0°C, oxygen concentration was relatively good in all lakes (6.4–10.8 mg O₂ dm⁻³), pH values ranged from 7.2 to 8.7 and conductivity from 199 to 577 μS cm⁻¹, except Lake Zielone, where it was clearly lower (100 μS cm⁻¹).

E × D values were higher in the deeper phytoplankton-dominated lakes (7.6 and 8.3) compared to the other lakes (2.2–5.5). Water content in the bottom sediments was relatively high, ranging from 93.3 to 97.4%. The percentage of organic matter content per unit of dry mass of the bottom sediments (OC-%) varied considerably among the studied lakes,

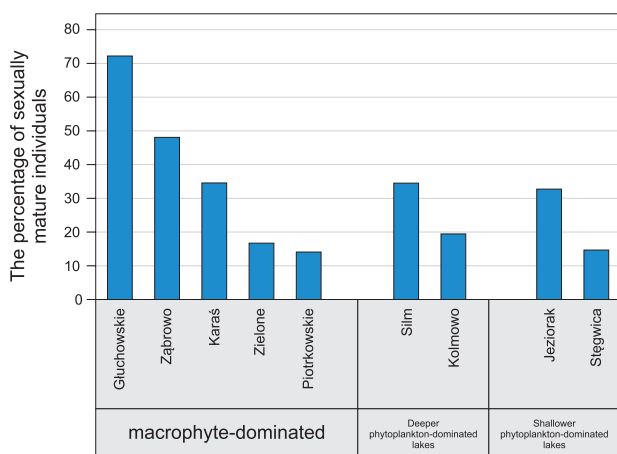


Figure 2 Percentage of sexually mature individuals of *Potamothenis hammoniensis* in the studied lakes

Table 4

Mean values of abiotic parameters of water and bottom sediments of the studied lakes

Parameter	Macrophyte-dominated lakes					Phytoplankton-dominated lakes			
	Zielone	Karaś	Piotrkowskie	Głuchowskie	Ząbrowo	shallower		deeper	
						Jeziorak*	Stęgowica	Kolmowo	Silm
Secchi depth (m)	2.2	2.1	2.1	2.0	1.7	0.8	0.7	1.0	1.4
Water above the bottom									
Temperature (°C)	13.5	13.4	14.0	12.6	12.3	12.1	11.2	12.3	13.4
Oxygen concentration (mg dm ⁻³)	8.0	7.8	9.3	6.4	10.0	10.8	6.9	7.2	7.2
pH	7.5	7.9	8.0	8.6	8.3	8.7	7.2	8.5	8.0
Conductivity (µS cm ⁻¹)	100	496	253	577	428	309	199	428	425
Bottom sediments									
E × D	2.4	2.7	2.2	5.5	2.7	4.4	2.9	8.3	7.6
Water content (%)	97.3	94.6	96.6	93.3	95.8	96.1	95.5	94.7	97.4
Organic matter (%) ¹	78.4	39.2	64.9	32.6	49.8	51.7	54.8	34.6	58.6
Organic matter (mg) ²	170	217	226	242	215	136	252	189	159
SOD ³	2.6	3.3	3.2	6.2	5.1	4.7	4.3	8.2	3.4

1 – percentage of dry mass of sediments

2 – in milligrams of dry mass per unit of fresh sediment volume (10 cm³)3 – sediment oxygen demand (mg O₂ per 20 cm³ of fresh sediments per 1 h)

ranging from 32.6 to 78.4%. Organic matter content (in mg) per 10 cm³ of the fresh bottom sediments ranged from 136 to 252 mg. SOD values varied considerably from 2.6 to 8.2 mg O₂ per 20 cm³ of fresh sediments per 1 h.

The highest values of the Pearson correlation coefficient between the percentage of individuals with a developed reproductive system and the measured parameters were found in the case of conductivity ($r = 0.69$; $p < 0.001$), pH ($r = 0.51$; $p = 0.002$) and OC-% ($r = -0.42$; $p = 0.012$) (Table 5). It is worth noting that there

was no correlation between the proportion of sexually mature specimens and the water temperature ($r = -0.22$, $p = 0.204$). It was observed, however, that the individuals with the developed reproductive system were recorded at temperatures below 2°C, while the proportion of reproducing individuals was very low when the water temperature was higher than 23°C (Fig. 4). Also no correlation between the water oxygen concentration and the proportion of sexually mature individuals was found ($r = -0.08$; $p = 0.648$). Even when the oxygen concentration was very low (< 1 mg dm⁻³),

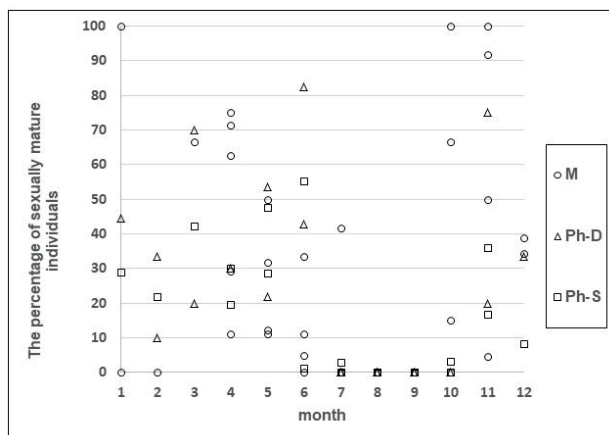


Figure 3

Percentage of sexually mature individuals of *Potamothenis hammoniensis* in each month

M – macrophyte-dominated lakes; Ph-D – deeper phytoplankton-dominated lakes; Ph-S – shallower phytoplankton-dominated lakes

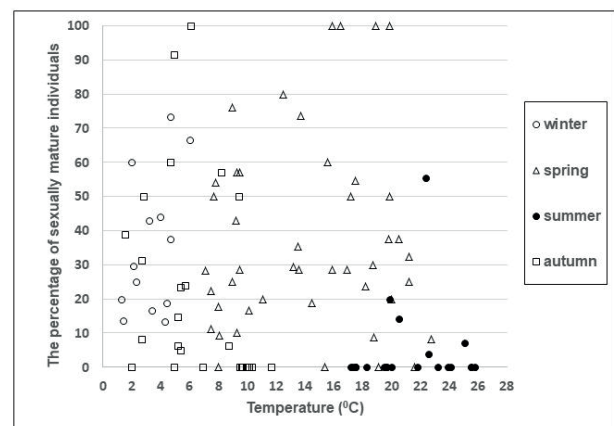


Figure 4

Relationship between the percentage of sexually mature individuals of *Potamothenis hammoniensis* and the water temperature near bottom

M – macrophyte-dominated lakes; Ph-D – deeper phytoplankton-dominated lakes; Ph-S – shallower phytoplankton-dominated lakes

Table 5

Values of Pearson's linear correlation coefficient (r) and the significance level (p) between the percentage of sexually mature individuals of *Potamothenis hammoniensis* and the environmental variables under study. Statistically significant values are boldfaced

Statistics	Near-bottom water layer				E × D	Bottom sediments			
	Temperature	Oxygen concentration	pH	Conductivity		WC	OC (%)	OC (mg)	SOD
r	-0.22	0.08	0.51	0.69	0.30	-0.21	-0.42	-0.10	0.22
p	0.204	0.648	0.002	< 0.000	0.080	0.226	0.012	0.568	0.204

E × D – index related to the light conditions at the lake bottom; WC – water content; OC (%) – organic matter content expressed as a percentage of dry mass of sediments; OC (mg) – organic matter content in milligrams of dry mass per unit of fresh sediment volume (10 cm³); SOD – sediment oxygen demand

specimens with the developed reproductive system were found (Fig. 5). The total lack of reproductive activity was recorded mainly in summer and early autumn, when the oxygen concentration was high (from 6 to 13 mg dm⁻³). On the other hand, in the same aerobic conditions, at other times of the year, the percentage of sexually mature individuals was high.

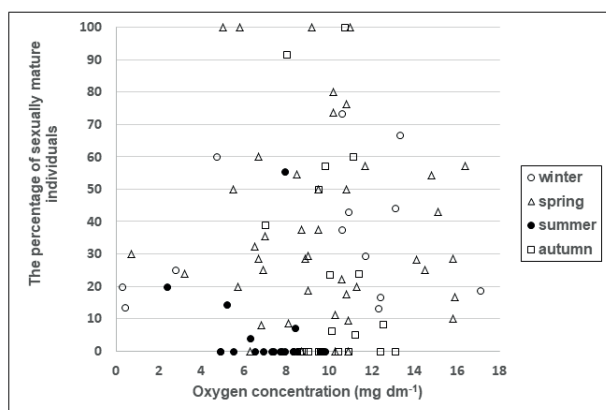


Figure 5
Relationship between the percentage of sexually mature individuals of *Potamothenis hammoniensis* and the oxygen concentration in the water near the bottom

Discussion

Research on abiotic parameters that significantly affect the reproduction of *Potamothenis hammoniensis* was carried out mainly in the 20th century. Discontinuation of such studies would suggest that the problem has already been solved. However, the results of this study do not fully confirm the previously observed (mainly in deep stratified lakes) regularities, which justifies the need to continue such studies also in shallow eutrophic lakes.

The percentage of sexually mature individuals

of *Potamothenis hammoniensis* varied in particular lakes and ranged from 14 to 72%. Due to different methodology (described in the Materials and methods section) used in this study, our results are in line with the expectations usually higher compared to the results of other authors (Wiśniewski 1979; Arkhipova 1980; Rîşnoveanu & Vadineanu 2002), defining the percentage of sexually mature individuals in the entire population, and not only in the group of specimens with the size indicating the capability to reproduce. It may be surprising that there was no correlation between the type of lake and the percentage of individuals with a developed reproductive system, because Żbikowski (2011) proved that the abiotic environment of the three types of shallow lakes distinguished in this paper varies greatly. Perhaps the reproduction of *P. hammoniensis* is significantly influenced by factors not included in the above-mentioned paper.

The percentage of sexually mature individuals of *Potamothenis hammoniensis* varied in particular months. It is worth noting that these specimens are almost absent only in summer (July to September). This may be surprising because in a shallow eutrophic lake in the Danube Delta, Rîşnoveanu & Vadineanu (2002) have identified the constant presence of reproductive specimens of this species from May to September. Furthermore, Arkhipova (1980) found even a slight increase in the percentage of breeding individuals in the Rybinsk Reservoir in August. The lack of breeding individuals in summer is characteristic of the deep profundal zone of stratified lakes, where the oxygen deficit in early summer ends the breeding season (Thorhauge 1975). In the lakes under study, only specimens with the developed reproductive system were identified in the period from March to May and in November and December, suggesting the occurrence of conditions favorable for reproduction. On the other hand, Moroz (1976) (in the temperate zone) and Matčinskaja & Pligin (1988) (in an Ukrainian reservoir)

report that *Potamothenis hammoniensis* breeds only once a year, from May to July. The above differences in the periods of reproductive activity of this species found between the studied lakes and literature data confirm the results of Thorhauge (1975) and Kravčenko & Šahmatova (1988), which show that *P. hammoniensis* can breed at different times of the year, depending on external conditions.

A very important aspect of this study was to identify the abiotic parameters of water and bottom sediments having an important impact on the sexual maturity of *Potamothenis hammoniensis*. The research has shown a significant correlation between the percentage of reproductive individuals and the conductivity, pH (positive correlations) and OC-% (negative correlation). Seasonal changes in the conductivity, pH and OC-% in the same lake were small, while these parameters varied in individual lakes. Data analysis shows that in some lakes, the worms generally reproduce more actively. Based on the research, it is difficult to explain the first two correlations. Whereas this study has confirmed the previous observations (Poddubnaja 1959; Arkhipova 1980; Reynoldson 1990) that the organic matter content in the sediments is one of the most important environmental factors affecting the life cycle of common Tubificidae.

In this study, no correlation between the water temperature and the percentage of individuals with a developed reproductive system was found. These results may be somewhat surprising, since the thermal conditions are considered as one of the most important environmental factors affecting the reproductive activity of aquatic worms. The researchers generally agree that the reproduction of *Potamothenis hammoniensis* begins when the water temperature reaches 5–7°C (Jónasson 1972; Arkhipova 1980). However, it is not easy to indicate the maximum temperature that limits the reproduction. Jónasson (1972) states that the species does not reproduce at a temperature above 13°C, while according to Rîşnoveanu & Vadineanu (2002) – above 20°C. The results obtained in this study may suggest that in shallow eutrophic lakes, *P. hammoniensis* could potentially breed already at temperatures of approx. 2–3°C, which is slightly lower than commonly believed. However, this hypothesis requires confirmation. The maximum temperature could be as high as 22–23°C, which is consistent with the results of Rîşnoveanu & Vadineanu (2002). It should be noted, however, that such a high temperature was recorded only in summer, when the reproductive activity was generally inhibited also at lower temperatures (17–20°C). On the other hand, the relative abundance of sexually mature individuals at the same temperature range

in spring (17–20°C) was quite high, similar to that at lower temperatures. Thus, there is no clear evidence that a temperature slightly above 20°C is a key factor inhibiting the species reproduction.

Low oxygen concentration is another important environmental factor affecting the reproductive activity of *Potamothenis hammoniensis* (Poddubnaja 1959; Thorhauge 1975; 1976). The results obtained in our study do not support this theory. The individuals with the developed reproductive system were found even when the water oxygen concentration was as low as $< 1 \text{ mg dm}^{-3}$. On the other hand, the lack of breeding individuals in summer and early autumn was unlikely due to the oxygen deficiency, because the oxygen concentration at that time was high enough and did not limit the reproduction in other seasons of the year. The results show that in shallow lakes, as opposed to deep lakes, oxygen conditions do not significantly affect the reproductive activity of *P. hammoniensis*.

Both in the shallow and deep lakes under study, we found no individuals of *Potamothenis hammoniensis* with a developed reproductive system in the second half of the summer. However, unlike the latter, the oxygen deficits were not a limiting factor for breeding in the shallow lakes. Furthermore, it cannot be concluded with certainty that the inhibition of species reproduction was mainly caused by too high water temperature near the bottom, because *P. hammoniensis* reproductive activity was high in spring when the temperature conditions were similar to those in summer. Perhaps the decisive factor is not only the absolute value, but also the time of exposure to the temperature considered to be close to the limit of reproduction. The spring temperature of approx. 20°C does not inhibit the reproductive activity of this species, but its maintenance in summer begins to limit the reproductive processes of *P. hammoniensis*. However, this hypothesis should be confirmed, which requires the continuation of this research.

Acknowledgements

We are very grateful to both anonymous reviewers for all their comments and suggestions that have undoubtedly contributed to improving the quality of this publication.

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