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Instability of spring environmental conditions as a driver of biotic interactions and crustacean structuring in meteorite crater ponds (Morasko, Poland)

by

Kasper Świdnicki^{1,*}, Anna M. Basińska^{2,3}, Natalia Kuczyńska-Kippen¹

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¹Department of Water Protection, Adam Mickiewicz University in Poznań, Faculty of Biology, ul. Umultowska 89, 61-614 Poznań, Poland

²Laboratory of Wetland Ecology and Monitoring, Faculty of Geography, Adam Mickiewicz University in Poznań, ul. Dzięgielowa 27, 61-680 Poznań, Poland

³Department of Meteorology, Poznań University of Life Sciences, ul. Piątkowska 94, 60-649 Poznań, Poland

Abstract

There are 150 meteorite craters worldwide, however, their aggregations are rarely noted. The nature reserve 'Meteoryt Morasko' in Poland with fishless meteorite ponds was analyzed as a unique ecosystem for biological analysis of invertebrate interactions. The aim of the study was to recognize the main environmental drivers of cladoceran and copepod community structure from among biotic (competitors and predators) and abiotic factors (i.e. oxygen and pH level) in the spring season.

The abundance of small cladocerans (Alonella excisa and Chydorus sphaericus) was the highest at the end of the spring season, i.e. in June, while large species (Daphnia pulex and Simocephalus exspinosus) were most abundant in May. Both size groups of Cladocera were negatively affected by invertebrate predators (Chaoborus crystallinus and carnivorous copepods), which are known to play an important role in structuring cladoceran communities due to the fishless character of the studied ponds. No negative effect of those predators was found for Copepoda, however, nauplii density was reduced by competitors (Aedes communis larvae and ostracods).

The temporary character of the examined ponds, oxygen depletion and low pH of water in the shallowest pond resulted in the abundant occurrence of cladoceran males, whose high densities are usually observed in autumn.

Key words: meteorite ponds, Cladocera, cladoceran males, Copepoda, invertebrate predators, competition

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^{*} Corresponding author: kaspers@amu.edu.pl

Introduction

Although there are over 150 identified meteorite craters in the world, the occurrence of their aggregations is highly scattered (Hodge 2010). The studied meteorite crater ponds are one of the largest groups of meteorite craters in the world (Stankowski 2001). The literature concerning such specific ecosystems mainly refers to large lakes located in very deep craters of over 100 m depth, e.g. Lake Siljan in Sweden (Joakim 1989; Bengtsson, Malm 1997) or Lake Karakul in Tajikistan (Mishke et al. 2010). Some of them were found to be inhabited by new species or those that are rare in the region or country, for instance Lake Elgygytgyn, Russia (Cremer et al. 2005; Kharitonov, Genkal 2010). The previous investigation conducted within the crater ponds in Poland (Morasko) also revealed the presence of some zooplankton species which are not commonly observed in Poland (Kuczyńska-Kippen

It was assumed that the fishless meteorite water bodies would be suitable sites to study interactions between microinvertebrate groups. As the seasonal variation of environmental factors may have a great impact on zooplankton structure (Czerniawski, Domagała 2012; Simões et al. 2012; Ziadi et al. 2015), we restricted the study period to the spring season. Many studies are based on the summer zooplankton dynamics (e.g. Chojnacki, Wegleńska 1984; Havens 1991; Srichandan et al. 2014; Wang et al. 2015). However, the spring season is crucial for the development of zooplankton, especially in shallow water bodies which freeze to the bottom during winter and often dry up in the summer. Every year, these types of ponds create completely new niches for zooplankton communities, shortly after the ice melts. On the other hand, the spring season is characterized by instability of environmental factors - abiotic and biotic conditions change rapidly during the transitional period between winter and spring, i.e. from April to June, and in the transitional period between the spring and summer season. Moreover, the studied meteorite ponds are very shallow and supplied only by rainwater, therefore they may dry up during summer and often persist only in spring and autumn. Thus, we decided to conduct the study to observe the succession, development and dynamics of the crustacean community during the spring season.

Due to the temporary character of the studied water bodies, the crucial factor for crustacean survival may lay in the resting egg bank and the high hatching rate following dry periods. In accordance with the parthenogenetic reproduction, the cladoceran community develops faster than the copepod community (Ekvall, Hansson 2012). On the other hand, immature forms of Copepoda may be more abundant in comparison with cladoceran individuals (Lampert, Sommer 2001). Furthermore, the males' occurrence helps cladocerans to survive under such unfavorable environmental conditions (Fryer 1968; Cáceres, Tessier 2004; Forró et al. 2008). The sexual eggs are much more resistant to harsh conditions than the parthenogenetic ones. Additionally, females hatched from sexual eggs supply their populations with new genetic material even after many years (Rybak, Błędzki 2010).

Vertebrate predators have a clear impact on the species composition and body size of crustaceans. Planktivorous fish feed on large Cladocera (e.g. from the Daphnidae family) more willingly than on smaller forms (e.g. from the Chydoridae family), therefore the dominance of small cladoceran species is characteristic of water bodies with fish. On the other hand, fishless water bodies are inhabited by large crustacean species which may be included exploitative and interference competition with smaller zooplankters (Lampert et al. 2014). In the conditions where no vertebrate predators occur, invertebrate planktivores may take control over the crustacean community structure. Some invertebrates, such as the phantom midge Chaoborus larvae and adult copepods, are predators that consume cladocerans (Fryer 1957; Pastorok 1981; Gliwicz, Umana 1994; Castilho-Noll, Arcifa 2007). Contrary to fish predation, invertebrate predators are limited by their mouth gape size and hence they may have a stronger limiting effect, especially on small-sized crustaceans. While microcrustaceans are able to win the competition with mosquito larvae (Meyabeme Elono et al. 2010; Duquesne et al. 2011; Kroeger et al. 2014), shallow and fishless water bodies may be inhabited by other groups of potential competitors for Cladocera and Copepoda, e.g. ostracods.

Biotic interactions are a key factor in structuring the crustacean community. Therefore, we analyzed the relationships between invertebrates (including cladoceran males), predators and competitors in meteorite crater ponds of varying depth. We hypothesize that meteorite crater depth will significantly affect the invertebrate community structure. Moreover, the zooplankton competitors in the studied ponds as well as invertebrate predators will have different impacts on particular groups of

crustaceans: small and large Cladocera, larvae and adult copepods.

Materials and methods

Study area

The studied meteorite craters originated 6000 years ago when an iron meteorite fell and its disintegrated parts created seven distinct craters in the ground (Stankowski 2001). The whole area is located within the city of Poznań (western Poland), among the forested area of Morasko Meteorite Nature Reserve (Fig. 1).

Within the craters, temporary shallow ponds exist due to rainwater accumulation. During the study period, only three craters were filled with water, while the remaining four were dry.

The analyzed water bodies varied in respect of size and depth (Table 1). The ponds are round in shape. Their maximum depth ranged from between a few dozen of centimetres to 2 metres. The water inside the craters was transparent to the bottom. Due to deciduous forest in their surroundings, dominated by oaks and hornbeams (Stankowski 2001), the water bodies had a large supply of organic matter.

Sampling and laboratory analyses

The research on the zooplankton community structure was carried out in the spring season of 2009. As a result of the temporal character of the studied ecosystems, only three ponds contained water were examined in the spring season of 2009. The studied ponds differed in terms of their depth and crater diameter, so we used three categories of their size throughout the whole article: a shallow pond (SP) of the maximum depth of 0.5 m, a medium pond (MP) of the maximum depth of 1.0 m and a deep pond (DP) of the maximum depth of 1.5 m.

Samples were collected weekly from the beginning of April to the end of June from the open water area of each pond in triplicate, using a calibrated vessel of a volume of 5 l. Samples were concentrated using a 45-µm plankton net and fixed immediately with 4% formalin. Identification of insect larvae and crustacean species was based on the identification key for Polish fauna (Skierska 1971; Sywula 1974; Rybak, Błędzki 2010). During the whole spring season, 39 samples in triplicates were collected from each pond (n=117).

Temperature, pH level and electric conductivity of water were measured *in situ* at the sampling sites. Moreover, water samples were also collected in order to conduct nutrient analyzes (the total

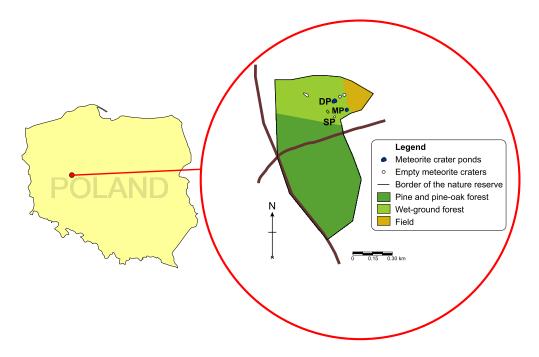


Figure 1

Location of the nature reserve "Meteorite Morasko" in Poland and location of the surveyed craters in the reserve (DP, MP and SP)



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Table 1

Mean values of physico-chemical parameters, abundance of competitors and predators, and morphometric parameters with the standard error and Kruskal-Wallis test (KW-H) in the studied meteorite crater ponds (DP – deep, MP – medium and SP – small) in different moths (A – April, M – May, J – June) (Temp – water temperature, O_2 – oxygen concentration, pH – pH value, Cond – electric conductivity, Chl a – chlorphyll a concentration, NO_3 – nitrate content, PO_4 – phosphorus content, A.com – Aedes communis, Ostrac – Ostracoda, Chaob – Chaoborus crystallinus, Comp Tot – the total number of competitors, Carn Cope – carnivorous copepods' abundance, Pred Tot – the total number of predators

		DP				MP				SP			
		A	М	J	KW-H	A	M	J	KW-H	A	М	J	KW-H
Abiotic parameters													
Temp	°C	9±3.0	13±1	14±4	10.6**	11±3	14±3	14±5	5.0	10±3	11±2	15±3	11.7**
O ₂	mg l-1	7.0±5.1	2.2±1.2	3.7±2.3	2.7	6.1±1.9	5.9±1.1	5.8±1.1	0.4	2.8±1.0	4.2±1.7	3.0±0.6	6.0*
pН	-	7.9±0.6	7.6±0.4	7.3±0.2	12.6**	7.6±0.1	7.4±0.3	7.4±0.7	0.1	6.4±0.3	6.9±0.4	7.0±0.0	17.3**
Cond	μS cm ⁻³	144±20	158±38	201±128	2.4	541±53	516±89	334±88	24.3**	362±240	695±221	429±12	19.0**
Chl a	μg l-1	84±51	14±11	5±5	19.5**	24±13	10±9	6±5	15.1**	24±17	25±16	7±4	14.8**
NO ₃	1.1	0.21±0.01	0.17±0.1	0.00±0.00	21.5**	0.19±0.02	0.18±0.11	0.00±0.00	20.5**	0.73±0.51	0.34±0.21	0.00±0.00	20.6**
PO ₄	mg l-1	2.27±0.25	3.21±0.31	2.03±0.63	24.3**	0.2±0.08	0.24±0.15	0.53±0.62	1.3	3.05±0.86	2.91±0.62	1.36±1.42	16.5**
Biotic parameters													
A.com		1±2	2±2	7±8	4.9	2±2	2±3	2±3	1.4	83.±130	4±3	4±4	7.4*
Ostrac		662±1014	1703±1631	27±64	21.7**	18±50	354±537	3±8	24.0**	6±9	22±23	0.1±0.3	19.0**
Chaob	ind. l-1	3±4	3±8	9±9	5.6	1±1	0.2±0.4	1±1	3.4	0.1±0.3	0±0	1±1	6.1*
Comp Tot	ind. i	663±1014	1705±1630	34±62	19.2**	20±50	357±536	5±7	22.5**	90±132	26±24	4±4	14.8**
Carn Cope		3±4	0.1±0.3	0±0	13.9**	5±6	0±0	0.1±0.3	18.5**	1±1	1±3	0±0	8.9*
Pred Tot		8±7	8±16	18±17	5.2	7±8	0.3±1	2±3	12.7**	1±2	1±2	1±1	3.1
Morphometric parameters													
Maximum crater diameter		40 35			27 25			16					
Maximum pond diameter	m							20					
Maximum pond depth		1.5				1			0.5				

^{*} p<0.05; ** p<0.01

phosphorus and nitrates) carried out according to the methods advised by Hermanowicz et al. (1999). Chlorophyll a was determined fluorometrically according to Lorenzen (1966). This method uses ethanol extraction and its concentrations were given as active photosynthetic pigments.

In accordance to the literature data (Flößner 2000; Rybak, Błędzki 2010), we classified the cladocerans into two size classes: large (the minimum size over 1 mm, e.g. *Daphnia* sp.) and small (the maximum size below 1 mm, e.g. *Alonella* sp.).

Among copepods, adult forms were identified to the species level (the density of nauplii and copepodite was analyzed along with adult community abundance).

The competitor group consisted of Ostracoda (the Cyprididae family) and mosquito larvae (*Aedes communis*), while phantom midge larvae, *Chaoborus crystallinus*, and carnivorous copepods were classified as predators.

The dominant species of Cladocera and Copepoda were determined as those whose density exceeded 10% of the total zooplankton abundance at each station.

Statistical analyzes

The species diversity of zooplankton inhabiting particular meteorite craters was evaluated using the Shannon index (Margalef 1957). Due to the data distribution and non-homogeneous variances, the non-parametric Kruskal-Wallis test and a multiple comparison of ranked data were used to determine the differences in zooplankton biocenotic parameters (species number, Shannon diversity and abundance) and environmental characteristics between particular months (April, May and June) and ponds (shallow – SP, medium – MP and deep – DP).

A redundancy analysis (RDA) of logarithmized data was carried out using the software Canoco 5.0 to examine the relationship between the environmental factors (physico-chemical parameters of water and ponds' depth categories) and their significance (Monte Carlo Permutation test with 999 permutations) for the distribution of the invertebrate abundance, species richness and diversity.



Results

Spatio-temporal fluctuations of physico-chemical parameters

Physico-chemical parameters varied during the study period in individual ponds (Table 1). The deepest and the shallowest pond were characterized by a clear increase in temperature from April to June (Table 1). However, the water in DP was characterized by a significantly reduced pH level, while pH of SP water significantly increased during the study period. The analyzed water bodies were also different in terms of water conductivity and PO₄ fluctuations. MP was characterized by a systematic decrease in water conductivity from April to June, whereas the highest values of this parameter in SP were noted in May. The maximum concentration of orthophosphates in DP was recorded in May, while

in SP – the concentration decreased from April to June. Significant oxygen concentration changes were observed only in SP, with the maximum value recorded in May. All three ponds were characterized by a significant decrease in chlorophyll *a* and nitrate content.

Zooplankton assemblage during the spring season

Zooplankton spring diversity

In total, 17 cladoceran and 20 copepod taxa were found. All meteorite crater ponds were characterized by poor species composition of Cladocera at the beginning of the study period (Fig. 2). Their species richness significantly increased in May in DP and MP and slightly decreased in June. On the other

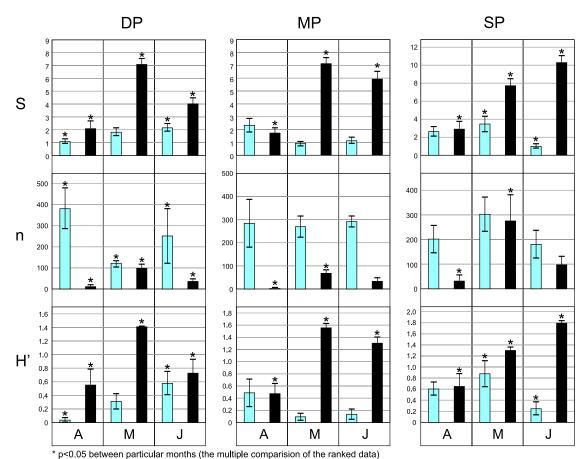


Figure 2

Mean values of copepod (blue bars) cladoceran (black bars) and species number (S), abundance (n; ind. I^{-1}) and Shannon diversity index (H') in meteorite crater ponds (DP – deep, MP – medium, SP – shallow) in different moths (A – April, M – May, J – June) with the standard error



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hand, SP was characterized by a gradual increase in the total number of cladoceran species from April to the end of the study period (p<0.01). The number of copepod species fluctuated throughout the study period from 1 to 3 taxa on average in every meteorite water body (Fig. 2). These changes were not significant in MP. The two other ponds were characterized by different dynamics of copepod species richness – the lowest in April in DP and increased gradually over the study period (p<0.01). On the other hand, the shallowest pond was characterized by a significantly larger number of Copepoda species in April and May compared to the last month of the study period.

Zooplankton spring abundance

The dominance of 9 species was observed (7 cladoceran species and 2 copepod species) (Table 2). Small Cladocera species (*Alonella excisa* and *Chydorus sphaericus*) dominated mainly in June, while large species (*Daphnia pulex* and *Simocephalus exspinosus*) were generally abundant in April and May (Table 2). Two copepod species (*Cyclops vicinus* and *Megacyclops viridis*) dominated in April and May and high density of *M. viridis* was noted only in June (ponds MP and SP).

The MP was characterized by the lowest mean cladoceran abundance throughout the study period in comparison with the other meteorite crater ponds. The most abundant Cladocera community was found in SP in May. However, the cladoceran density dynamics was similar in each water body and was characterized by a significant increase in the middle of the study period (Fig. 2).

The same trend was observed for Cladocera males, which each time showed the maximum abundance in May. The shallowest pond was characterized by the highest density of males in the middle of the spring season (Table 2).

The analysis of different size groups of cladocerans resulted in dissimilar observations. Large taxa revealed a density peak in May in each pond (p<0.01) (Fig. 3, Table 2). A similar pattern was found only in the case of small Cladocera in MP, while densities in the two other ponds revealed a significantly increasing pattern of their distribution.

The adult forms of copepods showed a strong decrease in the abundance dynamics in June in the shallowest pond. All the other fluctuations considering larvae and density of adult forms were insignificant (Fig. 2, Table 2).

Spring assemblage of predators and competitors

Strong fluctuations of potential competitors as well as predators of cladocerans and copepods were observed during the study period (Table 1). Each water body was characterized by a significant increase in the ostracod abundance in May and their virtual disappearance in June. At the same

Table 2

Mean values of cladoceran and copepod abundance with the list of dominant species in meteorite crater ponds (DP – deep, MP – medium, SP – shallow) in different months (A – April, M – May, J – June) with the standard error and Kruskal-Wallis test (KW-H) (Large Clad – large cladocerans, Small Clad – small cladocerans, Clad \mathring{o} – cladoceran males, Cope Larvae – copepod larvae, Cope Adult – adult forms of copepods)

	Unit	DP			MP				SP				
		A	M	J	KW-H	A	М	J	KW-H	A	М	J	KW-H
Large Clad		10±18	56±43	29±23	15.6**	3±4	33±26	7±5	19.3**	21±41	139±123	49.±58	14.2**
Small Clad		0.2±0.5	2±2	9±13	12.0**	1±2	25±17	22±19	17.9**	1±2	3±2	12±9	23.4**
Clad ♂	ind. l-1	0.3±1	8±10	0±0	11.6**	1±1	4±5	1±1	17.2**	8±17	85±90	3±3	21.5**
Cope Larvae		361±240	97±40	241±258	4.7	200±147	264±106	286±90	4.1	134±101	307±324	180±120	2.9
Cope Adult		12±18	19±16	10±9	3.4	10±11	5±5	5±4	0.8	5±4	11±10	1±1	14.8**
Alonella excisa				+			+	+					
Bosmina longirostris			+										
Chydorus sphaericus												+	
Daphnia pulex]	+	+			+	+			+	+	+	
Scapholeberis mucronata]											+	
Simocephalus exspinosus		+	+	+									
Cyclops vicinus		+				+							
Megacyclops viridis]	+	+	+		+		+					

^{**} p<0.01



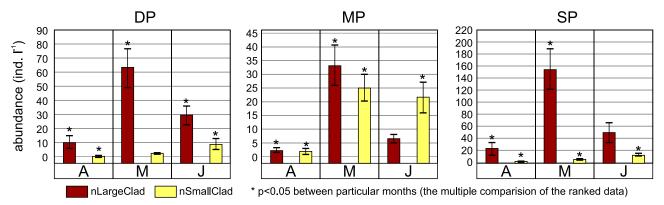


Figure 3

Mean number of large (nLargeClad) and small species (nSmallClad) of Cladocera (ind. I^{-1}) in the studied months (A – April, M – May, J – June) in meteorite crater ponds (DP – deep, MP – medium, SP – shallow) in different moths (A – April, M – May, J – June) with the standard error

time, *A. communis* densities slightly increased in DP (p>0.05), while a large decline was recorded in SP after the April peak (p<0.05).

The dynamics of invertebrate predators had a similar pattern in all three meteorite crater ponds. *Ch. crystallinus* abundance changed significantly only in SP (p<0.05). The density of predator copepods gradually decreased during the study period till they completely disappear in each pond by the end of the spring season (DP p<0.01, MP p<0.01, SP p<0.05) (Table 1).

Relationships between zooplankton, predators, competitors and environmental conditions

analysis Redundancy (RDA) revealed relationship between the zooplankton biocenotic parameters and physico-chemical parameters of water related to the depth of ponds. The high values of biocenotic parameters of crustacean communities were connected with SP. Moreover, the abundance of small and large cladoceran, their species richness and diversity were positively correlated with high values of water temperature and conductivity. Parameters of the Cladocera community were also negatively correlated with the predator density and chlorophyll a content. The species richness and the diversity of copepods as well as the density of cladoceran males and adult Copepoda were negatively affected by high oxygen concentration and pH of water. Copepod larvae and the above-mentioned environmental factors showed an inverse relation. Furthermore, nauplii were negatively correlated with competitor abundance (Fig. 4).

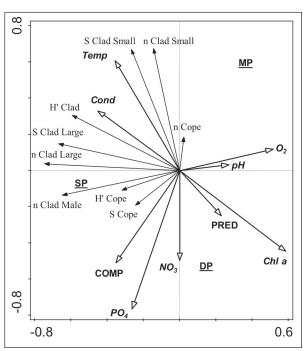


Figure 4

The redundancy analysis diagram showing the relationships between species richness (S), Shannon diversity index (H'), abundance (n)

(Clad Large – large cladocerans, Clad Small – small cladocerans, Clad Male – cladoceran males, Cope – copepods) and environmental factors (COMP – competitor numbers, PRED – predator numbers, Temp – water temperature, O_2 – oxygen concentration, pH – pH value, Cond – electric conductivity, ChI a – chlorophyll a concentration, NO_3 – nitrate content, PO_4 – phosphorus content) for the groups of invertebrate species in the studied meteorite crater ponds (DP – deep, MP – medium, SP – shallow)





The environmental factors used in RDA explained 53% of the zooplankton distribution (p<0.001). The most important factors structuring the crustacean community were chlorophyll a concentration, conductivity, oxygen concentration, PO $_4$ content, temperature, the presence of the medium pond, the shallow pond and the abundance of competitors (Table 3).

Table 3

Monte Carlo test for the significance of environmental factors in explaining the variation of biocenotic parameters of the crustacean community

Factor	variance explained (%)	F
Chl a	25.6	5.7**
Cond	18.6	3.9*
O_2	17.8	3.8*
PO_4	17.8	3.7*
Temp	17.5	3.7*
SP	16.2	3.4*
MP	15.8	3.3*
Comp	15.1	3.1*

^{**} p<0.001, * p<0.01

Discussion

The functioning of large and deep water bodies as well as the role of zooplankton has been the object of various research all over the world and over a relatively long period (e.g. Ikeda 1985; Jeppesen et al. 2011; Ejsmont-Karabin, Hutorowicz 2011). Although small water bodies have attracted the attention of scientists in the last two decades (e.g. Shurin 2000; Bhuiyan, Gupta 2007; Seminara et al. 2008; Czerniawski & Domagała 2013; Basińska et al. 2014), the knowledge of their role, the ecological mechanisms affecting their chemistry as well as the plant and animal communities that inhabit them is still insufficient, due to a great variety of pond types (Boix et al. 2012). This knowledge is insufficient especially in the case of rarer types of aquatic ecosystem, such as the meteorite craters presented in this study. The decomposition processes of organic matter (tree leaves) caused oxygen deficiencies and low pH, which together with the temporary character of the studied ponds resulted in a lack of fish, which makes those ecosystems suitable objects to study the biocenotic interactions in the invertebrate community.

The beginning of the spring season was characterized by low values of abundance and species richness for all the studied cladoceran groups, irrespective of the water body depth. This was a consequence of the specific character of small and shallow water bodies which freeze to the bottom during the winter season. Additionally, the location of ponds (forest surrounding, deep banks of craters) resulted in the shading of their surface which inhibited the spring increase in water temperature. Hence, the hatching rate of cladocerans from resting eggs was reduced after the ice had melted. The majority of Cladocera need a higher water temperature than that observed in April (mean 9-11°C) to build their community after the winter season. Vandekerkhove et al. (2005) suggest that the photoperiod is also important for the cladoceran development in the case of species richness as well as abundance. Moreover, we found a positive correlation in our study between the biocenotic parameters (abundance, species richness and diversity) of small and large cladocerans and water temperature, which is one of the crucial factors for the development of zooplankton communities in the early spring season.

After April, the total cladoceran abundance and species diversity increased, however, the trends were different in the case of small and large Cladocera. In general large cladocerans dominated over the small ones in all the studied ponds and periods. It is a typical phenomenon that large zooplankton organisms, e.g. representatives of *Daphnia* genus, often dominate in the absence of fish (Lampert et al. 2014), while in the case of water bodies with fish, the structuring often follows the direction of small forms of zooplankton (Havens, Beaver 2011; Iglesias et al. 2011; Vijverberg et al. 2014). Unlike the small cladocerans, the spring dynamics of large cladocerans was similar in every examined water body with the maximum values in May. Although the water temperature was higher in June than in May, the density and diversity of large cladocerans decreased toward the end of spring when the chlorophyll a concentration was the lowest, irrespective of the pond depth. Large cladocerans, e.g. from the Daphnia genus, are well known to be effective filtrators, which may reduce the phytoplankton development (Cottingham, Schindler 2000; Steiner 2002; Antilla et al. 2013). Therefore, the rapid increase in the abundance of large species, which was observed in May, might have led to phytoplankton food base depletion, which was also found in RDA results.

However, the abundance dynamics of small



and large species was different: while high species richness and density of large cladocerans occurred mainly in May in all ponds, the distribution of small cladocerans varied in the case of pond depth. The May peak in the number and abundance of small cladoceran species was observed only in the medium ponds while in the remaining ponds (deep and shallow meteorite water bodies), the abundance of small cladocerans increased up to the June maximum. This suggests that other factors affect the dynamics of small and large cladocerans in meteorite crater ponds. Small species from the family Chydoridae are well adapted not only to obtain the food by filtration (*Chydorus sphaericus*) (Eyto, Irvine 2001), but also to scrape it from organic or inorganic substrata (Alonella genus) (Fryer 1968). Therefore, they may not be so sensitive to algae depletion as typical filtrators, such as e.g. *Daphnia*. On the other hand, due to their small size, they may be more susceptible to displacement by larger competitors such as daphnids, ostracods or mosquito larvae. The negative effect of competitors on their community structure was assumed to be due to low densities of small cladocerans during the whole study period. However, the multivariate analysis did not confirm this expectation. The competitors negatively correlated only with nauplii abundance. Furthermore, the food base conditions were positively correlated with the deepest pond where invertebrate predators were most abundant. Both size groups of Cladocera were characterized by lower species richness, diversity and density in DP. Many authors (Preissen, Young 2005; Jäger et al. 2011; Juračka et al. 2011) have found that invertebrate predators have a negative effect on cladoceran communities in fishless water bodies. However, the observed negative correlation of small and large cladocerans with predator density strongly suggests a lack of selective predation impact by Chaoborus and carnivorous copepods. This result also suggests that the spring dynamics of small and large cladocerans was more affected by predatorprey interactions than by competition.

Similarly to small and large cladoceran densities, the males of Cladocera were also most abundant in May. Their occurrence was the highest in the case of the shallowest pond (SP) and negatively correlated with a high oxygen concentration as well as with high pH of water. The lowest values of these water parameters (recorded in SP) could have been unfavorable for most of the cladoceran taxa and could have been the reason for the high abundance of the cladoceran males. Forró et al. (2008)

established that a high contribution of males helps the community of cladocerans to survive and hence proves their resistance to harsh habitat conditions (Fryer 1968; Cáceres, Tessier 2004). This explain why cladoceran males usually occur in the autumn (Jankowski, Straile 2004; Nevalainen, Sarmaja-Korjonen 2008; Martin et al. 2014). However, the unfavorable conditions, observed in the studied meteorite ponds, resulted in the presence of an abundant community of Cladocera males in the spring. The abundance of cladoceran females was not negatively correlated with the conditions of low oxygen concentration. In general, they were represented by daphnids, which are known to be well adapted to unfavorable oxygen conditions through hemoglobin production. Even though it is connected with high metabolic costs, it enables them to survive in conditions of oxygen depletion, because transport of oxygen by hemoglobin is more efficient compare to hemocyanin (Fox 1948; Green 1956; Pirow et al.

Contrary to the cladoceran community, copepod species composition was characterized by minor spring fluctuations in each of the studied pond and revealed different relations to environmental factors. The number of Copepoda species did not depend on a temperature increase. Many of them are eurythermal. However, their adult forms are usually more frequently observed in cold seasons (including early spring months) than in the summer (Rybak, Błędzki 2010; Lampert, Sommer 2001).

Adult copepod species, which dominated during the study period (Cyclops vicinus and Megacyclops viridis), are referred to in the literature as often observed in shallow ponds or littoral zones of lakes (Rybak, Błędzki 2010; Kumar et al. 2010; Aygen 2011). Therefore, they showed a positive correlation with the shallowest meteorite water body, even though this small reservoir was the most susceptible to drying in comparison with the deeper ones. However, the drought periods occur in summer, which is a diapause time for many of the observed copepod species (e.g. C. vicinus and M. viridis), therefore they are able to survive those dry periods (Rybak, Błędzki 2010). Moreover, the number and diversity of adult copepod species were favored by a higher content of biogenic substance, such as phosphates and nitrates. These compounds are mainly allochthonous in ponds supplied only by rainwater, so the biogenic substances are released in the process of decomposition of tree leaves on the pond bottom (Lampert, Sommer 2001; Sobczyński, Joniak 2009). These kinds of sediments can be an





additional habitat for copepods as well as for other groups of organisms, such as bacteria, ciliates and ostracods which can also make up a supplementary food for some copepods.

The abundance of copepods was strongly dependent on the density of larvae, which usually reached ca. 95% of the total copepod abundance. In the case of the investigated meteor craters, Copepoda abundance was significantly higher than the cladoceran abundance. The high growth rate of copepods in the spring season may be connected with their ability to quickly colonize new ecosystems. On the other hand, the cladoceran resting egg bank may be a very important factor affecting the spring community structure of invertebrates. While drying or freezing of the water column may prevent adult individuals from surviving (Frisch, Green 2007), resting eggs can survive under these conditions and supply their population with new genetic material after the harsh conditions (Rybak, Błędzki 2010). Therefore, sexual eggs are important to cladoceran communities, especially in temporary water bodies. Cladocerans may also rapidly colonize ecosystems in the spring season, although they need a higher water temperature to develop quickly, compared to copepods (Rybak, Błędzki 2010). Thus, a seasonal segregation of both groups of crustaceans was observed as an effect of different life cycles of copepods and cladocerans as well as of the dependence of the Cladocera development on a high water temperature.

The abundance of copepods was not affected by predators. Nauplii and early copepodite stages are characterized by a small body size, therefore they can potentially be preyed upon by *Chaoborus* larvae. However, the fast swimming strategy of Copepoda and swift and rapid escape may prevent the success of predators (Reissen et al. 1984; Kiørboe et al. 2010). This suggests that despite the well-developed ability of copepod larvae to escape, invertebrate predators preferred to feed on cladocerans.

Conclusion

Despite the fact that the studied meteorite crater ponds were of the same origin and located in the same catchment area, and despite a small distance between the ponds, the spring dynamics of zooplankton was distinct different in particular water bodies. The spring succession of small cladocerans was modified by a pond depth, contrary to the dynamics of large cladocerans. The fishless character of the analyzed

ponds resulted in the co-occurrence of small and large cladocerans as well as in a strong impact from invertebrate predators (phantom midge *Chaoborus* larvae and adult copepods) on their community structure. A similar effect of invertebrate predators on both size groups of Cladocera suggests the lack of their feeding selectivity. Moreover, copepod larvae were negatively affected by high competitor abundance (*Aedes communis* and ostracods).

The meteorite crate ponds were characterized by a low water level and oxygen depletions. Those unfavorable abiotic conditions resulted in the high density of Cladocera males during the spring season. Moreover, cladocerans from the genus *Daphnia* produced hemoglobin, which better transports oxygen in the organism than hemocyanin, so they were not sensitive to oxygen deficiencies.

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