



Article Ephemeral Puddles—Potential Sites for Feeding and Reproduction of Hyporheic Copepoda

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Abstract: The hyporheic (phreatic) zone connects groundwater and surface water and hosts a diverse community of organisms that are adapted to its unique conditions. In order to investigate the hitherto poorly understood biotic connections between the hyporheic zone and temporary ponds, we analyzed changes in the community of Copepoda in a small and shallow ephemeral puddle in a meadow for one year, with comparison to the groundwater fauna of the surrounding region in northeastern Poland. In the puddle, three species of Cyclopoida (*Acanthocyclops vernalis, Diacyclops bisetosus,* and *Cyclops furcifer*) were present in large numbers throughout the year. These species were also common components of the region's groundwater fauna, but in much lower densities in the groundwater than in the puddle. These results suggest that temporary puddles can be a convenient place for copepods to feed and reproduce, while groundwater may serve as an important corridor for their dispersal. This study contributes to a more comprehensive understanding of copepod ecology and the functioning of ephemeral aquatic habitats.

Keywords: temporary ponds; phreatic zone; groundwater Copepoda; recolonization; seasonal succession; NE Poland



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1. Introduction

Ephemeral puddles in meadows are characterized by their cyclical nature. They form during wet periods when groundwater levels rise and the saturation zone (water table) reaches the surface. The hyporheic (phreatic) zone refers to the area underground where all the available spaces, such as the pore spaces in rocks or sediment, are filled with water. It represents a unique interface between surface water and deeper groundwater, a place where biogeochemical processes occur and create distinct ecological conditions [1,2]. The hyporheic zone is known to host a diverse community of organisms that are adapted to the unique physicochemical conditions and hydrological dynamics of this environment [3–5]. The extent to which temporary ponds interact with the hyporheic zone and their potential as a refuge or habitat for groundwater-inhabiting copepods, nonetheless, remains poorly understood.

The copepods, one of the major components of the groundwater fauna, are characterized by great species diversity in this habitat. About 1000 species and subspecies of Copepoda are known from continental groundwaters, and almost half of the newly described Copepoda species in recent years have been from groundwater habitats [6]. Previous work in northeastern Poland revealed a relatively stable composition but patchy distribution of the groundwater copepod community [7,8]. Seven species of stygophiles (species more frequently found in groundwater than surface water) occur there [7,8] and only one species of stygobiont—*Elaphoidella elaphoides* (Chappuis, 1924) [9]. Our study aimed to compare the copepod community composition of an ephemeral puddle and groundwater. Since the major environmental descriptors of groundwater habitats are oligotrophy and low food resources [6], we hypothesized that ephemeral puddles could serve as a favorable habitat for groundwater copepods due to a large amount of food available there and also as a place to produce offspring.

Temporary ponds are already well known as favorable habitats for copepods, including such typical species in northern Europe as *Cyclops furcifer* (Claus, 1857), *C. heberti* Einsle, 1996, and *C. singularis* Einsle, 1996 [10,11]. Diapause (dormancy) is well known in Copepoda, and it is crucial for their survival in temporary aquatic habitats, allowing them to endure harsh conditions and resume their life cycle when conditions become favorable [12]. Copepods fundamentally have a 13-stage life history, and diapause may occur in most of these stages, but in the freshwater Cyclopoida, it is most characteristic of late copepodite stages [13,14]. We hypothesize that the rapid colonization of temporary puddles occurs both through the revival of individuals in diapause and by the migration of copepods up from the hyporheic zone. Many previous studies have demonstrated the high dispersal capacity of crustacean zooplankton into isolated ponds [15,16], with the presumed vectors most often being wind [17,18] and animals—especially birds [19,20]; however, groundwater and the hyporheic zone have been ignored as a dispersal vector in research related to the re-establishment of zooplankton communities in temporary ponds [21,22].

Over the course of a year, we examined quantitative and qualitative aspects of the copepod community of a small and shallow ephemeral puddle in a meadow in northeastern Poland with the aim of comparing it to the community of groundwater copepods in that region. The studied puddle exists only in periods with intense rainfall (Figures 1 and 2) when the saturation level reaches the soil surface and a small depression in the terrain becomes filled with water. To document the copepod fauna, we present a morphological description of the adult females of each species encountered in the puddle, with an emphasis on the features that are most important for diagnosis. Studies of changes in its faunal composition ought to provide new insights into the role of the hyporheic zone in the ecology of temporary ponds as well as a more comprehensive understanding of copepod ecology and the functioning of temporary aquatic habitats in general.



Figure 1. Cont.



Figure 1. Views of a temporary puddle throughout the year (on sampling days): (**A**) 21 November 2021; (**B**) 5 December 2021; (**C**) 16 February 2022; (**D**) 19 March 2022; (**E**) 27 March 2022 (dry period); (**F**) 7 April 2022; (**G**) 13 July 2022; (**H**) 6 October 2022.



Figure 2. Daily rain precipitation (**A**) and daily maximum temperature (**B**) from September (IX) 2021 to October (X) 2022 at Białystok near the study site (data from www.tutiempo.net; accessed on 26 February 2024). The arrows indicate sampling dates. The bar between the graphs shows the periods when the puddle was present (white), dry (black), or either covered with ice or completely frozen (gray).

2. Materials and Methods

The analyzed temporary puddle was located in a meadow in the village of Kamionka (near the city of Białystok) in northeastern Poland (53°4'32.642″ N, 23°19'59.343″ E). The puddle occupied a small depression in a meadow near a drainage ditch (Figure 1). It appeared only after long-term rainfall when the soil saturation reached its maximum and the meadow was wet. Therefore, it was present mainly in the autumn and spring, while in the summer, only during the first half of July (Figure 2). It was covered with ice (Figure 1B) or completely frozen for a large part of the winter. The maximum surface area of the puddle was approximately 100 m², but in the summer, it was reduced to only a few square meters. Its depth when filled ranged from 20 to 40 cm. Views of the puddle throughout the year (on sampling days) are presented in Figure 1. Figure 2 shows the daily maximum temperature and daily precipitation data for the weather station in Białystok (near the study site) obtained from www.tutiempo.net (accessed on 26 February 2024).

At the beginning of the study period in 2021, the puddle appeared after intense rainfall in September and the beginning of October (Figure 2). The rest of October and the first half of November were characterized by sparse rainfall (Figure 2A) and high air temperatures (Figure 2B), which resulted in the puddle drying up. In the second half of November, the puddle reappeared after several days of light rainfall and lower air temperatures (Figure 2). It was present throughout the winter, but most of the time, it was either ice-covered or entirely frozen. The mean (\pm SD) maximum daily temperature in the winter was 3.3 \pm 4.0 °C, and the total precipitation in the winter amounted to 384 mm. In March 2022, the total rainfall was only 2 mm (Figure 2A) and the mean air temperature was 8.0 \pm 5.1 °C (Figure 2B), but the puddle was, nevertheless, sustained for most of March by rising groundwater levels due to snowmelt. At the end of March, due to a lack of rainfall and high temperatures, the puddle did dry up (Figure 1E), but it reappeared in early April after several days of rain. It then alternately dried up and reappeared after heavy rainfall in July and again in October (Figure 2).

In total, nine samples were collected on the following dates: 8 October 2021, 21 November 2021, 5 December 2021, 16 February 2022, 19 March 2022, 7 April 2022, 6 July 2022, 13 July 2022, and 6 October 2022 (Figure 2). Sampling usually took place every 3–4 weeks during periods when the temporary puddle existed, but the two sampling dates in July were just a week apart. The samples were collected using a 10 L bucket; 20 L of water was filtered each time through a 50 μ m plankton net and fixed with 96% alcohol. The Copepoda were analyzed using an Olympus BX53 optical microscope using the imaging software cellSens 2.1 (Olympus Corporation, Tokyo, Japan). The identification of species was determined for adult forms using taxonomical keys [23,24] and specialized publications [25,26]. All the individuals in the samples were enumerated, including the nauplii, copepodites, and adults of both sexes. For the purposes of documentation, an adult female of each species was dissected, and microphotographs were taken of the most important morphological features for diagnosis (thoracic legs P1–P5, furcal rami, antennule A1, cephalothorax, coxopodite of P4, etc.), as presented in Figures 3–5. Reference materials are deposited in the Department of Hydrobiology, University of Białystok as alcohol samples and microscopic slides. The developmental stages (nauplii and copepodites) and adults of both sexes of each encountered species of copepod were determined according to [23]. The body size (from the tip of the rostrum to the tips of the caudal rami) of at least 10 adult females and 10 males was measured for each species. The number of females with egg sacs, the number of free egg sacs, and the number of empty exoskeletons (copepodite and adult) in each sample were noted. The great majority of these exoskeletons were exuviae (molted cuticles) without any kind of predation-related mortality. Comparisons with the groundwater copepod fauna of the region were based on our previous comprehensive surveys of over 100 wells [7,8]. This allowed us to better understand the functioning and ecology of Copepoda in the temporary puddle and provide insight into the functioning of the hyporheic zone.



Figure 3. *Cyclops furcifer* (female): **(A)** habitus, right dorsolateral view; **(B)** furcal rami, dorsolateral view; **(C)** antennule (A1); **(D)** first pair of swimming legs (P1), dorsal view; **(E)** second pair of swimming legs (P2), dorsal view; **(F)** third pair of swimming legs (P3), dorsal view; **(G)** fourth pair of swimming legs (P4), dorsal view; **(H)** fifth pair of legs (P5), distal segment and distal part of proximal segment, lateral view; **(I)** ornamentation of coxopodite of P4, dorsal view.



Figure 4. *Acanthocyclops vernalis* (female): (**A**) habitus, left dorsolateral view; (**B**) antennule (A1), dorsal view; (**C**) furcal rami; (**D**) first pair of swimming legs (P1), dorsal view; (**E**) second pair of swimming legs (P2), dorsal view; (**F**) third pair of swimming legs (P3), dorsal view; (**G**) fourth pair of swimming legs (P4), dorsal view, with P5 (fifth leg) in upper left; (**H**) (enlarged from (**G**)) fifth pair of legs (P5), distal segment and distal part of proximal segment, lateral view.



Figure 5. *Diacyclops bisetosus* (female): (**A**) habitus, left lateral view; (**B**) antennule (A1) and antenna (A2), dorsal view; (**C**) furcal rami, left dorsolateral view; (**D**) first pair of swimming legs (P1), dorsal view; (**E**) second pair of swimming legs (P2), dorsal view; (**F**) third pair of swimming legs (P3), dorsal view; (**G**) fifth pair of legs (P5), lateral view; (**H**) fourth pair of swimming legs (P4), dorsal view.

3. Results

In the studied temporary puddle, we found three species of Copepoda, all of which belong to the Cyclopoida and were present for most of the year (Figure 6B): *Acanthocyclops vernalis* (Fischer, 1853), *Diacyclops bisetosus* (Rehberg, 1880), and *Cyclops furcifer* (Claus, 1857). All three species were characterized by large body size, with the adult females of *C. furcifer*, *A. vernalis*, and *D. bisetosus* being 1707 \pm 167 µm, 1420 \pm 184 µm, and 1116 \pm 91 µm long (mean \pm SD), respectively. The males were slightly smaller (81–88% as long) at 1383 \pm 105 µm, 1247 \pm 88 µm, and 937 \pm 86 µm long, respectively. A habitus view of the females of each species and illustrated descriptions of their most important morphological features for recognition are presented below. The molecular characteristics of the above three species from groundwater in northeastern Poland, based on a mitochondrial DNA marker (the COI gene), are presented elsewhere [7,8].



Figure 6. Characteristics of the copepod community in the studied temporary puddle on nine sampling dates throughout the year. (**A**) changes in densities of developmental stages (adults, copepodites, nauplii); (**B**) changes in density of each species and exoskeletons; (**C**) changes in densities of adult females and males; (**D**) changes in densities of females with egg sacs, of free egg sacs, and in the percentage of females bearing egg sacs.

The most distinguishing features of *C. furcifer* are the fifth pair of thoracic legs (P5) and the ornamentation of the coxopodite of P4. P5 has a strong spine that is longer than its second article (Figure 3H). The posterior coxopodal ornamentation of P4 includes two well-developed rows of spinules, a curved row in the proximal part, and two nearly colinear rows in the distal part, with one row composed of slightly longer spinules than the other (Figure 3I). Another characteristic feature is the pair of long, slender furcal rami, each ramus being up to 12 times longer than wide (Figure 3B) and bearing small hair-setae along its inner margin. The fourth and fifth thoracomeres (Th.4 and Th.5) point outwards (Figure 3A). The 17-segmented antennule (A1) reaches the middle of Th2 (Figure 3C). The most common spine formula for the swimming legs (the number of spines on the last segments of the exopodite of P1–P4) in the present material is 2333 (Figure 3D–G), whereas, in groundwater from this region, the most common formula for the swimming legs of *C. furcifer* is 3433 [7].

The most distinguishing feature of *A. vernalis* is its P5, which has a slender second article and quite a long spine (Figure 4H). Also, the characteristics of this species are an indentation in the outer margin of the first endopodal article of P4 and a long inner spine of the third endopodal segment that is longer than the outer spine (Figure 4G). The spine formula of the swimming legs is 3444 (Figure 4D–G). The 17-segmented A1 reaches the end of the cephalothorax (Figure 4B). The furcal rami are long and slender, up to eight times longer than wide (Figure 4C), with the terminal internal seta of each ramus about half as long as the ramus and longer than the terminal external seta (Figure 4C).

The most characteristic features of *D. bisetosus* concern P5, the swimming legs P1–P4, and the third endopodal segment of P4. P5 consists of two segments, and the second segment has a long and massive inner spine (Figure 5G). The swimming legs are three-segmented with a spine formula of 2333 (Figure 5D–F,H), with the inner spine of the third endopodal segment of P4 being longer than the outer one (Figure 5H). The 17-segmented A1 reaches the end of the cephalothorax (Figure 5A,B). The furcal rami are up to seven times longer than wide, with a lateral spine (FsII) located close to the outer margin of each ramus (Figure 5C).

The highest density was recorded for *C. furcifer*, reaching up to 77.9 adult ind. L⁻¹ (Figure 6B), with an average density of 14.9 \pm 26.0 ind. L⁻¹. *C. furcifer* was more numerous during the autumn (39.7 \pm 36.0 ind. L⁻¹), less abundant in the winter (3.8 \pm 2.0 ind. L⁻¹), and single individuals were found in the summer (Figure 6B). *A. vernalis* occurred throughout the year at similar densities (5.5 \pm 5.9 ind. L⁻¹). The average density of *D. bisetosus* was 3.1 \pm 3.6 ind. L⁻¹, with the highest abundance in the summer (Figure 6B).

The total density of adult individuals and copepodites for all three species combined ranged from 0.8 ind. L^{-1} (in the summer right after the puddle appeared) to 126.9 ind. L^{-1} in the autumn (Figure 6A), with a mean (±SD) density of 45.1 ± 46.7 ind. L^{-1} . The naupliar densities ranged from 0.1 ind. 198 L^{-1} to 229.6 ind. L^{-1} with a mean density of 21.6 ± 33.8 ind. L^{-1} . Larger numbers of nauplii occurred in the autumn; the rest of the time they were present in low numbers, except for increases in March and July (Figure 6A). Adult females were much more abundant than adult males in the autumn and summer but were only about twice as abundant as the males in the spring, while in the winter, the numbers of males and females were similar (Figure 6C). The females started to produce egg sacs at the beginning of the spring and continued to do so through the summer into the beginning of the autumn (Figure 6D). Many egg sacs were observed that were not attached to females (free egg sacs), often in numbers exceeding the number of females with egg sacs (Figure 6D). Empty exoskeletons were encountered in most samples, with the highest numbers in the autumn of 2021 (Figure 6B).

The peak in copepodite numbers observed in October 2021 was followed in November by a peak in the number of adult copepods (Figure 6A). The majority of the latter were female (Figure 6C), but only a few of them had egg sacs (Figure 6D). The relative dearth of nauplii that ensued lasted until the end of the winter (Figure 6A). An impressive increase in the abundance of copepods at the beginning of the autumn of 2022 was characterized by a high number of females (Figure 6C), many of which, unlike the previous year, bore egg sacs (Figure 6D). Additionally, there were a large number of 'free' egg sacs in the water (Figure 6D), and a large number of nauplii were present at the beginning of the autumn of 2022 (Figure 6A). A high proportion of females with egg sacs was also found in the spring and summer (Figure 6D), suggesting that copepod populations in temporary puddles may increase already in the spring and summer, although the maximum takes place at the beginning of the autumn.

4. Discussion

Temporary shallow-water structures in meadows and floodplains that are related to the hyporheic zone and groundwater level could be exceptionally rich in terms of biodiversity [27]. They also provide important ecological functions and ecosystem services such as hydrological regulation, nutrient retention, and wildlife protection [28]. However, these types of ecosystems are particularly vulnerable nowadays due to the widespread regulation of rivers and smaller watercourses as well as ubiquitous drainage ditches in meadows [29]. Changes caused by anthropogenic pressure were observed also in the studied site, where two years after field tests, the meadow moisture decreased due to the construction of houses and a road through the meadow.

Copepods were the dominant component of the fauna in the temporary puddle we studied, maintaining high population densities throughout most of the year. Their mean total abundance was 45.1 \pm 46.7 ind. L⁻¹, while in the groundwater of northeastern Poland, copepods occur at a much lower density: 0.6 ± 1.8 ind. L^{-1} [7,8]. Comprehensive surveys of the groundwater fauna in this region (129 wells, located 5 km to 80 km from the studied temporary puddle) had already revealed a patchy distribution of Copepoda with a, nonetheless, relatively stable community composition including eight stygophiles (species more common in groundwater than in surface waters) [7,8]. The three species recorded in the present study—Acanthocyclops vernalis, Diacyclops bisetosus, and Cyclops furcifer—were among those eight, and all three also occurred throughout the year and in much greater densities in the puddle than in the groundwater [7,8]. Acanthocyclops vernalis and Diacyclops bisetosus were also common components of the groundwater fauna in mountainous areas of southern Poland [30] and lowland areas of Central Europe [31], which confirms the common occurrence of these species in groundwater. Therefore, our research may indicate that groundwater serves as an important corridor for the dispersal of copepods, while temporary puddles serve as convenient places for them to find large amounts of food, in contrast to the meager food resources and oligotrophy typical of groundwater habitats [6]. This could be true, especially in the glaciated areas of the Holarctic, where Pleistocene glaciations impoverished groundwater fauna in northern Europe [31] and North America [32,33]. The copepod communities of alluvial aquifers of central and northern Europe are dominated by more widely distributed species [8,31,34], in contrast with the non-glaciated areas of Europe where large endemism was found and a distinctly higher number of stygobiont species [31,35,36].

The large number of females with egg sacs found in the present study suggests that temporary puddles are also favorable places for producing offspring, especially since female copepods with egg sacs are rarely found in the region's groundwater [7,8]. The large number of "free" egg sacs in the puddle may be an indication that some species there differ from most freshwater Cyclopoida, the females of which bear until hatching two egg sacs attached to the genital segment on either side of the urosome [14,24]. Some species of Cyclopoida, e.g., *Acanthocyclops venustus* (Norman, Scott, 1906), can lay eggs directly into the water [14,24,37], and one or more of the present three species may be intermediate, releasing sacs full of unhatched eggs when the conditions are favorable. A large number of free egg sacs observed in our study suggests that favorable conditions may have prompted a shift in the behavior of Copepoda. The experimental results clearly indicated that egg sacs impair the swimming of cyclopoid females and increase the energetic costs of movement [38].

All three species found in this study (*A. vernalis, D. bisetosus,* and *C. furcifer*) are widely distributed in Europe and have been frequently reported from various habitats including shallow lakes, pools, swamps, and especially temporary waters [10,11,23,24,39,40]. *Cyclops furcifer*, in particular, is a typical species of ephemeral waters, including sites that often experience long periods of desiccation; it is rarely found in other habitats [10,23], but it does occur in the groundwater of northeastern Poland, often in high abundance [7]. Many kinds of copepods undergo diapause during the life cycle at different developmental stages—as adults, copepodites, or eggs [41]. The three species found in the present study (*A. vernalis, D. bisetosus,* and *C. furcifer*) are well-adapted to desiccation, and their resting stages can survive drying for several years. They most often undergo diapause in copepodite stage C4 without encystment, buried at depths of up to 5 cm in the bottom sediment [24,42]. Furthermore, each cohort of *C. furcifer* can produce resting stages apart from the larvae that develop into adults [10,23]. Due to these adaptations, copepodites can appear immediately

after the refilling of a pond [10,23]. In our study, very low numbers of copepods were observed immediately after the puddle's refilling in July; nevertheless, a week later large numbers of copepods in all developmental stages (adults, copepodites, nauplii) were found (Figure 3A) as well as a large number of females with egg sacs (Figure 3D). The short delay in repopulation, along with the diversity of stages present, suggests that besides the cessation of diapause, the migration of copepods from the groundwater and hyporheic (phreatic) zone into the temporary puddles for the production of offspring may occur when the conditions are favorable.

The recolonization of temporary ponds has most often been attributed to recruitment from the dormant egg bank [43–46]. Other studies have pointed out the high dispersal capacity of crustacean zooplankton into isolated ponds [15,16], but the most frequently assumed vectors have been wind [17,18] and animals (birds, mammals, and amphibians) [19,20]. The present study shows that, for copepods at least, groundwater and the phreatic zone may be another important migration corridor, a possibility that has not yet been seriously considered in studies related to the re-establishment of zooplankton in temporary ponds [21,22]. The studies from Everglades National Park (USA) suggest that copepod communities after the re-wetting of ephemeral habitats are largely determined by the groundwater communities and by the re-emergence of dormant stages, both of which are affected by hydrological factors such as the hydroperiod and the extent of dry-down [47].

We found that three species of Copepoda (*A. vernalis*, *D. bisetosus*, and *C. furcifer*) can take advantage of the studied temporary puddle conditions to attain high densities and monopolize aquatic resources there. Mosquitoes also frequently colonize this type of ephemeral water body [48], but we found only a few mosquito larvae in our samples. The abundance of large-bodied copepods in the studied puddle may have prevented the development of mosquito larvae there, and such large copepods are promising candidates for the biological control of mosquito larvae more generally [49–51]. Cyclopoid copepods have proved to be more effective for practical mosquito control than any other invertebrate predator of mosquito larvae [49].

5. Conclusions

The findings of our study shed light on the significance of ephemeral puddles as crucial habitats for groundwater Cyclopoida. Three species of Cyclopoida, *Acanthocyclops vernalis, Diacyclops bisetosus,* and *Cyclops furcifer,* were found to be year-round residents of the temporary puddle under study. These species were also part of the groundwater fauna of the surrounding region, albeit they were far less common there. These findings shed light on the significance of ephemeral puddles and other temporary waters as crucial habitats for groundwater copepods, suggesting that they may provide an optimal environment for feeding and breeding. Our findings also highlight an intricate but under-appreciated interplay between temporary puddles and groundwater systems since the former may serve as vital hubs for population dynamics, while the latter may act as important corridors for dispersal. An appreciation of the ecological importance of ephemeral puddles as essential adjuncts of the hyporheic zone can also provide valuable insights into the life history strategies of copepods.

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