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Winners and Losers of Water Stress: Does the Drying Up of Peat Ponds Affect All Groups of Aquatic Organisms in the Same Way?

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Abstract

Climate change models point to a possible rise in air temperature, ranging from 2 °C to 4 °C. Global changes will therefore have a particularly pronounced effect on the functioning of shallow water bodies known as peat ponds, i.e., habitats formed after peat extraction in peatlands. However, the extent of this impact is still unknown. The main objective of the study was to determine the impact of water level and water physicochemical properties on the functioning of selected groups of aquatic organisms in peat ponds of different origins. The study was conducted in spring, summer and autumn of the years 2024 and 2025, in 10 peat ponds with different trophic status and typology, located in the Polesie National Park in eastern Poland. Considerable fluctuations in water levels, resulting from a scarcity of precipitation, accelerated the drying out and overgrowth of peat ponds, particularly the alkaline and acidic types. Within the zoocoenotic communities, a significant decline in the abundance of planktonic species and an increase in the abundance of littoral or periphytic species were recorded ($F = 6.24$, $p < 0.015$). Regarding trophic structure, an increase in the abundance of mixotrophic species and a decrease in the abundance of top-level predators were observed. Hydrological changes were reflected in an increase in species richness and abundance of communities of organisms with broad ecological tolerance (mainly ciliates), and a decrease in the number of species and abundance of planktonic crustaceans and macroinvertebrates. The RDA model explains over 84% of the total variability, indicating excellent model fit to the data and a strong correlation between environmental variables and species composition. Based on p values, water level, temperature, pH, and COD were selected as significant variables, with conductivity, O_2, and P_{tot} demonstrating less statistical significance. Peat ponds ecosystems can serve as an excellent model system for studying the impact of intensifying climate change on the functioning of shallow water bodies.

Keywords: peatlands; peat ponds; hydrology; zooplankton; macroinvertebrates

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1. Introduction

Peatland ecosystems serve an important role in global carbon and nitrogen cycles. At the same time, they are among the fastest-disappearing ecosystems with low resilience to anthropogenic impacts. These ecosystems were exploited particularly heavily in the 1960s and 1970s for peat extraction. As a result, a number of small water bodies, the so-called peat ponds, formed on their surface.

Due to decades of succession processes, these water bodies have become an interesting subject for ecological research, including studies in evolutionary biology and the monitoring of global environmental changes [1,2]. The current so-called Anthropocene period, with its dynamic climate changes, is leading to the degradation of hydrogenic soils, reduced habitat diversity, increased eutrophication of peatland habitats, lowered water tables and the frequent drying up of these water bodies.

Current climate change modelling indicates a possible rise in air temperature of 2–4 °C [3,4]. Consequently, rising temperatures affect the growth of primary producers, particularly phytoplankton, as well as the duration and frequency of ice formation on water bodies, and the trophic and hydrological conditions of small water bodies [5,6]. These changes particularly affect peat ponds [2]. While the functioning of shallow lakes in a warming climate is increasingly well understood [5,6], few studies have examined the impact of these changes on the biodiversity of peat ponds. Particularly little is known about the impact of changing hydrological conditions, combined with the trophic gradient, on communities of micro- and macroorganisms and the functioning of food webs.

Peat ponds, formed within raised bogs or transition bogs, are typically characterised by low primary production, low pH, and low nutrient concentrations. In contrast, peat ponds formed within fens or calcareous fens are most often characterised by higher pH values, higher nutrient concentrations, and higher primary production [7]. Due to their small surface area and shallow depth, these water bodies may be particularly sensitive to unstable hydrological conditions, and their changes may be highly dynamic. To date, only episodic studies have been conducted in these ecosystems, focusing on a limited number of aquatic organism groups.

Only a few studies have been published on the protozooplankton of small water bodies in peatland areas of Tierra del Fuego (Argentina) [2,3,8] and in the European temperate climate zone [9]. These studies demonstrated that the occurrence of protozoa was primarily influenced by pH and organic matter concentration. Research has also been conducted on zooplankton communities (rotifers, copepods and cladocerans) in small dystrophic lakes with habitat conditions slightly similar to those of acidic peat ponds [4,5] or rotifers in peatland ecosystems in habitats dominated by *Sphagnum* sp. [10,11]. However, there is no comprehensive research into the links between trophic and hydrological conditions and the functioning of micro- and macroorganisms in these habitats. The response of bacteria, testate amoebae or small metazoans, i.e., organisms that often dominate in peatland ecosystems, to changes in the hydrological conditions of these water bodies remains unknown [7].

Undoubtedly, however, hydrological and peat conditions have significant consequences for the global carbon cycle [12–15]. Direct effects of these impacts include, e.g., the influence on oxygen conditions and methanogenesis processes [12], while indirect effects are reflected in the decline of typically peat-forming plant species, mainly of the genus *Sphagnum*, and an increase in the proportion of vascular plant cover [15]. This may consequently result in the restructuring of the vegetation in these water bodies and have a particularly profound impact on microorganism communities, which respond much more rapidly to ongoing environmental changes than other groups of organisms or the vegetation itself [12,16,17].

Abiotic factors can influence biological parameters and, consequently, control the occurrence of individual communities of organisms. Among these communities, protozoans play a particularly important role as bioindicators, both in relation to changing hydrological conditions and anthropogenic pollution of peatlands [15,18,19].

The lack of comprehensive information regarding the responses of specific groups of organisms to rapidly changing environmental conditions in peat pond ecosystems amidst the climate crisis inspired this research. Knowledge of scenarios of changes in water level is extremely important in predicting the response of ecosystems to increasing human pressure, including climate change.

We tested the following hypotheses:

Hypothesis 1: *Due to their faster rate of multiplication, the response of bacteria, algae and ciliates to the decrease in water level will be much faster than that of testate amoebae and small metazoans, and a decrease in the water level in peat ponds will mediate changes in species richness and abundance of aqueous organism communities.*

Hypothesis 2: *Communities of microorganisms and small metazoans exhibit pronounced species diversity along the trophic gradient of peat ponds.*

Hypothesis 3: *A decreased water level in peat ponds causes changes in the significance and strength of relationships between dominant microbial consumers and food web.*

2. Materials and Methods

2.1. Study Area

The study was conducted during three seasons, spring, summer and autumn of the years 2024 and 2025 and covered 10 peat ponds of varied trophic status and typology, located within different types of peatlands in the Polesie National Park in eastern Poland (Figure 1).

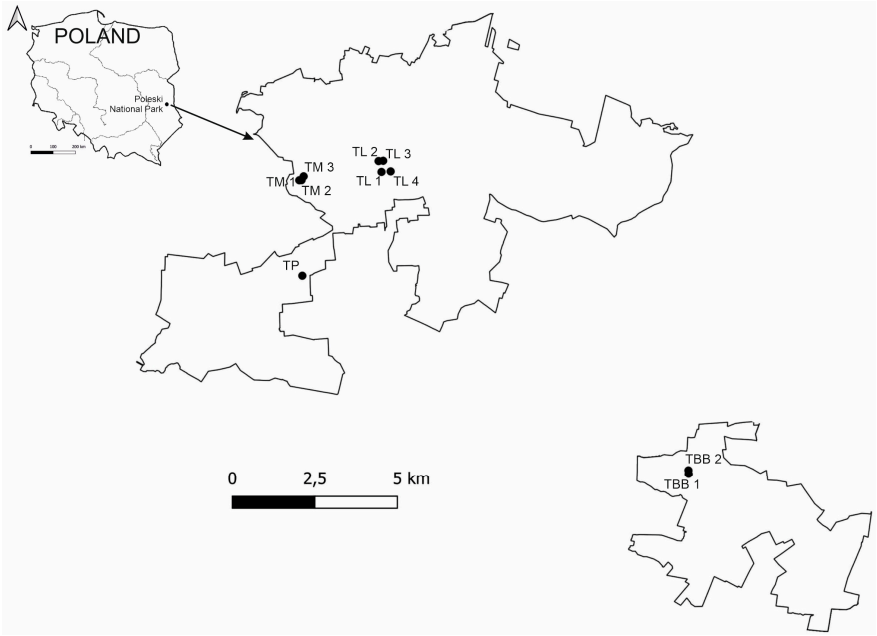

Figure 1. Location of the study area; explanation of abbreviations in Table 1.

These included alkaline peat ponds situated in fens in the Lipniak area (TL1, TL2, TL3, TL4) and the Podkaraśne peat pond (TP), as well as acidic peat ponds situated in raised bogs or transition bogs in the Lake Moszne area (TM1, TM2, TM3), and calcareous peat ponds situated in the Bagno Bubnów calcareous fen (TBB1, TBB2) (Table 1).

In total, 60 samples were collected each year across three seasons for each of the studied groups of organisms (10 peat ponds × 3 seasons × 2 sites: littoral/pelagic). The vegetation of the peat ponds showed considerable variation, depending on pond type. Alkaline peat ponds were dominated by *Hottonia palustris*, *Oenanthe aquatica*, and a few true sedges and grasses. Acidic peat ponds were dominated by *Sphagnum* sp., with *Utricularia vulgaris* and *Calla palustris* also found there. In calcareous peat ponds, *Phragmites australis*, *Chara fragilis*, *Utricularia vulgaris* and *Potamogeton natans* were dominant.

Table 1. List of the examined peat ponds, their location and abbreviations of the site names used in the text.

Site/Peat Pond	Abbreviation of the Position Name	Location
Peat pond Lipniak 1	TL1	51,458 N, 23,147 E
Peat pond Lipniak 2	TL2	51,461 N, 23,146 E
Peat pond Lipniak 3	TL3	51,461 N, 23,148 E
Peat pond Lipniak 4	TL4	51,458 N, 23,151 E
Peat pond Moszne 1	TM1	51,457 N, 23,111 E
Peat pond Moszne 2	TM2	51,457 N, 23,112 E
Peat pond Moszne 3	TM3	51,458 N, 23,113 E
Peat pond Podkaraśne	TP	51,431 N, 23,110 E
Peat pond Bagno Bubnów 1	TBB1	51,371 N, 23,273 E
Peat pond Bagno Bubnów 2	TBB2	51,372 N, 23,273 E

2.2. Hydrological and Physico-Chemical Analyses

Hydrological and the physicochemical analyses of the water included water level (WL) and temperature, pH, conductivity, oxygen, oxygen saturation, and nutrients: phosphates ($P\text{-}PO_4^{3-}$), ammonium nitrogen ($N\text{-}NH_4^+$), nitrogen total (N_{tot}), total phosphorus (P_{tot}), total suspended solids (TSS), total organic carbon (TOC), chemical oxygen demand (COD), biochemical oxygen demand (BOD), nephelometric turbidity unit (NTU) and chlorophyll *a*. Temperature, oxygen, electrical conductivity, pH, NTU and chlorophyll *a* were determined directly in the waters of peat ponds using multi-parameter probes (YSI 556 MES; OMC ENVAG, Yellow Spring, OH, USA). Nutrients were analysed using colorimetric methods [20]. COD, BOD, TSS and TOC were determined using a UV spectrophotometer.

2.3. Aquatic Organisms

Plankton samples were collected using a TOŃ water sampler from the littoral and pelagic zones, and identified using an inverted microscope Nikon Eclipse TE 200 (Nikon Corporation, Tokio, Japan).

To assess the abundance of algae, 1 L of water from the collected samples was preserved with Lugol's iodine. A portion of the preserved sample (50 mL) was concentrated by 48-h settling, and then phycoflora was counted by means of light microscopy in a 1 mL plankton chamber. The remaining portion was used to prepare slides, which assisted in the taxonomic identification of phytoplankton. The biomass of microalgae was estimated by cell volume measurements [21]. Algal systematics was based on Van den Hoek et al. [22].

The abundance and biomass of the heterotrophic bacteria were determined using DAPI (4′6-diamino-2-phenylindole) [23]. Ten millilitres of water was preserved in formaldehyde to a final concentration of 2%. The preserved sample was stored in the dark at 4 °C and analysed within 24 h. Sub-samples of 2 mL were concentrated on polycarbonate filters coated with Irgalan black with a pore size of 0.2 µm, and enumerated by epifluorescence microscope (Nikon Eclipse TE 200).

The abundance of ciliates and testate amoebae was determined using the Utermöhl method [24]. Samples of testate amoebae and ciliates (3 samples; total sample volume = 500 mL) were allowed to settle for 24 h in a cylinder sealed with parafilm, and the upper 400 mL was then gently removed. To determine abundance and biomass, three samples were preserved in Lugol's iodine. In each case, live samples were observed for taxonomic and trophic identification. Morphological identifications of protozoans were mainly

based on studies by Foissner and Berger [25], Foissner et al. [26], and Charman et al. [27]. Biovolumes were estimated by assuming geometric shapes and converting to carbon using the following conversion factors: heterotrophic bacteria: 1 $\mu m^3 = 5.6 \times 10^{-7}$ µgC; ciliates and testate amoebae: 1 $\mu m^3 = 1.1 \times 10^{-7}$ µgC [13].

Rotifers, cladocerans and copepods were collected using a 5 L sampler. Samples were sieved through a 25 µm mesh, dispersed into a 100 mL bottle, and fixed in a formalin-glycerol solution. The studies of Ruttner-Kolisko [28] and Koste [29] were used to identify metazoans. The biomass of rotifers was calculated using the standard dry weight method of Bottrell et al. [30]. In the laboratory, crustacean classification and counts were made using the Sedgewick–Rafter cell to calculate abundance as individuals per 1 L^{-1}. Crustacean biomass was estimated via the relations between body length and body mass of a given specimen [30,31] by applying established mathematical formulas. The carbon content of metazoans was calculated using a conversion factor of 0.48 µg C per µg dry weight [32].

Quantitative zoobenthos samples were collected using a Kajak tube sampler with a sampling area of 19.6 cm^2. The bottom sediment was collected in this way and rinsed using a benthic net with a mesh size of 0.28 mm, while zoopleuston was collected using a rectangular frame with an area of 0.25 m^2, made of duraluminum sheet, from which the material was taken using a hydrobiological dip net. Samples of benthos and zoopleuston were collected on each date in triplicate, and placed in plastic bags. In the laboratory, the samples were placed on white photo-processing trays, and the invertebrates were transferred to containers and preserved in 80% ethanol. Morphological identification was carried out using a Nikon SMZ 800 stereo microscope (Nikon Corporation, Tokio, Japan), based on identification keys by Kołodziejczyk and Koperski [33] and Tończyk and Siciński [34]. The number of identified individuals was converted to 1 m^2 of water surface area (zoopleuston) or bottom surface area (benthos). The biomass of the macrofauna was determined by weighing individual specimens on an Ohaus Explorer analytical balance with an accuracy of 0.1 mg. The values provided are gross wet weight.

2.4. Statistical Analysis

Statistical analyses were performed using R software (version 4.3.1) and STATISTICA 7.0 (StatSoft, Hamburg, Germany). Differences in the physicochemical parameters as well as in the abundance of aquatic organism communities within the studied sites were tested using factorial ANOVA (peat ponds, season). Subsequently, pairwise differences between peat pond types were identified using post-hoc comparisons. Statistical significance was accepted at $p < 0.05$. Pearson's correlation coefficients were calculated in order to specify the interactions between physicochemical parameters and aquatic organism communities and between food web components. Statistical significance was accepted at $p < 0.05$. We performed non-metric multidimensional scaling (NMDS) based on the taxonomic composition of hydrobionts in relation to seasonal variability in individual peat ponds types. Data including biological parameters were mapped to NMDS using the envfit function. NMDS was calculated using the Bray–Curtis distance. The RDA ordination analysis used data specific to the individual taxonomic groups analyzed and subjected them to a Hellinger transformation. Environmental data were not standardized as explanatory variables. The significance of the RDA model, individual environmental variables and canonical axes was assessed using Monte Carlo permutation tests with 999 permutations. The significance of the model was assessed using a permutation test (ANOVA); the obtained result ($p = 0.001$) indicates that the model is statistically significant, meaning that environmental variables significantly explain the variability of the species data. The results of the classification were presented graphically in the form of a combination of dendrograms and heatmaps.

3. Results

3.1. Hydrological and Physicochemical Parameters

In the studied water bodies, the lowest mean water level (WL) was observed in peat ponds TL1–TL4 and TM1–TM3 (4–5 cm); in peat pond TP, it reached 43 cm, while in TBB1–TBB2, it reached 66–70 cm. Water levels showed significant seasonal variability ($F = 12.23$, $p < 0.001$). WL in peat ponds L1–L4 reaching a maximum of approximately 10 cm in spring, and dropping to 3–4 cm in summer. In autumn, no open water was observed, as these peat ponds had completely dried out. In TP, the water level fluctuated significantly throughout the study period, reaching approximately 60 cm in spring, 40 cm in summer and 30 cm in autumn. In TM1–TM3, the water level was very low, reaching a maximum of approximately 10 cm in spring and 5 cm in summer, whereas in autumn, no open water surface was observed in TM3. A relatively stable water level was observed in the peat ponds TBB1–2, ranging from approximately 60 to 80 cm.

The waters of the peat ponds exhibited particular physicochemical properties that were linked to the genetic type of the peatland. The pH varied distinctly, ranging from 4.3 in peat ponds TM1–3 to 7.0–7.4 in ponds TL1–4 and TP, and up to 7.3–7.4 in TBB1–2 ($F = 11.87$, $p < 0.001$). Water temperature values were similar across all water bodies under study, with significantly higher values during the summer season, while water oxygen content was highest in peat ponds TL4 and TBB1. Electrical conductivity was significantly higher in the peat pond TL1 (360 µS cm^{-1}), while distinctly lower values were noted in the acidic peat ponds ($F = 12.37$, $p < 0.001$). The highest nutrient concentrations and the highest TOC, BOD and COD values were found in the peat ponds TL1–4 and TM1–3 and increased considerably in summer and autumn. Similar patterns were observed for total suspended solids (TSS) ($F = 11.82$, $p < 0.001$). Chlorophyll *a* concentrations were the highest in the peat ponds TM1–3, and the lowest in TBB1–2 and TL1–2, with this parameter increasing markedly during the summer season ($F = 4.28$, $p < 0.015$) (Table 2).

Table 2. Physicochemical properties of the waters of the investigated peat pools (average values for three seasons, 2024–2025).

Parameter	Unit	TL1	TL2	TL3	TL4	TM1	TM2	TM3	TP	TBB1	TBB2
Water level	cm	4	5	4	4	5	5	5	43	66	70
Temperature	°C	19.1	20.2	19.2	19.4	19.1	18.2	17.9	20.1	20.8	20.53
pH	pH	7.2	7.1	7.0	7.1	4.8	4.3	5.2	6.8	7.4	7.30
Conductivity	µS/cm	360.5	241.2	140.4	192.7	246.2	69.7	80.9	124.6	251.9	250.90
O_2	$\%O_2$	58.7	72.3	63.4	76.4	39.6	60.8	39.1	74.9	82.6	79.77
O_2	mg O_2/dm^3	5.5	6.4	6.0	7.5	3.8	5.6	3.8	6.7	7.4	6.93
NTU	NTU	166.4	60.5	74.3	65.3	50.8	123.1	45.3	43.0	46.8	46.68
Chlorophyll *a*	µg/L	22.0	34.7	22.1	32.4	81.5	33.3	47.9	21.6	13.1	11.93
$N\text{-}NH_4^+$	mg N/L	0.071	0.930	0.012	0.9	2.182	1.402	1.207	0.307	0.031	0.021
$N\text{-}NO_3$	mg N/L	0.093	1.063	0.725	1.913	0.015	0.029	0.043	0.022	0.012	0.013
$P\text{-}PO_4^{3-}$	mg P/L	0.006	0.087	0.005	0.005	0.017	0.047	0.015	0.048	0.027	0.024
P tot	mg P/L	0.081	0.489	0.072	0.057	0.479	0.264	0.242	0.134	0.072	0.070
N tot	mgN/L	2.528	7.300	2.796	2.066	5.109	2.764	4.021	2.263	1.291	1.327
TSS	mg/L	103.5	450.0	160.5	202.0	401.5	713.3	460.0	59.4	70.3	69.47
TOC	mg C/L	35.0	78.0	34.5	34.2	31.1	81.2	72.0	16.5	17.1	17.10
COD	mg O_2/L	78.5	180.0	47.8	80.3	143.3	187.3	163.7	37.8	36.1	36.13
BOD	mg O_2/L	47.3	106.5	46.3	46.8	81.8	108.8	95.7	22.5	22.6	21.20

3.2. Bacterioplankton and Phytoplankton

The abundance and biomass of bacterioplankton showed significant variation between the peat ponds (F = 18.5–19.56, p = 0.001) (Figures 2b and 3). The TBB1–2 and TM1–3 peat ponds exhibited the highest abundance and biomass of heterotrophic bacteria (8×10^6 mL^{-1} and 7×10^6 mL^{-1}, respectively), while lower values were recorded in TP at 6.4×10^6 mL^{-1}. Regardless of the type of peat pond, bacteria reached their highest abundance and biomass in spring and/or autumn for the peat ponds containing water during those seasons (TM1–3, TBB1,2), and their lowest values in summer (F = 4.37, $p < 0.015$).

In total, 36 phytoplankton taxa were identified in the water bodies under study. The peat ponds TM1–TM3 (12) and TL1–TL4 (16) exhibited the fewest species, and TP (18) and TBB1–2 (19) had the most. The phytoplankton community was dominated mainly by Cryptophyceae and Bacillariophyceae. Phytoplankton abundance and biomass varied significantly between the peat pond types under study, ranging from 0.06×10^6 individuals dm^{-3} in TM1–3 to 2.21×10^6 individuals dm^{-3} in TBB1–2 and from 98 to 32 µg $\times$ dm^{-3} (F = 6.26–6.96, $p < 0.015$), with significantly higher abundance noted during the summer season (Figures 2a and 3).

Figure 2. Abundance of particular group of hydrobionts in investigated peat ponds.

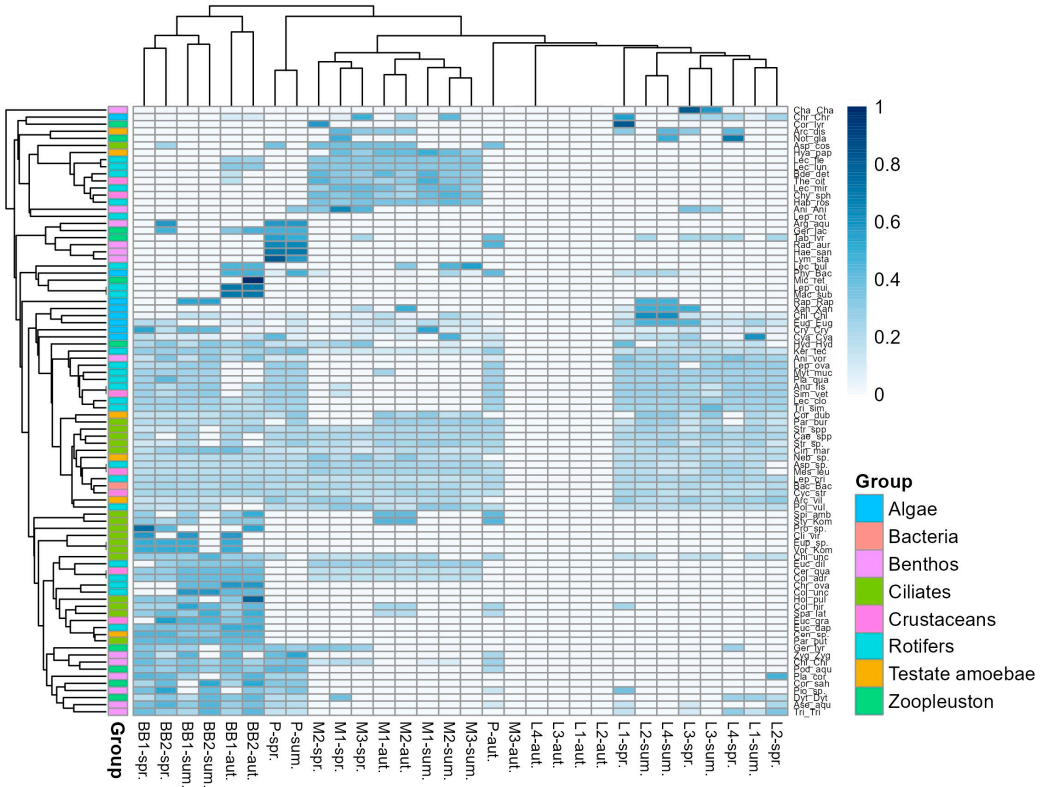

Figure 3. Index of similarity of hydrobionts community between investigated peat ponds; spr.—spring; sum.—summer; aut.—autumn.

3.3. Zooplankton

In total, only 6 taxa of testate amoebae were identified in the peat ponds under study, with 6 taxa noted in acidic peat ponds, and only 3 taxa in calcareous peat ponds. The highest abundance and biomass of these organisms were noted in acidic peat ponds, while the lowest were noted in calcareous peat ponds (14 and 6 individuals mL^{-1} and 3 and 0.4 μg × mL^{-1}, respectively) (F = 6.27–6.96, $p < 0.015$). In acidic peat ponds, *Arcella vulgaris* and *Nebela* sp. represented the largest proportion of the total abundance, while in calcareous peat ponds, it was *Centropyxis* sp.

Ciliates were represented by 17 taxa. The number of ciliate taxa ranged from 7 in the peat ponds TL1–TL4, through 9–11 in TM1–3, to 16 in TBB1–2. The results of factorial ANOVA showed that the abundance and biomass of ciliates were affected by the peat pond type (F = 22.84, $p < 0.001$) and the season (F = 24.28, $p < 0.001$). The highest abundance and biomass of these microorganisms were noted in calcareous peat ponds, whereas the lowest were found in acidic peat ponds (44 and 22 individuals mL^{-1}, and 6 and 2.1 μg × mL^{-1}, respectively). In all the water bodies under study, Scuticociliatida (mainly *Cinetochilum margaritaceum*) and Oligotrichida were dominant.

The species richness of rotifers ranged from 12 species in TP, 14–16 species in the peat ponds TL1–4 and TM1–3, and 26 species in TBB1–2. The abundance and biomass of rotifers were significantly higher in alkaline or calcareous peat ponds, regardless of the peat pond type, reaching their peak during the summer (F = 5.28, $p < 0.014$). Among the crustacean plankton in the peat ponds of Polesie National Park, 17 species of water fleas, or cladocerans, and 8 species of copepods were noted, with the highest number of species found in TBB1–2 (14).

The abundance and biomass of cladocerans in the ponds under study ranged from 18 individuals dm^{-3} to 34 dm^{-3}, whereas the abundance and biomass of individuals copepods (ranged from 6 individuals dm^{-3} to 18 individuals dm^{-3} and 19 and 498 μg × mL^{-1},

respectively) (F = 6.24, $p < 0.015$). Among Cladocera, *Chydorus sphaericus* dominated in acidic peat ponds, while *Ceriodaphnia quadrangula* dominated in alkaline or calcareous peat ponds. Among the copepods, the dominant species included *Mesocyclops leuckartii* in TP, *Thermocyclops crassus* in TM1–3 and TL1–4, and *Eucyclops graciloides* in TBB1–2 (Figures 2c–f and 3).

3.4. Macroinvertebrates

In the peat ponds under study, the presence of between 2 and 12 taxa of benthic fauna was recorded. The highest number of zoobenthic taxa (12) was noted in TP, with Chironomidae dominating in both this peat pond and the calcareous peat ponds. In the remaining peat ponds, a significantly lower number of benthic invertebrate taxa was observed during summer and autumn, and even a complete absence of zoobenthos was noted in the autumn months. Similar patterns were observed for the density of benthic organisms (F = 8.28, $p < 0.016$).

The zoopleuston community was represented by 2 to 10 taxa, including aquatic bugs (Heteroptera aquatica), aquatic beetles (Coleoptera aquatica), springtails (Collembola) and flies (Diptera). TBB1–2 and TP exhibited the highest number of taxa (7–10 taxa). In the remaining water bodies, significantly fewer taxa were found, ranging from 2 to a maximum of 5 taxa, which occurred almost exclusively during the spring. At the study sites, a significantly higher density (50–55 individuals m^{-2}, F = 22.14, $p < 0.001$) was observed in TP and TBB1–2, while the lowest density was recorded in TL1–4 and TM1–3 (50–55 individuals m^{-2}) (Figure 2g,h and Figure 3).

3.5. Ordination Analyses and Correlations Between the Physicochemical Parameters of the Water and Aquatic Organisms

Two-dimensional NMDS analysis showed clear gradients of changes in individual types of peat bogs and seasons (Figure 4).

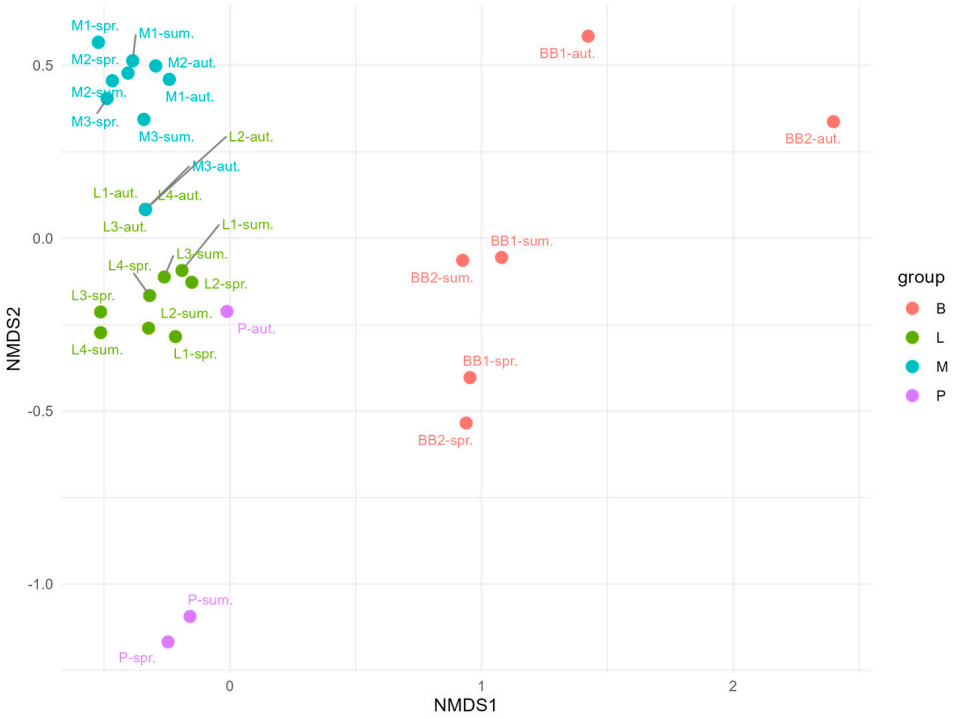

Figure 4. NMDS ordination of hydrobionts community data based on Bray–Curtis distance; spr.—spring; sum.—summer; aut.—autumn.

The RDA model explains over 84% of the total variability, indicating excellent model fit to the data and a strong correlation between environmental variables and species composition. Detailed analysis of individual variables (ANOVA by = "terms") allowed us to select statistically significant variables. Based on *p* values, WL, temperature, pH, and COD were selected as significant variables, with conductivity, O_2, and P_{tot} demonstrating less statistical significance. The first axis (RDA1) explains the largest proportion of the variability (over 50%) and is statistically significant, meaning it constitutes the main gradient in the data. WL, pH, and O_2 are strongly related to the positive part of axis 1 (RDA1), while COD and P_{tot} are strongly related to the negative part. The second axis (RDA2) explains a smaller proportion of the variability and is borderline significant, therefore it is interpreted as an additional, weaker gradient. Temperature is strongly related to this axis (Figures 5 and 6a–c).

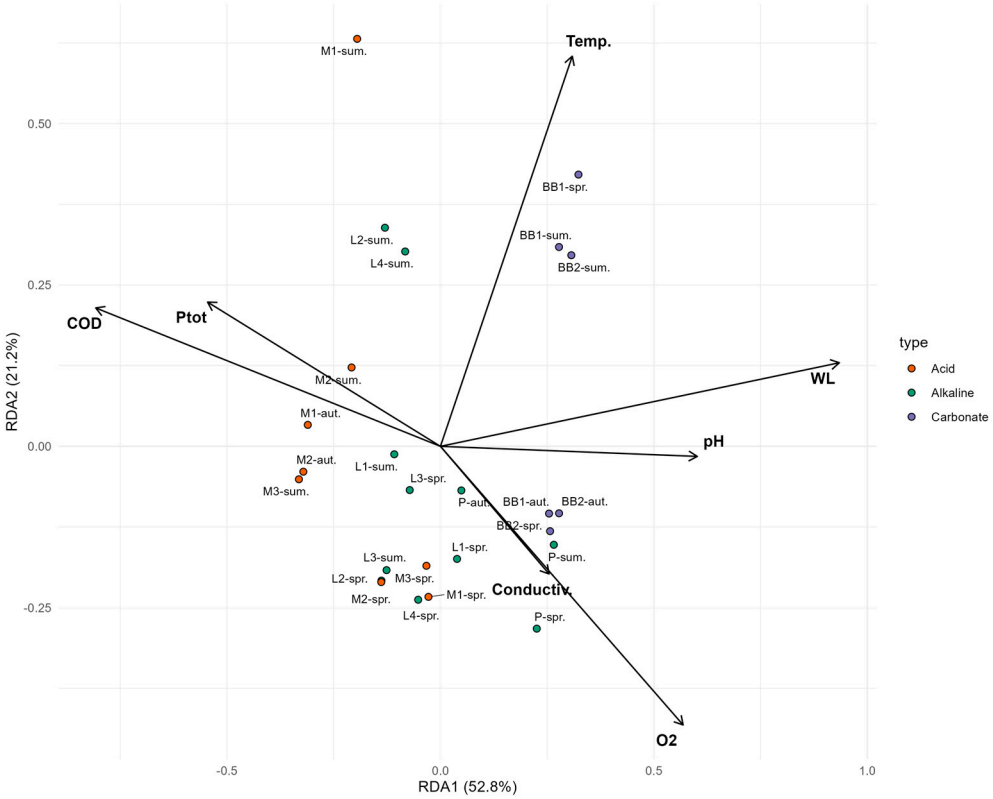

Figure 5. Redundancy analysis biplots showing communities of hydrobionts and environmental variables; spr.—spring; sum.—summer; aut.—autumn; WL—water level; Temp—water temperature; pH—water reaction; P_{tot}—total phosphorus; COD—chemical oxygen demand; Conductiv.—conductivity; O_2—dissolved oxygen.

Water level (λ = 0.200; F = 8.123; p = 0.001) showed the significant effect on the abundance of bacteria and Cryptophyceae. On the RDA biplot the presence of *Lecane* sp., *Arcella vulgaris* and *Arcella discoides* showed the relation with temperature, conductivity and pH. Water level affected the abundance of *Paramecium bursaria*, *Paramecium putrinum* and *Stylonychia mytilus* (λ = 0.054–0.324; F = 2.089–12.369; p = 0.001). Temperature, water level and pH showed the significant effect on the abundance of Zygoptera, *Microvelia reticulata*, *Asselllus aquaticus* (λ = 0.054–0.324; F = 2.315–2.809; p = 0.018–0.043) (Figure 6a–c).

Correlation analysis showed the highest strength of relationships between WL, temperature and oxygen content in water (Figure 7). The degree of correlation between the physicochemical properties of water and aquatic organisms varied considerably across the individual peat ponds. In acidic peat ponds, a strong correlation was noted for the water level, nutrients–phytoplankton and ciliates (from r = 0.89 to r = −0.58, $p \leq 0.01$).

In calcareous peat ponds, a significantly weaker correlation was observed between TOC and bacteria (r = 0.37, $p \leq 0.05$), while in alkaline peat ponds, associated with fens, the strongest correlations were noted between nutrient concentrations and protozoans and macroinvertebrates (from r = 0.53 to r = 0.64, $p \leq 0.01$).

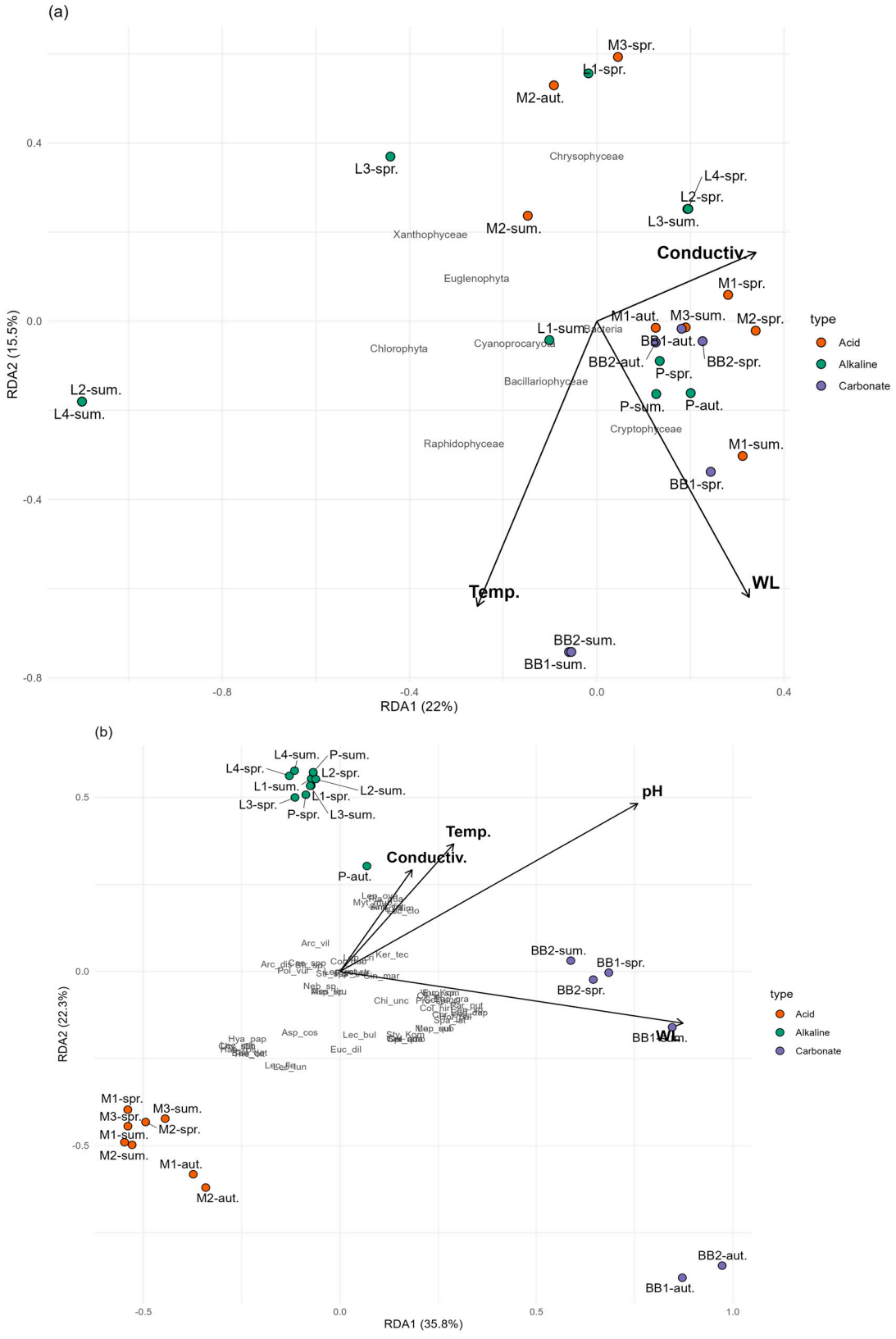

Figure 6. *Cont.*

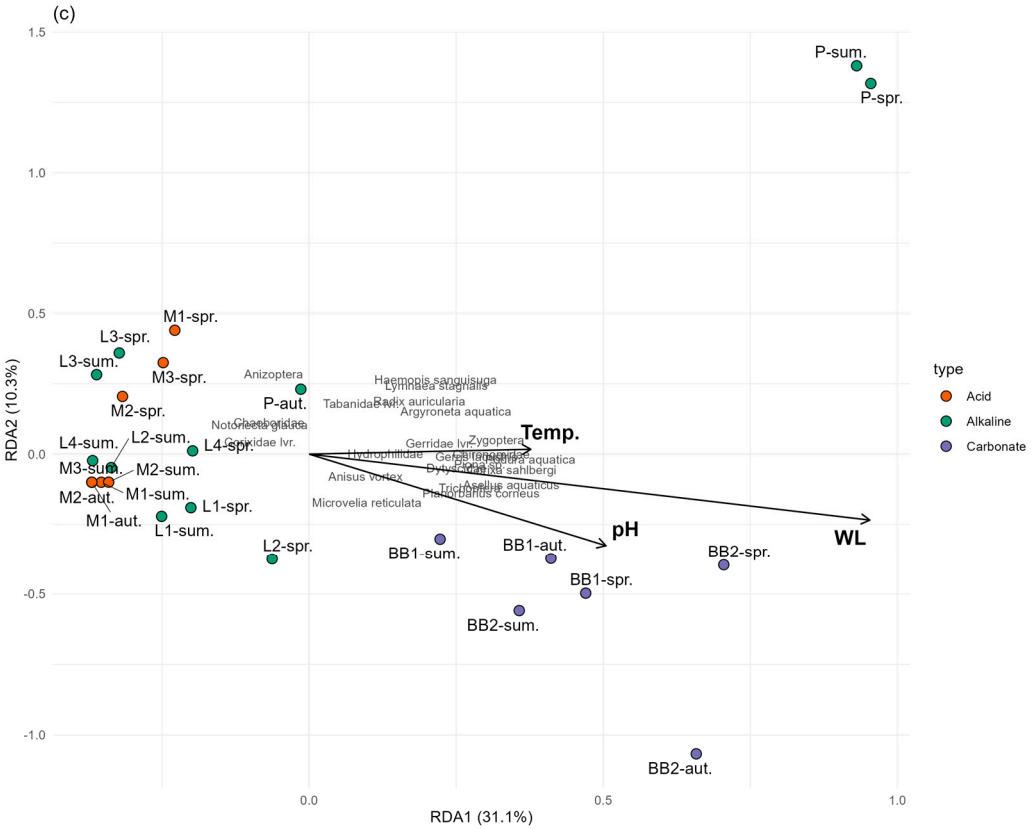

Figure 6. Redundancy analysis biplots showing communities of hydrobionts; (**a**) bacteria and algae, (**b**) zooplankton, (**c**) zoobenthos and zoopleuston and environmental variables; spr.—spring; sum.—summer; aut.—autumn; WL—water level; Temp—water temperature; pH—water reaction; Conductiv.—conductivity.

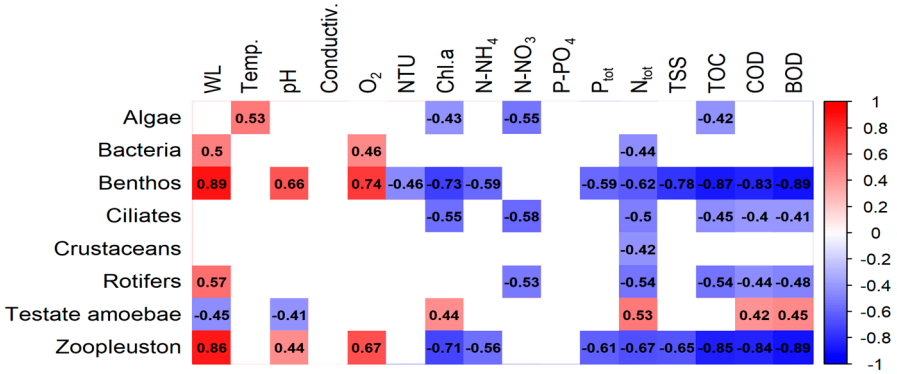

Figure 7. Linear correlation coefficients between abundance of hydrobionts community and environmental parameters in investigated peat ponds; WL—water level; Temp—water temperature; pH—water reaction; Conductiv.—conductivity; O_2—dissolved oxygen. NTU—nephelometric turbidity unit; N-NH_4—ammonium nitrogen; N_{tot}—nitrogen total; P-PO_4—dissolved orthophosphates. N-NO_3—nitrates; N_{tot}—nitrogen total; P-PO_4—dissolved orthophosphates. P_{tot}—total phosphorus; TSS—total suspended solids; TOC—total organic carbon; COD—chemical oxygen demand; BOD—biochemical oxygen demand.

3.6. Correlations Between Food Web Components

The degree of correlation between the groups of organisms under study varied considerably across the individual types of peat ponds. In acidic peat ponds, the abundance of protists was correlated with phytoplankton abundance (from r = 0.37, $p \leq 0.05$ to r = 0.59, $p \leq 0.01$, $n = 56$). In the calcareous peat ponds, bacterial density correlated positively with

the density of testate amoebae (r = 0.51, $p \leq 0.01$) and ciliates (r = 0.51, $p \leq 0.01$). The density of zooplankton correlated positively with the phytoplankton (r = 0.47, $p \leq 0.01$). The most significant relationship was found between the density of zoopleuston and the density of crustaceans (r = 0.50, $p \leq 0.01$).

4. Discussion

4.1. Physicochemical Parameters

To date, there have been almost no comparative data on the physicochemical properties of the water in peat ponds, particularly those located in fens (TL1–TL4). In contrast, the physicochemical properties of the water in acidic peat ponds located in raised bogs and/or transition bogs were similar to those found in dystrophic lakes [35], as well as to those recorded within peat ponds situated in Tierra del Fuego, Argentina [8].

Regardless of the type of peat pond, it was found that as surface water levels fell, pH values increased, oxygen conditions deteriorated, and water mineralisation increased. These processes were particularly evident during summer and autumn. Furthermore, there was an increase in chlorophyll *a* and total organic carbon concentrations in the water. It appears that the increase in chlorophyll *a* may result from algae colonising *Sphagnum* sp. patches in many shallow areas that enter the water during sampling, or it may reflect the increase in nutrient concentration. This effect was particularly pronounced in the water bodies where the greatest decreases in water levels were recorded. An increase in pH and a decrease in oxygen concentration in the water, combined with deterioration in hydrological conditions, were also observed in small peat moss hollows within the Pradeaux peatland in France [13].

4.2. Bacterioplankton and Phytoplankton

Bacterial abundance increased in peat ponds associated with transition bogs (acidic peat ponds) and in calcareous peat ponds. Bacterial abundance in acidic peat ponds was similar to that recorded in peatlands dominated by *Sphagnum* [36]. However, there is a lack of comparative data on peat ponds associated with fens and calcareous fens. The study results indicate that as trophic levels increased, total organic carbon (TOC) and chemical oxygen demand (COD) increased. In acidic and alkaline peat ponds, bacterial abundance correlated strongly with the WL and organic matter pool, whereas in calcareous peat ponds, this correlation was significantly lower. It is likely that concentrations of organic matter, including dissolved organic carbon (DOC), may influence the abundance of bacterial communities.

A study conducted by Chróst et al. [37] shows that bacterial abundance is linked not to the amount of DOC itself, but to its availability, which is determined by the presence of refractory carbon compounds that are utilised in enzymatic decomposition processes. At the same time, peaks in bacterial abundance during the autumn period were associated with a drop in water level and an increase in the organic matter content of the water. Meanwhile, the highest phytoplankton abundance was noted in calcareous peat ponds. Undoubtedly, one of the major factors influencing this was the more favourable light conditions prevailing there compared to those in the other peat ponds. Both the species composition and abundance of phytoplankton in acidic peat ponds were typical of this habitat type and, in this respect, showed similarities to communities found in dystrophic lakes or peatlands dominated by *Sphagnum* mosses [13,35].

In most peat ponds, the phytoplankton was dominated by *Cryptomonas* sp. The dominance of flagellates has also been observed by other authors in the ecosystems of small dystrophic lakes [38]. An exception was one of the acidic peat ponds, TM2, where the diatom *Fragilaria ulna* was dominant. Its dominance in phytoplankton may indicate

the increasing trophic status of the water in this pond. Furthermore, the invasive species *Gonyostomum semen* was found in the phytoplankton of acidic peat ponds (TM2). This species was already recorded in 2008, and its appearance is likely due to ongoing climate change [38].

The variation in phytoplankton structure is, therefore, undoubtedly due to the trophic and hydrological conditions of the water bodies, while the significant decrease in its abundance during the summer period may result, on the one hand, from considerable amounts of organic matter and humic compounds originating from peatlands, which adversely affect light conditions, and, on the other hand, from an increase in the abundance of zooplankton, which may control phytoplankton abundance. At the same time, an increase in the proportion of mixotrophic phytoplankton species may be an adaptive strategy in response to deteriorating light conditions and/or low nutrient concentration, as well as deteriorating hydrological conditions [35]. The deterioration in hydrological conditions also resulted in the decline of typically planktonic species, and an increase in the proportion of periphyton taxa, mainly diatoms of the genus *Eunotia*, which may have a significant bioindicator value.

Diatoms of the genus *Eunotia* are likely the potential "winners" in this race for survival amidst significant water-level drops and the onset of peat-pit overgrowth. At the same time, bacterial communities also rapidly adapt to the abruptly changing environmental conditions, although this is primarily reflected in an increase in their overall abundance.

4.3. Zooplankton

Individual zooplankton groups showed significant variation across the peat ponds. As the nutrient concentration increased, so did the species diversity of testate amoebae, ciliates and crustaceans. Such patterns were also observed in sphagnum peatland ecosystems located in north-eastern France [39,40].

The testate amoeba community was dominated mainly by *Arcella vulgaris*. This may be due to the broad ecological tolerance of this species. As demonstrated by a study by Gilbert et al. [13], species of this genus are found in both oligotrophic and nutrient-rich habitats. The dominance of this species in the peat ponds under study may affect the functioning of bacterial communities and phytoplankton, because, as shown by a study by Mieczan and Pawlik-Skowrońska [7], this species, under experimental conditions, clearly contributed to a decrease in diatom abundance, and altered the bacterial cell size structure, showing a trend towards increasing the proportion of large cells (>1 μm). Such an alteration in cell size may result from the bacterial communities activating defence mechanisms against predation pressure [7]. However, as water levels dropped and nutrient concentrations increased, the proportion of species belonging to the genera *Nebela* and *Centropyxis* increased. These are regarded as species characteristic of drier habitats or those with higher trophic levels [40,41]. It was also observed that as temperatures rose and hydrological conditions deteriorated, there was a decrease in the proportion of large testate amoeba taxa with a large diameter of shell aperture. These species feed primarily on ciliates, rotifers, and even small nematodes, i.e., organisms from higher trophic levels. They may, therefore, have helped control the abundance of potential consumers of bacteria or other protozoans. It is, therefore, likely that the increased efficiency of consumption by top predators contributed to the decrease in the abundance of other groups of microorganisms. It appears that the combined effects of rising temperatures, declining water levels, increased organic matter content, and nutrient concentrations may have the greatest impact on protozoan diversity and abundance. This regularity is also confirmed by studies conducted in lake ecosystems [18].

Ciliates respond very quickly to changing environmental conditions. Regardless of the type of water body, ciliate abundance peaked in spring and summer and was lowest in autumn. Spring and summer abundance peaks were also noted by Gilbert et al. [13] in *Sphagnum*-dominated peatlands. At the same time, an increase in the proportion of mixotrophic species was observed, particularly in summer, and an increase in bacteriophagous species in autumn. The physiological plasticity conferred by mixotrophy in ciliates may be one of the mechanisms that adapt this group of organisms to the highly unstable environmental conditions found in peat pond ecosystems, driven by pronounced fluctuations in temperature, water level, and light conditions.

In the rotifer community of acidic peat ponds, *Habrotrocha* sp. and *Lecane lunaris* accounted for a significant proportion. These species were recorded, e.g., in acidic peatlands in the north-eastern USA and in raised bogs in Poland [10,11]. Furthermore, within the community of rotifers and planktonic crustaceans, a significant proportion of eutrophication indicators was observed, including the genera *Keratella* and *Asplanchna* (Rotatoria); *Alona guttata*, *Diaphanosoma brachyurum* and *Polyphemus pediculus* (Cladocera), as well as *Cyclops strenuus* and *Thermocyclops oithonoides* (Copepoda). The high abundance of the genus *Asplanchna*, particularly in acidic peat ponds, may result from favourable feeding conditions (the abundance of the flagellate *Gonyostomum semen*), because, as shown by the study conducted by Karpowicz et al. [42], this species has been found in the digestive tracts of predatory rotifer species. At the same time, the considerable abundance of rotifers in alkaline and calcareous peat ponds may reflect not only their trophic status, but also a significant microhabitat diversity resulting from the presence of macrophyte stands with varied spatial structure, which represent excellent habitats for zooplankton [43].

Among Cladocera, *Chydorus sphaericus* dominated in acidic peat ponds, whereas *Ceriodaphnia quadrangula* dominated in calcareous peat ponds. Among the copepods, the dominant species included *Mesocyclops leuckartii* in TP, *Thermocyclops crassus* in TM1–3 and TL1–4, and *Eucyclops graciloides* in TBB1–2. According to studies by other authors, *Ceriodaphnia quadrangula* has also been found in acidic and dystrophic lakes, particularly in the pelagic zone, while the other species have been recorded in various types of trophic lakes in Eastern Europe [44]. *Mesocyclops leuckartii* often dominates in acidic water bodies, whereas *Thermocyclops crassus* has frequently dominated in various types of water bodies with an alkaline pH throughout Europe [45]. However, the evident increase in crustacean abundance in calcareous peat ponds may result not only from their higher trophic levels, but also from more stable hydrological conditions and greater microhabitat diversity (emergent and submerged macrophytes), compared with acidic peat ponds, where the open water zone and the *Sphagnum* mat zone were mainly present.

It thus appears that, within the zooplankton community, ciliates *(Paramecium bursaria* and *Paramecium putrinum)* are the primary winners in terms of adaptation to harsh environmental conditions—though this applies mainly to functional groups rather than individual species. Furthermore, bdelloid rotifers—which colonize the vegetation emerging in peat ponds—exhibit a high degree of resilience, whereas planktonic crustaceans proved to be the least resistant to environmental stress.

4.4. Macroinvertebrates

Between 2 and 12 taxa of benthic fauna were found in the peat ponds under study. This is an exceptionally low result, indicating a short period of water accumulation in the analysed water bodies. The highest number of zoobenthic taxa (12) was noted in an alkaline peat pond located in a fen (TP). Water was present there in all study seasons, and benthic invertebrates characteristic of eutrophic waters were found. Furthermore, the complex

vegetation structure, similar to that of a pond phytolittoral, likely provided more optimal habitats for aquatic fauna than the other peat ponds.

In calcareous peat ponds, the proportion of Chironomidae larvae reached as much as 88% of the total benthic fauna abundance, with molluscs and *Zygoptera* larvae also accounting for a significant proportion. Among the Chironomidae, taxa typical of eutrophic waters were clearly dominant [46]. In contrast, the very low number of taxa and the abundance of zooplankton, particularly in peat ponds TL1–4 and TM1–3, is probably a reflection of a significant decrease in the water level, which dropped considerably after the spring period. For water bodies that dry up during the breeding season of pleuston insects, this group often moves to other habitats in search of optimal breeding conditions. In turn, high zoopleuston abundance in calcareous peat ponds was caused by the appearance of springtails (*Podura aquatica*), which dominated habitats with relatively constant water levels. Springtails found in high numbers in the littoral zone are frequently observed in lake littorals as well as in water bodies with a constant water level and a stable water/land interface [46,47]. They may serve as useful indicators of the stability of peat pond ecosystems.

It is likely that the pleuston community served a significant role in controlling the abundance of planktonic crustaceans in the calcareous peat pond, particularly during the autumn period, which is reflected in a clear decrease in the abundance of this zooplankton group in parallel with the increase in the abundance of the zoopleuston. It should be noted that the literature contains little information on the importance of planktonic crustaceans as an element of the diet of predatory Heteroptera, while it is known that they can be their food. Previous studies have devoted much attention to the Notonectidae, which play a significant role in regulating water invertebrates [47]. It has been demonstrated that they can be effective regulators of mosquitoes and help to control them, and that, if necessary, they can also feed on Chironomidae [47,48]. As shown in small water bodies, they can regulate the abundance and diversity of the entire invertebrate population (including plankton) [48].

Macroinvertebrates thus clearly responded to adverse environmental conditions—primarily deteriorating hydrological conditions—with zoopleuston organisms proving particularly sensitive to these changes; they disappeared from the studied peat pits as the intensity of hydrological stress and successional processes increased.

5. Conclusions

The physicochemical properties of peat pond waters under conditions of water scarcity show signs of eutrophication, and this applies in particular to acidic peat ponds. It is microorganisms that responded particularly strongly to these changes, with an increase in the diversity and abundance of bacteria and ciliates. In zoocenotic communities, there was a decrease in the proportion of planktonic species and an increase in the proportion of littoral or periphyton species. At the same time, an increase in the proportion of mixotrophic species and a decrease in the abundance of top predators were noted, which may represent a mechanism by which aquatic organisms adapt to environmental stress. Undoubtedly, the winners in terms of survival under these adverse hydrological and climatic conditions were microbial assemblages (primarily bacteria, ciliates, and Bdelloidea), although the assessment of this resilience should rely chiefly on functional groups (mixotrophic and bacterivorous taxa versus predatory, planktonic, and periphytic taxa). Conversely, the losers amidst these changes were planktonic crustaceans and zoopleustonic organisms.

Considerable fluctuations in water levels, resulting from precipitation scarcity, accelerated the drying out and overgrowth of peat ponds, particularly the alkaline and acidic ones, the decline of *Sphagnum* mosses, and an increase in the proportion of vascular plants.

The current shape and depth of the basin of these small water bodies indicate that they dry out completely during periods of low water levels.

These water bodies may provide an excellent model system for investigating the impact of intensifying climate change on shallow water bodies, while future research should also consider the role of biogenic sediments, which can serve as a kind of "bank" of resting stages for certain groups of organisms, as well as a source of biogenic compounds.

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