

Article

Gastropod Assemblages Associated with Habitat Heterogeneity and Hydrological Shifts in Two Shallow Waterbodies

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Abstract: We aimed to determine the effects of water level and habitat heterogeneity on gastropod fauna in the littoral zone, and the differentiation of functional feeding guilds (FFG) of gastropods. Two periods were analyzed: 2012 (low water level, LWL) and 2013 (high water level, HWL) in the littoral zone of two shallow waterbodies (Sutla backwater, NW Croatia). Waterbody S1, covered with *Ceratophyllum demersum*, was sampled in the macrophyte stands, and the littoral benthic area, while waterbody S2, without macrophytes, was sampled only in the littoral benthic area. It was observed that among the macrophyte stands in S1, gastropods were significantly more abundant during LWL. The same trend was observed in the littoral benthic area of S2. In contrast, gastropod abundance was higher in the littoral benthic area of S1 during HWL. Comparing gastropods in the two waterbodies, the abundance in S1 was ten times higher than in S2. The most abundant species was *Gyraulus parvus*, which accounted for 51–92% of the gastropods observed among the macrophytes of S1 and 86% in the adjacent benthic zone. Among the FFG groups, grazers (particularly those feeding on gymnamoebae and rotifers) had the largest proportion, followed by shredders feeding on small pieces of macrophytes. In our research, we indicate the important role of microhabitat diversity and submerged macrophytes as a rich food source for gastropods and safe shelter from predators.

Keywords: littoral zone; macrophytes; pulmonate snails; functional feeding group; invasive species



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1. Introduction

Shallow water bodies (SWB) are unique freshwater ecosystems that have long been neglected in limnological research, despite their great contribution to overall biodiversity, including phyto- and zooplankton, macrophytes, benthos, nekton, amphibians, and waterbirds [1–4]. These ecosystems, regardless of their poor morphological features, are particularly vulnerable to global climate changes, including hydrological regimes that cause frequent and significant fluctuations in water levels [2,5–7], which is one of the most important aspects of limnology research in our time. The fluctuations in water level and occasional lack of water may alter several environmental conditions such as light availability, but they can also affect the occurrence and distribution of aquatic organisms, including submerged macrophytes [8–10] or various animals [11]. The littoral zone of the SWB is of critical ecological importance for aquatic food webs, being the main site for secondary production [12], enhancing habitat complexity and thus providing high diversity and abundance of invertebrates that support specific ecosystem functions, e.g., nutrient retention and water cycling [13,14]. The littoral zone is subjected to frequent and extreme water level fluctuations that often result in changes in the functioning of shallow ecosystems, such as modifications in water transparency [15–17], macrophyte cover [7], nutrient levels [7], and

food resources [18,19]. All these shifts will influence habitat function, nutrition quality and availability, reproduction, and general life cycle conditions for littoral communities [5,7,20].

Among the macroinvertebrates inhabiting the benthic area of SWB, there are more records of the occurrence of insect larvae [7,21–23] and crustaceans [2,24,25] than of gastropod mollusks, although they play a significant role in the macroinvertebrate community in the SWB [26] and are a particularly important element in the production and transformation of detritus [27]. When sufficient calcium ions are available, gastropod assemblages in lakes are regulated primarily by fish and crayfish predation; assemblages in shallow, fishless ponds are mainly regulated by competition, whereas gastropod assemblages in temporary ponds are largely influenced by the frequency and extent of desiccation [28,29].

In littoral food webs, gastropods may primarily affect epiphyton (detritus, bacteria, algae, fungi, protozoa, and metazoans), while rarely consuming live macrophytes [30–34]. Accordingly, the distribution of macrophytes in the littoral zone is critical for both gastropods and ecosystem functioning, and the role of gastropods is multifaceted. Submerged macrophytes with complex architecture provide a greater surface area for epiphyton, which leads to greater food source [35–38] and habitat availability, in addition to increased protection from visual predators and diversification of suitable sites for oviposition [39]. Conversely, several studies have confirmed that gastropods can promote macrophyte growth by grazing light-limiting vegetation, which indirectly leads to changes in nutrient regeneration [26,40,41]. All of this may also be reflected in total biomass, abundance, and richness of macroinvertebrates, which are significantly higher in submerged vegetation than in emergent and floating vegetation e.g., [5,37]. Habitat type is often stated as a factor that influences species distribution of gastropods, besides e.g., substrate composition, meteorological and physiographical factors, environmental tolerance, or anthropogenic disturbance [42,43].

Compared to lakes with low water level fluctuations, lakes with high water level fluctuations may have the following characteristics: (i) significantly coarser-grained littoral substrates with lower macrophyte cover, and (ii) greater proportions of omnivorous benthic invertebrates in the littoral zone, in addition to (iii) a generally altered taxonomic and trophic structure of benthic consumers and a more homogeneous benthic invertebrate assemblage [16]. Gastropod response to hydrologic stress (i.e., water level fluctuations) and their trophic interactions are poorly studied in SWB. Lakes with low water level fluctuations have been proven to host greater numbers of pulmonate (non-operculate) gastropod taxa, while lakes with high water level fluctuations have few gastropods [16]. In intermediate or deep habitats, gastropods are mostly represented by prosobranchs (operculate taxa) (e.g., *Bithynia tentaculata*, *Viviparus viviparus*), which are more resistant to desiccation and drought [16,44].

In this study, we analyzed gastropod assemblages and their role in food webs in two SWB (S1 with submerged macrophytes and S2 without macrophytes) during summer in two consecutive years (2012, 2013) that differed in hydrological regime. According to Špoljar et al. [7], lower precipitation and lower water levels (LWL) were recorded in 2012, while higher water levels (HWL) were measured in both SWB in 2013. The primary objectives of this study were to assess gastropod assemblages during periods of LWL and HWL, considering: (i) habitat heterogeneity of the littoral zone, (ii) epiphyton as a food source, and (iii) fish as predators. The results of this study will help highlight gastropods as an important link in trophic interactions and as indicators of water quality in SWB. They will also provide a basis for using gastropods as indicator organisms responding to potential changes in SWB functioning due to water level fluctuations.

2. Materials and Methods

2.1. Study Area

This study was conducted in NW Croatia (about 30 km from Zagreb) in the littoral zone of the Sutla River backwater. The Sutla backwater is a natural water body connected to the Sutla River and divided into two barely connected basins: (a) the upper basin (S1) covered

by submerged macrophytes dominated by *Ceratophyllum demersum*, and (b) the lower basin (S2) without macrophyte stands (Figure 1). These basins differed in their morphometry, water transparency, and macrophyte cover. The study area has been described in detail in previous studies [2,7].

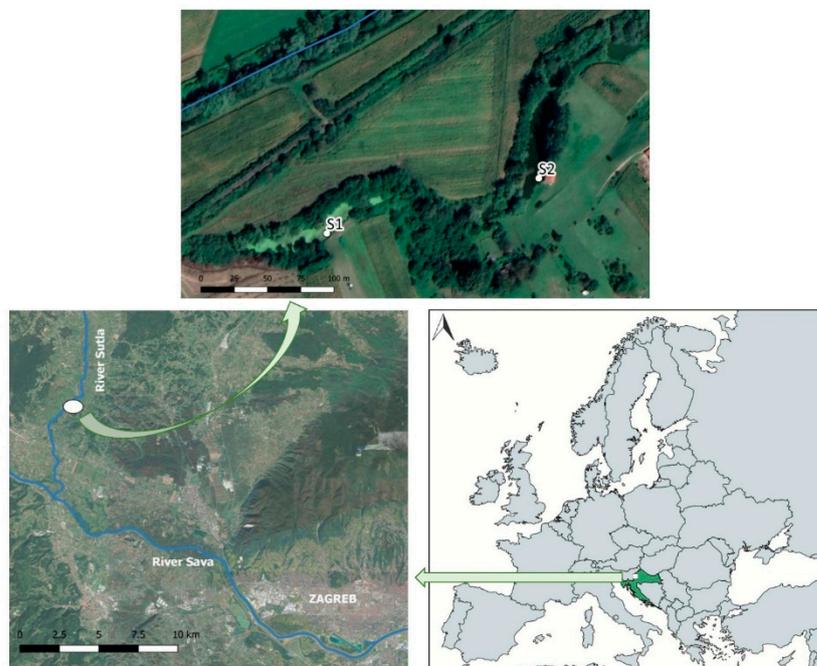


Figure 1. Map with the location of the two studied shallow water bodies of the Sutla River backwater (S1—with submerged macrophytes covered littoral and S2—without macrophytes) and the ground-plan of the investigated water bodies with marked positions of sampling points in the littoral zone.

2.2. Macroinvertebrates and Epiphyton Sampling and Biocoenotical Analyses

Samples were collected monthly, from July to September (in Roman numerals: July VII, August VIII, September IX), in 2012 and 2013. Triplicate samples of macroinvertebrates (i.e., macrozoobenthos) were collected at each water body (S1 and S2) in the littoral zone. We used the following sampling protocol: first, we measured environmental parameters in the field and collected samples for analysis of water physicochemical parameters; second, we collected macroinvertebrates from among macrophytes in S1 and from the littoral benthal area of both waterbodies S1 and S2; and third, we collected fish by electrofishing.

In both waterbodies, littoral benthos (i.e., littoral benthic macroinvertebrates), including gastropods, were sampled using a Surber sampler (25 × 25 cm frame; 300 µm mesh size) and preserved in 75% ethanol. In S1, macroinvertebrates were additionally sampled within macrophytes and macrophyte epiphyton. Sampling was performed by cutting the submerged portion of the macrophytes at a length of 10 to 15 cm (2 stems in triplicate for macroinvertebrates, and the same sampling protocol for epiphyton). Macrophytes were placed in a plastic bag filled with ambient water and transported to the laboratory in a cooler. Gastropods and macroinvertebrates were isolated from stems manually or under a stereomicroscope, and all animals were preserved in 75% ethanol. For epiphyton collection, stems were scraped with a small brush, and biocenotic microscopic analyses were performed on the live material several hours after sampling. The stems of *C. demersum* were dried (to constant mass) at 104 °C for 24 h. Abundance of gastropods among macrophytes and epiphyton (i.e., zooperiphyton: Gymnamoeba, Testacea, Ciliophora, Rotifera) was expressed as the number of individuals per 1 g of dried mass of *Ceratophyllum* (Ind. g⁻¹ DM), while abundance of gastropods, and macroinvertebrates in littoral benthos was expressed as the number of individuals per square metre (Ind. m⁻²).

All macroinvertebrate samples were analyzed under an Olympus SZ61 stereomicroscope (Hamburg, Germany; 10× to 40× magnification). Epiphyton samples were divided into groups according to the higher taxonomic levels (Gymnamoeba, Testacea, Ciliophora, Rotifera) and counted using the Opton-Axiovert 35 microscope (Carl Zeiss Jena, 100× to 400×). Gastropods were identified to species level based on Glöer [45] and classified into functional feeding groups (FFG) based on their feeding preferences as shredders (SHR), grazers (GRA), passive filterers (PFIL), detritivores (DET), and others (OTH) according to Moog [46].

2.3. Environmental Parameters

The analyses of environmental parameters for both years 2012 and 2013 have already been described in detail in previous studies [2,7]. During the summer period in each year, environmental data did not indicate a significant difference between two SWB, S1 and S2 (Mann-Whitney, $p > 0.05$), thus we indicated those values as average for both SWB during the summer season at LWL and HWL, respectively. Physicochemical water parameters [water temperature (Temp), dissolved oxygen concentration (DO) and pH] were measured with a portable pH and dissolved oxygen meter (Hach HQ30d, Loveland, CO, USA); electrical conductivity (EC) with a portable conductivity meter (Hach sensION 5, Loveland, CO, USA); pelagic water transparency (Trans) with a Secchi disc (z_{SD}) to determine the environmental characteristics of the SWB. Macrophyte cover was expressed as a percentage (MC, %). An additional 1-litre water sample was collected at each site (and stored at 4 °C) for laboratory analysis of chemical parameters and food sources (algae, detritus). Total nitrogen (TN) and total phosphorus (TP) were determined according to APHA [47] and dissolved organic matter (DOM) was determined by estimating chemical oxygen demand, $COD_{(Mn)}$ [48]. Phytoplankton (based on chlorophyll *a*) and particulate organic matter (based on POM) concentrations were considered as possible food sources for the littoral community. Chlorophyll *a* (Chl *a*) concentration (a proxy for phytoplankton biomass) was analyzed using an ethanol extraction method [49] in plankton ($\mu\text{g L}^{-1}$) and in epiphyton ($\mu\text{g g}^{-1}$ DM). POM was evaluated as ash-free dry mass (AFDM), calculated as the difference between the mass of the water sample after drying at 104 °C (to constant mass) and its mass after ashing at 600 °C/6 h.

2.4. Data Analysis

The parameters analyzed were not normally distributed and could not be normalized by common transformations [50], so we used non-parametric tests. The Mann–Whitney U test was applied to test differences in environmental variables between years (2012 vs. 2013), and the Kruskal–Wallis test and accompanying post-hoc multiple comparisons were used to test differences in gastropod abundance among years and habitats.

Multivariate similarity analysis (ANOSIM) was used to identify differences or similarities in water depth and other environmental variables between the two years studied, while SIMPER analysis was used to calculate the contribution of each gastropod species (%) to dissimilarity between LWL (2012) and HWL (2013) years [7]. Interactions between selected environmental parameters and food resources LL—leaf litter; ML—macrophyte litter; macrophyte coverage—MC; fish length—Fish; particulate organic matter in benthos—POMb; macrozoobenthos excluding gastropods—MZB; chlorophyll *a* concentration in epiphyton—Echl; epiphyton abundance of Gymnamoeba—EGam, Testacea—ETest, Ciliophora—ECili, Rotifera—ERot; abundances of the gastropod species (*Fc*—*Ferrissia californica*; *Hc*—*Hippeutis complanatus*; *Gc*—*Gyraulus crista*; *Gp*—*Gyraulus parvus*; *Gt*—*Galba truncatula*; *Pa*—*Physella acuta*; *Ra*—*Radix auricularia*; *Vp*—*Valvata piscinalis*) and gastropod functional feeding groups (FFG) at each study site (S1 and S2) were analyzed by canonical correspondence analysis (CCA) or redundancy analysis (RDA) using the Canoco 4.5 program [51]. The statistical significance of the analyzed correlations was tested using the Monte Carlo permutation test (499 permutations). For all statistical tests, a *p*-value of 0.05 was used as an indicator of statistical significance.

3. Results

3.1. Environmental Variables

For summer environmental conditions, when the research took place, the preceding winter and spring hydrometeorological conditions were crucial. There was a total of 219 mm more precipitation in the second year of examination [2013 (total 1201 mm)] than in the first year [2012 (total 982 mm)]. The average water depth in summer 2013 was up to 0.4 m higher than in 2012 (Mann–Whitney U test, $p < 0.05$). Macrophyte cover in S1 was significantly (20%) higher in 2012 compared to 2013 (Mann–Whitney U test, $Z = 2.09$ $p < 0.05$). Due to the observed decrease in macrophyte cover, POM and Chl *a*, and the increase in TP, environmental conditions differed significantly between LWL and HWL (ANOSIM, $r = 0.872$, $p < 0.002$) during the summer periods in SWB, S1, and S2 (Table 1). The NMDS analysis also clearly separated LWL from HWL, based on the measured environmental variables (Figure 2).

Table 1. Mean and standard deviation (SD) of the physicochemical parameters during the study period. Temperature—water temperature; DO—dissolved oxygen concentration; EC—electrical conductivity; DOM—dissolved organic matter; POM—particulate organic matter; TN—total nitrogen concentration; TP—total phosphorous concentration; Chl *a*—chlorophyll concentration.

Variable	Mean \pm SD	
	LWL	HWL
Temperature ($^{\circ}$ C)	23.2 \pm 4.8	19.7 \pm 3.0
DO ($\text{mg O}_2 \text{ L}^{-1}$)	6.8 \pm 2.7	5.9 \pm 1.3
pH	8.33 \pm 0.70	7.95 \pm 0.35
EC ($\mu\text{S cm}^{-1}$)	485.8 \pm 159.5	430.5 \pm 124.3
DOM ($\text{mg O}_{2(\text{Mn})} \text{ L}^{-1}$)	17.0 \pm 3.8	21.5 \pm 5.6
POM ($\mu\text{g L}^{-1} (\times 10^{-3})$)	6.395 \pm 6.215	13.503 \pm 18.404
TN (mg N L^{-1})	0.896 \pm 0.327	0.399 \pm 0.113
TP (mg P L^{-1})	0.362 \pm 0.086	0.318 \pm 0.026
Chl <i>a</i> ($\mu\text{g L}^{-1}$)	27.528 \pm 18.549	26.668 \pm 34.119

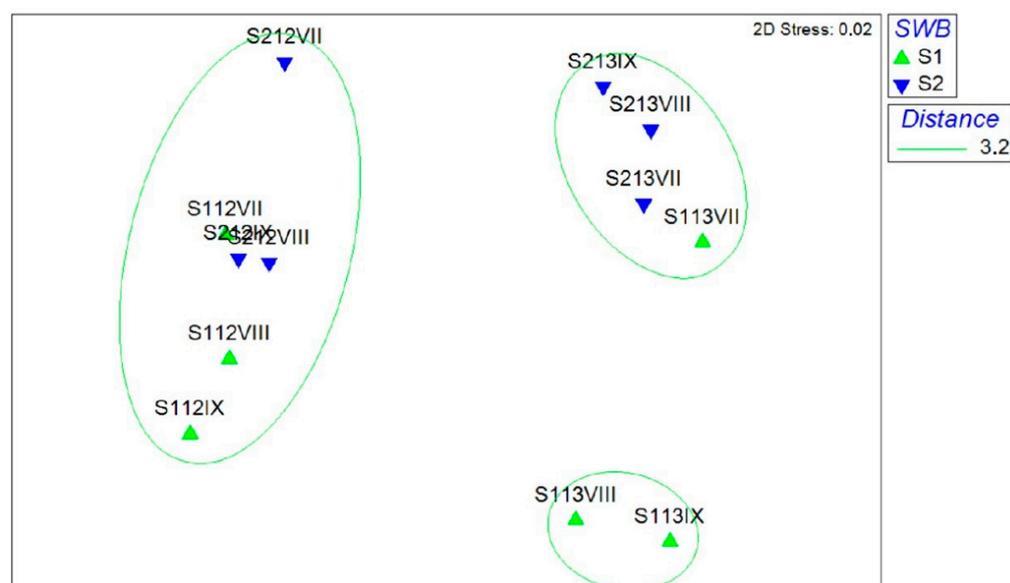


Figure 2. Non-metric multidimensional scaling (NMDS) ordination based on differences in summer environmental conditions in 2012 (LWL) and in 2013 (HWL). Explanation of symbol codes plotted in the diagram: e.g., S112IX refers to S1—shallow water body, 12—year 2012, roman numerals indicate the months.

At an increased water level, chlorophyll *a* in epiphyton over macrophyte in S1 was significantly reduced to $5.964 \pm 3.425 \mu\text{g Chl } a \text{ g}^{-1} \text{ DM}$ in comparison to its value at LWL, $52.125 \pm 33.177 \mu\text{g Chl } a \text{ g}^{-1} \text{ DM}$ (Mann–Whitney U test, $Z = 3.09$ $p < 0.05$).

3.2. Gastropod Assemblage

During the research, a total of eight gastropod species were recorded—pulmonate *Ferrissia californica* (Rowell, 1863), *Galba truncatula* (O. F. Müller, 1774), *Gyraulus crista* (Linnaeus, 1758), *G. parvus* (Say, 1817), *Hippeutis complanatus* (Linnaeus, 1758), *Physella acuta* (Draparnaud, 1805), *Radix auricularia* (Linnaeus, 1758), and prosobranch *Valvata piscinalis* (O. F. Müller, 1774). Three of them, *F. californica*, *G. parvus*, and *P. acuta*, are alien invasive species. The most common is the family Planorbidae (*F. californica*, *G. crista*, *G. parvus* and *H. complanatus*), followed by Lymnaeidae (*G. truncatula* and *R. auricularia*), while Physidae (*P. acuta*) and Valvatidae (*V. piscinalis*) are families represented by only one species.

At waterbody S1, a total of six species of freshwater gastropods were detected within macrophytes: *F. californica*, *G. crista*, *G. parvus*, *H. complanatus*, *P. acuta*, and *R. auricularia* (Figure 3). Total abundance was significantly higher (Kruskal–Wallis test, $H = 9.48$, $p < 0.03$) in the LWL period, which was directly related to the abundance of *G. parvus*, $9 \pm 12 \text{ Ind. g}^{-1} \text{ DW}$ in LWL and $4 \pm 3 \text{ Ind. g}^{-1} \text{ DW}$ in HWL, respectively. The species *H. complanatus* had the lowest abundance in both periods. Abundances of *F. californica* and *R. auricularia* were similar during both hydrological periods. Abundance of *G. crista* and *P. acuta* was low, but higher during the HWL period, but these differences were not statistically significant (Mann–Whitney U test, $p > 0.05$).

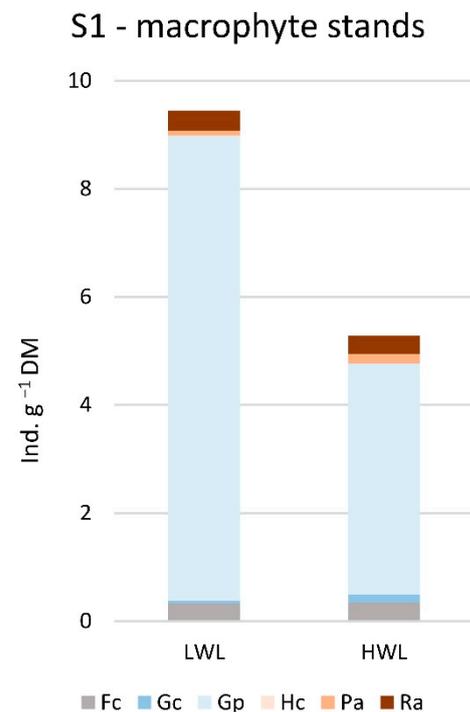


Figure 3. Gastropod abundance within the macrophyte stands of S1. Abbreviations of species names are given in Materials and Methods.

Seven gastropod species were discovered in the littoral benthic area of S1 (Figure 4a). In addition to the species already mentioned within macrophytes, *G. truncatula* and *V. piscinalis* were also discovered in the benthic area of S1. A significantly higher abundance of gastropods was discovered during the HWL period (LWL up to 150 Ind. m^{-2} , HWL up to 600 Ind. m^{-2} , Figure 4a). The Kruskal–Wallis test ($H = 3.86$, $p < 0.05$) indicated that gastropod abundance differed between the two years studied with different hydrological regimes, with gastropods being more abundant in the macrophyte-covered littoral during HWL. In both periods (LWL

and HWL), the abundance of *G. parvus* was the highest (61 ± 54 and 483 ± 325 Ind. m^{-2} , respectively). Abundances of *F. californica* and *G. crista* were equal (ca. 45 Ind. m^{-2} and 3 Ind. m^{-2} , respectively), *R. auricularia* was most abundant in the LWL period, and *P. acuta* in the HWL period.

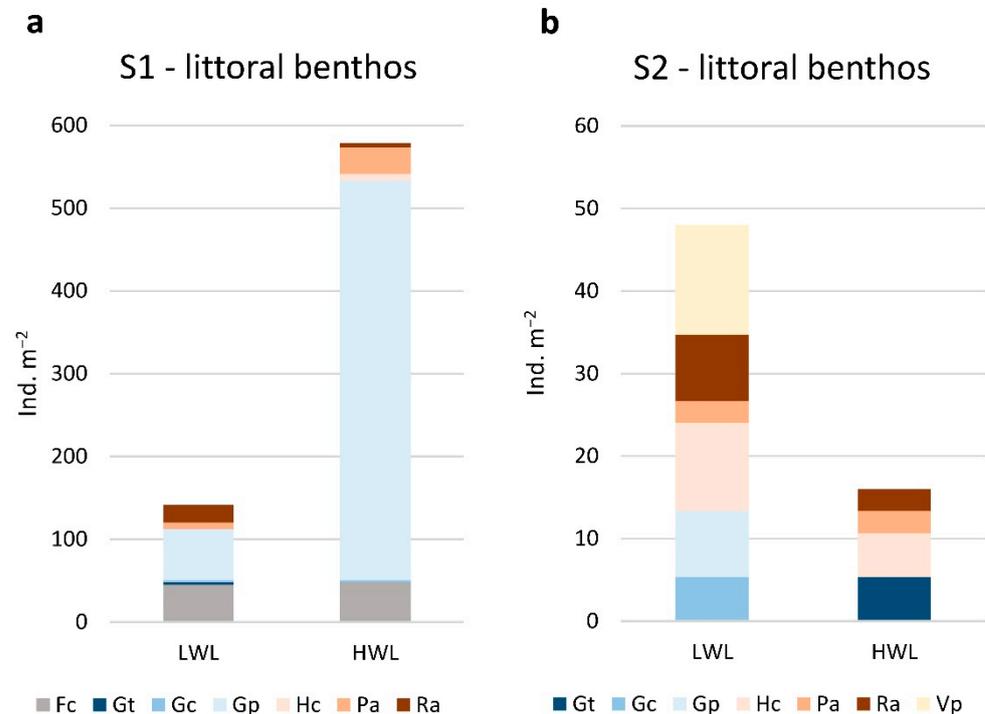


Figure 4. Gastropod abundance in the littoral benthal area of S1 (a) and S2 (b). Abbreviations of species names are given in Materials and Methods.

In waterbody S2, a total of seven gastropod species were discovered in the littoral benthal area (Figure 4b). While *V. piscinalis* was not detected in S1, *F. californica* was not detected in S2. The highest numbers of all species were recorded during the LWL period, with *V. piscinalis* and *H. complanatus* having the highest abundance. The exception was *P. acuta*, which was equally abundant during both periods. Gastropod abundance did not differ significantly (Kruskal–Wallis test, $H = 1.34$, $p > 0.05$), between LWL and HWL. The gastropod abundance in the littoral benthal area was significantly lower in S2 than in S1 (Kruskal–Wallis test, $H = 3.65$, $p < 0.05$).

The difference in total gastropod abundance was statistically significant (Kruskal–Wallis test, $H = 7.67$, $p < 0.05$) when we compared LWL and HWL; this was primarily due to the high abundance of *G. parvus* during HWL (Kruskal–Wallis test, $H = 10.73$, $p < 0.02$). The SIMPER analysis was used to identify the littoral benthic taxa that were responsible for the greatest differences between the LWL and the HWL period (Table 2). It was discovered that the species *G. parvus* was a primary contributor to assemblage structure in both periods. Together with the aforementioned species, *R. auricularia* and *F. californica* played a significant role in structuring the assemblages during LWL, while *P. acuta* and *H. complanatus* were characteristic representatives during the HWL period. The SIMPER test indicated that the assemblages of LWL and HWL were quite dissimilar (average dissimilarity = 78.50). Table 2 indicates that the HWL assemblages were better defined and had higher internal similarity (average similarity = 22.23) than the LWL (average similarity = 10.84).

Table 2. Results of SIMPER analysis for gastropod assemblage during LWL and HWL of investigated waterbodies in S1 and S2 littoral benthal area. Av. Ab.—average abundance of specific species; Av. Sim.—average similarity of specific species; Contrib. (%)—percentage of contribution for specific species in the assemblage.

Species	Av. Ab.	Av. Sim.	Contrib. (%)
LWL			
<i>Gyraulus parvus</i>	2.04	5.72	52.8
<i>Radix auricularia</i>	1.23	1.45	13.35
<i>Ferrissia californica</i>	1.27	1.42	13.12
<i>Physella acuta</i>	0.9	1.26	11.62
HWL			
<i>Gyraulus parvus</i>	3.02	7.16	32.21
<i>Physella acuta</i>	1.64	5.17	23.24
<i>Hippeutis complanatus</i>	1.31	3.5	15.75
<i>Ferrissia californica</i>	1.69	3.22	14.47
<i>Radix auricularia</i>	1.1	3.18	14.32

3.3. Gastropod Functional Feeding Groups

When analyzing the composition of FFG in macrophyte stands of S1, grazers dominated in both time periods, followed by shredders (Figure 5). Abundance values for all groups were higher in the LWL period, except for detritivores, whose values were very low in both periods.

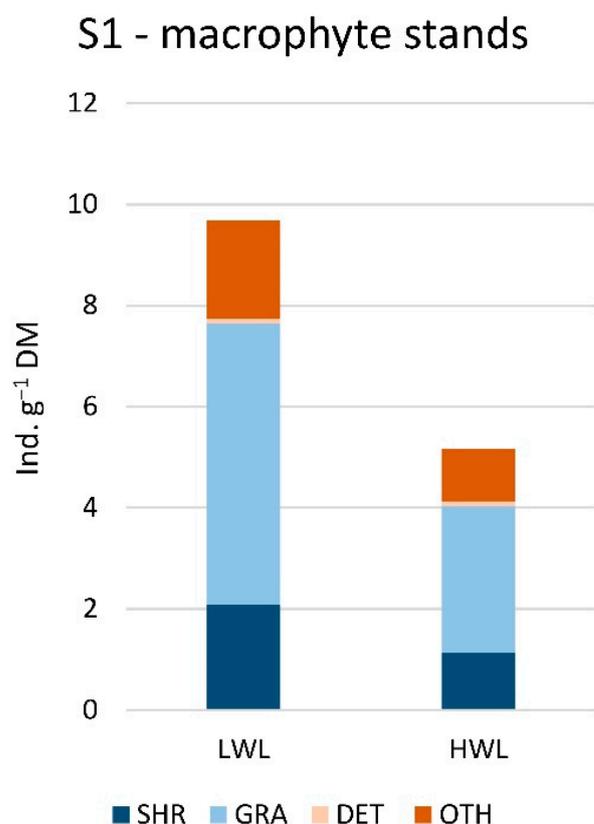


Figure 5. Gastropod functional feeding groups within the macrophyte stands of S1. Abbreviations are provided in Materials and Methods.

In the littoral benthal area of S1 (Figure 6a) grazers also dominated in both periods, but in contrast to the macrophyte stands, the number of all groups was significantly higher in the HWL season, and there were no detritivores.

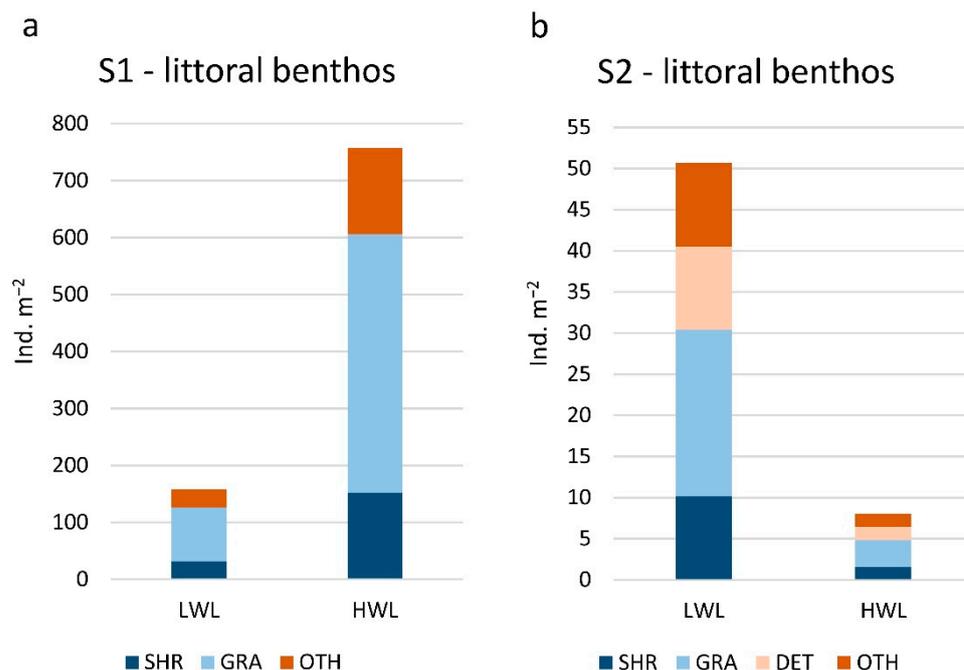


Figure 6. Gastropod functional feeding groups in the littoral benthic area of S1 (a) and S2 (b). Abbreviations are provided in Materials and Methods.

At site S2 (Figure 6b), a significantly higher abundance of all FFG was recorded during the LWL period. Grazing gastropods dominated in both periods, but the numbers of shredders, detritivores, and others were equal.

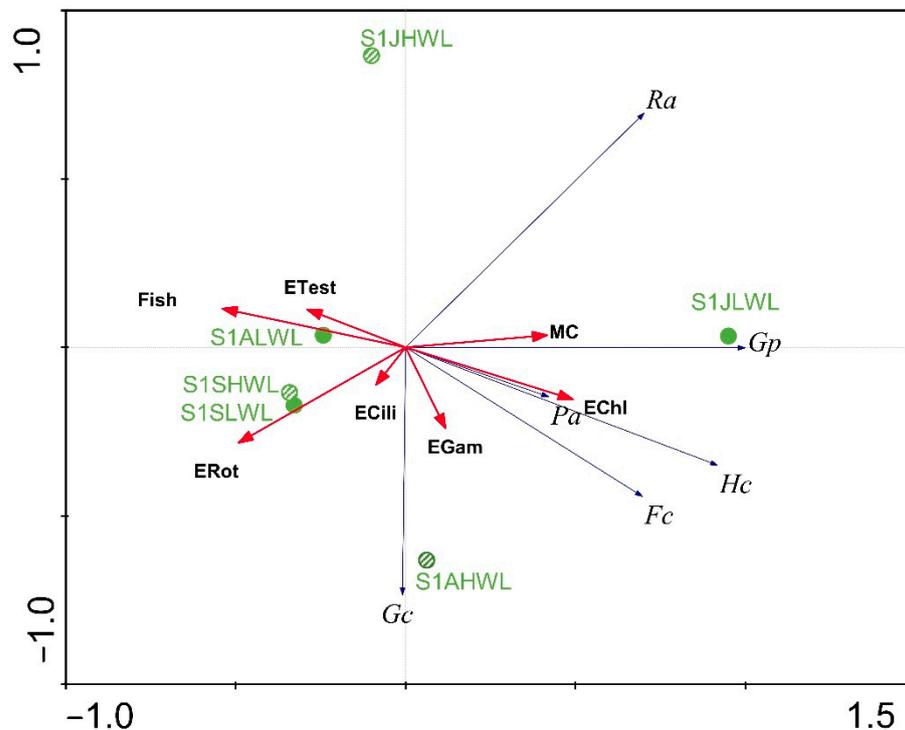


Figure 7. RDA-plot illustrating relationships among sampling sites, physicochemical variables, and gastropod abundance within the macrophyte stands at S1. Abbreviations are provided in Materials and Methods.

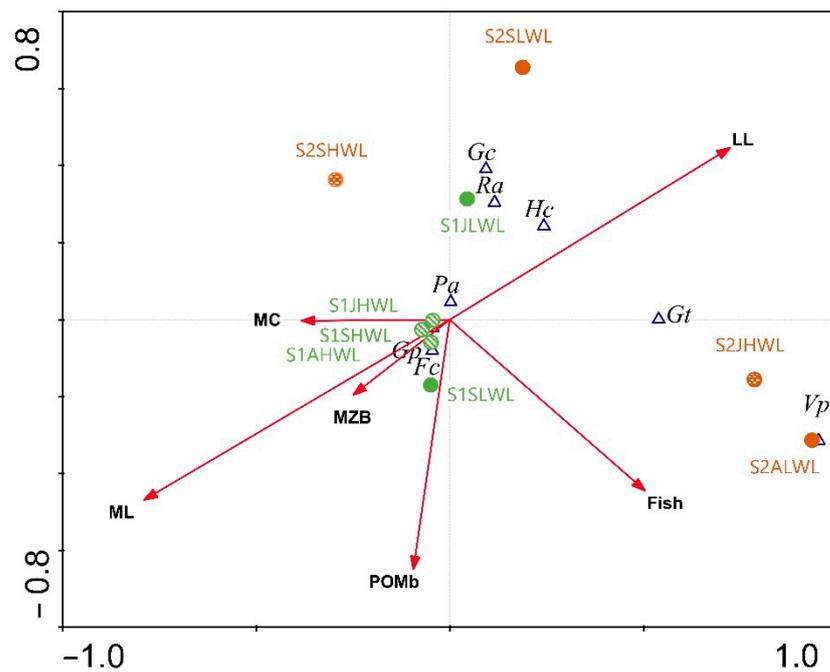


Figure 8. CCA-plot indicating relationships among sampling sites, physicochemical variables, and abundance of common gastropod species in the littoral benthal areas of S1 and S2. Abbreviations are provided in Materials and Methods.

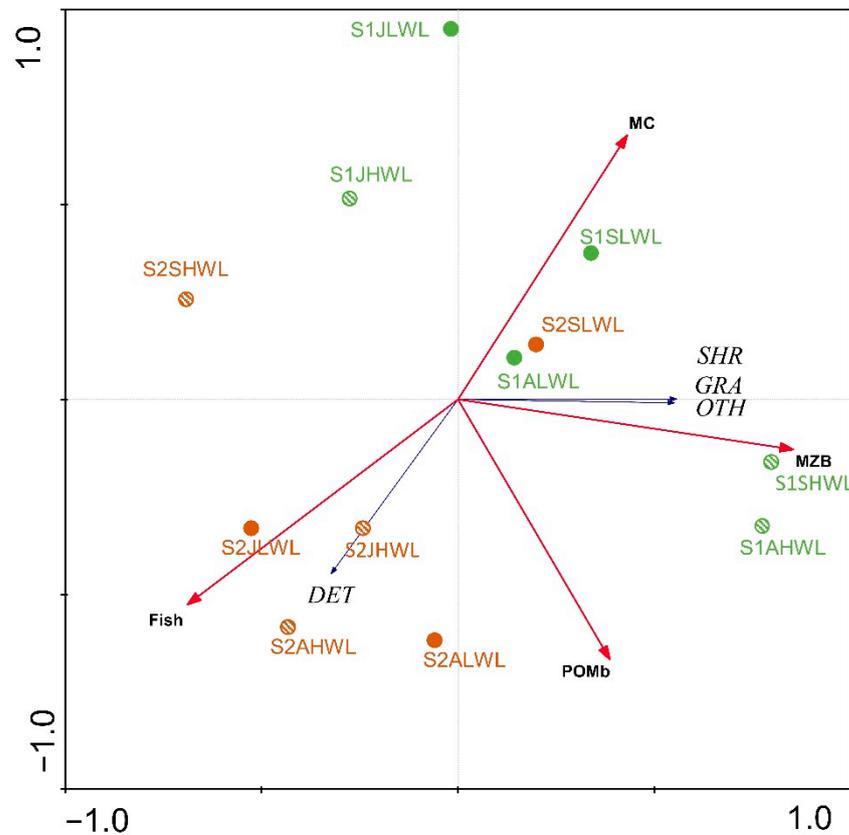


Figure 9. RDA-plot illustrating relationships among sampling sites, physicochemical variables, and functional feeding guilds of gastropods in the littoral benthal area of S1 and S2. Abbreviations are provided in Materials and Methods.

An analysis of relationships among sampling sites, physicochemical variables, and gastropod abundance was also performed. In the macrophyte stands of S1 (Figure 7), the first two axes of the RDA analysis explained 98% of the variance in gastropod interactions (Axis 1: 56%, Axis 2: 42%). The RDA results indicated that the most important food sources for gastropods were Rotifera (ERot: $F = 12.28$, $p = 0.038$), and Gymnamoebae (EGam: $F = 31.68$, $p = 0.032$). According to the CCA results for the littoral benthic area, the first two axes explained 78% of the variance (Axis 1: 52%, Axis 2: 26%, Figure 8). Waterbodies differed as demonstrated in Figure 8, indicating that the gastropod community in the littoral benthic area of S1 was significantly influenced by macrophyte litter (ML: $F = 2.42$, $p = 0.012$), while gastropods in the littoral benthic area of S2 were primarily influenced by leaf litter (LL: $F = 1.00$, $p = 0.0422$). RDA analysis of gastropod FFG composition (Figure 9) indicates that macrophyte cover (MC) increased the number of gastropod shredders and grazers, while particulate organic matter in the benthos (POMb) was significantly positively correlated with the number of gastropod detritivores. In S1, small fish dominated and coexisted with gastropods, while the presence of larger fish in S2 negatively affected the gastropod abundance and, consequently, FFG composition.

4. Discussion

Environmental conditions in ponds and other small waterbodies are far less stable than in lakes and can be profoundly altered by comparatively minor pressures or small changes in the environment [16,20,52,53]. The fluctuations of the water level may greatly affect the functioning of the water body and therefore have an impact on the whole food web. In our study conducted on a Sutla backwater, NW Croatia, it was ascertained that the rise in water level in 2013, caused primarily by high precipitation in the autumn of 2012 and winter of 2013 [2,7], had a strong impact on overall environmental conditions, particularly a 20% reduction in macrophyte cover in one (S1) of the two examined waterbodies.

The results of our study clearly suggest that extreme weather events not only determine environmental conditions, but also gastropod assemblage in small water bodies, which are closely associated with macrophytes and sediments due to their manner of feeding and habitat requirements. During the HWL period, a decrease in diversity and abundance was observed in the littoral benthic area of macrophyte-free waterbody S2 and within the macrophyte stands of macrophyte-covered waterbody S1. In contrast, gastropod abundance increased in the second site of the macrophyte-covered waterbody S1—in the littoral benthic area. These results are consistent with previous studies reporting that gastropods in lakes with large water level fluctuations are subjected not only to direct physical disturbance, but also to significant trophic stress due to reductions in macrophyte biomass and diversity, which create a favorable food base for gastropods [52,54].

All the species identified in our study are typical for shallow waters and the littoral zone of lakes, in addition to floodplains and wetlands with high trophic levels [45], which confirms both the trophic state and the shallow character of the Sutla waterbodies [2,7]. We demonstrated that during the study, pulmonate gastropods dominated, particularly *G. parvus*, while only *V. piscinalis* was observed among prosobranch gastropods. A similar composition was detected by Jezidžić [55], who conducted malacological surveys in the Kopački Rit area at sites with well-developed aquatic vegetation. This author reports that pulmonate gastropods from the family Lymnaeidae are the most represented in the number of species and their abundance, and the highest abundance was observed on submerged vegetation (*C. demersum*), as opposed to emergent and floating plant beds. Lodge et al. [28] note that prosobranchs are absent from ponds and smaller lakes that dry out in summer, or lakes with poor oxygen conditions. Prosobranchs were also absent in small ponds during the water-filled period [56]. It is possible that prosobranchs are outcompeted by pulmonates in water bodies where fish predation levels are low or fish predators are absent. Indeed, when predators are abundant in the environment, prosobranchs with thick shells survive, whereas pulmonates with thin shells do not [28].

The significantly higher abundance of gastropods in S1 compared to S2 SWB during the two hydrological periods can be explained by the greater heterogeneity of habitats in S1 caused by the cover of the complex macrophyte *C. demersum*. This suggests that gastropods use the macrophytes as a safe shelter from potential predators, particularly fish, and that the cover of macrophytes is an important food source for gastropods in addition to other micro- and macroinvertebrates [2,7]. Namely, the leaves of *C. demersum* form bowl-shaped whorls that are close together, particularly near the top of the stem. This may provide additional protection and a stable attachment surface particularly for gastropods being the largest organisms of the epiphytic fauna [57].

Considering the *Ceratophyllum* stand in S1, the observed decline in gastropod abundance during the HWL was primarily a result of the decline in the abundance of the dominant pulmonate species *G. parvus*. According to Lorencova et al. [58] this North American planorbid gastropod was reported from Europe (Germany) in the 1970s, but it is possible that this species was introduced to Europe several centuries earlier and described as a species of *G. laevis*. Recent molecular research has indicated that *G. parvus* and *G. laevis* are indeed members of the same species-level clade, with the former taking nomenclatural precedence [58]. Possible routes of dispersal included freshwater ballast in the holds of transcontinental ships [59] or migratory waterfowl [60]. Since then, it has spread to Central and Western Europe, where it mostly lives in artificial and highly modified habitats in shallow standing waters of different sizes with rich vegetation, mostly in reservoirs or artificial water bodies in gardens, with few competing species [58,61]. In our study, it can be assumed that the lower abundance of *G. parvus* is directly affected by the reduction of macrophytes in the HWL. Additionally, this species likely has a strong preference for macrophyte habitats, as it feeds preferentially by scraping epiphyton and shredding macrophyte tissue and leaves [45,46].

Comparing the gastropod abundance in the littoral benthic area between LWL and HWL, the opposite trends were observed in the studied SWB, namely an increase in S1 and a decrease in S2. After the water level increased in S1, the decrease in macrophyte cover likely resulted in a loss of habitat for the dominant *G. parvus* specimens, and they chose the adjacent littoral benthos, which was rich in macrophyte detritus, as an alternative habitat. This sediment was also observed to be a suitable habitat for other macroinvertebrates in the same SWB [7]. In contrast, in macrophyte-free S2, the decreasing trend in gastropod abundance and diversity with the water rise could be explained by differences in habitat heterogeneity. During LWL, occasional tree branches and roots, in addition to ecotonal vegetation, were partially submerged and likely allowed gastropods to inhabit such organic epiphyton-covered surfaces. Concurrently, these vegetation fragments, along with leaf litter, contributed to the increase in diversity and abundance in S1 during LWL. Decreasing abundance and diversity in S2 during HWL may be associated with flooding of the ecotone zone and adjacent vegetation (primarily grass) as an important habitat for pulmonate gastropods. Thus, the flooding period reduces the habitat and diversification of the gastropod community. Generally, the remaining muddy substrate during the HWL was an unfavorable environment (e.g., lack of epiphyton) for their life in S2. Consistent with our results, there are records of decreases in the abundance of *Chilina ovalis* G. B. Sowerby I, 1838 in the muddy sediment of the Queule River Estuary, in the south-central region of Chile [62].

The occurrence of alien species is often regarded as one of the major threats to biodiversity, both on a local and global scale. Therefore, it is important to monitor communities of freshwater organisms to assess their taxonomic affiliation and changes in the abundance of alien species. We observed three alien invasive species: *F. californica*, *P. acuta*, and the previously mentioned *G. parvus*. Two of these species, *P. acuta* and *F. californica*, are also native to North America [63–67], similarly to *G. parvus*. The possible pathway of introduction for these three species into the studied SWB is human activities (e.g., fish stocking), but spread by animals (particularly birds) should not be excluded. The abundance of *P. acuta* and *F. californica* suggests that these species have significant influence in structuring

the assemblage in the littoral benthos of both SWB, particularly during HWL. The species *P. acuta* is known to be one of the most effective and spectacular invaders among freshwater gastropods [66], and in our study it indicated an increasing trend of abundance and a higher proportion of the gastropod assemblage during HWL (LWL 12%, HWL 23%) compared to *F. californica* (LWL 13%, HWL 15%). Like other invaders, both species displayed resistance to stressors. The rising water levels in our study resulted in an increase in their abundance and more uniform species composition. From a biogeographic perspective, molluscan invasions lead to homogenization of faunas, the extinction of sensitive endemic species, and changes in the biotic composition of invaded ecosystems [65–69].

Not only single species will react to changes in the environmental conditions. Very often, a functional group, which is a set of organisms that share similar characteristics within a community, will also reveal a strong response. As mentioned, the analyses of FFG were performed based on their feeding preferences as suggested by Moog [46], according to which one species can be classified into several groups. Species such as *G. parvus*, *G. crista*, and *H. complanatus* are primarily grazers but could be classified as shredders as well; *F. californica* is a shredder and grazer in the same ratio; *P. acuta* was primarily a grazer but is also shredder and detritivore; *R. auricularia* is a shredder and grazer in the same ratio while to a lesser extent detritivore; *V. piscinalis* is a detritivore [46]. The decrease in the numbers of grazers and shredders among macrophytes in S1 during HWL is directly related to the decrease in the abundance of *G. parvus*. The same explanation can be applied to the increasing number of grazers and shredders due to HWL in the littoral benthic area in S1. The decreasing numbers of shredders and grazers in S2 in HWL are a consequence of the absence of *G. parvus*, *G. crista* and *H. complanatus*, while the decreasing abundance of *R. auricularia* and the absence of *V. piscinalis* result in fewer detritivores. These results were also confirmed by the RDA analysis, which indicated that macrophyte stands increased the number of gastropod shredders and grazers, while particulate organic matter in the benthic area was significantly positively correlated with the number of gastropod detritivores. According to the CCA analysis in the macrophyte stands of S1, the most important food sources for gastropods were Rotifera and Gymnamoebae. It is known that these groups are common and abundant in epiphytic assemblages of freshwaters [7,70]. In contrast, CCA results indicate that macrophyte litter in the littoral benthic area of S1 and leaf litter in the littoral benthic area of S2 significantly influenced the gastropod assemblages.

It is important to emphasize that through analyzing the percentages of FFG, it is evident that the ratios of individual FFG remained exactly the same in the littoral benthic area of both SWB. Minor discrepancies were observed only in S1 among macrophytes, where there was a slight decrease in grazers and others, while there has been an increase in detritivores and shredders. These changes can be attributed to higher abundances of *P. acuta* and *R. auricularia*.

Although all gastropod species observed during the study in both SWB are very small (shell width for planorbids and shell length for other species are less than 5 mm), we can assume that small-sized fish in S1 did not consume gastropods. Therefore, the abundance of gastropods was significantly higher in S1 than in S2, where larger-sized fish species, including carp, which can effectively feed on snails, predominated.

Finally, we can conclude that both methods of assessing environmental conditions using the taxonomic approach and functional diversity of gastropod assemblages may be useful tools that can be applied for monitoring changes in ecosystem functions in the SWB that are influenced by water level fluctuations.

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