Sediment as a Refuge Spot for Planktonic Crustaceans

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Abstract: The littoral zone of shallow water bodies (SWB) is often considered in relation to predator–prey interactions. In this study we assumed that the littoral sediment serves as a refuge for planktonic microcrustaceans, mediated by size-dependent fish predation. In order to recognise the impact of fish on their prey, we determined: (i) the assemblage and size structure of crustaceans and fish; and (ii) the biotic interactions along the gradient of the heterogeneity of the littoral zone. The results showed that in the sediment of macrophyte-dominated SWB, large-sized cladocerans predominated and were preyed upon by smaller-sized fish. In the sediment of macrophyte-absent SWB, large-sized copepods dominated, due to the predation risk of larger-sized fish. Cladoceran females with egg broods mostly selected sediment as shelter. Cladocera/Copepoda ratios were lower in the littoral of vegetated SWB, and higher in unvegetated SWB. The ratios in the adjacent sediment revealed an opposite pattern. It is important to point out the findings of planktonic crustacean species in the sediment of SWB are not recorded in the littoral water. The result of this study will contribute to the knowledge of defence strategy mechanisms developed by zooplankters against predators.

Keywords: Cladocera; Copepoda; fish; predator-prey interactions; shallow lakes

1. Introduction

In freshwater ecosystems, fish, as visual and size-selective predators, are the main regulators in top-down ecosystem control. They can easily detect large-sized prey such as crustacean plankton, e.g., *Daphnia* [1] on which zooplanktonivorous fish (e.g., perch—*Perca fluviatilis* L. 1758 and roach—*Rutilus rutilus* L. 1758) have a strong negative impact [2,3]. In addition, fish often affect crustacean fecundity, as females with eggs are more conspicuous and therefore more vulnerable to predation [4]. Females not only produce eggs but also may actively care for their eggs. This strategy is known for the majority of freshwater planktonic organisms as an evolutionary adaptation to inhabit inland waters [5]. Experimental studies on fish feeding upon copepod females with subitaneous eggs—two calanoid species (*Eudiaptomus gracilis* (Sars, 1863) and *E. graciloides* (Lilljeborg, 1888)) and two cyclopoid species (*Cyclops abyssorum* Sars, 1863 and *Macrocyclops albidus*, Jurine, 1820)—revealed that 50–70% of the calanoid eggs and 11–29% of the cyclopoid eggs survived fish ingestion [6]. The above-mentioned authors concluded that digestion

resistance of eggs in copepods is likely to be an adaptation of copepod egg-carrying females to fish predation.

To survive, microcrustaceans have evolved various strategies to avoid or minimise fish predator pressure. One such strategy is diel migration, which differs depending on the lake depth. In deep lakes diel vertical migrations are most important, where zooplankton avoid fish during the daytime by migrating vertically into the deeper, darker, hypolimnetic water layer [7–11]. In shallow lakes, zooplankton undertake horizontal migrations into vegetated littoral zones during the day, and back to the pelagial zone at night [7–13]. These defence mechanisms are defined as diel horizontal migration. Macrophytes play an important role for zooplankton organisms in this case. The results of a study conducted on shallow wetlands in South Korea [14] showed that the physical structure of microhabitats strongly influences the distribution of various aquatic animals. The complex habitus architecture of macrophytes provides food resources of high quality and quantity, and ensures zooplankton refuge and protection against visual predators by reducing predator–prey encounters and positively influences zooplankton survival rates [8,15–17]. The efficiency of horizontal migrations also depends on the predation pressure from tactile, macroinvertebrate predators, i.e., insect larvae, within the macrophyte stands [7,18]. Namely, within stands of structurally complex submerged plants, predation pressure by invertebrates is higher than among free-floating macrophytes [7,17]. Furthermore, in the presence of piscivorous fish, macrophyte stands may also provide a refuge for juvenile fish, and in this way increase predation pressure on zooplankton [8]. Adult and juvenile fish mostly feed upon large-bodied zooplankters, including females carrying eggs, while invertebrate predators mostly prey upon smaller zooplankton individuals, including rotifers [4].

Recent studies related to predation in the shallow water bodies (SWB) mainly indicate that fish size selective predation at first affects large-sized zooplankters, especially cladocerans (efficient algivores), and shifts the population size in favour of small-sized cladocerans and rotifers (less efficient algivores), and also brings alteration from a transparent to a turbid state and a consequent deterioration of water quality [7,8]. A key abiotic factor in fish–zooplankton interplays is water transparency or turbidity, determining the impact of fish predation on zooplankton as well as its defence mechanisms against predators [12]. At a high turbidity, zooplankton are generally uniformly distributed in the lake, while in transparent lakes their distribution shows different spatial patterns, depending on the lake depth and macrophyte coverage [19]. Accordingly, large-sized zooplankters in SWB seek shelter within macrophyte stands [8,20–23]. Although aquatic vegetation as refuge has been investigated intensively, the analogous role of sediments in water bodies has still not been fully described and proven. Some studies indicate that planktonic zooplankters hide in the near-bottom water layer [7,8,24,25] and above or in lake sediment [9,16], thus suggesting zooplankton vertical movement in SWB. It has been confirmed that in the macrophyte-dominated areas of SWB, zooplankton may undertake both types of migrations, typical horizontal between the plant stand and adjacent waters, but also vertical within the plant bed [21]. The structure of zooplankton inhabiting the littoral zone of three SWB, S1, S2, and SK, has previously been assessed [26], and in this study it will be presented mainly as the background for comparisons with the assemblage occupying the sediment zone. In the present study we tested a selection of sediment as a refuge for planktonic crustaceans against fish predation, based on fish size-efficiency at different water transparencies, macrophyte coverages, and sediment types. The goals of this research were to assess: (i) the assemblage and size structure of planktonic crustaceans and fish in the littoral area and sediment; and (ii) the biotic interactions along the gradient of the heterogeneity of the littoral zone. This study will make an important contribution to research on the defence strategy mechanisms developed by invertebrates against predators in SWB, which are ecosystems highly vulnerable to growing land-use pressures and environmental change, particularly those associated with human-originated changes [27].

2. Materials and Methods

2.1. Study Sites

The research was carried out in small, shallow waterbodies (SWB) located in NW Croatia (Europe; Figure 1): Škrčev kut (SK; Length$_{max}$ =300 m, Width$_{max}$ = 12 m, Depth$_{max}$ = 4.5 m) an oxbow of the Krapina River and backwater of the Sutla River, divided into two basins S1 (Length$_{max}$ =124 m, Width$_{max}$ = 12.2 m, Depth$_{max}$ = 3.3 m), and S2 (Length$_{max}$ =188 m, Width$_{max}$ = 14.4 m, Depth$_{max}$ = 4.6 m). Detailed information related to the studied waterbodies has been provided in our previous papers [16,26]. The three studied localities differed greatly in respect to the water transparency and macrophyte cover. SK was turbid, covered very rarely with free-floating macrophytes (0–3% coverage with *Nuphar lutea* (L.)); Sm. S1 was a more transparent waterbody, moderately covered (10–50%) with submerged macrophytes, mostly, hornwort *Ceratophyllum demersum* L.; and S2 was turbid and lacked macrophytes. All SWB were under intense pressure from recreational fishing.
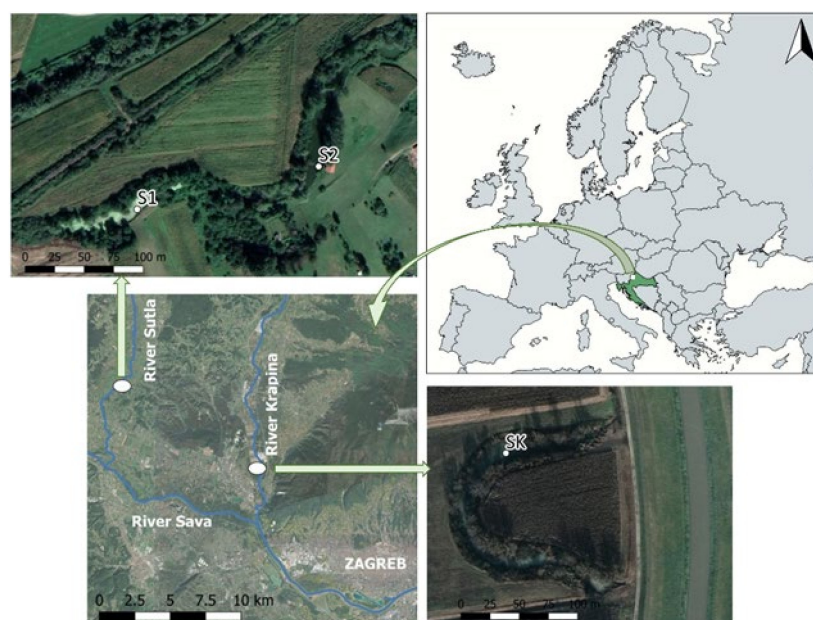

Figure 1. Map showing the schematic and satellite location of the investigated shallow waterbodies in Croatia with marked sampling sites in the littoral of: S1—Sutla backwater basin with submerged macrophytes (45°54′51″ N, 15°41′48″ E), S2—Sutla backwater without macrophytes (45°54′53″ N, 15°41′56″ E), SK—Škrčev kut oxbow (45°51′45″ N, 15°49′29″ E).

2.2. Collection and Analysis of Biocoenotic Components

Samples were collected from May to October of 2013, on nine sampling occasions: once a month in May (V), September (IX), and October (X), and twice a month in June (VI/1, VI/2), July (VII/1, VII/2), and August (VIII/1, VIII/2) in the littoral zone of three SWB (S1, S2, and SK). For determination of the planktonic crustaceans, the following literature were used: coverage [28] for Cladocera, and [29] for Copepoda.

Zooplankton samples in the littoral water zone were gathered in triplicates (plankton net mesh size 26-μm) after filtering 3 × 10 L of the water, and were fixed with 4% formalin. Sample volumes were concentrated to 5–12 mL using a centrifuge (EBA, Hettich, 3500 rpm for 5 min). Total number of the samples used in our analysis were 54. Each sample was counted using the Opton-Axiovert 35 microscope (Carl Zeiss Jena, 100× to 400×) and shown as abundance in ind. L^{-1}.

Planktonic crustaceans, Cladocera (Cla) and Copepoda (Cop), in the sediment zone were also collected in triplicates, together with macrozoobenthos using a Surber sampler (25 × 25 cm frame; 300 μm mesh size), preserved in 75% ethanol and analysed under an

Olympus SZ61 stereomicroscope (Hamburg, Germany; $10\times$ to $40\times$ magnification) and an Opton-Axiovert 35 microscope (Carl Zeiss Jena, $100\times$ to $400\times$). Specimens were identified to the lowest possible taxon, and their abundance was expressed in ind. m^{-2}. Abundance of Cladocera and Copepoda females with eggs (Cla_{egg}, Cop_{egg}), in brood chambers and egg sacks, respectively, was also recorded in the littoral plankton and sediment samples. Their abundances were extracted and merged in the total abundances of cladocerans and copepods. In the benthos samples we also found semiplanktonic benthic microcrustaceans Copepoda-Harpacticoida and Ostracoda. Their abundances were counted but not included in the further analyses.

According to the body length, by measuring individual body size of approximately 30 specimens of each species, planktonic crustaceans were grouped into 3 size categories: ClaI/CopI 300–600 μm (Cla: *Bosmina longirostris*; Cop: nauplii), ClaII/CopII 600 μm–1 mm (Cla: *Ceriodaphnia pulchella*; Cop: copepodites), and ClaIII/CopIII > 1 mm (Cla: *Daphnia* sp., *Illiocryptus agilis*, *Simocephalus exspinosus*, *S. serrulatus*, *S. vetulus*, *Eudiaptomus gracilis*, *Macrocyclops* spp.).

Electrofishing (employed by Hans Grassl EL 63 II, 220/440 V, 17.8/8.9 A; Hans Grassl Schönau am Königssee, Germany) was undertaken in the littoral zone for 15 min and fish abundance was shown as catch per unit effort (CPUE per 15′). Fish identification was performed according to [30]. Several fish traits were considered in the study: abundance, biomass (g), and size structure. Fish were divided into three size categories based on their body length: FI (<5 cm), FII (5–10 cm), and FIII (>10 cm).

2.3. Determination of Limnological Factors and Sediment Analysis

Limnological parameters analysis has extensively been described in our previous paper that dealt with the littoral zone of S1, S2, and SK waterbodies [26]. The study confirmed significantly higher macrophyte coverage, transparency, and POM in S1 in comparison to S2 and SK. Field measurements and collection of water samples for laboratory analyses were taken at each sampling point. In the field, pelagic water transparency was measured with a Secchi disc (z_{SD}), and portable instruments were used to determine temperature, oxygen concentration, pH (Hach HQ30d, Loveland, CO, USA), and conductivity (Hach sensION 5, Loveland, CO, USA). Macrophyte coverage (MC, %) was estimated as an average from the ratio of transect length occupied by macrophytes to total transect length at five locations in each SWB. All nutrients, orthophosphates, total phosphorus, nitrates, and Kjeldahl total nitrogen were determined in the laboratory [31]. Nitrites and ammonium were measured using an ion chromatograph (Dionex ICS-3000), and dissolved organic matter (DOM) through the estimation of chemical oxygen demand, $COD_{(Mn)}$ [17]. Phytoplankton and concentration of suspended and particulate organic matter (POM) were regarded as food resources. Phytoplankton biomass (indicated by chlorophyl *a* in plankton, Chl *a*) was determined using an ethanol extraction method by [32]. POM values (measured as ash free dry mass, AFDM) were obtained after drying each sample at 104 °C for 4 h and ashing at 600 °C for 6 h [19]. The determination of the sediment type (SIM—Sediment Inorganic Matter; SOM—Sediment Organic Matter; LL—Leaf litter; WL—Wood Litter; and ML—Macrophyte Litter) in the littoral zone of three SWB was conducted according to mass analyses after drying each sample at 104 °C for 4 h. SIM and SOM were calculated after exposing mud sediment at 600 °C for 6 h.

2.4. Statistical Analysis

Non-metric multidimensional scaling (NMDS) was used to determine similarities between stations based on based on fish traits, sediment type, and macrophyte coverage. In addition, we applied multivariate analysis of similarities (ANOSIM) to identify differences/similarities in environmental conditions and main drivers. ANOSIM generates an r-value ($p < 0.05$) ranging between −1 and +1; r < 1 indicate similarities, r = 0—indicates no difference, and r > 0.5 indicate differences among study sites [33]. Both analyses were performed using the analytical package PRIMER v6 [34].

Data for the analysed abiotic and biotic parameters did not show normal distribution (Shapiro–Wilk test, $p < 0.05$) and could not be normalized by common transformations. Thus, a nonparametric Kruskal–Wallis test ($p < 0.05$) and accompanying *post-hoc* Tukey test were used for testing differences between the three SWB, and the Mann–Whitney U test ($p < 0.05$) for comparison of the percentage of planktonic crustaceans in the littoral plankton and sediment (Statistica 9.1, StatSoft, 2010, Tulsa, OK, USA). A correlation matrix was obtained by the R function "*cor*" using the Spearman test ($p < 0.05$), and a correlogram was made using the package "*corrplot*" (RStudio). GAM models were used to assess the relationships between Cladocera and Copepoda abundance as dependent variables and potential drivers FI, FII, FIII, M%, and SD as independent variables with the "mgcv" package in R (Wood, 2017), R version 4.1.2 [35]. Parameter estimation was determined using the restricted maximum likelihood method (REML). We started with the most complex model that included all independent factors and reformulated it by removing different smoothers. All models were then compared using the Akaike information criterion, AIC [36].

3. Results

3.1. Abiotic and Biotic Drivers in the Zooplankton Shelter Selection

Environmental conditions in the water column of the littoral zone of the three shallow waterbodies, including 12 environmental parameters—z_{SD}, MC, temperature, dissolved oxygen, conductivity, phosphorous and nitrogen nutrients, DOM, Chl *a*, and POM—altogether showed significant differences among three SWB (ANOSIM r = 0.80, $p < 0.001$). Comparison of environmental conditions between each combination of two SWB (S1 vs. S2, S1 vs. SK, and S2 vs. SK) also indicated significant variation (ANOSM, r = 0.7–0.96, $p < 0.01$).

The chosen drivers (transparency, macrophyte coverage, sediment type, and visual predator size categories) in the zooplankton shelter selection differed significantly among three SWB (Kruskal–Wallis test, $p < 0.05$). Macrophyte coverage ($25 \pm 6.1\%$) and transparency (1.1 ± 0.1 m) were significantly higher in S1 in comparison to SK (MC $0.5 \pm 0.3\%$, $z_{SD} = 0.4 \pm 0.1$ m) with rare macrophyte coverage and S2 ($z_{SD} = 0.7 \pm 0.1$ m) without macrophyte coverage (Kruskal–Wallis test, $H_{MC} = 13.28$, $p = 0.0013$; $Hz_{SD} = 14.84$, $p = 0.0006$). Sediment composition showed a 50% to 70% share of organic matter in the littoral sediment of the three SWB (Figure 2a). Significant differences among SWB arose from a higher share of ML (20%; 39.8 g m^{-2}) in S1, in comparison to a higher contribution of LL, 20% (22 g m^{-2}) and 10% (25.2 g m^{-2}), in S2 and SK, respectively (Kruskal–Wallis test, $p < 0.05$; Table 1).

Studies sites differ in fish composition: in S1 the dominant species was *Carassius gibelio* (Bloch, 1782) (27% in abundance), followed by *Rutilus rutilus* (Linnaeus, 1758) (18%), and *Lepomis gibbosus* (Linnaeus, 1758) (11%); in S2 the dominant species was *Alburnus alburnus* Linnaeus, 1758 (27), followed by *L. gibbosus* (20%) and *Cobitis* sp. (13%); *Pseudorasbora parva* (Temminck and Schlegel, 1846) with 26% in abundance was the dominant species in SK, followed by *L. gibbosus* (22%) and *A. alburnus* (14%). Fish appeared in significantly higher abundances in SK in comparison to S1 and S2, which resulted from the highest abundance of mid-sized specimens, and the lowest abundance of small-sized fish (Table 1, Figure 2b). The submerged macrophyte-covered littoral of S1 had abundant small-sized fish (8 ± 7 Ind. CPUE), which differed significantly from their abundance (≈ 2 Ind. CPUE) in the littoral of SWB with an extremely sparse or absence of macrophytes, SK and S2, respectively (Figure 2b, Table 1).

Planktonic crustaceans in sediment were confronted by slightly overlapping, but clearly different environmental conditions, including fish traits (abundance, biomass, and size structure), percentage of sediment type, and macrophyte coverage, when seeking shelter across the three SWB (ANOSIM, r = 0.52, $p < 0.001$), (Figure 3). Notably pronounced imparity was observed between conditions in the macrophyte covered S1 in comparison to the sparsely free-floating macrophyte covered SK (ANOSIM, S1 vs. SK, r = 0.75 $p < 0.001$) or macrophyte absent S2 (ANOSIM, S1 vs. S2, r = 0.818, $p < 0.001$), while related features did not differ significantly between S2 and SK. These results were also confirmed by NMDS

analysis, which separates the S1 site with dense macrophyte stands and the abundant small-sized fish size category (Figure 2b) from the other two locations (Figure 3). The results of the Kruskal–Wallis test ($p < 0.05$) agreed with these discoveries, suggesting that distinctions among the three SWB resulted from significantly more extended submerged macrophyte coverage, a higher amount of ML, and a lower amount of LL, as well as a higher abundance of smaller fish in S1 in comparison to SK and S2 (Table 1).
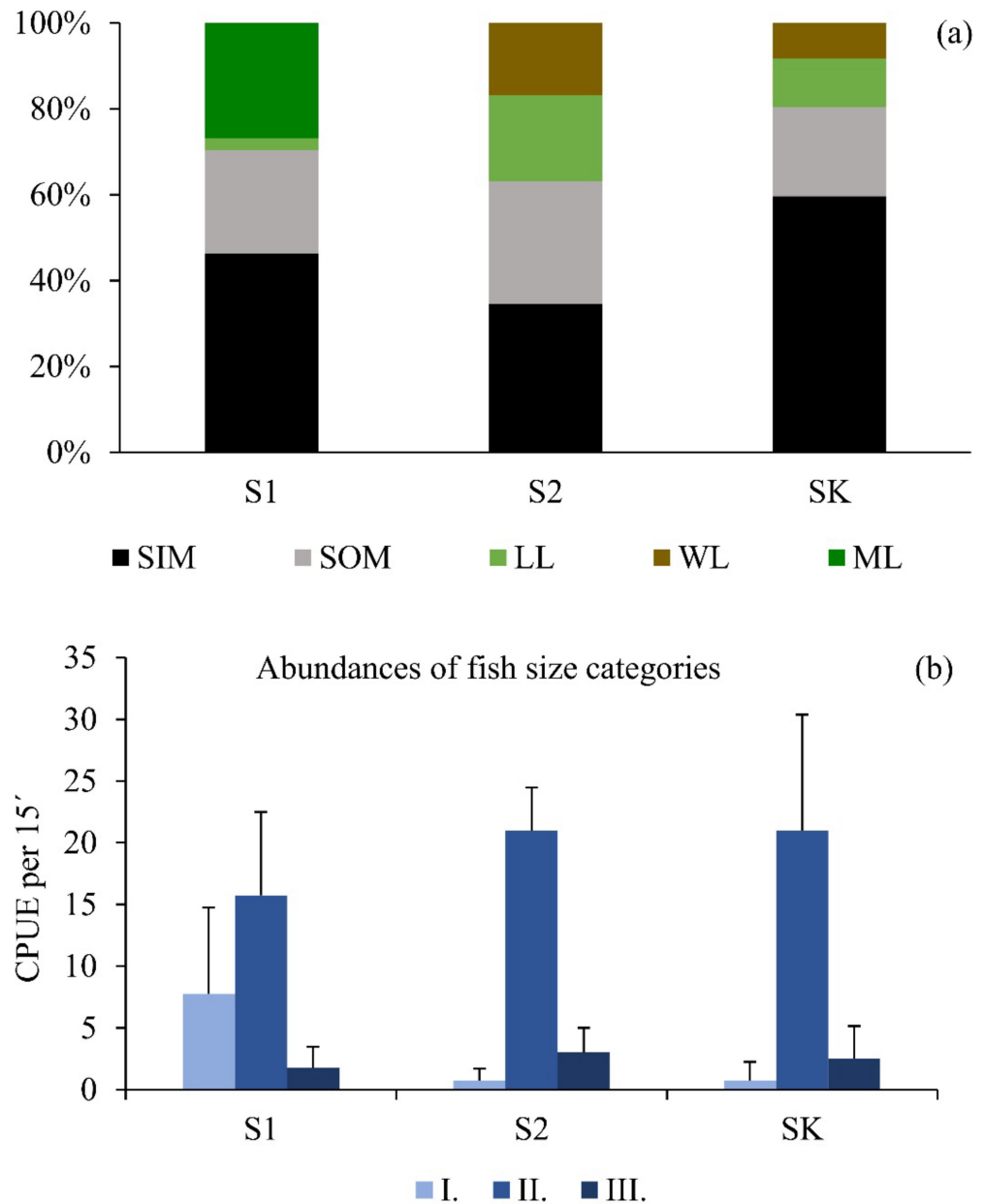

Figure 2. Contribution of (**a**) sediment type and (**b**) fish size distribution in the littoral zone of three SWB (S1, S2, SK). (**a**) abbreviations: SIM—Sediment Inorganic Matter, SOM—Sediment Organic Matter; LL—Leaf litter; WL—Wood Litter; ML—Macrophyte Litter. (**b**) abbreviations for fish size categories based on their body length: FI (<5 cm), FII (5–10 cm), and FIII (>10 cm).

Table 1. Significant differences (Kruskal–Wallis test, $p < 0.05$) in the sediment type and traits of fish, zooplankton, and planktonic crustaceans in the littoral sediment among the study sites (S1, S2, and SK).

	H	*p*	*Post-Hoc* Test
Sediment type			
LL (g m^{-2})	10.88	0.0043	S1 < S2, SK
ML (g m^{-2})	17.68	0.0001	S1 > S2, SK
Fish			
Total fish abundance	8.856	0.0119	SK > S1, S2
Fish I	13.59	0.0011	S1 > S2, SK
Average fish length (cm)	10.66	0.0048	S1 < S2, SK
Littoral Sediment			
No. of taxa	6.73	0.0346	SK < S1
Total Crustacea (Ind. m^{-2})	7.89	0.0193	SK < S2
Cladocera females with eggs (Ind. m^{-2})	8.24	0.0163	SK < S2

Figure 3. Non-metric multidimensional scaling (NMDS) ordination based on fish traits, sediment type, and macrophyte coverage in three SWB based on Euclidian distance.

3.2. Planktonic Crustaceans in the Littoral Sediment and Connection with the Littoral Plankton

Fourteen species of planktonic crustaceans, seven species each of cladocerans and copepods, were observed in the littoral sediment of the three SWB. The total number of species was highest in S2 (10 species), and statistically significant in comparison to SK (Tables 1 and 2). Cladocerans were the most diverse in S2 (six species), while copepods were equally present in each SWB with four species. Cladoceran species of the genus *Simocephalus*, and copepods *Macrocyclops albidus* (Jurine, 1820) and *Cyclops* sp. in SK, dominated in assemblage across the three SWB (Table 2).

Table 2. Composition and abundance (AVE ± SD) of planktonic crustaceans in the littoral sediment of three SWB.

Taxa/Station	S1			S2			SK		
Cladocera									
Bosmina longirostris (O.F.Müller, 1776)				512	±	540			
B. longirostris with eggs				339	±	358			
Ceriodaphnia pulchella				13	±	13			
Daphnia curvirostris Eylmann, 1887				38	±	40			
D. curvirostris with eggs				19	±	20			
Ilyocryptus agilis Kurz, 1878	1	±	1	1	±	1			
Pleuroxus sp.	1	±	1						
Simocephalus vetulus (O.F. Müller, 1776)	773	±	279	256	±	105	149	±	146
S. vetulus with eggs	223	±	108	68	±	36	9	±	8
Simocephalus exspinosus (Koch, 1841)	261	±	79	159	±	79	100	±	104
S. exspinosus with eggs	77	±	38	39	±	18	5	±	5
Simocephalus serrulatus (Koch, 1841)							12	±	11
S. serrulatus with eggs							10	±	10
Cladocera total	1031	±	350	978	±	594	260	±	160
Cladocera total eggs	262	±	127	469	±	368	24	±	23
Cyclopoida									
Acanthocyclops robustus (Sars, 1863)	88	±	93						
A. robustus with eggs	2	±	3						
Cyclops sp.	35	±	17	61	±	64	96	±	66
Cyclops sp. *with eggs*	1	±	1	7	±	8	1	±	1
Ectocyclops sp.							1	±	1
Macrocyclops albidus (Jurine, 1820)	44	±	25	51	±	27	64	±	60
M. albidus with eggs	44	±	25	30	±	19			
Macrocyclops fuscus (Jurine, 1820)	3	±	3						
Mesocyclops leuckarti (Claus, 1857)				218	±	229			
M. leuckarti with eggs				38	±	40			
nauplii	1	±	1	26	±	27			
copepodites	26	±	13	2265	±	2292			
Cyclopoida total	285	±	134	2621	±	2539	154	±	118
Cyclopoida total eggs	15	±	4	61	±	40	1	±	1
Calanoida									
Eudiaptomus gracilis (Sars, 1863)				6	±	7	3	±	3
Calanoida total				6	±	7	3	±	3
Harpacticoida total				3	±	3			
Ostracoda total	2	±	2	10	±	7	9	±	9

In sediment, the total abundance of planktonic crustaceans was almost tenfold higher in S2 without macrophytes (3609 ± 3127 Ind. m^{-2}), in comparison to SK with sparsely free-floating macrophyte coverage (418 ± 380 Ind. m^{-2}; Tables 1 and 2). Planktonic cladocerans prevailed in the sediment of S1 and SK up to 70%, and copepods dominated in S2 up to 80%. In the littoral zone of the studied SWB, the share of cladocerans and copepods was opposite to that in the sediment (Figure 4). Overall, a significantly higher share of copepods was found in the littoral zone than in the sediment (Mann–Whitney U test, Z = 4.9, $p < 0.0001$).
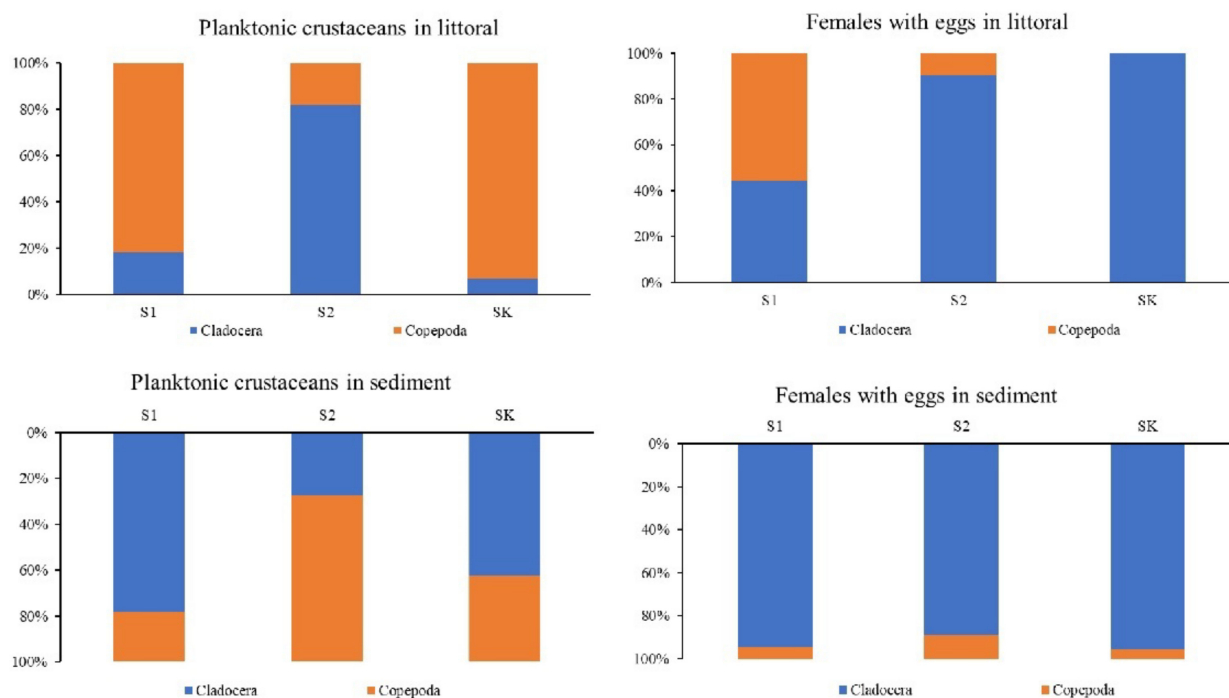
Figure 4. Relative abundance of planktonic crustaceans, Cladocera and Copepoda, and females with eggs in littoral water zone and sediment in the three SWB.

In total, crustacean females with eggs occurred in a lower abundance in SK, particularly significantly cladocerans, in comparison to S2 (Table 2). In S2, females with eggs made up a 15% abundance of planktonic crustaceans in sediment (Cru_{egg} 530 ± 408 Ind. m^{-2}), and around 6% in SK (Cru_{egg} 24 ± 23 Ind. m^{-2}). Interestingly, females with eggs contributed up to 30% to the abundance of planktonic crustaceans in the sediment of S1 (Cru_{egg} 277 ± 130 Ind. m^{-2}), although their abundance was smaller than in S2. In all ponds, Cla_{egg} dominated and contributed 95 to 99% in sediment abundance (Figure 4). In the littoral zone plankton females with eggs made up <5% of total crustacean abundance, and the ratio of cladocerans differed in comparison to the sediment (Table 2). In the littoral, plankton of S1, the ratio of Cladocera and Copepoda females with eggs was almost equal, and in S2 and SK, 10% and 0%, respectively (Figure 4).

Planktonic crustaceans in sediment were mainly representatives of large-sized categories, up to 75% of ClaIII and up to 25% CopIII in S1 and SK waterbodies (Figure 5). The share of large-sized planktonic crustaceans, particularly the share of ClaIII, appeared significantly higher in the sediment than in the littoral zone of the unvegetated S2 (Mann–Whitney U test, $Z_{ClaIII} = -2.472$, $p < 0.01$) and the sparsely floating-leaved covered SK (Mann–Whitney U test, $Z_{ClaIII} = -2.122$, $p < 0.03$; Figure 5). In the littoral water zone, large-sized cladocerans (ClaIII) occurred only in S1 in a share of less than 10%, while CopIII dominated within the macrophyte stands of S1 and SK, 40% and 25%, respectively. Generally, small-sized specimens prevailed in the littoral zone of S2 (90%) and SK (70%; Figure 5). These records resulted in a significantly higher share of ClaI, CopI, and CopIII in the littoral water in comparison to the sediment (Mann–Whitney U test, $Z_{ClaI} = 4.680$, $p < 0.0001$; $Z_{CopI} = 5.870$, $p < 0.0001$; $Z_{CopIII} = 2.200$, $p < 0.027$).
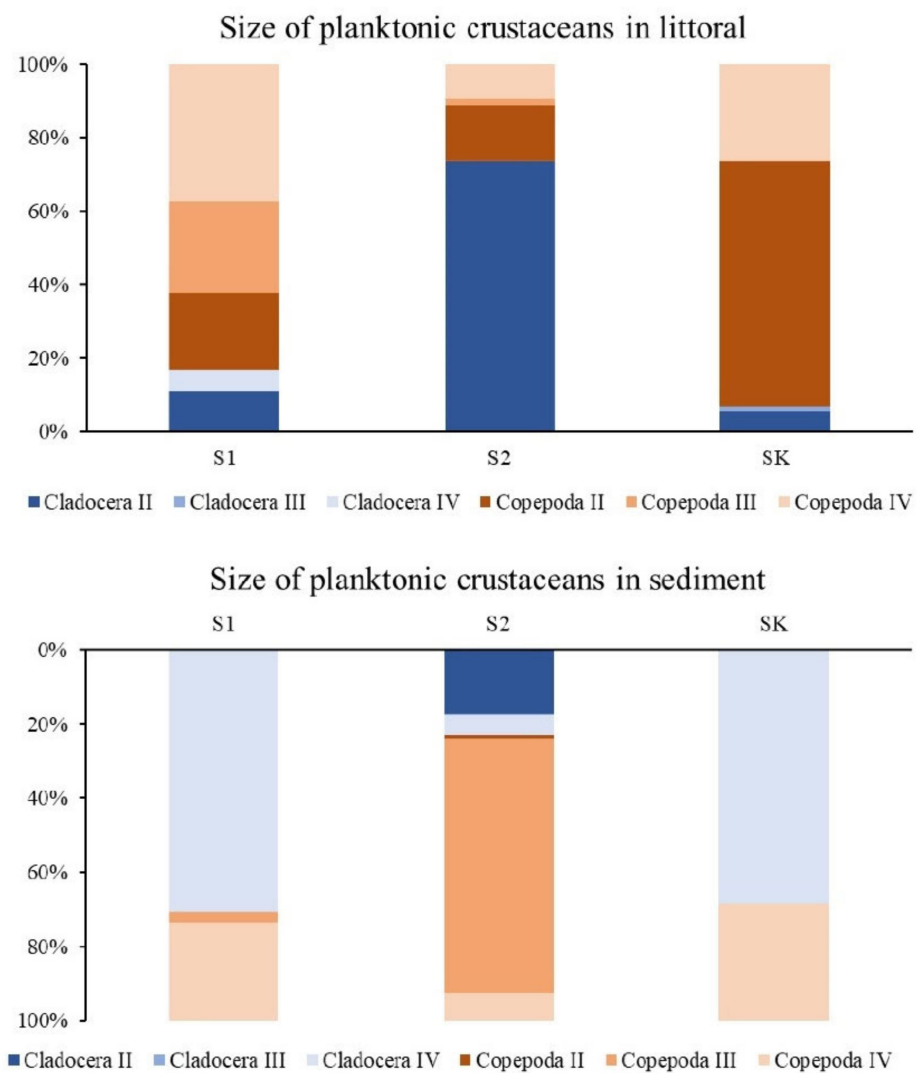
Figure 5. Relative abundance of body size categories of planktonic crustaceans in the littoral water zone and sediment. Size ranges of categories are given in the Section 2.2.

Overall interplays among planktonic crustaceans in the sediment and abiotic and biotic parameters (Figure 6) indicated that a higher transparency positively affected the total crustacean diversity and abundance in the sediment, as well as the abundance of cladocerans and their females with eggs and larger-sized specimens of copepods. The results suggested that sediments made up of wood and leaf litter mainly negatively affected cladoceran abundance in sediment, as opposed to the sediment with macrophyte litter that supported an abundance of larger-sized cladocerans and their females with eggs. The abundance of fish had an impact on the increased diversity and abundances of all studied traits of planktonic crustaceans in the sediment. The results of the correlations indicated the expected positive correlations between cladoceran specimens in the littoral zone and their abundance in the sediment, and opposite findings indicated abundances of copepods among the littoral plankton and sediment (Figure 6). However, the abundance of planktonic larger-sized copepod females with eggs correlated positively (Spearman correlation, r = 0.170, $p > 0.05$) with their abundance in the sediment.
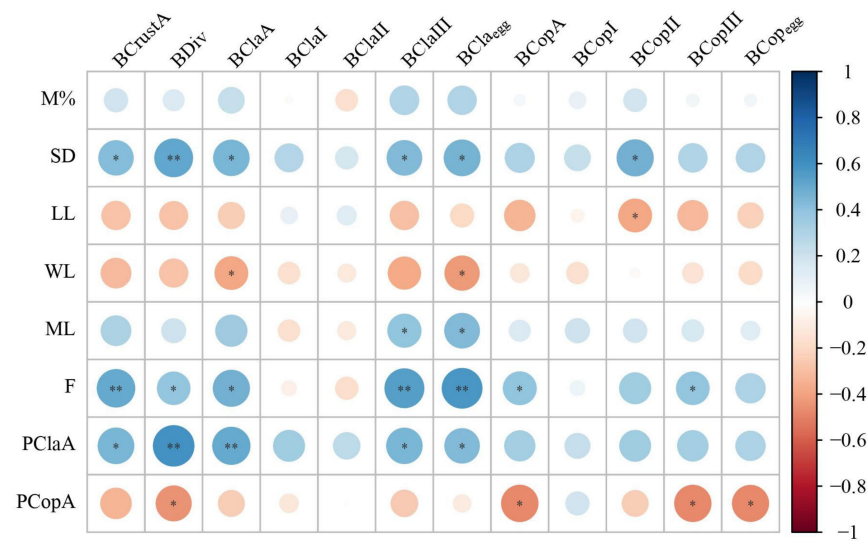
Figure 6. Spearman correlations ($p < 0.05$) among planktonic crustaceans in sediment and abiotic and biotic parameters. Prefix B indicated traits in benthal, prefix p indicated traits in plankton. Significance codes are as follows: $p < 0.01$ '**' and $p < 0.5$ '*'. Other abbreviations are given in Section 2.

Large-sized cladocerans and copepods were highlighted through the analyses as very sensitive to fish predation, and accordingly, GAM analyses against the main drivers were conducted. The values of best fitted models with the lowest AIC (BClaIII 439.9 and BCopIII 417.1, respectively) are given in Table 3. Selected models explained 47.2% and 37.3% of the deviance, in BClaIII and BCopIII abundance, respectively, using the smooth terms FI ($p < 0.05$) and FII ($p < 0.05$), and M% ($p = 0.05$) and SD ($p < 0.05$) (Figure 7). GAM indicates that the higher abundance of large-sized copepods in the sediment was mainly caused by increased transparency and abundance of FII, and decreasing macrophyte coverage. The selection of sediment as a shelter for large-sized cladocerans was significantly influenced by the increased abundance of FI (Figure 7, Table 3).

Table 3. Parameters of GAMs describing the factors involved as drivers of changes in BClaIII and BCopIII during the experiment. Significant p values are given in the table.

| Model Terms	Family: Gaussian		Scale est. 5.17×10^5		$n = 27$	
	Parametric coefficients	Estimate	Std. Error	T value	Pr ($> \lvert t \rvert$)	
	(Intercept)	647.1	138.4	4.678	<0.001	
BClaIII abundance	Aproximate significance of smooth terms	**s (FI)**	**s (FII)**	**s (FIII)**	**s (M%)**	
		$p < 0.05$	-	-	-	
	R^2_{adj}			**0.338**		
	Deviance explained (%)			**47.2**		
Model Terms	Family: Gaussian		Scale est. 2.19×10^5		$n = 27$	
	Parametric coefficients	Estimate	Std. Error	T value	Pr ($> \lvert t \rvert$)	
	(Intercept)	283.56	90.21	3.143	<0.01	
BCopIII abundance	Aproximate significance of smooth terms	**s (FI)**	**s (FII)**	**s (FIII)**	**s (M%)**	**s (SD)**
		-	**<0.05**	-	**0.05**	**<0.05**
	R^2_{adj}			**0.198**		
	Deviance explained (%)			**37.3**		
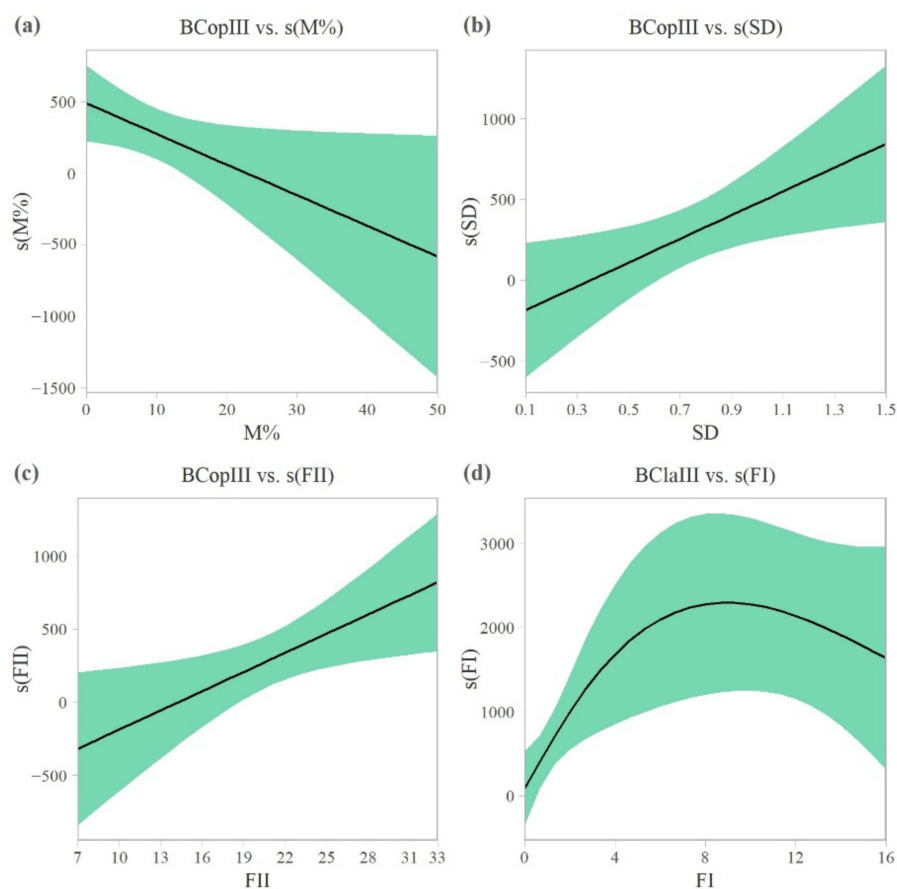
Figure 7. Generalized additive model (GAM) plots showing the partial effects of the four selected independent variables (FI, FII, M%, and SD) on BClaIII and BCopIII abundance. Y-axis indicates the partial effect of the variable and shaded areas represent the 95% confidence intervals. (**a**) Abundance of large size copepods (BCopIII) vs. percentage macrophyte coverage (M%). (**b**) Abundance of large size copepods (BCopIII) vs. Secchi disk transparency (SD). (**c**) Abundance of large size copepods (BCopIII) vs. abundance of medium-sized fish (FII). (**d**) Abundance of large size cladocerans (BClaIII) vs. small sized fish (FI). Abbreviations: BClaIII—large-sized Cladocera in benthal; BCopIII—large-sized Copepoda in benthal.

4. Discussion

In the pilot study [16], conducted on a group of shallow lakes throughout the summer of 2012, we reported that zooplankton are not only distributed horizontally but also in a vertical profile since the presence of planktonic crustaceans inhabiting the sediment zone was also ascertained. This was the starting point to expand our understanding of the functioning of shallow ecosystems. Thus, during the study carried out in 2013, we continued the analysis on planktonic microcrustaceans in sediments, directed towards the activity of visual predators, i.e., fish, as a factor structuring the spatial distribution of zooplankton. The results of this study suggest that the sediment layer in the littoral zone greatly contributes to the provision of shelter against fish predation for planktonic crustaceans, particularly those prone to fish predation, i.e., larger-sized specimens and females of cladocerans and copepods with eggs, being conspicuous in the non-vegetated SWB. Furthermore, the results highlighted that the sediment of macrophyte covered SWB hosted particularly large-sized cladoceran specimens, while in the sediment of macrophyte-absent SWB, large-sized copepod specimens dominated. The selection of sediment as a refuge spot against predation risk for large-sized cladocerans (e.g., *Simocephalus*) was determined by the behaviour of small-sized fish (<5 cm) of the genus *Carassius*, which occurred in the littoral of one of the investigated water bodies (S1) covered with submerged macrophytes [16]. Large-sized copepods showed a high degree of sensitivity to medium-sized

fish (5–10 cm) of *A. alburnus* and *L. gibbosus*, particularly in the unvegetated littoral of the second SWB (S2) [25,26]. *L. gibbosus* is a non-native, invasive species, with a strong negative impact on zooplankton population and biomass [26,27]. A higher abundance of small-sized fish among submerged macrophyte stands has also been attested from temperate and (sub)tropic climates [7,8,20,37]. Namely, small sized fish also seek shelter against piscivores, and their abundance increases with a warmer climate due to a prolonged reproduction period and more potential hatching opportunities [38,39]. Encounters attributed to the high share of larger-sized specimens of planktonic cladocerans in sediment, i.e., the genera *Daphnia* and *Simocephalus*, were also of interest as they were generally not found or had an extremely low share in the littoral or pelagial plankton, where mainly *Bosmina longirostris* (O.F. Müller, 1776) prevailed [13,25,39,40]. These findings concur with results from several shallow lakes in Uruguay as well as in 16 Turkish Mediterranean SWB, where ephippia and the remains of *Daphnia* and other large-sized cladocerans were found in the sediments, while at the same time these taxa were absent from the water samples [8,9]. The assessment of shelter efficiency related to the impact of sediment structure (macrophyte, leaf, or wood litter) in the littoral zone of the three studied SWB indicated that macrophyte remains in the form of loose sediment enhanced the refuge effect of sediments, particularly for cladocerans. Leaf and wood litter revealed a negative interplay with planktonic crustaceans, probably due to their dense structure, suggesting that these types of bottom sediments will not act as a favourable hiding place for planktonic crustaceans.

The main shortcoming of this study could be the non-implementation of horizontal/vertical migration analyses. As was mentioned above, other authors have also recorded the remains of planktonic crustaceans in sediment, but detailed studies have not yet been presented, probably also due to the absence of migration analyses. However, intensive research and continuous sampling as well as many previous studies in SWB [15,17,41,42], have clearly shown that fish as daylight predators cause the vertical segregation of plankton in shallow water bodies. Most of the published studies concerning plankton–benthic coupling in SWB, point primarily to lake sediment as an egg bank for planktonic crustaceans [43–45], or refer to macroinvertebrate predation upon zooplankters [7,17,26]. Thus, the results of our research provide a new perspective, indicating that the larval and adult stages of planktonic crustaceans select sediments as a refuge in natural SWB.

The results of our study have also identified biotic interactions within the varying levels of the habitat spatial structure of the littoral zone. The assessment of planktonic crustaceans in sediment along the gradient of habitat heterogeneity (submerged macrophytes, sparse floating-leaved macrophytes, and the macrophyte free littoral of the studied SWB), clearly indicated that in SWB without macrophyte cover, where planktonic crustaceans generally lack habitats to hide, the littoral sediment offered an important refuge against fish predation. Similar observations, where it was suggested that sediments can provide an additional habitat for copepods as well as for other groups of aquatic organisms, have been made in the case of small water bodies [46]. An opposite share of cladocerans and copepods was found between littoral plankton and sediment, where small- and medium-sized copepods prevailed among the macrophyte stands of S1 and SK, and cladocerans with small-sized *Bosmina* prevailed in the littoral water without macrophytes. What is also of interest was the reverse share of cladocerans and copepods in the adjacent sediment, where large-sized cladocerans prevailed in the macrophyte covered sediment of S1 and SK, and large-sized copepods featured in the macrophyte-absent sediment of S2.

In the sediment zone of the turbid and unvegetated SWB, S2, even small-sized cladocerans (*Bosmina*) and medium-sized copepods were potentially threatened by encounters with fish, thus these microcrustaceans tended to bury themselves in the sediment, which constituted the only refuge in unvegetated SWB. From the obtained results it can be seen that the abundance of large-sized and fast swimming copepods in the sediment increased along with transparency and this phenomenon also confirms a high predation risk in the absence of macrophytes. This concurs with some data from other temperate SWB presented by [8]. Namely, in the littoral of Danish shallow lakes cyclopoid copepods dominated over

calanoid copepods, i.e., an overall feature of temperate lakes, and underwent diel vertical migration in transparent water bodies. It is possible that macrophytes offered a sufficient temporary shelter for cyclopoids, since they were dominant over cladocerans in the littoral plankton of the macrophyte-covered SWB, S1 and SK. This finding is in accordance with the results of several studies pointing to the increase in cyclopoid abundance along with macrophyte complexity [8,21]. Therefore, when macrophyte stands were present, it seems that macrophyte stems were a sufficient shelter for cyclopoids and presumably they did not seek for additional protection in the sediment, as confirmed by the negative correlation between the abundance of large-sized copepods in the sediment and macrophyte coverage.

Cladocerans prevailed in the littoral plankton of SWB S1, within the stands of complex macrophyte hornwort (*C. demersum*), with specimens of all body sizes, including smaller individuals, which probably appeared due to the hatching from ephippia and eggs sedimented in the littoral [47]. The opposite pattern was observed in the case of the next SWB (SK), with free-floating yellow water-lilies (*N. lutea*), where a fourfold lower abundance of cladocerans were found. Such discrepancies in the abundance of cladocerans inhabiting macrophyte stands with a different degree of morphological and spatial differentiation have also been observed by other researchers. Moreover, in experiments carried out with both artificial and natural macrophytes it was demonstrated that cladocerans may avoid certain macrophyte stands [9,20]. Namely, free-floating macrophytes may limit light penetration and thus restrict phytoplankton production, leading to a lower food availability for algivore cladocerans [48]. This may have also been the case in our study.

The high abundance of large-sized specimens of cladocerans and copepods, *Simocephalus vetulus* and *Macrocyclops albidus*, even in the sediment area of macrophyte covered SWB, indicated the distinct influence of fish, as well as macroinvertebrates. In the macrophyte-covered SWB littoral zone (S1), the complex architecture of *C. demersum* presumably provided a shelter and hatching zone for numerous copepods, occurring in equal shares made up of smaller-sized and medium-sized specimens, larval stages (nauplii), copepodites, and adults of *M. albidus*, respectively. The higher abundance of larval stages is probably associated with the placing and retaining of eggs directly on macrophytes. In Bullhead Pond (USA) *Diaptomus sanguineus* Forbes S.A., 1876 was found to deposit a large fraction of diapausing eggs on macrophytes, even up to five months before either hatching or sinking to the sediment [43,49].

Particularly important are females with eggs, which are more vulnerable to fish predation. Macrophyte stands in the littoral area of the transparent waterbody, which was moderately covered with submerged macrophytes (S1), provided sufficient shelter for copepods, and this could explain their lower percentage in the sediment. Generally, cladocerans as slower swimmers, and being much more visible with eggs, presumably undertook all measures to escape fish in the vegetated and unvegetated littoral zone, water, and sediment, respectively. We have demonstrated that cladoceran females with egg chambers mostly selected sediment as shelter in comparison to copepod females with egg sacks, which had a similar share irrespective of the habitat heterogeneity. These findings concur with the explanation of a crustacean defence strategy against visual predators who can selectively choose females with eggs that are more visible, have a higher nutritional value, as well as slower movements [1].

5. Conclusions

Due to different sampling strategies and research aims, plankton–benthic coupled research very rarely presents data with respect to planktonic organisms in the sediment of lakes or ponds. The results of this study could be extended to include other planktonic organisms, i.e., rotifers, and thus reveal sediments as a refuge in terms of interference or exploitative competition or predation. Moreover, it is confirmed that the sediment of the littoral zone plays an important role not only for paleontological reconstruction or a zone of hatching for a multiplicity of organisms, but it is also full of life, where ongoing planktonic organisms remain in order to find a secure refuge from fish predation.

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