Electronic Journal of Polish Agricultural Universities is the very first Polish scientific journal published exclusively on the Internet, founded on January 1, 1998 by the following agricultural universities and higher schools of agriculture: University of Technology and Agriculture of Bydgoszcz, Agricultural University of Cracow, Agricultural University of Lublin, Agricultural University of Poznan, Higher School of Agriculture and Teacher Training Siedlce, Agricultural University of Szczecin, and Agricultural University of Wroclaw.

ELECTRONIC JOURNAL OF POLISH AGRICULTURAL UNIVERSITIES

2006
Volume 9
Issue 2
Topic
BIOLOGY


BOWSZYS M. , HIRSZ E. , PATUREJ E. 2006. THE ROLE OF MACROPHYTES IN THE DIURNAL DISTRIBUTION OF CRUSTACEAN ZOOPLANKTON IN A LITTORAL OF A SHALLOW, MACROPHYTE-DOMINATED LAKE **Electronic Journal of Polish Agricultural Universities**, Biology, Volume 9, Issue 2.
Available Online http://www.ejpau.media.pl/volume9/issue2/art-18.html

# THE ROLE OF MACROPHYTES IN THE DIURNAL DISTRIBUTION OF CRUSTACEAN ZOOPLANKTON IN A LITTORAL OF A SHALLOW, MACROPHYTE-DOMINATED LAKE

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## ABSTRACT

In a mesotrophic, shallow, macrophyte-dominated lake, stable plant cover can be attractive for zooplankton species being a grazer or a prey; dense submerged vegetation, *Chara* beds in particular, can offer a day-time refuge for cladocerans and some adult copepods. The former use this shelter also at night; on the contrary, young stages of Copepoda distinctively avoided both types of plant covered areas during the day and migrated towards open water. That might resulted from the increased grazing upon zooplankton. The pressure of predatory fish in open water probably forced young fish to seek for a shelter. As *Chara* beds are too dense to be penetrated, they preferred emergent plant zone. That might encourage copepods to undertake reversed DHM. The present study suggests a significant role of plant cover on diurnal zooplankton distribution. Dense charophyte patches could offer a daytime refuge for cladocerans, and some adult forms of Copepoda, while both groups of planktonic invertebrates did not take the advantage of emergent macrophytes cover to avoid fish predation.

**Key words:** zooplankton migration, shallow lakes, macrophytes.

## INTRODUCTION

Shallow lakes are of a significant ecological value by providing high biodiversity for different trophic levels as well as being the “area” of complex biogeochemical transformations. A littoral zone of a lake is the field of diversified interactions, between biota as well as biotic and abiotic features, affecting the entire water body. Due to presence of zooplankton among macrophytes, the acceleration of the process towards clear water can be observed, thereby improving the growth conditions for macrophytes [17]. In stable, macrophyte-dominated lakes, plants can offer a daytime refuge for crustacean zooplankton against predation by zooplanktivorous fish. The likelihood of a refuge effect increases with increasing macrophyte cover [15]. Daytime aggregations of zooplankton among plants, diel horizontal migrations (DHM), were recorded in some eutrophic lakes [8, 12, 24, 31] or ponds [36]. However, the studies usually emphasized the role of submerged vegetation. Only few studies focused on emergent plants [13, 19]. Emergent macrophytes expand the zone attractive to zooplankton as a day-time shelter against zooplanktivorous fish predation. Zooplankton diurnal distribution is also affected by planktivorous invertebrates. A numerous studies have

documented the influence of Chaoborus larvae or notonectids on zooplankton size structure or diurnal migrations [5,16,18,30]. However, the effect of predatory invertebrates is more pronounced in fishless reservoirs.

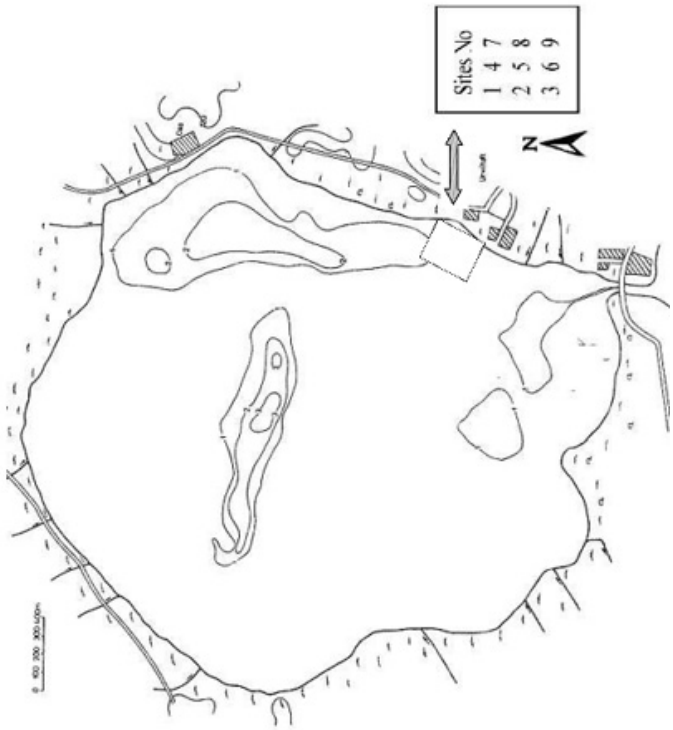
Recent studies suggest clearer DHM in eutrophic waters than in lakes of a lower trophy [28]. Little is known about day and night-time distribution of zooplankton in mesotrophic, macrophyte-dominated lakes, where due to water transparency the potential predatory pressure of zooplanktivorous fish may be higher. Then, zooplankton can be forced to seek for a refuge to avoid grazing pressure among submerged macrophytes as well as congregate among emergent plants or migrate towards the shore [12]. On the other hand, numerous studies suggest that zooplankton avoid macrophytes [e.g.22, 28]. Nevertheless, that plant avoidance is reversaly correlated with the fish pressure [13]. The aim of the present study was to determine the role of submerged vegetation and emergent plants in diurnal distribution of zooplankton in a mesotrophic, macrophyte-dominated lake as well as to assess the usefulness of macrophytes beds as a potential refuge for zooplankton avoiding fish predation.

## MATERIALS AND METHODS

Studies were carried out in Lake Łuknajno (Masurian Lakeland, NE Poland) – a shallow (mean depth 0.6 m; maximal – 3.0 m), macrophyte-dominated reservoir. That mesotrophic, relatively large (surface are 623 ha) lake due to abundant and diversified waterfowl has been protected as a biosphere reserve. The lake is, to a great extent, overgrown by submerged vegetation, in 50% composed of *Chara* species and surrounded by a wide belt of emergent plants [10]. It is connected by a channel with the biggest Polish lake, Lake Sniardwy, to which delivers its waters [11]. Due to dense vegetation, the lake is attractive for ichtiofauna. Experimental netting (Terlecki, unpublished) revealed numerous and diversified fish community, mainly composed of perch *Perca fluviatilis*, roach *Rutilus rutilus*, rudd *Scardinius erythrophthalmus,* bleak (*Alburnus alburnus*), pike (*Essox lucius*), tench (*Tinca tinca*) and abundant juvenile, feeding on zooplankton fish. Personal observations of the authors indicated high density of young-of-the-year-fish, mainly perch and roach.

Zooplankton was sampled along 3 pararell transects crossing 3 different habitats i.e. open water (site 1-3), submerged macrophytes (site 4-6) and emergent plants (7-9) what gave an overall number of 9 stations (fig.1). To test for DHM and the importance of the macrophytes, zooplankton was sampled day and night in the period from 5-8 August 2004. The sampling took place every 12 hours, two times a day: between 1-3 am and 1-3 pm. Totally, it was collected 54 samples (18 samples at each zone). At each station, it was taken 25 liters of water in 5 subsamples (5l) to avoid zooplankton swarming error. Samples were taken from submerged vegetation by a tube sampler (7 cm diameter). To confirm the hypothesis that crustaceans take advantage of macrophytes during the day, we tested if the zooplankton density was higher during day than night (Man-Whitney test); the same test was used to find out which zone the animals prefered.

**Fig. 1. The location of sampling sites in the littoral zone of Lake Łuknajno. Sites 1-3 are situated in the open water zone, 4-6 among submerged macrophytes and 7-9 within the belt of emergent plants**



To determine helophytes density, at each station the number of individuals were counted at three, randomly chosen areas (the square of 0,1 $m^2$). In case of submerged vegetation, three repeated random samples were taken, dried at 105 °C to constant mass and weighted (with 0,1g accuracy). To estimate mean dry weight of the individual, for each sample, 10 individuals were selected, dried at 105 °C to a constant mass and weighted (with 0.01g accuracy). Plant density was calculated by dividing overall dry weight by mean dry individual weight.

## RESULTS

The role of patches of submerged vegetation and the belt of emergent plants as the refuge for planktonic crustaceans were studied at the peak of the vegetation season (August). The studies were carried out in a sheltered bay, which littoral was overgrown by emergent plants and submerged vegetation. The study area was covered in 14.5 % by a dense, single-species (*Phragmites australis* ) belt of rushes (Tab. 1). Submerged vegetation (67.7 % of the total area) was mainly composed of *Chara tomentosa* (89.8 % on average). Charophyte patches reached there relatively high density (exceeding 1500 indiv. /$m^2$). The PVI calculated for that zone was about 60-70%.

**Table 1. The level of plant and dominating species coverage in particular zones (open water, submerged macrophytes, and emergent plants) of the studied area in August 2004**

| Zone | Plant coverage | Dominating species coverage |
|---|---|---|
| | [%] | [%] |
| Open water | < 2.0 | - |
| Submerged plants | 98.0 | 89.8 *(Chara tomentosa)* |
| Emergent plants | 100.0 | 100.0 *(Phragmites australis)* |

During the study, the weather conditions were calm (sunny weather, weak wind from the shore – not exceeding 1-2 $m^{s-1}$ ). Within diel cycles, both, thermal and oxygen conditions were stable. Temperature of water at particular sites varied between 22.2 °C and 24.9 °C. Oxygen concentrations in water at particular zones did not vary noticeably (6.26 mg $O_2$ /$dm^3$ – 8.91 mg $O_2$ /$dm^3$) except for a single daytime record that once, at site 7, reached 11.43 mg $O_2$ /$dm^3$. The temperature and oxygen concentrations were not correlated with zooplankton density at any station. Water transparency always reached the bottom.

In general, higher zooplankton densities were recorded in the night-time than during the day (Tab. 2). At night, mean crustacean density achieved 205 indiv. /$dm^3$ (min. 63.3; max. 448), while in day hours it was 114 (min. 34; max. 281, respectively). The difference was statistically significant ($P<0,05$; $n=27$).

**Table 2. Daytime and night-time mean density of the total zooplankton community in Lake Łuknajno in the studied period**

| Mean density of zooplankton [indiv./$dm^3$] | | |
|---|---|---|
| Zones (stations) | Day | Night |
| Open water (1,2,3) | 161.1 | 142.1 |
| Submerged plants (4,5,6) | 161.7 | 272.5 |
| Emergent plants (7,8,9) | 109.1 | 201.2 |

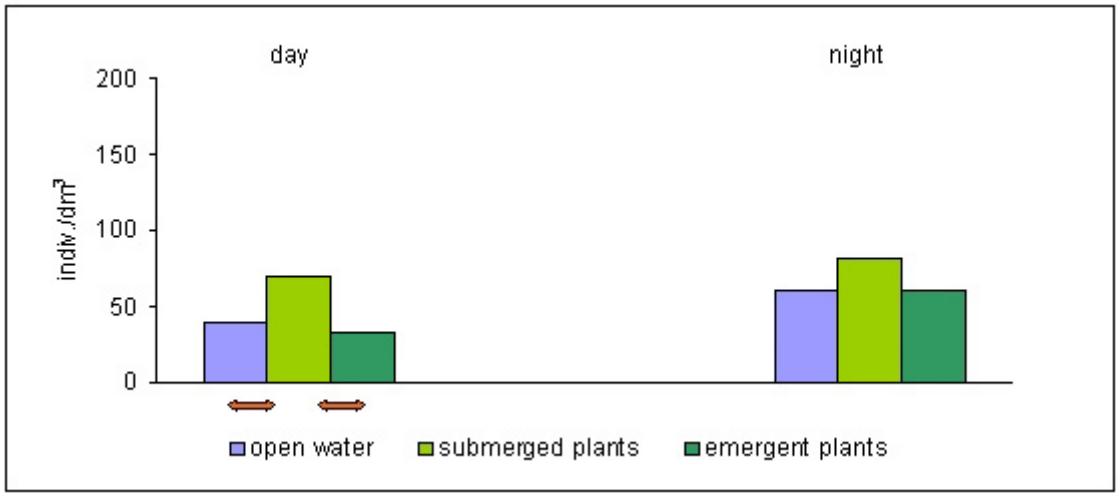
Zooplankton of Lake Łuknajno was dominated by small-bodied forms e.g. *Ceriodaphnia quadranguala* (O.F. Muller), *Bosmina longirostris* (O.F. Muller), *Diaphanosoma brachyurum* (Lievin), *Mesocyclops leuckarti* (Claus) and young stages of Copepoda (Tab. 3). However, both crustaceans groups showed different patterns of spatial distribution. Cladocerans usually preferred areas covered by charophytes. The submerged plant zone was intensively penetrated by ubiquistic, distinctly dominating species *C. quadranguala* (within the whole diel cycle). During the day, its density reached 50 indiv./$dm^3$ being 2-fold higher than in the two remaining zones. At night, among charophytes, *C. quadranguala* was more abundant (80 indiv./$dm^3$) than in day-time, also in other areas reaching there 60 indiv./$dm^3$. The avoidance of open water zone was also recorded in case of another relatively abundant cladocerans representative – *B. longiristris*, while *Chydorus sphaericus* (O.F.Muller) usually avoided zones covered by submerged plants. Some large-bodied, littoral species from the genera *Simocephalus* and *Eurycercus* occurred exclusively in charophyte beds.

**Table 3. Daytime and night-time maximal and mean density (sites 1-9) of dominating species of zooplankton in Lake Łuknajno in the studied period**

| Mean density of zooplankton dominants [indiv./dm$^3$] | | | | |
|---|---|---|---|---|
| Taxon | Day | | Night | |
| | Maximal | Mean | Maximal | Mean |
| Bosmina longirostris | 18 | 5.3 | 30.4 | 9.1 |
| Ceriodaphnia quadranguala | 78 | 36.4 | 154 | 52.4 |
| Diaphanosoma brachyurum | 10 | 4.3 | 20.8 | 5.3 |
| Mesocyclops leuckarti | 17.6 | 4.6 | 28 | 8.2 |
| kopepodit | 67.2 | 33.2 | 124.8 | 43.4 |
| nauplius | 156 | 69.2 | 168.6 | 85.7 |

Copepoda predominated over Cladocera (Tab. 3, fig. 2, 3) within each studied zone (submerged plants, emergent plants, and open water) mainly due to abundant occurrence of copepodits and naupliar stages. Their highest density was recorded in the area covered by submerged macrophytes (above 300 indiv./ dm$^3$l), at night; cladocerans achieved there 2-fold lower maximal density (149 indiv./ dm$^3$), also in nocturnal hours. Copepods were more abundant at night than during the day. Then, adult forms of Cyclopoida (*M. leuckarti, Eucyclops* sp.) and Calanoida (*Eudiaptomus graciloides* Lilljeborg) occurred more abundantly.

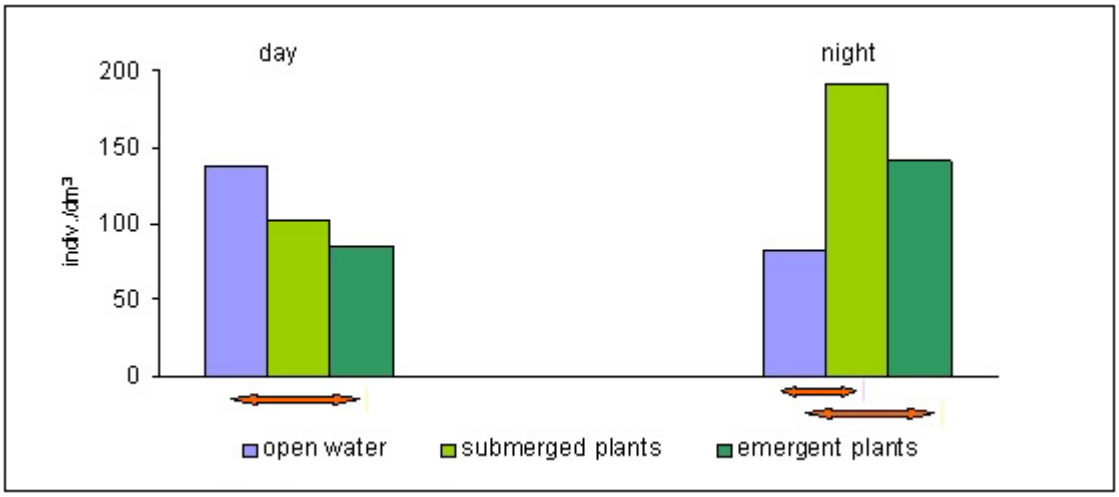
**Fig. 2. Mean day-time and night time Cladocera density in different habitats of Lake Łuknajno. The statistical significance of the differences between zones is indicated by arrows (p<0,05; n=9). Lack of arrow means not significant cases**




Both crustacean groups showed different patterns of diel migrations. During the day, cladocerans avoided the open water and areas covered by emergent macrophytes and concentrated in the zone overgrown by charophytes; there their density (maximal – 111indiv./l dm$^3$) was 2-fold higher (fig. 2) in comparison with the remaining zones. The differences between cladocerans density in *Chara* beds and open water as well as rush belt were statistically significant. At night, Cladocera evenly spread over the entire littoral (fig. 2). Although, the dominating species – *C. quadranguala* – was still strongly associated with charophytes.

Copepoda (mainly copepodits and naupliar stages) undertook day migrations from the plant – covered areas to the open water (fig. 3). They were significantly more abundant in the open water zone than among emergent plants (fig. 3). The opposite situation was observed at night when copepods aggregated in *Chara* beds as well as within emergent plant belt. The differences in their density between open water and plant-covered areas were statistically significant (fig. 3). Outstanding tendency was found for *M. leuckarti,* especially larger, adult forms, that during the day and night preferred dense *Chara* patches.

**Fig. 3. Mean day-time and night time Copepoda density in different habitats of Lake Łuknajno. The statistical significance of the differences between zones is indicated by arrows (p<0,05; n=9). Lack of arrow means not significant cases.**




We also investigated if, in general, there is a correlation between crustaceans occurrence and chlorophyll *a* concentration which could determine their distribution at particular zones. The correlation was performed for data obtained in July and August 2004. Copepods showed weak positive correlation ($r=0.36$ $p< 0.05$) with the concentration of chlorophyll in the emergent plant zone.

The studies revealed that dense charophytes patches could offer a daytime refuge for cladocerans, and some adult forms of Copepoda, while both groups of planktonic invertebrates did not take the advantage of emergent macrophytes cover to avoid fish predation.

## DISCUSSION

Shallow lakes are very often covered by vegetation. Macrophytes can affect zooplankton community in different ways, providing a structure as well as a shelter for animals. Lake Łuknajno is, to a great extent, overgrown by plant cover among which *Chara* patches play an important role [10], having impact on the entire ecosystem functioning. Characeae may have an effect on planktonic food chain [4] as the conditions inside macrophyte beds can lead to a decreased availability of nutrients and limit phytoplankton growth. Effects on phytoplankton may subsequently affect higher trophic levels – zooplankton and fish. Submerged macrophytes can also reduce mixing of water and resuspension of seston [1] and in that way create environmental conditions for zooplankton development. Moreover, macrophytes can produce allelopathic substances affecting phytoplankton and periphyton [7] and perhaps higher trophic levels [2]. Finally, submerged vegetation is inhabited by very specific communities and plant associated invertebrates [14] as well provide a spatial refuge against predators for zooplankton [31] and small fish [21]. Lake Łuknajno status (Natural reserve) and, in a consequence, lack of fish catching as well as the studies on zooplankton community [9] suggest noticeable impact of fish on planktonic crustaceans. It is in accordance with the preliminary studies (experimental netting, Terlecki unpublished) of ichtiofauna.

In the studied lake, crustacean zooplankton was composed of typical "midsummer" forms achieving moderate densities, like *C. quadranguala, B.longirostris, Ch. Sphaericus,* benefiting from high concentrations of fine suspended matter and algal food that was mainly composed of non-filamentous, edible species (Jaworska, unpublished). The latter should favor the development of large, filtering *Daphnia* species, common in the Masurian Lake system. However, in the studied period, *Daphnia* spp. did not occurr. They were scarce even in spring (personal observations). As the pressure on prey depend on PVI, that genera, developing mainly in late spring and early summer when the vegetation is poor, is particularly endangered to fish predation [24]. Moreover, *Daphnia* species prefer to stay in open water despite the risk of fish predation due to repellent effect of submerged macrophytes [13]. With this strategy *Daphnia* can decline to extinction in the presence of a high density of zooplanktivorous fish [27]. The potential effect of invertebrate predators on *Dapnia* should also be taken into account. Latest study [30] provided evidence that notonectids can significantly inflict reductions in *Daphnia* population. In the absence of *Daphnia, Ceriodaphnia spp*. can develop because of lack of competitive suppression [33]. Moreover, it was found a positive relationship of *Ceriodaphnia* sp. and *Simocephalus* sp. with an increasing macrophyte cover [24]. That leaded to the pronounced domination of *C. quadranguala* in the studied lake. Food resources may determine distribution of some species. *Ch. sphaericus* is usually randomly distributed in water mass

as this relatively minute species is considered to be less vulnerable to fish predation [3]. The availability of food in Lake Łuknajno might favor its spatial pattern. As a consequence of the above factors, zooplankton of Lake Łuknajno was dominated by small-bodied cladoceran species.

In the studied lake, cladocerans showed distinct tendency to avoid fish predation achieving density peak in *Chara* beds which is in accordance with some earlier studies [3,23]. The degree of aggregation depends on habitat size. Large, homogenous macrophyte beds are not very effective as a daytime refuge for zooplankton against fish predation as they have little edge relative to the surface area [3, 12, 25]. On the other hand, it was found that the more dense macrophyte bed, the higher zooplankton density and the more pronounced refuge effect. In Majcz Wielki Lake, the maximal numbers of Cladocera and Copepoda were recorded within the densest *Chara* beds [23]. In Lake Łuknajno, where large-size Characeae beds achieved very high densities, the refuge effect was found for cladocerans. According to some findings [15] such dense macrophytes provide an effective refuge for zooplankton avoiding fish predation as open water feeders e.g. roach cause little threat in dense vegetation [24]. In the studied lake, Cladocera aggregated in *Chara* beds also at night. It is known that the refuge effect can also occur in nocturnal hours [32] as many common fish species are capable of feeding in darkness. The significance of macrophytes as a shelter for planktonic crustaceans was related to the size of a prey population [29]. When a large population of a particular species (> 50 indiv./$dm^3$) is maintained during the summer months, the refuge effect is achieved, what in Lake Łuknajno was recorded for the dominating species (*C. quadranguala*). In addition, stable oxygen and thermal conditions suggest rather biotic factors influencing their density. Cladocerans did not take the advantage of emergent plants, probably due to negative impact of young-of the-year-fish that usually abundantly inhabiting rush belt [19]. Young fish may search for a refuge to avoid pike that is common in waters of Lake Łuknajno (Terlecki, unbublished). As *Chara* beds are too dense in the studied lake (very high PVI) to be penetrated by some young fish, they might seek a shelter among emergent plants [24]. This theory is in accordance with study [28] reporting that young-of–the-year-fish can congregate within the emergent vegetation during the day to avoid predators, thereby inducing opposite diurnal migrations of zooplankton.

Quite striking is the fact that zooplankton was significantly more numerous at night than during the day. This phenomenon could be explained by vertical migrations of Cladocera from the bottom of a shallow lake littoral – a kind of a daytime refuge – to the surface at night [3,20,25]. Some cladocerans (e.g. *Sida crystalina*) can also migrate between the surface of plants and water-body [34]. The same might be the reasons of more abundant nocturnal occurrence of Cladocera in Lake Łuknajno. Moreover, some large pelagic species like e.g. *Eurycercus lammelatus* (O.F. Muler) where recorded exclusively at night. Vertical migrations in shallow lakes were also reported for large Copepoda [3]. In Lake Łuknajno adult copepods (*Mesocyclops sp, Eucyclops sp. Eudiaptomus sp.*) occurred more abundantly in nocturnal hours. That might be induced by negative impact of notonectides, efficient predators in daylight, that are unable to feed effectively in the dark or even in full moonlight [5]. Chaoborus predation was less possible as its larval stages usually spend the day near the bottom sediments when the fish pressure is high [e.g. 5, 18]. Also the density of young Cyclopoids within both macrophytes zones was markedly higher in nocturnal hours, being lower in daytime. The same was recorded in earlier studies [3]. Those diel variations in Cyclopoid density may indicate that these organisms could undergo migrations from open water areas towards both types of plant-covered zones. This is in contrast with earlier findings [6, 20]. However, some authors suggested [12] that zooplankton species during the day could aggregate very close to the shore (0.5 m) while at night might migrate towards plants – off the shoreline. But this hypothesis was not tested in the present study. On the other hand, copepodits could be more efficiently consumed within emergent plants zone during the day; as larger cladocerans and scarce adult copepods species use *Chara* beds as a daytime refuge, the stronger fish pressure is aimed into abundant younger stages of Copepoda. Moreover, under some circumstances young perch (abundant in Lake Łuknajno) may prefer to feed on copepods than grazing Cladocera [28]. That might by the reasons of generally lower number of Copepoda among plants during the day. In a consequence, their number might significantly decrease. These assumptions are supported by some findings [e.g. 14, 35]. The deteriorating impact of macrophytes on Copepoda also should be considered; however it usually is true in case of pelagic species [26], like *Eudiaptomus sp.*, that occurred in Lake Łuknajno rather scarcely. All the discussed factors could be responsible for the significant differences in diurnal copepods distribution.

In general, some observations on zooplankton distribution might also be a consequence of complicated direct and indirect interactions between organisms and abiotic factors in the entire littoral. Therefore, more detailed study on the multiple relations in that zone affecting zooplankton distribution needs to be conducted.

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