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Jan Igor RYBAK[1)], Teresa WĘGLEŃSKA[2)]

[1)]Department of Hydrobiology, University of Warsaw, Banacha 2, 02-097 Warszawa, Poland, e-mail: igor@hydro.biol.uw.edu.pl

[2)]Formerly: Department of Hydrobiology, Institute of Ecology, Polish Academy of Sciences, Dziekanów Leśny, Poland

TEMPORAL AND SPATIAL CHANGES IN THE HORIZONTAL DISTRIBUTION OF PLANKTONIC CRUSTACEA BETWEEN VEGETATED LITTORAL ZONE AND THE ZONE OF OPEN WATER

ABSTRACT: The research concerned the density, dominance structure and species composition of planktonic Crustacea community, as well as their diel horizontal migrations between aggregations of vegetation and open water in the littoral zone of two lakes. The *Cladocera* communities of sparse beds of submerged macrophyte showed a sharp domination (70%) of individuals of large-sized tycholimnetic species. In the Cladocera community in a dense beds of macrophyte also individuals of littoral species occurred in greater numbers. The filamentous algal mats were mainly dominated by Copepoda and small tycholimnetic species of Cladocera.

We observed a sharp daily gradient of Crustacea density across macrophyte beds and open water. The greatest diel changes were found near the edge of the macrophyte beds (ecotone zone). Daytime density of Cladocera was several times greater in the macrophyte beds than in the open zone, while during the night-time density differences were not so marked. In contrast, in the case of filamentous algal mat, the sharp gradient of abundance remained constant by both day and night.

An inverse relationship between chlorophyll *a* concentration and Cladocera density was noted in the transect between beds of submerged macrophytes and open water, provide to effective control of phytoplankton biomass by Cladocera during their diel migrations.

KEY WORDS: plankton Crustacea, submerged macrophytes, filamentous algae, diel horizontal migrations

1. INTRODUCTION

A key role in the processes by which shallow water bodies are reclaimed is often assigned to macrophytes (Carpenter and Lodge 1986, Reynoldson 1994). Much field and experimental work has shown the zone of submerged macrophytes to be the subject of intensive periodic use as a place of refuge by large pelagic species of plankton, especially *Daphnia*. These animals migrate

during the day to the littoral in the presence of a vertebrate predator (Timms and Moss 1984, Davies 1985, Beklioglu and Moss 1996, Lauridsen *et al.* 1996). Intensive feeding by pelagic filter-feeding plankton hiding in the zone of macrophytes by day gives rise to a considerable reduction in phytoplankton biomass and an improvement in water quality in the littoral and open-water zones (De Stasio 1993, Lauridsen and Buenk 1996, Lauridsen and Lodge 1996, Søndergaard and Moss 1997). The zone of submerged macrophytes, as well as the filamentous algal mats are first and foremost a place of occurring for many littoral species of filter-feeding planktonic Crustacea. These are the communities of species more or less permanently associated with the area of macrophytes, as well as those that float freely between plants, for which both plant communities and the open-water zone are natural habitats. These species have been sometimes termed tycholimnetic, after Straškraba (1967). Some littoral species migrate periodically to and from the open-water zone in the course of the diel cycle (Kairesalo 1980, Walls *et al.* 1990, Rybak unpubl. data). What is not yet clear is the ecological role of these species in the elimination of phytoplankton and the nutrient cycling between the littoral and the pelagial.

The first step in understanding the structural and functional significance of these animals is the analysis of density, biological diversity and temporal and spatial variation within the littoral, and most especially between the edge of macrophytes bed (ecotone zone) and that of open water.

The aim of this work was thus to analyse the diel horizontal migrations of planktonic *Crustacea* between aggregations of plants and the open water in the mesotrophic and the eutrophic lake. This was related to the density, dominance structure, species composition and distribution of different ecological groups of planktonic Crustacea (littoral, tycholimnetic and pelagic species) in beds of submerged macrophyte of different size, density and species composition, as well as in filamentous algal mats.

2. SITE, MATERIALS AND METHODS

The study was undertaken in two lakes – the deep, stratified and mesotrophic Lake Majcz Wielki and the shallow, eutrophic Lake Zełwążek (both in the Masurian Lakeland, North Eastern Poland). Their morphometric and trophic characteristics are given in Table 1.

At Lake Majcz Wielki, the studies were carried out in July 1997, in the submerged macrophytes involved one large (c. 50 m^2), as well as one small (c. 20 m^2) beds exclusively covered by the single species of *Potamogeton lucens* L. Both beds were situated in a bay of the lake at a distance of c. 50 m from the shore and a depth of 1.5 m. The distance between the two beds was of c. 100 m, and the plants of both reached the water surface. The density of plants expressed as Plant Volume Infested index (*PVI*), Canfield *et al.* (1984) was sparse, at c. 20%. Index of *PVI* was calculated according to the formula:

$$PVI=A*B/C \qquad (1)$$

where: A – macrophyte covered (%); B – macrophyte height (m); C – water depth (m).

The research at Lake Zełwążek was done in July 1997, in the littoral zone 150 m from the shore, at a depth of 3 m. The site had a c. 50 m^2 bed of *Ceratophyllum demersum* L. with dense cover (c. 70% *PVI*), extending to the water surface. This submerged macrophyte is the dominant species in the lake.

The research was also done in a c. 9 m^2 floating surface mat of filamentous algae in which the dominant was *Mougeotia* sp.

Samples of zooplankton were taken from the center and edge of the beds of submerged macrophytes, as well as from the zone of open water 2–3 m away, using a plexiglass tube (length 3 m, diameter 7 cm). Sampling was done at the day time (11 a.m.) and at night (2 a.m.) at each point, with five 4-litre replicates being taken. In turn, zooplankton samples from the algal mat (again with five replicates) were collected with the aid of a 1-litre Czernik and Rybak-type sampler

Table 1. Limnological characteristics of studied lakes

Lake	Trophy type	Surface area (ha)	Littoral area (% total lake area)	Maximal depth (m)
Majcz Wielki	mesotrophic	161.5	42.4	16.4
Zełwążek	eutrophic	11.5	58.2	7.4

(Czernik and Rybak 1995). In addition, samples of zooplankton were taken in the epi-meta- and hypolimnion (in the case of Lake Majcz Wielkie) or the epilimnion (Lake Zełwążek), in the deepest part of the lakes, using a 5-litre Bernatowicz-type water sampler. The samples were pooled and filtered through 60 μm plankton net and fixed in 4% formalin. Quantitative estimations were made using widely-accepted methods (Bottrell *et al.* 1976), while analysis applied the index of Percentage Similarity of community (*PSc*) after Whittaker and Fairbanks (1958). Index of *PSc* was calculated according to the formula:

$$PSc = 100–0.5\Sigma\ (a–b) = E_{min.}\ (a,\ b) \quad (2)$$

where: *a*, b – percentage of individuals of each species of Cladocera in total number of the communities observed in studied habitats *A* and *B*, compared in pairs. Measurements of temperature, dissolved oxygen concentration (YSI probe), electrolytic conductivity, chlorophyll *a* (<30 μm, acetone method) and seston content (<30 μm by weighing) were also made. To test the differences between day and night zooplankton density in the macrophyte beds and in the open water we used the non-parametric Mann-Whitney U-test.

3. RESULTS

Irrespective of species composition, body size and density, the centre of beds of submerged macrophytes were dominated throughout the diel cycle by Cladocera, as opposed to Copepoda. The percentage representation of the latter (especially Cyclopoida and Calanoida nauplii) was steadily greater along the gradient towards open water, especially during daytime (Table 2, Fig. 1 A-C). In contrast, in the filamentous algal mat, it was Copepoda (Cyclopoida only) that showed a strong predominance over Cladocera both day and night (Table 2, Fig. 1 D).

Sampling in Lake Majcz Wielki revealed a relatively poorly-represented and non-diverse communities of planktonic Crustacea in the large and small, sparse density (c. 20% *PVI*) beds of *Potamogeton lucens*. Though this communities resembled that from the lake's pelagial in abundance (Fig. 2 A). In contrast the zooplankton species composition and dominance structure differed markedly in the two environments, as it is shown by an exceptionally low (c. 26%) Percentage Similarity of community index between centre of beds of submerged macrophytes and pelagial (Fig. 3 A).

The Cladocera community of sparse beds of macrophyte in Lake Majcz Wielki was dominated (to more than 70% of all individuals) by tycholimnetic species, notably *Ceriodaphnia quadrangula* (O. F. Müller) and *Diaphanosoma brachyurum* (Lievin). The only well-represented littoral species in that zone was *Sida crystallina* (O.F. Müller) (Fig. 4 A, B). In contrast, the pelagial of the lake showed a large dominance of *Daphnia* species (notably *D. cucullata* Sars, *D. hyaline* Leydig and *D. cristata* Sars).

In the dense (>70% *PVI*) bed of *Ceratophyllum demersum* at Lake Zełwążek, the abundance of planktonic Crustacea exceeded that in the lake's pelagial by several orders of magnitude (Fig. 2 B). The high diversity of the macrophyte bed's Cladocera community was mainly a result of the occurrence of species unique to this zone. Values for the PSc index comparing the centre and edge of the macrophyte beds with the pelagial did not exceed 27% (Fig. 3 B). Along with a main dominant (*C. quadrangula*), the community had high numbers of the littoral species: *Acroperus harpae* (Baird), *Simocephalus vetulus* (O. F. Müller) and *Pleuroxus aduncus* (Jurine) (Fig. 5 A). The community of the filamentous algal mat in turn had large numbers of the tycholimnetic *Chydorus sphaericus* (O. F. Müller), as well as of the aforementioned, typically-littoral *A. harpae* and *P. aduncus* (Fig. 5 B). In contrast, the pelagial of Lake Zełwążek was dominated in the study period by *Daphnia cucullata* and *Bosmina coregoni crassicornis* Lilljeborg.

Compared with that carried out in the day, night sampling revealed higher abundances of zooplankton, and especially of tycholimnetic and littoral Cladocera species (Figs 6 and 7). This was most marked and statistically significant ($P<0.05$) in the edge zone of macrophyte beds (ecotone) and in open water, but was not noted as far as the total abundance of Crustacea in mats of filamentous algae was concerned. This situation was mainly determined by the Copepoda dominant in the mats and the littoral Cladocera species (Figs 9 and 10).

There was a very sharp daytime gradient of the abundance of Crustacea along horizontal transects, especially that in the large beds

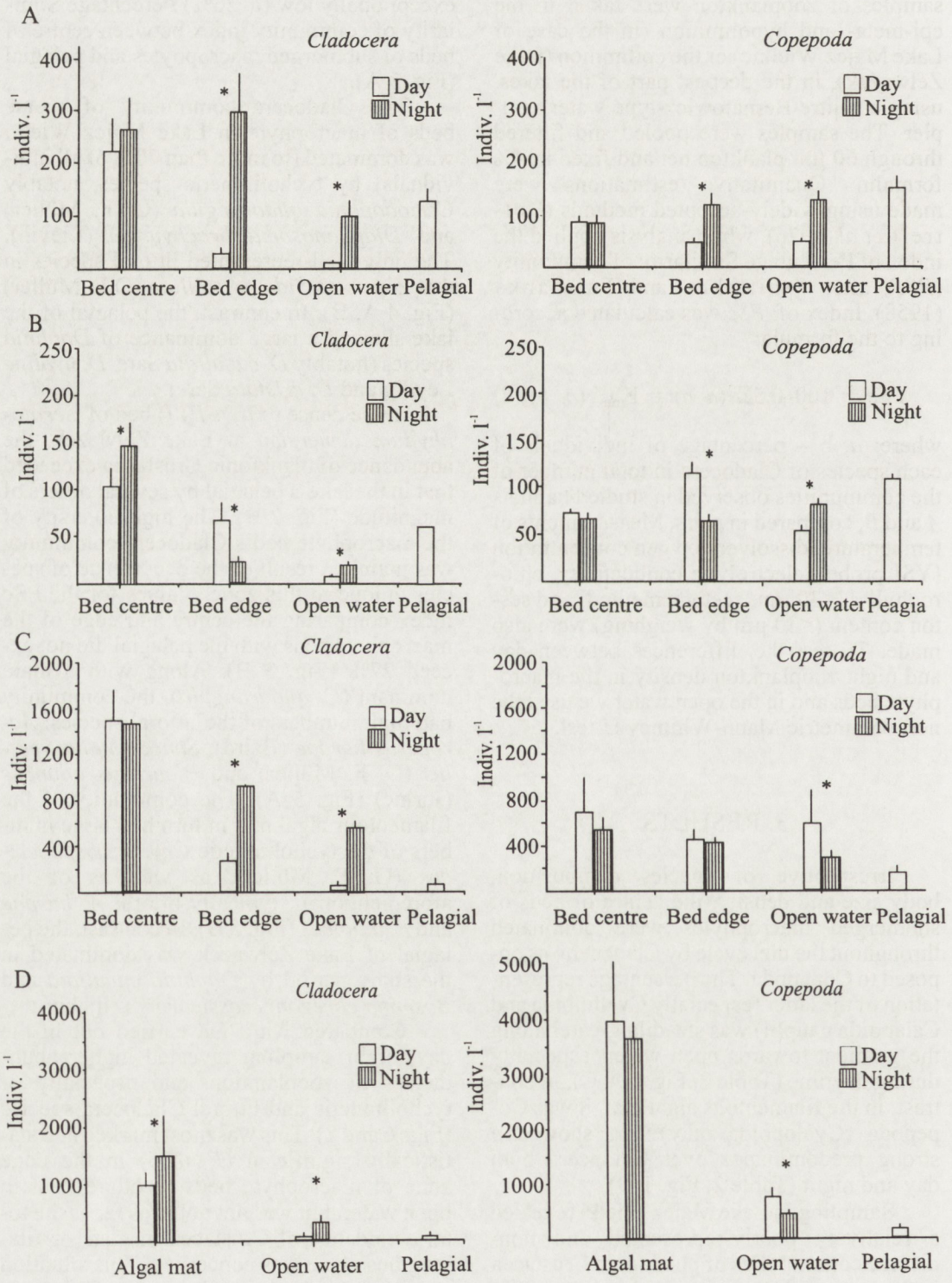

Fig. 1. Daytime (open columns) and night-time (shadow columns) mean density (N=5) of Cladocera and Copepoda along transect: centre macrophytes bed, edge bed, open water near bed, pelagial. Large (A) and small bed (B) of *Potamogeton lucens* in Lake Majcz Wielki; bed of *Ceratophyllum demersum* (C) and filamentous algal mat (D) in Lake Zełwążek; July 1997. SD is indicated by the vertical bars. The statistical significance ($P<0.05$, Mann-Whitney U-test) of the night-day differences are marked with asterisks.

Table 2. Structure of planktonic communities in beds of submerged macrophytes, in filamentous algal mat and open water in Lakes Majcz Wielki and Zełwążek (July 1997)
I – ratio of abundances of Calanoida to Cyclopoida
II – ratio of abundances of Cladocera to Copepoda

	Habitat	Time of day	Centre	Edge	Open water	Pelagial
	Lake Majcz W.					
I	Large bed *P. lucens*	Day	0			
		Night	0.05 00.03	0.04 0.07	0.55 0.41	0.74 –
I	Small bed *P. lucens*	Day	0.02	0.05	0.55	0.74
		Night	0.24	0.23	0.41	–
II	Large bed *P. lucens*	Day	4.4	0.32	0.16	0.55
		Night	3.0	1.0	0.25	–
II	Small bed *P. lucens*	Day	1.6	0.64	0.16	0.55
		Night	2.0	0.40	0.25	–
	Lake Zełwążek					
I	Bed *C. demersum*	Day	0	0	0	0.26
		Night	0.01	0.02	0.01	–
II	Bed *C. demersum*	Day	2.3	0.57	0.07	0.41
		Night	2.8	2.1	1.6	–
I	Filamentous algal mat	Day	0	–	0	0.26
		Night	0	–	0	–
II	Filamentous algal mat	Day	0.25	–	0.07	0.41
		Night	0.41	–	0.67	–

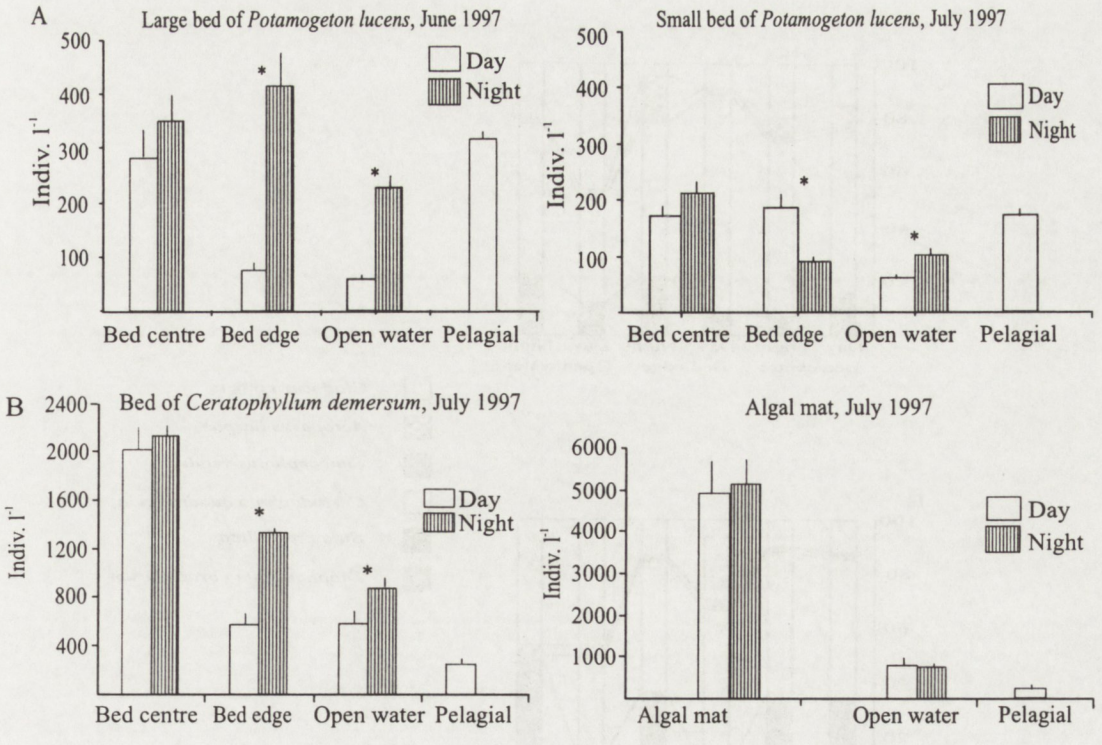

Fig. 2. Daytime (open columns) and night – time (shadow columns) mean density (N=5) of Crustacea along horizontal transect (see legend of Fig. 1) in large and small beds (A) of *Potamogeton lucens* in Lake Majcz Wielki and in a bed of *Ceratophyllum demersum* and filamentous algal mat (B) in Lake Zełwążek, July 1997
SD is indicated by the vertical bars. The statistical significance ($P<0.05$, Mann-Whitney U-test) of the night-day differences are marked with asterisks.

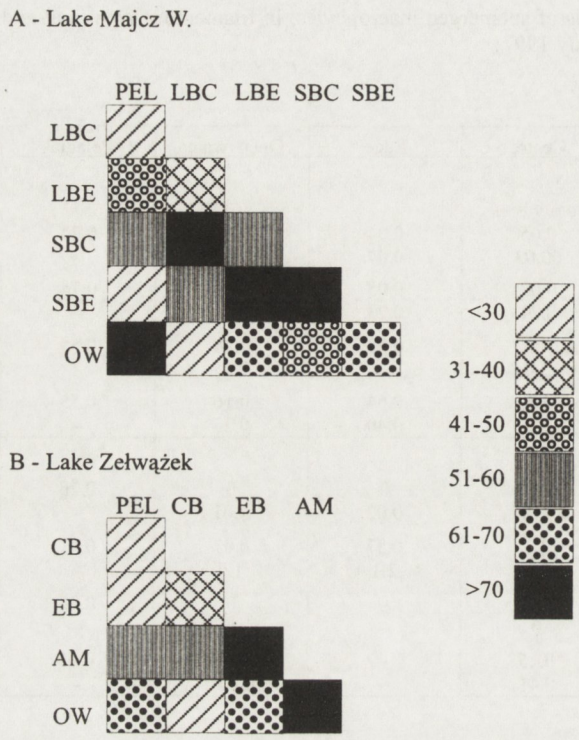

Fig. 3. Percentage Similarity coefficient (*PSc*) of Cladocera community (see the equation no 2) in the studied habitats in Lake Majcz Wielki (A) and Lake Zełwążek (B), July 1997.
PEL – pelagial; LBC – centre of large bed; LBE – edge of large bed; SBC – centre of small bed; SBE – edge of small bed; CB – centre of bed; EB – edge of bed; AM – filamentous algal mat; OW – open water (by bed or filamentous algal mat).

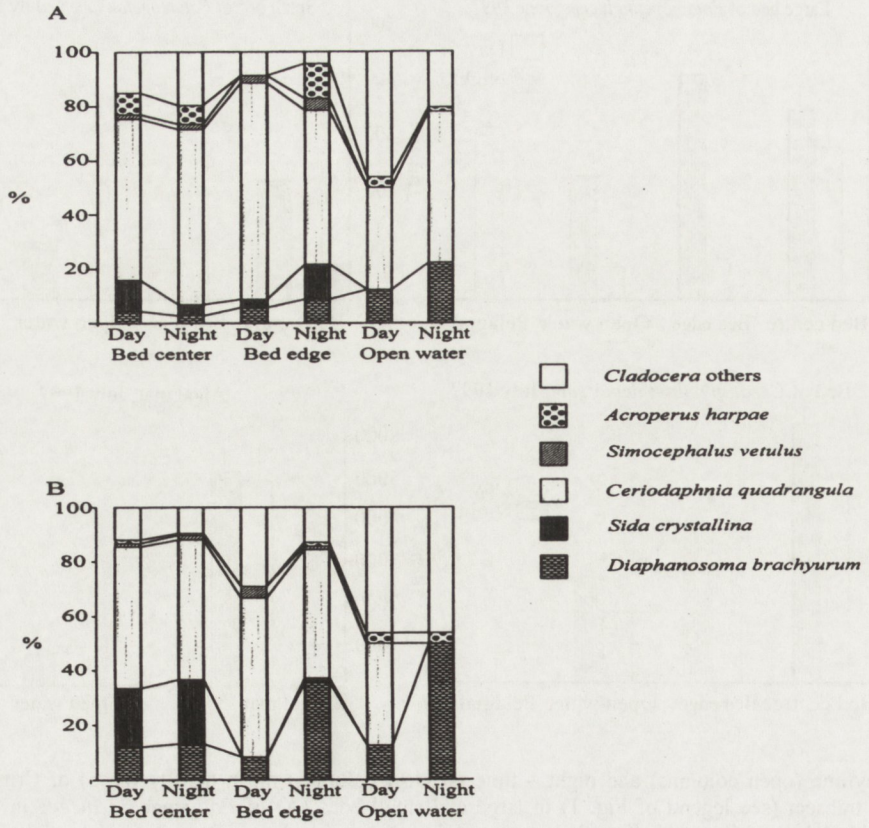

Fig. 4. Share of dominant species in total abundance of Cladocera in the small (A), and large (B) beds of *Potamogeton lucens* in Lake Majcz Wielki, July 1997
Mean value for five samplings. See description of habitats in Fig. 1.

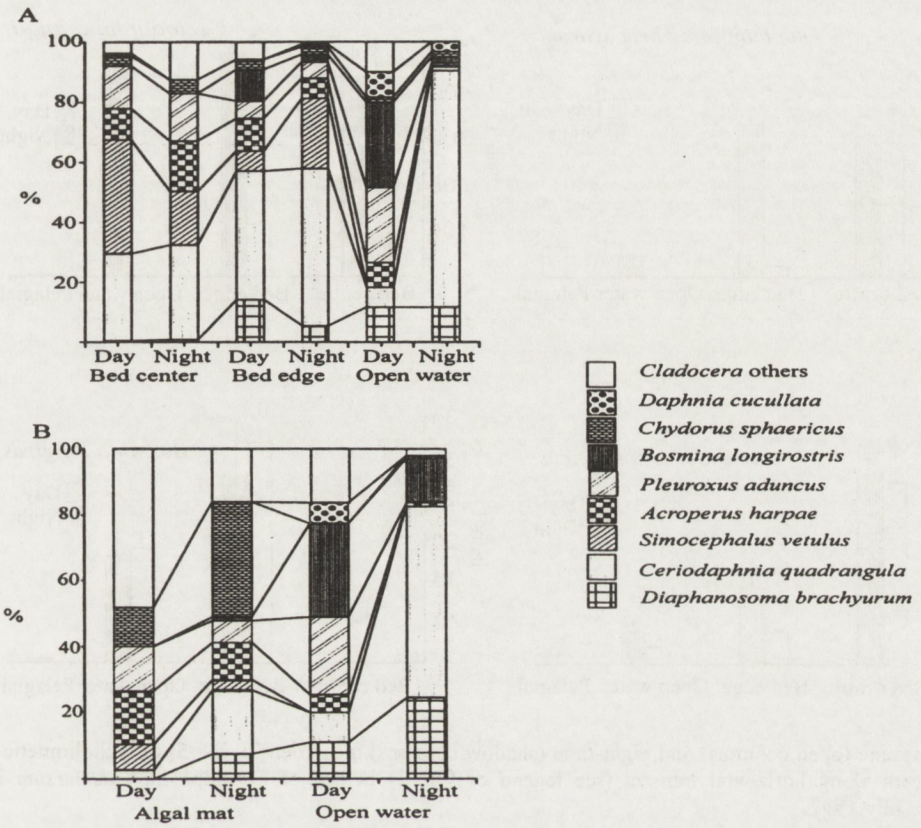

Fig. 5. Share of dominant species in total abundance of Cladocera in the bed of *Ceratophyllum demersum* (A), the filamentous algal mat (B) in Lake Zełwążek, July 1997

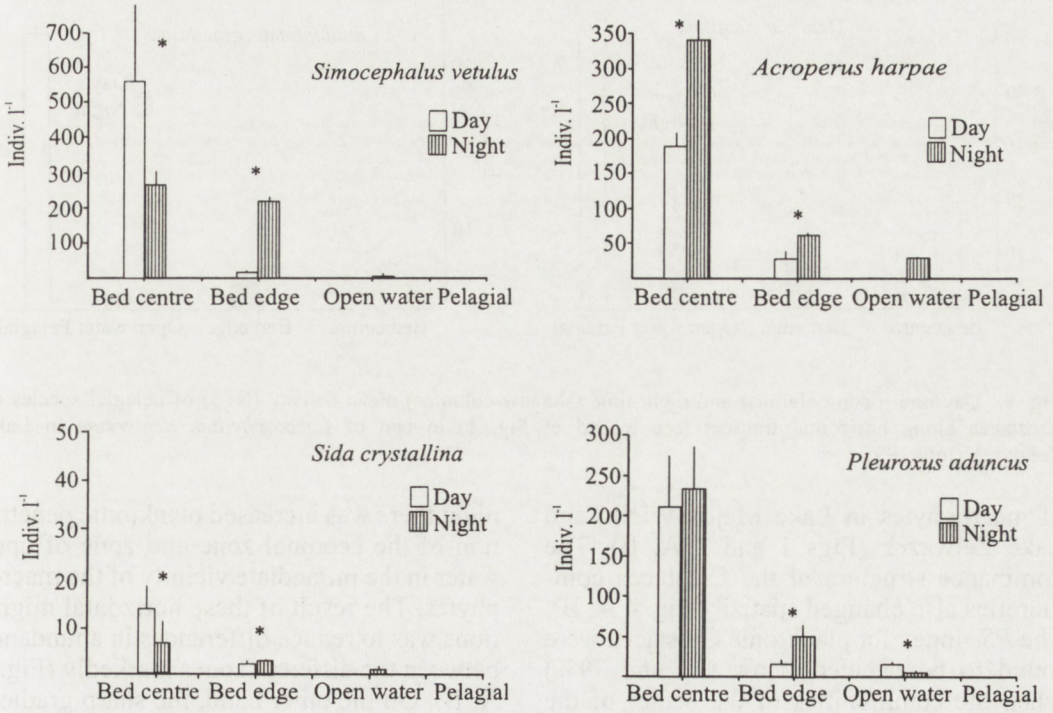

Fig. 6. Daytime (open columns) and night-time (shadow columns) mean density (N=5) of littoral species of Cladocera along horizontal transect (see legend of Fig. 1) in bed of *Ceratophyllum demersum* in Lake Zełwążek, July 1997.

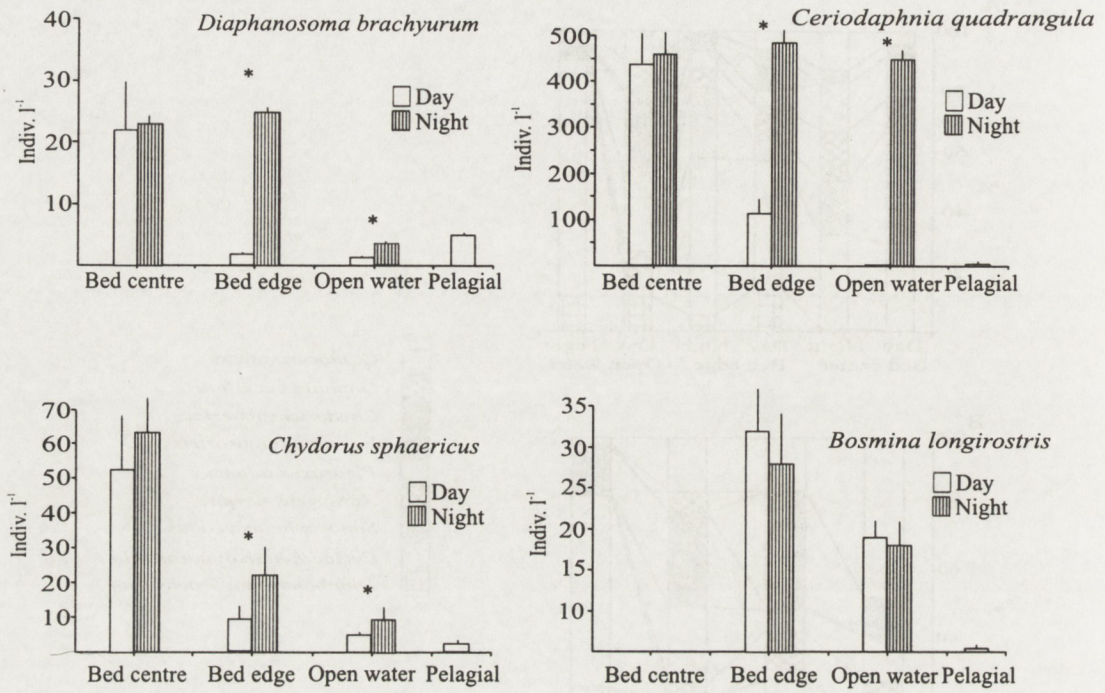

Fig. 7. Daytime (open columns) and night-time (shadow columns) mean density (N=5) of tycholimnetic species of Cladocera along horizontal transect (see legend of Fig. 1) in bed of *Ceratophyllum demersum* in Lake Zełwążek, July 1997.

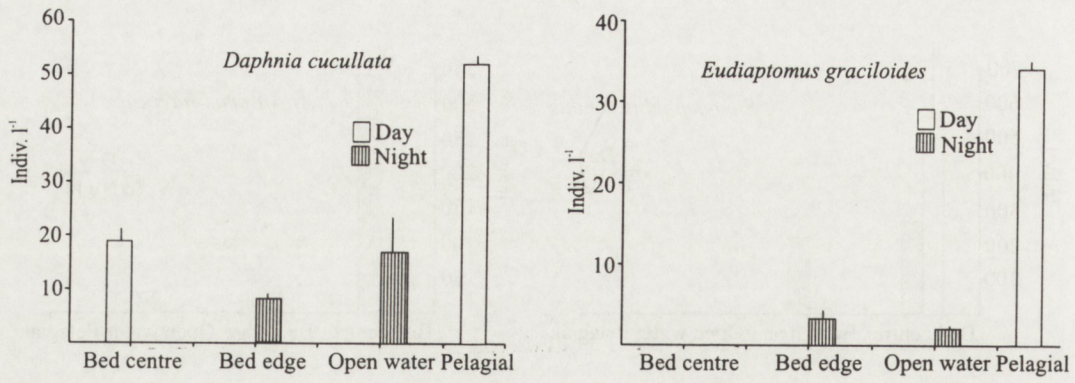

Fig. 8. Daytime (open columns) and night-time (shadow columns) mean density (N=5) of pelagial species of Crustacea along horizontal transect (see legend of Fig. 1) in bed of *Ceratophyllum demersum* in Lake Zełwążek, July 1997.

of macrophytes in Lake Majcz Wielki and Lake Zełwążek (Figs 1 and 2 A, B). The dominance structure of the Crustacea communities also changed spatially Fig. 4 A, B). The *PSc* index for planktonic Crustacea were found to be decidedly low (28 and 39%) when the communities of the center of the large bed of macrophytes and of its edge (ecotone) were compared with that of the zone of open water (Fig. 3 A, B). However, at night there was increased planktonic penetration of the ecotonal zone and zone of open water in the immediate vicinity of the macrophytes. The result of these horizontal migrations was to reduce differences in abundance between the different zones markedly (Fig. 2 A, B). On the other hand, the sharp gradient of zooplankton abundance between the filamentous algal mat and the nearby open water remained stable day and night (Fig. 2 B).

Table 3. Share of adult forms (%) in total abundance of selected *Crustacea* species in beds of macrophytes

		Taxons																	
Lake		*Sida crystallina*			*Acroperus harpae*			*Diaphanosoma brachyurum*			*Ceriodaphnia quadrangula*			*Daphnia cucullata*			*Eudiaptomus graciloides*		
		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Majcz W.	D	55	–	–	85	–	–	78	0	0	89	0	0	100	–	–	0	0	0
Large bed	N	50	0	0	90	30	0	23	15	30	46	13	26	–	–	25	0	0	9
Majcz W.	D	69	0	–	75	–	–	100	41	0	77	25	0	–	–	–	0	0	–
Small bed	N	46	0	0	80	60	0	0	0	30	66	24	26	–	–	25	28	8	9
Zełwążek	D	50	0	–	80	75	0	0	0	0	80	10	0	75	0	–	–	–	–
	N	50	0	–	64	65	0	20	20	10	50	41	30	–	–	30	0	0	0

D – day, N – night, 0 – only immature forms, – not present.

1– Bed centre; 2 – Bed edge; 3 – Open water

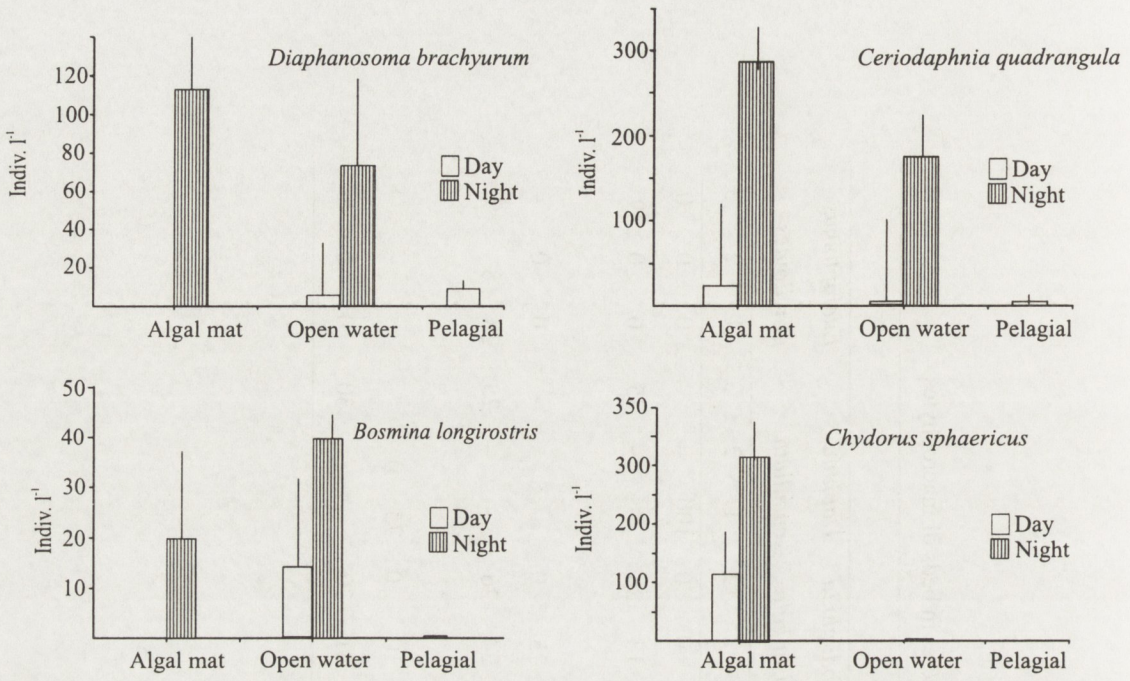

Fig. 9. Daytime (open columns) and night-time (shadow columns) mean density (N=5) of tycholimnetic species of Cladocera along horizontal transect (see legend of Fig. 1) in the filamentous algal mat in Lake Zełwążek, July 1997.

The diel gradient of horizontal distribution was different for different species. The littoral species gathered mainly within beds of macrophytes and filamentous algae during the day, but then both young and adult individuals extended their area of occurrence somewhat into the ecotonal and open-water zones at night (Figs 9 and 10, Table 3). In the case of *Sida crystallina* the nocturnal migration into open water involved young individuals only (Table 3).

During the day, the zone of submerged macrophytes is also penetrated intensively by large (>500 μm) tycholimnetic Cladocera like *Ceriodaphnia quadrangula* and *Diaphanosoma brachyurum*, especially in their adult forms (Table 3 and Fig. 7). Both this Cladocera species were characterised by significant ($P<0.05$) day – night differences in density. The maximum daytime abundance of *C. quadrangula* was noted in the dense bed of macrophytes of *Ceratophyllum demersum*, while *D. brachyurum* was more abundant in the sparse bed of *Potamogeton lucens*. During the night a considerable increase in the numbers of both species has been noted in the ecotonal zone and zone of open water (Fig. 7). In contrast, from among the small (<350 μm) tycholimnetic species, *Bosmina longirostris* (O. F. Müller) showed a marked avoidance of aggregations of vegetation both day and night (Fig. 7), while in filamentous algal mat, this species was only present during the night (Fig. 9).

Pelagic species were only present in the zone of submerged macrophytes in small numbers, and showed a distinct avoidance of filamentous algal mat. From among the three *Daphnia* species dominant in the pelagial of Lakes Majcz Wielki and Zełwążek, only one, *D. cucullata* (and then mainly adults of this species) migrated to the macrophyte zone during the course of the day. This migration was sporadic in Lake Majcz Wielki, but more frequent in Lake Zełwążek (Table 3, Fig. 8). In contrast, this species moved into the zone of open water at night. A completely different diel gradient of horizontal distribution is manifested by *Eudiaptomus graciloides* (Lilljeborg). In the day, older developmental stages showed marked avoidance of the zone of macrophytes, while at night they migrated horizontally in the direction of the littoral until they reached edge of the macrophyte zone (Table 3, Fig. 8).

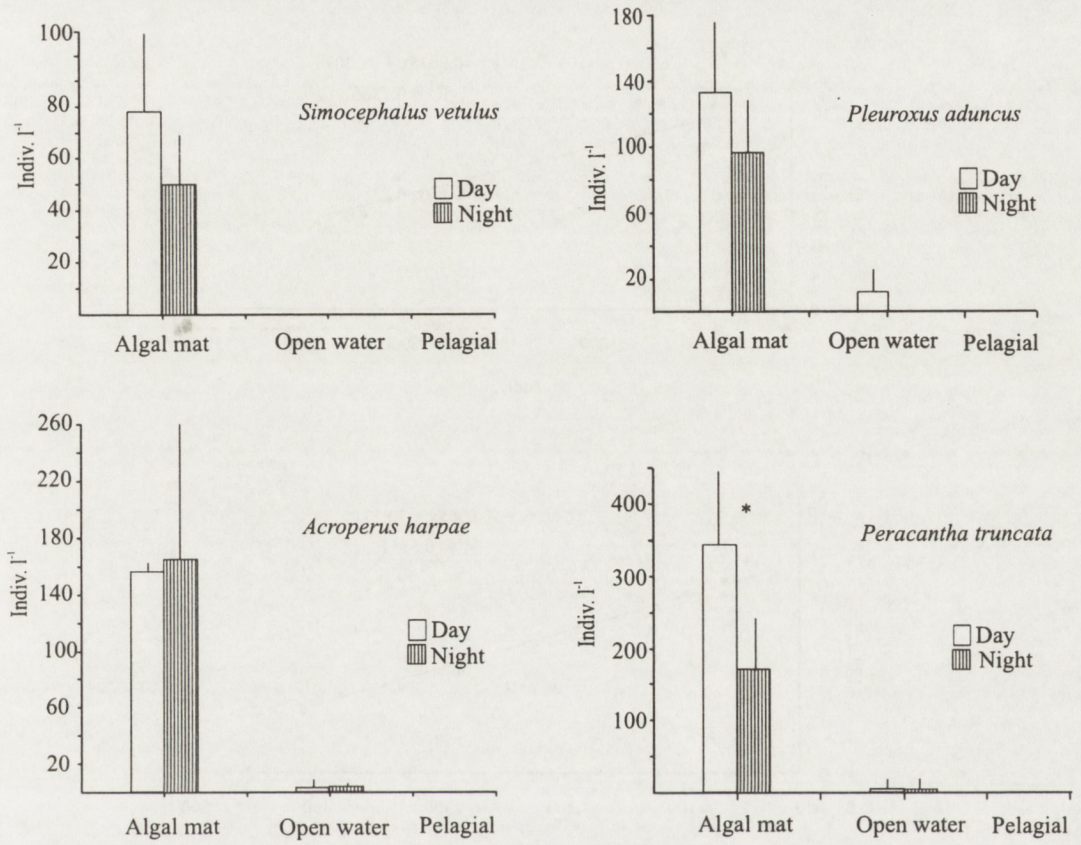

Fig. 10. Daytime (open columns) and night-time (shadow columns) mean density (N=5) of littoral species of Cladocera along horizontal transect (see legend of Fig. 1) in the filamentous algal mat in Lake Zełwążek, July 1997.

4. DISCUSSION

The problem of submerged macrophytes functioning as a refuge for zooplankton is a very complex one, not only in regard to pelagial species. Attention should first and foremost be paid to the mass occurrence of free-floating or periodically fixed species of littoral and tycholimnetic planktonic filter-feeders in the zone of macrophytes, and filamentous algal mats. The abundance and species diversity of Crustacea in beds of submerged macrophyte increases with the increased density of the latter. It may be that denser macrophytes provide zooplankton with a more attractive "environmental offer" – a greater supply of food and a safer refuge. Our work revealed that concentrations of potential food for filter-feeders (seston of <30 μm) were greater in the denser bed of *Ceratophyllum demersum* (*PVI*>70%) than in the sparse bed of *Potamogeton lucens* (*PVI* c. 20%). In turn Jeppesen *et al.* (1997) and Lauridsen *et al.* (1998) showed that the effectiveness of foraging by fish is lower where macrophyte density is higher. Macrophytes at a density of *PVI* >15–20% function as refuges for zooplankton where moderate predation pressure is imposed by planktivorous fish, typical of both lakes studied (Węgleńska unpubl. data).

Clearly greater abundances of zooplankton were noted at night than in the day, though the greatest diel differences characterised the edge zone of a bed and open water. Such a phenomenon was observed previously (Szlauer 1963, De Stasio 1993, Paterson 1993). One of the most probable interpretations here is the occurrence in the littoral of a daily vertical *Cladocera* migration between the surface layer of bottom sediments – treated as a daytime refuge – and the open water, as well as – in the case of *Sida crystallina* for example – a migration between the surface of macrophyte leaves and stems and open water.

The diel gradient of the distribution of planktonic Crustacea would thus result from

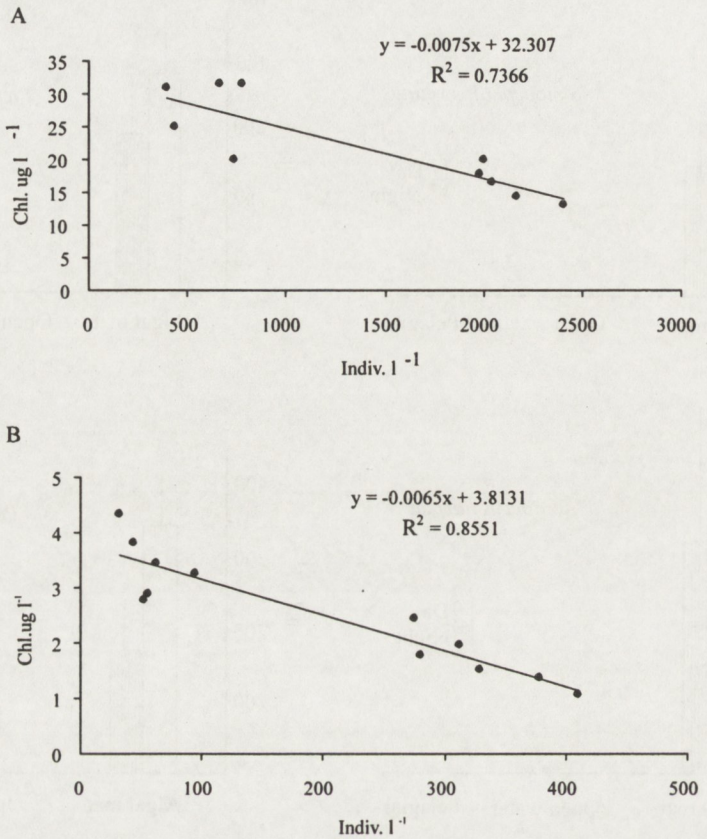

Fig. 11. Relationship between mean density of Cladocera and chlorophyll *a* concentration within beds of submerged macrophytes and in open water in Lake Zełwążek (N=10) (A), and in Lake Majcz Wielki (N=12) (B), June and July 1997.

simultaneous vertical and horizontal migrations in the transect between macrophytes and open water. A similar observation was made by Węgleńska *et al.* (1997).

The decisive factors regarding the behavioural strategy adopted by planktonic Crustacea as they migrated between macrophytes and open water were not in the nature of abiotic conditions (since electrolytic conductivity, temperature and oxygen concentrations were stable day and night), but rather a reflection of biotic impacts, above all the avoidance of planktivorous fish. Through the day, littoral and large tycholimnetic species (especially adult forms) gather in large beds of macrophytes, irrespective of their density, but mainly in their center. Attesting to this is the steep gradient in the abundance of Crustacea between the centers and edges of macrophyte beds and the open water. However, in the case of a small bed of macrophytes it is not merely the center but mainly the edge zone that functions as a refuge, as is witnessed by the much less pronounced gradient of the abundance of Crustacea between the center and the edge zone, and the much sharper one between the bed and the open water. The edge zone of macrophyte (ecotone) thus plays a particular role during the migrations of tycholimnetic species, seeming to constitute a barrier delaying movements and thereby generating an exceptionally high concentration of Crustracea. A similar phenomenon was observed by Lauridsen and Buenk (1996) for submerged macrophytes, and by Rybak (1960) for emergent macrophytes.

In the case of the pelagic *Daphnia cucullata* inhabiting the relatively-deep Lake Majcz Wielki, the refuge was first and foremost provided by the deeper parts of the lake, rather than by macrophytes. In contrast, the latter were the only available refuge in the shallow, unstratified Lake Zełwążek.

The reverse migration of the pelagic *Eudiaptomus graciloides* (which avoids macrophytes during the day) is a reflection of factors other then the predation pressure imposed by planktivorous fish. Probably what is involved here is the phenomenon of the repel-

lent effect induced by plants, of a kind observed previously for many pelagic species by Pennak (1973) and Siebeck (1980).

Unlike the macrophytes, the filamentous algal mats do not represent a refuge for zooplankton since pelagic species do not migrate into them, while tycholimnetic species (both large and small) are most abundant in them at night, rather than in the day. The marked gradient of abundance between the mat and the open water zone is retained day and night, perhaps reflecting vertical nocturnal migration in the direction of surface filamentous algal mat of the kind seen within macrophytes. The mass daily occurrence of Crustacea in the filamentous algal mat is probably a consequence of the favorable feeding conditions, because – in comparison with open water – there is a higher density of the seston of >30 μm that is available as potential food to most filter-feeding planktonic Crustacea (Rybak, unpubl. data).

Analysis of changes in the chlorophyll *a* concentration and densities of filter-feeding *Cladocera* (Fig. 11) revealed the high effectiveness of zooplankton in controlling phytoplankton biomass. Thus, the existence of a refuge in the form of beds of macrophyte and the possibility for zooplankton to hide within them during the day favours the elimination of phytoplankton, especially by the littoral species occurring permanently within the macrophytes, as well as the pelagic and tycholimnetic species present in the macrophytes by day and in open water (the pelagial) at night. This relationship is clearer in Lake Majcz Wielki, where large tycholimnetic species occur at lower concentrations, albeit with greater filtering effectiveness than the microfiltrators also occurring within the community of planktonic Crustacea in Lake Zełwążek and feeding to a great extent on small detritus and bacteria.

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5. SUMMARY

The diel horizontal migrations of Crustacea between beds of submerged macrophytes and filamentous algae on the one hand and open water on the other were studied in the mesotrophic-type Lake Majcz Wielki and the eutrophic-type Lake Zełwążek (Table 1).

The work considered the density, dominance structure, species composition and horizontal distribution of different ecological groups of planktonic Crustacea (plant-associated, tycholimnetic and pelagic) in beds of submerged macrophytes differing in size, density and species composition, as well as in filamentous algal mats (Tables 2 and 3).

The numbers and dominance structure of Crustacea in beds of submerged macrophytes were dependent upon the density of the latter. Large tycholimnetic species of Cladocera dominated (with <70% of all individuals) in a sparse bed of macrophytes (Figs 3 A, 4 A, B, 6, 7 and 8). In a dense bed, plant-associated species were found, as well as tycholimnetic species (Figs 3 B and 5 A). Copepoda and small tycholimnetic Cladocera dominated in the mats of filamentous algae (Figs 3 B, 5 B, 9 and 10).

The numbers of zooplankton (mainly Cladocera) in a macrophytes bed were higher at night than in the day, while differences between night and day were not observed in filamentous algal mat (Fig. 1 A-D).

A strong gradient to numbers of Crustacea was observed in the day along horizontal transect, particularly in large bed of macrophytes. At night, the Crustacea migrated horizontally from the macrophytes bed to open water. Differences in Crustacea numbers between the middle of the macrophytes bed, its edge and the open water showed a clear decrease that reflected the effect of migration during night. The strong gradient of numbers of Crustacea was present permanently (day and night) in the filamentous algal mat (Fig. 2 A, B).

There was an inverse relationship between chlorophyll concentration and differences in Cladocera community density between the macrophytes bed and the open water. This reflects the efficiency of Cladocera in controlling phytoplankton biomass, as well as the diel migration they participate in (Fig. 11).

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