Turkish Journal of Zoology

Volume 23 | Number 4 Article 4

1-1-1999

Diurnal Variation of Water Chemistry andZooplankton in Little Mere, Cheshire, UK, in 1993 and 1994

MERYEM BEKLİOĞLU

BRIAN MOSS

Tr. J. of Zoology
23 (1999) 337–348

Diurnal Variation of Water Chemistry and Zooplankton in Little Mere, Cheshire, UK, in 1993 and 1994

Meryem BEKLİOĞLU
Middle East Technical University, Biology Department, 06531, Ankara-TURKEY
Brian MOSS
The University of Liverpool, Biological Sciences Department, Derby Building, P.O Box 147 Liverpool L69 3BX, UK.

Received: 24.01.1997

Abstract: In Little Mere, diurnal sampling of the zooplankton at three different habitats in 1993 provided little evidence to support the data of Timms and Moss (10) that cladocerans move out from refugia at night to graze in open water. The floating-leaved water lily, appeared to be more efficient at providing refuge to *D. hyalina* in the presence of high planktivore fish predation than the submerged plant beds and the open water. This might be due to unfavourable physical and chemical environmental conditions associated with the water lily bed for fish feeding, a possibility supported by the findings of very low dissolved oxygen and pH values in the water lily beds. *Potamogeton berchtoldii* beds appeared to be more favourable habitats for submerged plant associated zooplankters than for open water grazers, probably due to the high predation pressure of planktivorous fish on the latter. The findings of this study suggest that it is important to have a better understanding of effectivness of submerged plants at provison of refuges for open water Cladocera against fish predation to combat eutrophication by using biomanipulation.

Key Words: Floating-leaved plants, submerged plants, *Daphnia,* plant-bed associated grazers, refuge.

Little Mere (Cheshire, İngiltere) Su Kimyası ve Zooplankton Topluluklarının 1993 ve 1994 Yıllarında Günlük Değişimi

Özet: 1993 yılında, Little Mere'de yapılan, üç farklı habitattaki zooplankton günlük örneklemesi, Timms ve Moss'un (10) Cladocera'ların gece sığınak olarak kullandıkları makrofitlerin yoğun bulunduğu habitatlardan açık suya çıkarak fitoplankton üzerinden beslendikleri temeline dayanan 'sığınak hipotez'ni desteklememektedir. Yüzen yapraklı su nilüferinin *D. hyalina*'ya planktivor balık avlama baskısına karşı barınak sağlamada sualtı bitkisi olan *Potamogeton berchtoldii* ye göre daha etkin olduğu bulgulanmıştır. Bu durum su nilüferinin yoğun olarak bulunduğu ortamlarda yarattığı fiziksel ve kimyasal değişmeler sonucu balık beslenmesini olumsuz olarak etkilemesi ile ilgili olabilir. Su nilüferinin yoğun bulunduğu ortamlarda balık beslenmesinin olumsuz etkilenmesi, 1994 yılında yapılan günlük örneklemede gözlenen çok düşük pH ve çözünmüş oksijen ile desteklenmektedir. *P. berchtoldii*'nin su bitkilerine bağlı yaşayan zooplakton gruplarına (Eurycercus, Sida, Simocephalus vb.) barınak sağlamada pelajik Cladocera'lara göre daha etkin olduğu bulgulanmıştır. Bu durum planktivor balık beslenmesinin sualtı bitkilerinin bulunduğu ortamdan olumsuz etkilenmemesi ile açıklanabilir. Bu çalışmanın bulguları, ötrofikasyonu kontrol etmek için uygulanan biyomanipulasyon tekniğinin daha etkin olarak kullanılabilmesinde, sualtı makrofitlerin pelajik Cladocera'lara planktivor balık avlanma baskısına karşı barınak sağlamadaki rolünün daha iyi anlaşılmasının önemini vurgulamaktadır.

Anahtar Sözcükler: Yüzen yapraklı su bitkisi, su altı bitkisi, *Daphnia*, Su bitkisine bağlı yaşayan zooplankton, barınak.

Introduction

Many taxa of both marine and freshwater zooplankton perform diurnal vertical migrations (1). The normal pattern is an evening ascent and a morning descent. The persence of diurnal vertical migration in so many taxa suggests that it has some adaptive value (2). This has been explained by several competing hypotheses, including metabolic and demographic advantages (3) and resource-related diurnal migration (4). Probably the strongest argument is in favour of demographic advantage through predation avoidance that has been provided by Gliwicz (5). He found a clear relationship between the amplitude of diurnal vertical migration and the period for which there had been fish populations in various lakes of the Tatra mountains.

This behavioural defence of planktonic herbivores appears to avoid fish predation pressure through exploitation of physical and chemical factors as refuges in deep lakes. The most common defensive behaviour of planktonic animals is to move to safer habitats in deep strata where low light intensity does not allow plantivorous fish to feed efficiently during the daytime (6). Taking visual refuge appears to be one of the most important defence mechanisms in Peter Lake, where removal of the visual refuge by alum treatment resulted in disappearance of *Daphnia pulex,* which had previously been abundant in the presence of high rainbow trout density (7). Another potential refuge need by diurnally migrating *Daphnia* is low dissolved oxygen (DO) concentrations which are tolerated by zooplankton but in which fish can not survive continuously (8). Diurnal shift to safer but cooler hypolimnetic habitats to use low temperature as refuge (9) is also widely used by zooplankton. In deep lakes, diurnal vertical migration of zooplankters to lower light, DO and temperature refuges appear to be efficient defence strategies to protect against fish predation.

Contary to studies on deep lakes and their open water cladoceran defence strategies, little is known about the potential similar defence strategies of cladocerans against fish predation in shallow lakes. Stands of macrophytes, however, have been shown to act as refuges for large *Daphnia* in the presene of planktivorous fish (10). A study by Timms & Moss (10) suggested that large-bodied, open-water grazers move horizontally out of the plant beds in darkness to feed on the phytoplankton crop. In the 1993 diurnal sampling described below, this suggestion was investigated.

Timms & Moss' (10) study also showed the efficiency of water lilies for sheltering *Daphnia,* and this has been recorded in several other shallow lakes (11, 12, 13). The disappearance of *Daphnia* and the increase of plant-associated zooplankters have been recorded in *C. demersum* beds (14, 15). We hypothesised that floating-leaved plants are more effective than submerged plants for providing refuges to open water Cladocera against fish predation because floating-leaved macrophytes and submerged plants have very different physical and chemical effects on the associated water, depending on the daily intensity of photosynthesis and respiration (16). No avoidance of macrophytes by fish has been recorded (17). Thus, the intensity of changes created in floating-leaved plant beds during day time might be severe enough to impair feeding of fish and in turn provide predation-free habitat to zooplankton, just as large zooplankters in stratified lakes use deeper hypolimnetic water as a refuge against fish predation.

Little attention has been paid to loosely or firmly plant-associated zooplankters of shallow lakes and the littoral zone of deep lakes, though within submerged plant beds a wide range of invertebrate species is found, including the herbivorous filter-feeders *Simocephalus* species and *Sida crystallina* (18). Most studies on zooplankton communities within submerged plant beds have tended to be descriptive (19), with a few exceptions (14, 20). Fairchild (20) found no diurnal migration of weed-associated *Simocephalus* and *Sida,* which hardly moved from the submerged plant beds during the day and night. However, *Chydrous* and *Eurycercus lamellatus* showed clear diurnal migration, staying in the plant beds during the day and moving up to the water surface at night (20). We hypothesised that submerged plants would be safer refuges for plant-associated zooplankters due to their evolutionary adaptations to the plant beds, but not for open-water zooplankters because the physical and chemical changes in the associated water may not be severe enough to impair feeding of fish.

Having a better understanding of interactions between zooplankton and fish in macrophyte beds would allow us to improve control of eutrophication. We made use of the current dense stands of floating-leaved plants, and the submerged plant, *P. berchtodii,* in Little Mere, to examine possible diurnal migration of both open-water and plant-associated zooplankters and the efficiency of both macrophytes for sheltering cladocerans against fish predation in relation to chemical and physical changes in the associated water caused by the plants.

Materials and Methods

Diurnal sampling in 1993

Diurnal sampling of zooplankton and chlorophyll a were carried out on the 14th and 15th of August, 1993, in Little Mere. Five sampling stations were chosen among the existant macrophyte communities and the open water of the lake. Two of the sampling stations were densely covered by water lilies (*Nymphaea alba* and *Nuphar lutea*). Two other stations were in open water, though one of them had a very small patch of *Elodea canadensis.* The last station had a medium density stand of *P. berchtoldii*, and there was a small patch of *E. canadensis* as well.

Samples were taken from the stations at 10:00, 15:00, 20:30, 01:30 and 06:00 BST. The weather was warm but not very bright and relatively clam. For zooplankton sampling, 101 of water were taken using a 1m-long plastic tube sampler from each station. The zooplankters were promptly narcotised with chloroform water (21) and preserved in a solution of formaldehyde, yielding a final formaldehyde concentration of about 4%. Samples were normally sub-sampled, and counted under a Kyowa stereo-microscope (22). The species of the animals were identified whenever possible using standard references (23). Chlorophyll a was extracted from phytoplankton and filtered through GF/C filters into 90% acetone, and concentrations were calculated from the absorbance reading at 663 nm (24).

Diurnal sampling in 1994

Diurnal sampling of zooplankton, chlorophyll a, alkalinity, temperature, dissolved oxygen and pH were carried out on the 12th and 13th of August, 1994. Five sampling stations were chosen, as in the previous year, but the macrophyte density and communities were different as the lake had changed. Two of the sampling stations were densely covered with water lilies (*N. alba* and *N. lutea*) as in the previous year. The total coverage of macrophytes was greater in 1994 than in the previous year, and the open water station was only nominal and had a substantial patch of *E. canadensis* in the bottom. The last two stations were densely covered by *P. berchtoldii*, and some filamentous algae were presents.

Samples were taken at 10:30, 13:00, 15:00, 19:30, 00:00 and 08:00. The weather was warm but not sunny, and there were spells of rain and wind. Sampling of zooplankton and chlorophyll a was carried out as described above. Temperature and dissolved oxygen concentrations were measured using a WTW oxygen meter to a precision of ±0.1˚C% and ±1% saturation respectively. Free-CO_2 and total alkalinity were determined according to Mackereth *et al.* to precisions of ±10 and 5%, respectively (25). For pH measurement, small water samples were collected from the surface, mid-depth and bottom of the each station with a remote sampler consisting of a 60 cm^3 hypodermic syringe without a needle, attached to a long, stiff graduated pole. The water was tranferred into a 30 ml beaker with minimum disturbance and the pH was measured with a 3050/3070 Jenway field pH meter.

Results

Diurnal sampling in 1993

Two-way ANOVA performed on chlorophyll a concentrations showed that whilst the habitats had significant effects on the concentrations (P=0.02) (Table 1), sampling time and interaction effect, had no significant effect on the chlorophyll a concentrations (P=0.7 and P=0.7 respectively). The highest concentrations of chlorophyll a were found associated with *P. berchtoldii* and the lowest were in the lily beds (Figure 1a). Two-way ANOVA performed on zooplankton densities revealed singnificant effects of the habitats on densities of *D. hyalina*, *Bosmina longirostris* and *Ceriodaphnia* sp. (P=0.0018, P=0.007 and P=0.034, respectively) (Table 1). No significant effects of sampling time on the densities of these species were found (P=0.18, P=0.1 and P=0.17, respectively) (Table 1). Whilst the interaction effect of sampling time and habitat revealed a significant effect on the density of *D. hyalina* (P=0.004), no significant interaction effect was found on the densities of *B. longirostris* and *Ceriodaphnia* sp. (P=0.76 and P=0.44, respectively) (Table 1). Whilst the highest densities of *D. hyalina* were recorded in lily beds, *B. longirostris* had its highest density in *P. berchtoldii* beds and *Ceriodaphnia* sp. in the open water (Figure 2 a, b and c). Two-way ANOVA employed on densities of *Euryercus lamellatus, Chydorus* sp, *Polyhemus pediculus, Simocephalus* sp., *Cyclops*+nauplii and rotifers showed that the sampling time, the habitats and the interaction effects of the sampling time and the habitats had no significant effects (Table 1).

Diurnal sampling in 1994

Two-way ANOVA performed on the water chemistry and chlorophyll a showed that the different habitats had significant effects on chlorophyll a, dissolved oxygen, free-CO_2 concentrations and pH (P<0.001, P=0.0012, P<0.001 and P<0.001, respectively) (Table 2). The sampling time had a significant effect only on dissolved oxygen concentrations (P=0.02) whilst the interaction between sampling time and habitats had significant effects on the chlorophyll a concentrations, free-CO_2 and pH (P=0.005, P=0.04 and P=0.02 respectively) (Table 2). The highest concentrations of chlorophyll a were found in the lily beds (Figure 1b). The dissolved oxygen concentratins reached their highest values in the afternoon and gradually decreased in the evening to the lowest values at midnight in all three habitats. The highest dissolved oxygen concentrations were found in *P. berchtoldii* beds and the lowest values were recorded in the lily beds (Figure 3a). The highest free-CO_2 concentrations and the lowest pH values were recorded in the lily beds, and the opposite was found in *P. berchtoldii* beds, as free-CO_2 concentration is closely related to pH values (Figure 3b and c).

Two-way ANOVA performed on the densities of the

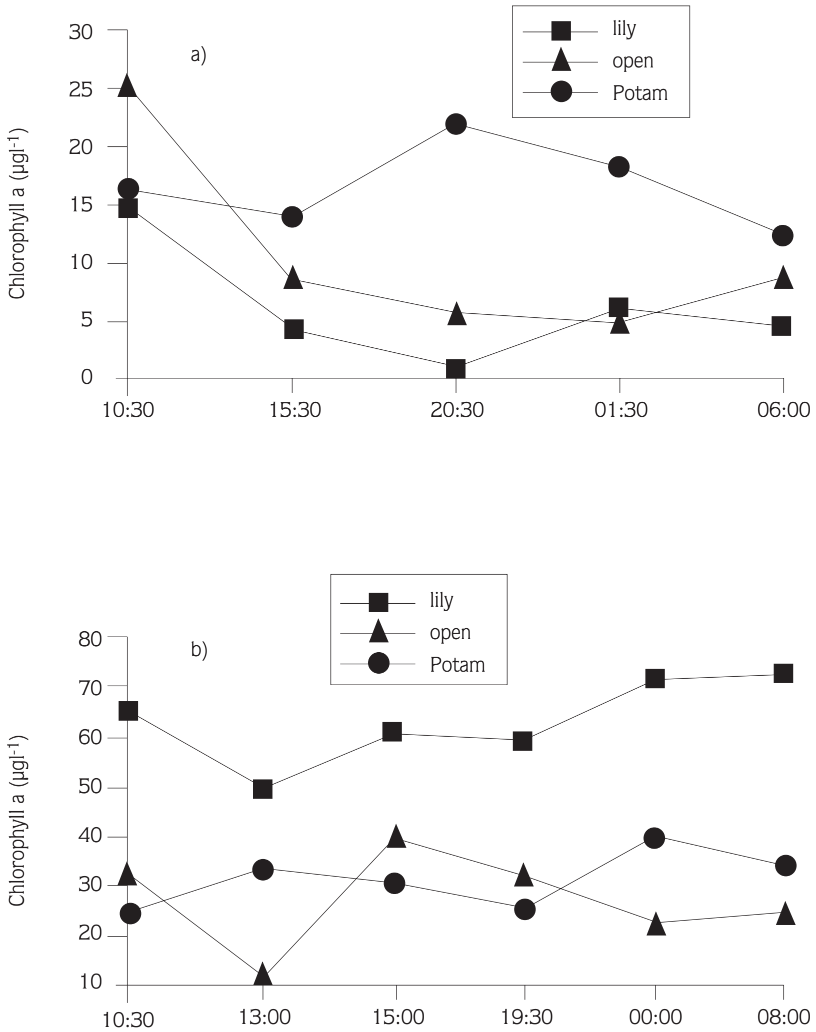

Figure 1. Changes in the concentrations of chlorophyll a in diurnal sampling a) on the 14th and 15th of August, 1993 and b) on 12th/13th August 1994 in Little Mere (lily= water lily beds, open: open water and Potam= *P. berchtodii* beds).

			Interactions
	Time	Habitats	Time*Habitat
Chlorophyll a (µg l^{-1})	NS	*	NS
D. hyalina (ind l^{-1})	NS	***	*
Bosmina longirostris (inds l^{-1})	NS	**	NS
Ceriodaphnia sp. (ind l^{-1})	NS	*	NS
Polyphemus pediculus (ind l^{-1})	NS	NS	NS
Eurycercus lamellatus (ind l^{-1})	NS	NS	NS
Chydorus sp. (ind l^{-1})	NS	NS	NS
Simocephalus sp. (ind l^{-1})	NS	NS	NS
Cyclops + nauplii (ind l^{-1})	NS	NS	NS
Rotifers (ind l^{-1})	NS	NS	NS

Table 1. Summary of effects of the sampling time, the different habitats and the time-habitats interaction on the chlorophyll a concentrations and zooplankton densities in diurnal sampling on the 14th and 15th of August, 1993 in Little Mere following two-way ANOVA. Symbols *P<0.05, **P<0.01, ***P<0.01 and NS: no significance.

	Time	Habitats	Interactions Time*Habitat
Chlorophyll a (µg l^{-1})	NS	***	**
Dissolved-oxygen (mgl^{-1})	*	**	NS
Free-CO2 (µg l^{-1})	NS	***	*
pH	NS	***	*
B. longirostris (ind.l^{-1})	NS	NS	NS
Ceriodaphnia sp. (ind. l^{-1})	NS	***	*
E. lamellatus (ind.l^{-1})	NS	***	*
Chydorus sp. (ind.l^{-1})	NS	**	NS
P. pediculus (ind.l^{-1})	NS	*	NS
Simoncephalus sp.(ind.l^{-1})	NS	**	NS
D. brachyurum (ind.l^{-1})	NS	***	NS
Cyclops+nauplii (ind.l^{-1})	NS	*	*
Rotifers (ind.l^{-1})	NS	NS	NS

Table 2. Summary of effects of the sampling time, the different habitats and the time-habittas interaction on the water chemistry, cholorophyll a concentrations and zooplankton densities in diurnal sampling on the 12th and 13th of August, 1994 in Little Mere following two-way ANOVA. Symbols *P<0.05, **P<0.01, ***P<0.01 and NS: no significance.

dominant zooplankton species revealed significant effects of the different habitats on densities of *Ceriodaphnia* sp, *E. lamellatus, Chydorus* sp., *P. pediculus, Simocephalus vetulus, Diaphanosoma brachuyrum* and *Cyclops+*nauplii (P=0.002, P<0.001, P=0.003, P=0.0014, P=0.0044, P=0.001 and P=0.045 respectivley) (Table 2). Whilst the sampling time had no significant effects on any of these zooplankton species, the interaction effect of sampling time and the habitats on densities of *Ceriodaphnia* sp, *E. lamellatus* and *Cyclops+*nauplii was significant (P=0.042, P=0.034 and P=0.02 respectively) (Table 2). The highest densities of *Ceriodaphnia* sp, *D. brachyurum* and *P. pediculus* were ecorded in the lily beds (Figure 4 a, b and c). The highest densities of the plant-bed associated zooplankters, *E. lamellatus, Chydorus* sp. and *S. vetulus,* were recorded in *P. berchtoldii* beds, but their densities were near zero in the lily beds and the open water (Figure 5a, b and c). Though two-way ANOVA did not reveal a significant effect of sampling time, the densities of *E. lamellatus, Chydorus* sp. and *S. vetulus* showed a similar trend throughout the 24-hr period with their densities gradually increasing from the first sampling (10:30 in the morning to the highest densities in the afternoon at 15:00, followed by a gradual decrease to the lowest values at midnight. One-way ANOVA was carried out to examine the effect of sampling time on the densities of *E. lamellatus, Chydorus* sp. and *S. vetulus* in the *P. berchtoldii* beds and revealed a significant effect of sampling time on the densities of these weed-bed zooplankters (F=6.24, P=0.0023; F=11.79, P=0.006 and F=9.3, P=0.0058, respectively).

Discussion

Diurnal sampling in 1993

The chlorophyll a concentrations were significantly lower in the lily beds where the highest *D. hyalina* densities were recorded. The effectivenes of the grazing pressure of large filter-feeding *Daphnia* on phytoplankton crops has been recorded elsewhere(11). Thus, the high density of *D. hyalina* was probably very important in

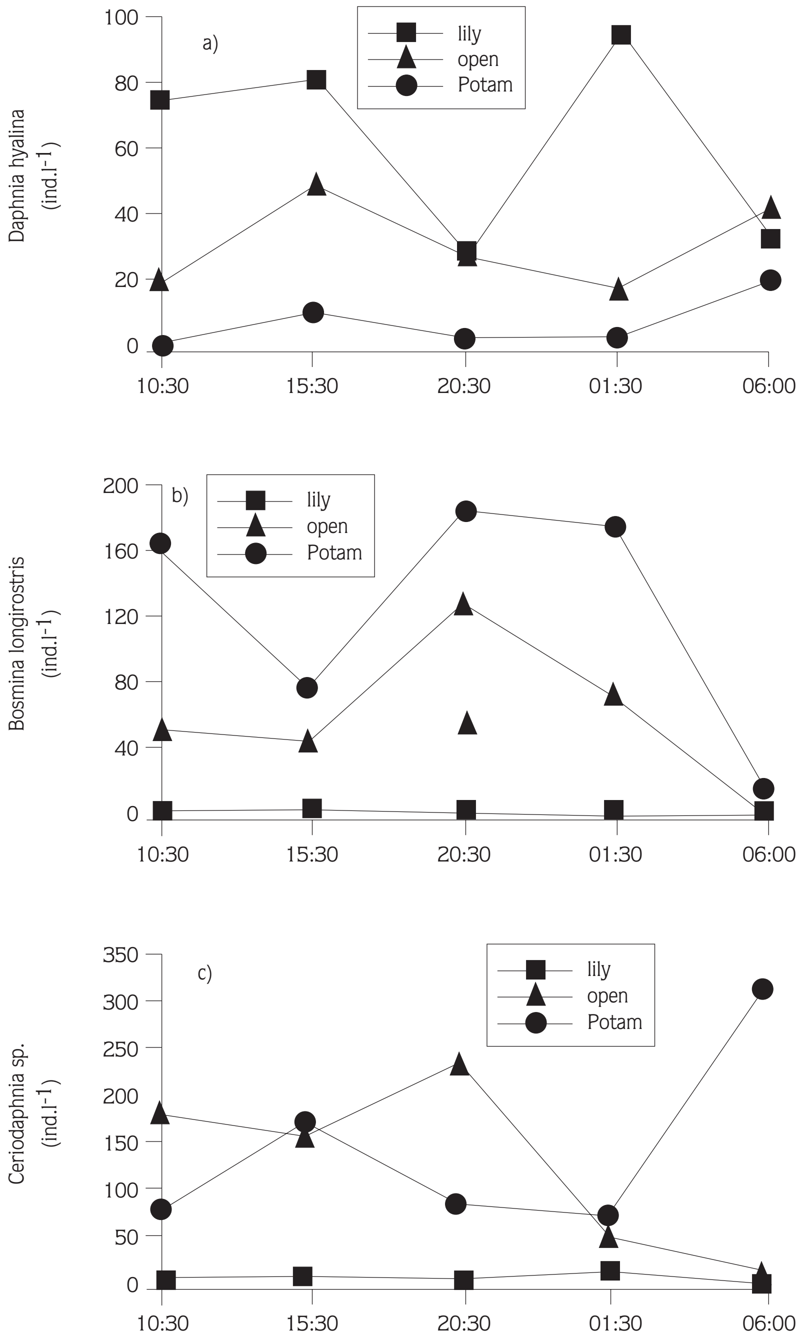

Figure 2. Changes in densities of a) *Daphnia hyalina*, b) *Bosmina longirostris* and c) *Ceriodaphnia* sp. in diurnal sampling on the 14th and 15th of August, 1993 in Little Mere. (lily= water lily beds, open= open water and Potam= *P. berchtodii* beds).

decreasing the chrolophyll a concentrations to near zero in the lily beds, although it did not seem to be a function of the absence of potential fish predation because perch had strongly recolonized the lake (12, 13, 15), and substantial fish populations have been recorded in lily beds in small shallow lakes elsewhere (17). In little Mere, the floating-leaved water lilies appeared to provide better refuges for *D. hyalina* than the submerged *P. berchtoldii*, where the lowest *D. hyalina* density was recorded. Though in the 1993 diurnal sampling no physical and chemical variables were sampled, the lily bed's greater efficiency at harbouring *D. hyalina* might be due to differences between floating-leaved plants and submerged plants in terms of structural effects or how

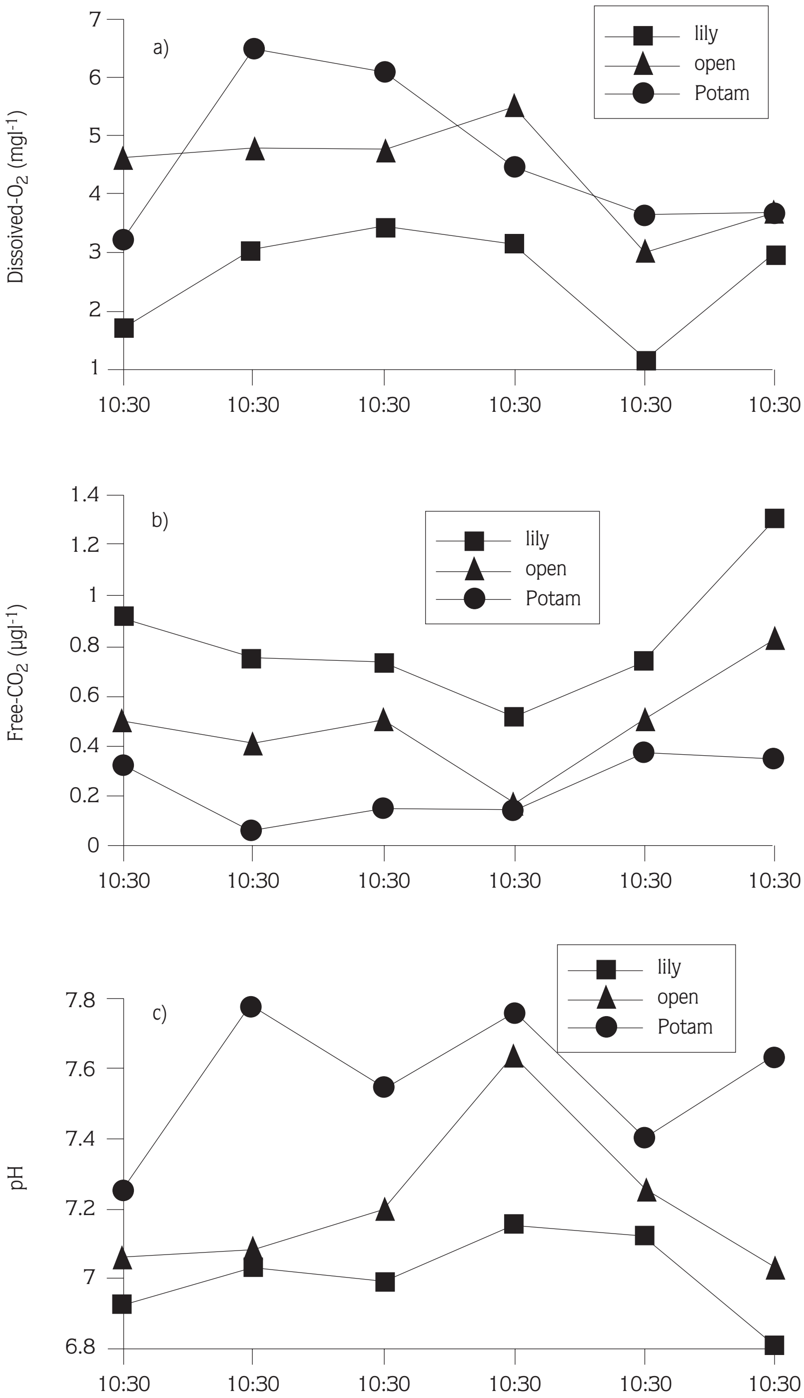

Figure 3. Chpanges in concentrations of a) dissolved-oxygen, b) free-CO_2 and c) pH in diurnal sampling on the 12th and 13th of August, 1994 in Little Mere. (lily= water lily beds, open: water and *P. berchtoldii* beds).

they change associated water chemistry and physical conditions (16).

The density of *D. hyalina* decreased at 20:30 at night in the lily beds but it reached its peak density at 01:30. Thus, there was a little evidence to support the data of Timms & Moss (10) that cladocerans move out from refugia at night to graze in open water. Taking into account the possibility that many zooplanktivorous fish are capable of preying efficiently on large cladocerans in virtual darkness by using cues other than vision (26), the finding of this diurnal study may not be surprising. The

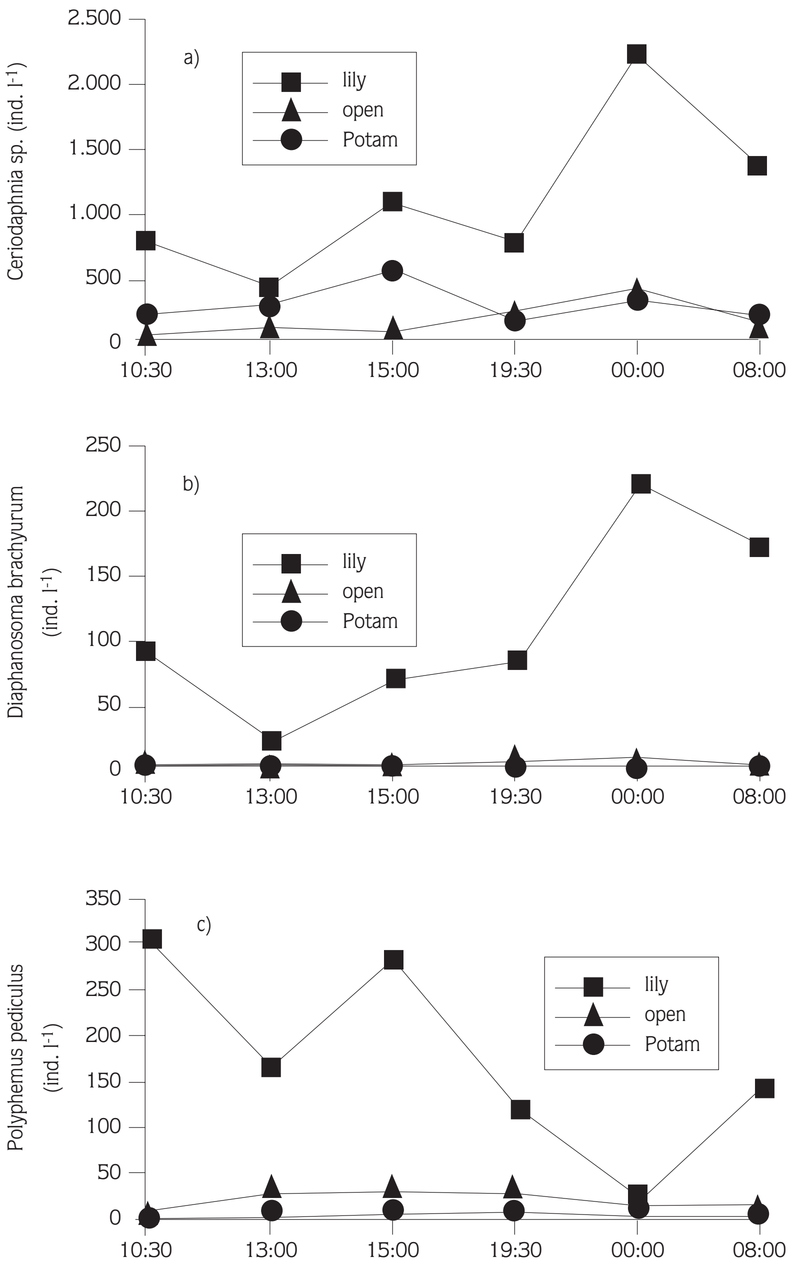

Figure 4. Changes in densities of a) *Ceriodaphnia* sp., b) *Diaphanosoma brachyurum* and c) *Polyphemus pediculus* in diurnal sampling on the 12th and 13th of August, 1994 in Little Mere.
(lily= water lily beds, open= open water and Potam= *P. berchtoldii* beds).

results are in accordance with the findings of Perrow & Stansfield (27).

The densities both of *Ceriodaphnia* sp. and *B. longirostris* were near zero in the lily beds but high with varying densities both in the open-water and *P. berchtoldii* bed. *Ceriodaphnia* sp. and *B. longirostris* might have been disadvantaged by the high *D. hyalina* density in tle lily beds, perhaps due to competition for food, because the lowest chlorophyll a concentrations were recorded in the lily beds. *Ceriodaphnia* sp and *Bosmina* appear to be less efficient grazers on phytoplankton crops than *D. hyalina* (28).

Diurnal Sampling in 1994

Frodge *et al.* (16) suggested that floated-leaved plants and submerged plants are very different in terms of creating different physical and chemical environments in

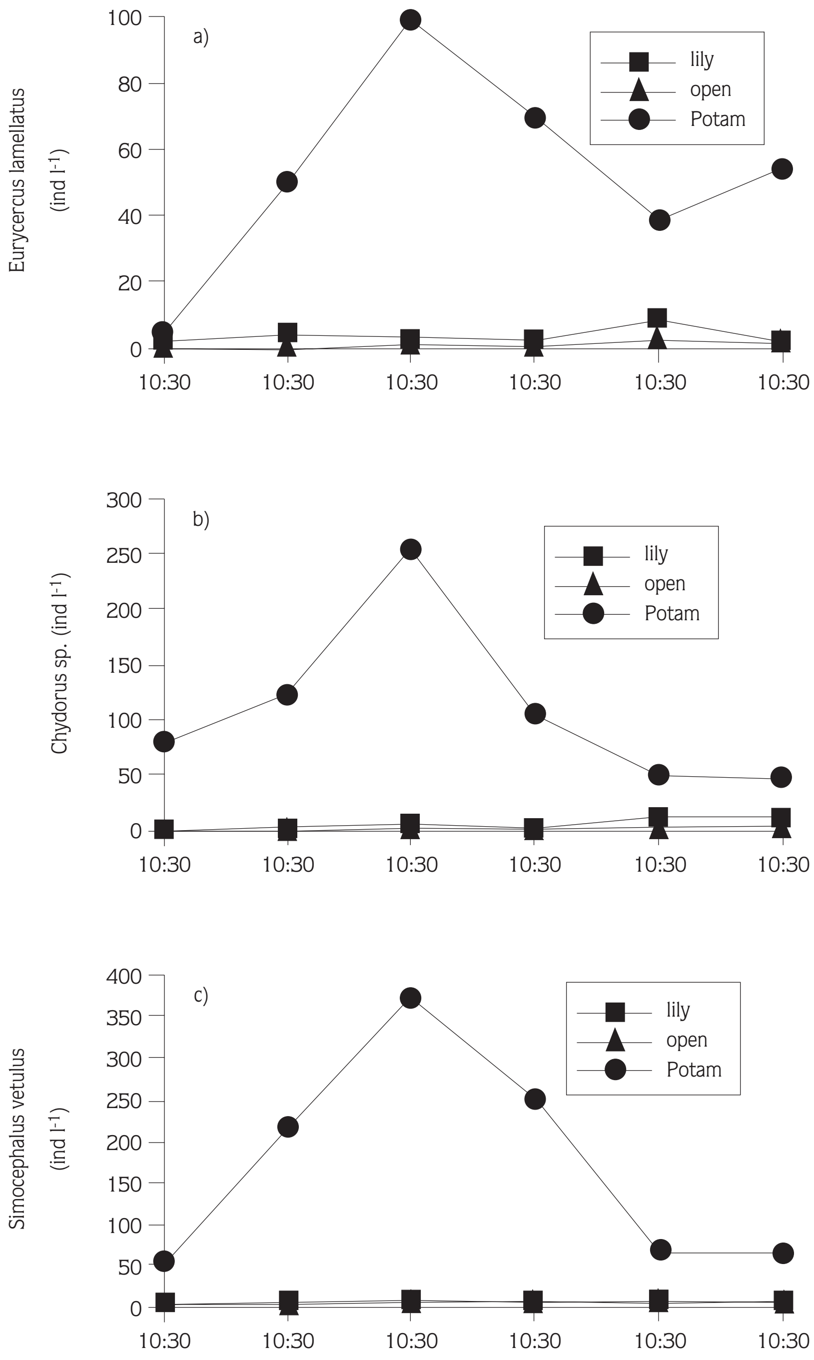

Figure 5. Changes in the densities of a) *Eurycercus lamellatus,* b) *Chydorus* sp. and c) *Simocephalus vetulus* in diurnal sampling on the 12th and 13th of August, 1994 in Little Mere. (lily= water lily beds, open= open water and Potam= *P. berchtoldii* beds).

water bodies. The dissolved oxygen concentrations and pH varied significantly among the habitats, with much lower values in the lily beds than in the open water and the submerged plant beds. This might be due to floating-leaved plants like lilies forming a layer on top of the water surface, creating a physical barrier between the surface water and the atmosphere and restricting oxgyen diffusion inwards and carbon dioxide diffusion outwards. It was likely to have been relatively low in the lily beds. Free CO_2 concentrations were higher in the lily beds, as expected from the lower pH. Significantly higher dissolved oxygen concentrations and pH values were recorded in *P. berchtoldii* beds than in the open water and in the water lily beds throughout the 24-hr period. Summerfelt (8) suggested that 3 mg l^{-1} would be critically low for typical planktivores. The mean dissolved oxygen concentrations of the lily beds were 2.4 to 2.7 mg l^{-1}. Thus, the recorded values of dissolved oxygen concentrations are likely to have impaired the feeding of fish in the lily beds. However, in *P. berchtoldii* beds, the oxygen concentrations were high enough not to have detrimental effects on the feeding of fish over 24 hrs.

The zooplankton community of Little Mere has shown great changes from the bright red, large-bodied *D. magna* to *D. hyalina* following sewage effluent diversion (13), and to the near absence of *D. hyalina* in summer 1994 (D. Stephen, unpublished data). The density of *D. hyalina* was negligible in this study, consistent with its general density in the lake throughout summer 1994. Factors linked with dense physical habitat structures, like interference of zooplankton filtering appendages by detritus material trapped by submerged plant, may have been significant in the disappearence of *D. hyalina.* Reduction of *Daphina* abundance and increase of plant-associated zooplankton in submerged plant beds has been recorded elsewhere (14).

Neither *Ceriodaphnia* nor *D. brachyurum* showed signs of moving out of the lily beds at night. It is probable that *Ceriodaphnia* and *D. brachyurum* were easy prey to fish in the absence of *D. hyalina.* It has been shown in Lake Chorea Bass that *D. lumholzi* was the preferable prey to the fish due to its large size, but when it disappeared, the smaller *Ceriodaphnia* became desriable prey and the fish predation drove *Ceridophnia* to very low densities. Lastly, the even smaller and less opaque *Diaphanosoma* became undetectable in the lake (29). In plant beds, high densities of *P. pediculus* have been recorded elsewhere (18), consistent wiht the high densities of *P. pediculus* found here. The highest chlorophyll a concentrations were found in the lily beds, in contrast to the previous year. This might be due to the small cladocerans being less efficient at grazing phytoplankton crops than large cladocerans like *Daphnia,* as grazing efficiency is a function of body size (28).

Large submerged plant-associated cladocerans like *Simocephalus* and *Eurycercus,* whose densities were much higher in *P. berchtoldii* beds than in the previous year, may have been responsible for reducing the phytoplankton crop in this habitat. Though two-way ANOVA did not reveal an overall significant effect of sampling time on these species in this habitat, one-way ANOVA did. The reason these species had peak numbers in the afternoon is not clear. Fish predation may have increased in the late afternoon. The animals harboured in the beds might be numerous enough to replace the populations at high densities in the adjacent water during the next day, or *E. lamellatus, Chydorus* sp. and *S. vetulus* may have moved to the bottom or attached themselves to the plants stems to avoid fish predation. In submerged plant beds, low night densities of *E. lamellatus* and *Chydorus* sp. (19, 20) have been recorded elsewhere. Both *Sida* and *Simocephalus* share the same adaption method of attaching to aquatic plants and filter feeding. *Sida* was rarely found away from plant surfaces (20). A similar pattern might be expected for *Simocephalus,* but in this study in abundance largely decreased at night. Detailed research on plant bed associated zooplankton and fish interactions is needed.

We hypothesised that floating-leaved plants are better for sheltering open water cladocerans due to the physical and chemical conditions they create in the associated water, and this was accepted. The water lily beds (*N. lutea* and *N. alba*) appeared to play an important role in harbouring and maintaining high densities of the open water cladocerans against fish predation in Little Mere, as suggested by Timms and Moss' (10) refuge theory, perhaps by depleting dissolved oxygen and cutting off light to an extent dependent on the density of the plant surface canopy (16), as very low dissolved oxygen concentrations were recorded in this study. This might impair the feeding of fish in dense stands of floating-leaved lilies without necesarrily affecting the abundance of fish (17). We hypothesised that submerged plants are more efficient for sheltering loosely or firmly plant bed-associated zooplankters but not open water zooplankters, and this appears to be the case. The submerged *P. berchtoldii* appeared to be efficient at shelterig loosely or firmly plant bed-associated zooplankters but not the open water zooplankters in Litte Mere. The reason submerged plants are less efficient in harbouring open water zooplankters might be that the plant-bed environment was unfavourable. The highest pH and dissolved oxygen values recorded in this study were found in *P. berchtoldii* beds. Serafy and Harrell (1993) found a lack of significant avoidance response by the fish tested at pH 9.52 to 9.83 when accompanied by 204 to 250% dissolved oxygen concentration. Fish apparently benefit from the increased oxygen levels, which counterbalance the adverse effects of high pH, perhaps allowing them to feed on open water cladocerans in submerged plant beds. Thus detailed studies are necessary to understand the difference between floating-leaved and submerged plants in terms of their effects on the associated water chemistry and in turn provision of refuges and the effectiveness of submerged plants for harbouring of open water Cladocera against fish predation.

References

1. Hutchinson, G.E.A. Treatise on Limnology. Introduction to Lake Biology and the Limnoplankton. Vol.II., New York. 1967, Wiley.
2. Lampert, W., The adaptive significance of diel vertical migration of zooplankton. Finc. Ecol. 3: 21-27, 1989.
3. Swift, M.C., Energetics of vertical migration in Chaborus trivittatus larvae. Ecology 57: 900-914, 1976.
4. Stich, H.-B., and Lampert, W., Growth and reproduction of migrating and non-migrating Daphnia species under simulated food and temperature conditions of diurnal vertical migration. Oecologia 61: 192-196, 1984.
5. Gliwicz, Z.M., Predation and the evaluation of vertical migration behaviour in zooplankton. Nature 320: 746-748, 1986.
6. Confer, J.L., Howick, G.L., Corzette, M.H., Kramer, S.L., Fitzgibbon, S., and Landesberg, R., Visual predation by planktivorous. Oikos 31: 27-37, 1978.
7. Kitchell, J.A., and Kitchell, J.F., Size-selective predation, light transmission and oxygen starification: evidence from recent sediments of manipulated lakes. Limnol. & Oceanogr. 25: 389-402, 1980.
8. Summerfelts, R.C., Fisheries benefits of lake aeration: A review. in F.L. Bruns andI.J. Powling, editors. Destratification of lakes and reservoirs to improve water quality. Sydney, 1981, Australian Gov. Pub. Serv., pages 419-445.
9. Dawidowicz, P., and Loose, C.J., Cost of swimming by Daphnia during diel vertical migration. Limnol. & Oceanogr. 37(3): 665-669, 1992.
10. Timms, R.M., and Moss, B., Prevention of growth of potentially dense phytoplankton by zooplankton grazing, in the presence of zooplantivorous fish, in a shallow wetland ecosystem. Limnol. & Oceanogr. 29(3): 472-486, 1984.
11. Moss, B., McGowan, S. and Carvalho, L., Determination of phytoplankton crops by top-down and bottom-up mechanisms in a group of English lakes, the West Midland Meres. Limnol. & Oceanogr. 35(9): 1020-1029, 1994.
12. Beklioğlu, M., and Moss, B., The impact of pH on interactions among phytoplankton algae, zooplankton and perch (Perca fluviatilis L.) in a shallow, fertile lake. Freshwat. Biol. 33: 497-509, 1995.
13. Beklioğlu, M., and Moss, B., Existence of a macrophyta-dominated clear water state over a very wide range of nutrient concentrations in a small shallow lake. Hydrobiologia x: 1-14, 1996.
14. Irvine, K., Balls, H., and Moss, B., The entomostraacan and rotifer communities associated with submerged plants in the Norfolk Broadland-effects of plant biomass and species composition. Int. Revue ges. Hydrobiol. 75(2): 121-141, 1990.
15. Beklioğlu, M., and Moss, B., Mesocosm experiments on the interaction of sediment influence, fish predation and aquatic plants on the structuref phytoplankon and zooplankton communities. Freshwat. Biol. 36: 315-325, 1996.
16. Frodge, J.D., Thomas, G.L., and Pauley, G.B., Effects of surface canopy formation by floating and submergent aquatic macrophytes on the water quality of two shallow Pacific North West lakes. Aquat. Bot. 38: 231-248, 1990.
17. Venugopal, M.N., and Winfield, I.J., The distribution of wuvenile fishes in a hypertrophic pond: can macrophytes potentially offer a refuge for zooplankton? J. Freshwat. Biol. 8: 389-396, 1993.
18. Smirnow, N.N., and Davis, C.C., Concerning some littoral Cladocera from Avalon Peninsula, Newfoundland. Can. J. Zool. 51: 65-67, 1973.
19. Whiteside, M.C., Chydorid (Cladocera) ecology: seasonal abundance patterns and abundance of populations in Elk Lake, Minnesota. Ecology 55: 538-550, 1974.
20. Fairchild, G.W., Movement and microdistribution of Sida crystallina and other littoral microcrustacea. Ecology 62(5): 1341-1352, 1981.
21. Gannon, J.E., and Gannon, S., Observation on the nacrotization of crustacean zooplankton. Crustaceana 28: 220-224, 1975.
22. Bottrell, H.H., Duncan, A., Gliwicz, Z.M., Grygiereg, E., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larrson, P., and Weyleleuska, T., A review of some problems in zooplankton production studies. Norw. J. Zool. 24: 419-456, 1976.
23. Scourfield, D.J., and Harding, J.P., A Key to Brisith Freshwater Cladocera, 3rd Edition, 1966, F.B.A Scientific Publication No:5.
24. Talling, J.F., and Driver, D., Some problems in the estimation of chlorophyll a in phytoplankton. In Productivity measurements in Marine and freshwater. Eds. M.S. Doty. University of Hawaii, US Atomic Energy Commission Publication, THD 7633, 1961.
25. Mackereth, F.J., Heron, H.J., and Talling, J.F., Water Analysis: some Methods for Limnologists. 1978, Freshwater Biological Association Scientific Publication No:36.
26. Townsend, C.R., and Riserbrow, A., The influence of light level on the functional response of a zooplantivorous fish. Oecologia 53: 293-295, 1982.

27. Perrow, M., and Stansifeld, J., Possible role of macrophytes as refuges from predation for zooplankton. Pages 133-157 in The development of biomanipulation techniques and control of phosphorus relase from sediment. 1994, National Rivers Authority and The Broads Authority Progress Report April 1994. NRA Report Number 475/2/A.

28. Brooks, J.L., and Dodson, S.I., Predation, body size, and composition of plankton. Science 150: 28-34, 1965.

29. Gliwicz, Z.M., Relative significance of direct and indirect effects of predation by planktivorous fish on zooplankton. Hydrobiologia 272(1/3): 201-210, 1994.

30. Serafy, J.E., and Harrell, R.M., Behavioural response of fishes to increasing pH and dissolved oxygen: filed and laboratory observation. Freshwat. Biol. 30: 53-61, 1993.