

The importance of macrophyte bed size for cladoceran composition and horizontal migration in a shallow lake

Torben L. Lauridsen, Leif Junge Pedersen, Erik Jeppesen and Martin Søndergaard

National Environmental Research Institute, Department of Lake and Estuarine Ecology, Vejlshøjvej 25, PO Box 314, DK-8600 Silkeborg, Denmark

Abstract. Cladoceran composition and diel horizontal migration were studied in 2, 10 and 25 m diameter macrophyte enclosures established in the littoral zone of shallow Lake Stigsholm, Denmark. The enclosures were protected from waterfowl grazing, but open to fish. The macrophyte community comprised *Potamogeton pectinatus*, *Potamogeton pusillus* and *Callitriche hermaphroditica*. Cladocerans were sampled randomly every third hour inside and outside the macrophyte enclosures during a 24 h period. In the 2 m enclosure, the pelagic species *Ceriodaphnia* spp. and *Bosmina* spp. dominated during the day, mean density being as high as 3430 indiv. l⁻¹. During the night, density decreased to 10–20% of the daytime density, thus indicating diel horizontal migration. In the 10 and 25 m enclosures, the daytime mean density of *Ceriodaphnia* spp. was 865 and 202 indiv. l⁻¹, respectively, and did not decrease at night. In contrast to the pelagic species, the density of macrophyte-associated species tended to be higher in the 10 and 25 m enclosure than in the 2 m enclosure. In the daytime, *Eurycerus lamellatus* density in the 2, 10 and 25 m macrophyte enclosures was 7, 28 and 16 indiv. l⁻¹, respectively, while that of *Simocephalus vetulus* was 11, 171 and 92 indiv. l⁻¹, respectively. There was no day–night difference in the density of macrophyte-associated species. We conclude that cladoceran community composition varies with macrophyte bed size, and that the edge zone between the bed and open water is an important daytime refuge for potentially migrating pelagic cladocerans.

Introduction

Submerged macrophytes can have an important stabilizing effect on the clear-water stage in eutrophic freshwater lakes (Moss, 1990; Scheffer, 1990; Jeppesen *et al.*, 1991). One of the reasons is that the macrophyte beds act as a spatial daytime refuge for cladocerans (Timms and Moss, 1984; Davies, 1985; Lauridsen and Buenk, 1996; Lauridsen and Lodge, 1996), thereby enabling the zooplankton to survive despite the presence of fish, and hence maintain a high grazing pressure on the phytoplankton.

In many eutrophic lakes, however, submerged vegetation is lacking due to the low transparency. Attempts to restore macrophytes by reducing external nutrient loading are often thwarted by resilience caused by internal nutrient loading or biological resistance (Ryding, 1981; Sas, 1989; Jeppesen *et al.*, 1991). One approach used to reduce the recovery period is fish manipulation (Gulati *et al.*, 1990; Jeppesen *et al.*, 1990), a measure that in some lakes has led to the reappearance of submerged macrophytes within 1 or 2 years (Ozimek *et al.*, 1990; Van Donk *et al.*, 1990; Hanson and Butler, 1994; Meijer *et al.*, 1994). In other cases, however, the response time has been longer (Lauridsen *et al.*, 1993), the delay being attributable to factors such as a lack of seeds or other propagules, resistance related to sediment composition (Barko and Smart, 1986) and waterfowl grazing (Lauridsen *et al.*, 1993; Søndergaard *et al.*, 1996). In such cases, it would be relevant to promote macrophyte growth actively, for instance by improving conditions for a sparse natural stand, e.g. by fencing in the potential growth areas or by transplantation.

Such measures may also have implications for the survival of cladocerans seeking refuge in the plant beds. The findings of Lauridsen and Buenk (1996) indicate that the boundary zone between macrophyte beds and the open water is particularly important as a refuge for cladocerans. This suggests that a high macrophyte bed edge: area ratio would favour migrating cladocerans, while a low edge:area ratio would favour the non-migrating littoral species that usually dominate in macrophyte-covered shallow areas (e.g. Quade, 1969; DiFonzo and Campbell, 1988; Paterson, 1993). In the present study, we have therefore evaluated how macrophyte bed size affects the composition and diel migration of a number of pelagic and littoral cladoceran species.

Study area

The study was undertaken in shallow eutrophic Lake Stigsholm situated in central Jutland, Denmark. The lake area is 21 ha and it has a maximum and mean depth of 1.2 and 0.8 m, respectively. In the period 1988–1992, average summer (May–October) total phosphorus (P) ranged from 105 to 151 $\mu\text{g P l}^{-1}$. The vegetation was dominated by submerged macrophytes until the 1950s, but has since been alternately dominated by macrophytes and phytoplankton. At the time of the study, the fish stock was dominated by roach (*Rutilus rutilus* L.) and perch (*Perca fluviatilis* L.), which comprised 79 and 18%, respectively, of the total number of fish caught in multiple mesh size survey nets (Schriver *et al.*, 1995).

Method

The study was conducted in August 1992 as part of a larger project. Triplicate circular macrophyte exclosures with diameters of 2, 10 and 25m, respectively, were established ~15 m from the shore in the littoral region of the lake bed. However, the macrophyte development in the exclosures deviated substantially among the replicates. Since the importance of macrophytes as a refuge for cladocerans is highly dependent on the per cent plant volume infested (PVI) (Schriver *et al.*, 1995; Jeppesen *et al.*, 1996), we decided to concentrate this study on three exclosures (one of each diameter) with identical and high PVI (60–70%).

Water depth in each of the three exclosures ranged from ~0.6 to 0.9 m. The exclosure fencing consisted of 60 mm mesh polyethylene netting projecting 1.6 m above the sediment surface, thereby preventing the macrophytes from being grazed by the lake waterfowl [mainly coot (*Fulica atra* L.) and mute swan (*Cygnus olor* Gmelin)] and large fish, but leaving the exclosures open to lake water and sediment. The macrophytes in the exclosures were left to grow naturally. A 10–20 m wide macrophyte-free zone was cleared around the exclosures to create a sharp demarcation between the macrophyte beds and the open water. The dominant macrophytes present were *Potamogeton pectinatus* L., *Potamogeton pusillus* L. and *Callitriche hermaphroditica* L. Macrophyte coverage, height and water depth were measured 1 week before the study at 5, 10 or 25 locations equidistant along the diameter of the three exclosures, the number depending on exclosure size. Macrophyte density was expressed as PVI (Canfield *et al.*, 1984) calculated

as the product of per cent coverage and height divided by the water depth. The macrophyte beds and the adjacent open-water reference areas were sampled every 3 h during a 24 h period using a core sampler (diameter 7.2 cm) to collect an entire water column. The method only allows sampling of animals inhabiting the water between the macrophytes together with individuals shaken off the plants during sample collection. The number of macrophyte-associated species is therefore likely to be underestimated. Samples for cladoceran enumeration were collected randomly at four locations within each macrophyte bed and at three open-water reference stations located 5–10 m from each enclosure. The composite enclosure and reference samples (6–12 l) were filtered through an 80 μm mesh net and fixed in acid Lugol's solution. Cladocerans $>140 \mu\text{m}$ were determined to genus or species level and counted using a stereomicroscope. Dense samples were subsampled, but at least 100 individuals of the dominant species were counted. A zooplankton sample was also taken in the open water of the central part of the lake on 11 August in connection with routine lake sampling.

Because of the lack of replicates, we tested horizontal migration from the macrophyte beds by comparing day data (mean density at 11 a.m., 2 p.m. and 5 p.m.) with night data (8 p.m., 11 p.m. and 1 a.m.) using Student's *t*-test. Eight p.m. was included as 'night' because zooplankton densities generally resembled night more than day at that time (Figure 1). Such a test can only give a rough estimate of the difference, as the triplicate samples cannot be assumed to be mutually independent. However, the reference samples are true replicates. Student's *t*-test was also used when testing for differences in cladoceran density between macrophyte-covered and open areas.

Results

Macrophyte composition was identical in the three enclosures, with *C. hermannophroditica* covering the bottom, and PVI being mainly accounted for by *P. pectinatus* and *P. pusillus*. PVI in the 2, 10 and 25 m macrophyte enclosures was 70, 60 and 61%, respectively.

As the diameter of the macrophyte enclosures increased, daytime cladoceran mean density decreased: from 5527 indiv. l^{-1} in the 2 m enclosure to 1864 indiv. l^{-1} in the 10 m enclosure, and 894 indiv. l^{-1} in the 25 m enclosure (Table I). This was mainly attributable to a marked decrease in the number of *Ceriodaphnia* spp. and *Bosmina* spp. with increasing macrophyte enclosure size (Table I, Figure 1). Most other cladocerans in fact increased in density, but as they were only present in small numbers, this could not compensate for the decrease in the two dominant species (Table I, Figure 1). Total cladoceran daytime mean density at the reference and mid-lake stations was 243 and 121 indiv. l^{-1} , respectively, *Ceriodaphnia* spp. and *Bosmina* spp. being completely dominant (Table I).

Ceriodaphnia spp. and *Bosmina* spp. accounted for 96% of total cladoceran numbers in the 2 m macrophyte enclosure, 62% in the 10 m enclosure and 26% in the 25 m enclosure (Table I). The corresponding figures for the reference and mid-lake stations were 89 and 94%, respectively. *Diaphanosoma brachyurum* accounted for 4% of the mid-lake population, 1% of the total cladoceran numbers

Table 1. Cladoceran daytime mean densities ($\pm 95\%$ CL) and percentage of total cladoceran numbers in macrophyte exclosures of diameter 2, 10 and 25 m ($n = 3$), at the open-water reference stations (all sampled 5–6 August; $n = 9$) and at the mid-lake station (sampled 11 August; $n = 1$)

	2 m enclosure		10 m enclosure		25 m enclosure		Reference stations		Mid-lake	
	No. l ⁻¹	%	No. l ⁻¹	%	No. l ⁻¹	%	No. l ⁻¹	%	No. l ⁻¹	%
<i>Ceriodaphnia</i> spp.	3430	62	865	46	202	23	99 \pm 38	41 \pm 16	92	76
<i>Bosmina</i> spp.	1876	34	300	16	28	3	118 \pm 45	48 \pm 18	22	18
<i>Diaphanosoma brachyurum</i>	70	1	278	15	138	15	3 \pm 1	1 \pm 0.3	5	4
<i>Sida crystallina</i>	1	0	10	0.5	10	1	0.1 \pm 0.1	0 \pm 0	0	0
<i>Eurycercus lamellatus</i>	7	0.1	28	1.5	16	2	0.1 \pm 0.1	0 \pm 0	0	0
<i>Simocephalus vetulus</i>	11	0.2	171	9	92	11	0 \pm 0	0 \pm 0	0	0
<i>Pleuroxus</i> sp.	109	2	72	4	82	9	16 \pm 13	7 \pm 5	0	0
<i>Chydorus sphaericus</i>	23	0.4	140	8	325	36	7 \pm 4	3 \pm 2	2	2
Total no. l ⁻¹	5527	100	1864	100	893	100	243	100	121	100

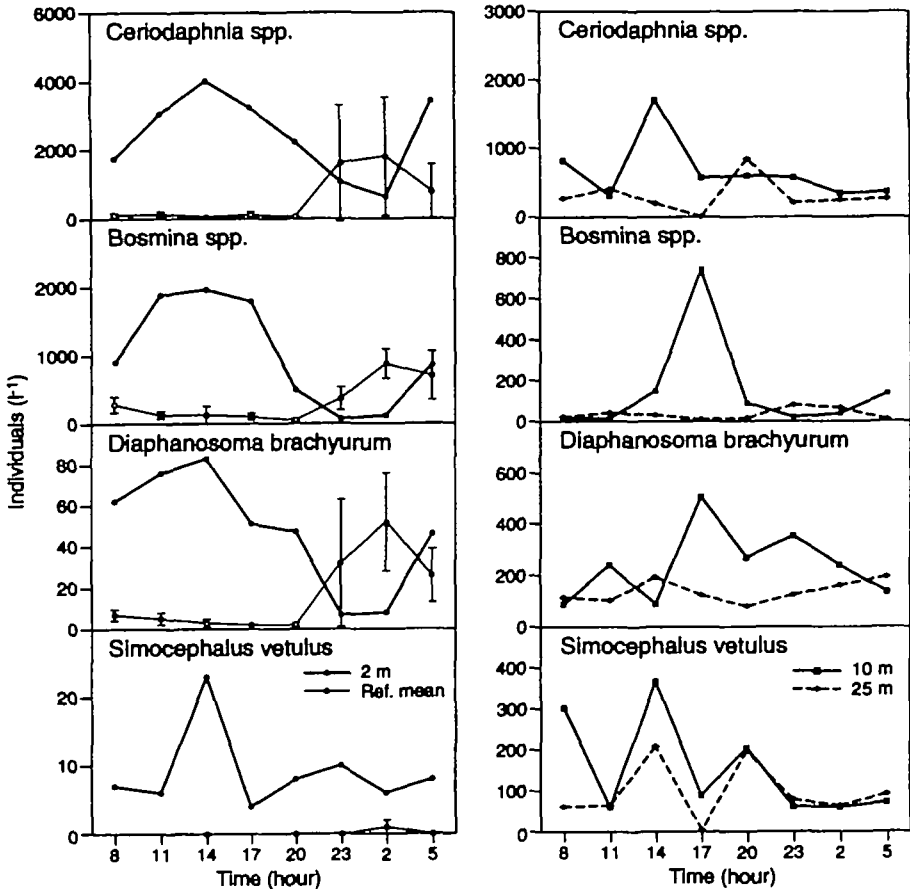


Fig. 1. Cladoceran density in macrophyte enclosures of three sizes during a 24 h period (5–6 August). **Left panel:** 2 m diameter enclosure (●), reference station mean value \pm 95% CL (○). **Right panel:** 10 m diameter enclosure (■) and 25 m diameter enclosure (◻).

in the 2 m enclosure, and 15% in the 10 and 25 m enclosures. The percentage of the macrophyte-associated species *Sida crystallina*, *Eurycercus lamellatus* and *Simocephalus vetulus* increased with size, comprising 0.3, 11 and 14% of the total cladoceran numbers in the 2, 10 and 25 m enclosures, respectively (Table I).

Daytime mean densities of *Ceriodaphnia* spp. and *Bosmina* spp. in the 2 m enclosure were significantly ($P = 0.0078$ and $P = 0.00008$ higher (340 and 1876 indiv. l^{-1} , respectively) than in the reference area (99 and 118 indiv. l^{-1} , respectively) and at the mid-lake station (92 and 22 indiv. l^{-1} , respectively) (Table I and Figure 2). At night, no difference was found, density being ~ 1000 and 300 indiv. l^{-1} , respectively (Figure 2). In the 10 m macrophyte enclosure, both *Bosmina* spp. and *Ceriodaphnia* spp. density did not differ from that at the reference stations, either during the day or during the night. However, in the 25 m macrophyte enclosure, *Bosmina* spp. density was lower during the day ($P = 0.035$) than at the

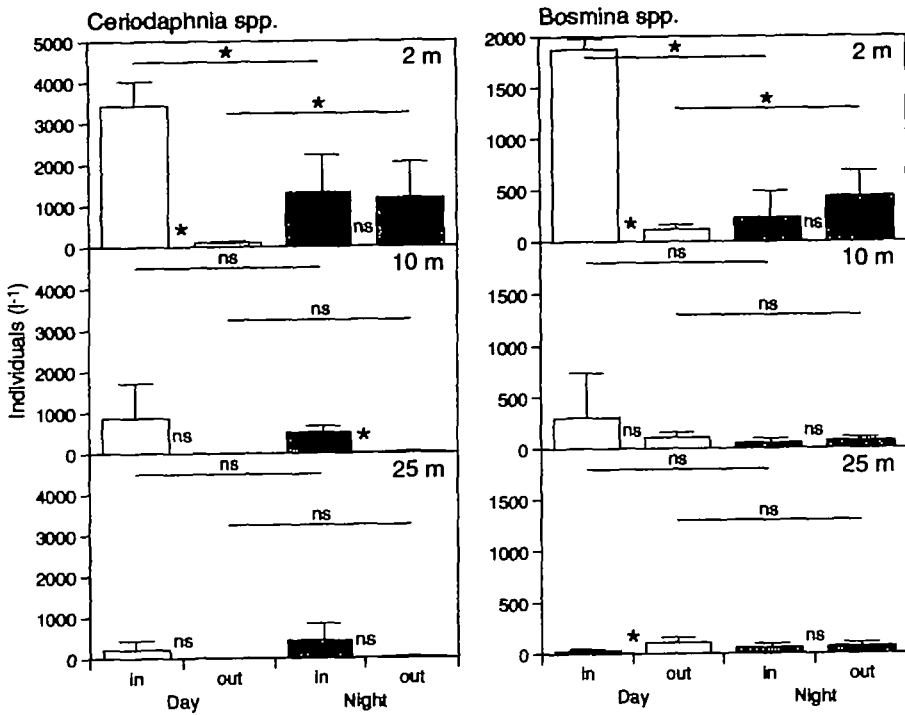


Fig. 2. Mean daytime and night-time density of *Ceriodaphnia* spp. and *Bosmina* spp. inside and outside macrophyte enclosures of diameter 2, 10 and 25 m. Statistically significant differences are indicated by an asterisk (see the text for *P* values; ns, not significant). The vertical bars indicate 95% CL ($n = 3-9$).

reference stations. Moreover, the daytime density of *Ceriodaphnia* spp. was significantly higher in the 2 m macrophyte enclosure (3430 indiv. l⁻¹) than in the 10 m ($P = 0.008$) and the 25 m ($P = 0.0002$) macrophyte enclosures (865 and 202 indiv. l⁻¹, respectively) (Table I and Figure 2). No consistent pattern was found for *D.brachyurum*. The density was significantly higher during the day than at night in the 2 m macrophyte enclosure ($P = 0.04$). During the night, a significantly higher density was found in the 10 and 25 m macrophyte enclosures than at the reference stations, while no differences were found between the 2 m macrophyte enclosure and the reference stations, except during the day ($P = 0.02$). There was a tendency towards higher densities in the 10 and 25 m enclosures than in the 2 m enclosure: 278 and 138 indiv. l⁻¹, respectively, versus 70 indiv. l⁻¹ (Table I, Figure 3). At the mid-lake station, the density was only 5 indiv. l⁻¹.

Sida crystallina daytime density was <1 indiv. l⁻¹ both inside and outside the 2 m enclosure, whereas in the 10 and 25 m enclosures it was 10 indiv. l⁻¹ and substantially greater ($P = 0.003$ and 0.04, respectively) than at the reference stations (Table I, Figure 3). During the night, no significant difference was found in the density between the macrophyte beds and the reference stations. Neither was any significant day-night difference in *D.brachyurum* and *S.crystallina* density found

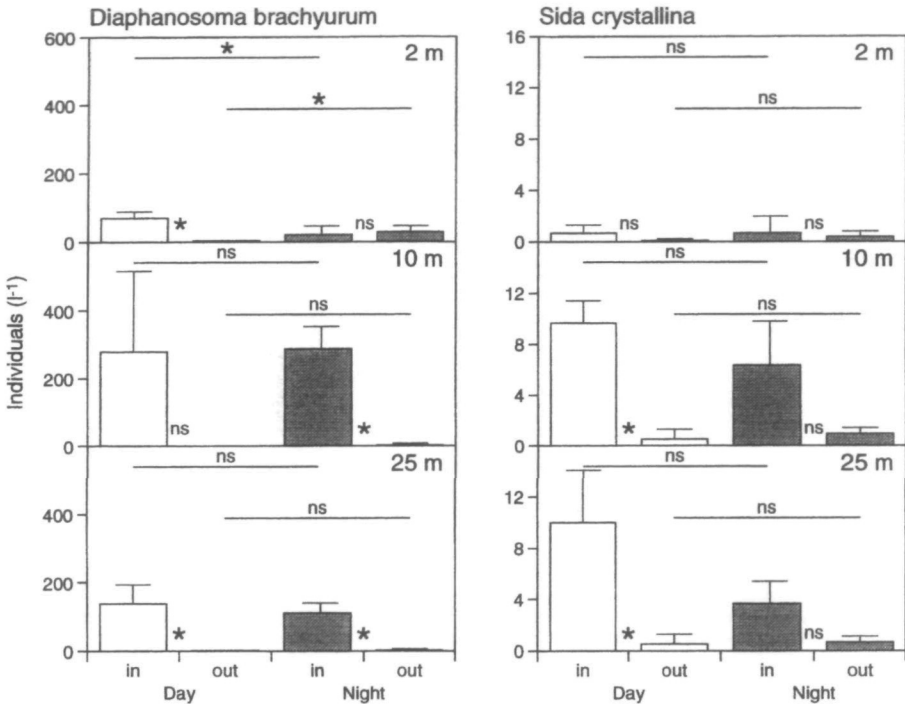


Fig. 3. Mean daytime and night-time density of *Diaphanosoma brachyurum* and *Sida crystallina* inside and outside macrophyte enclosures of diameter 2, 10 and 25 m. See Figure 2 for further information.

within the different macrophyte enclosures. However, the density of *S. crystallina* in the 10 and 25 m enclosures was significantly higher ($P = 0.002$, $P = 0.022$ and $P = 0.035$, $P = 0.028$) than in the 2 m enclosure during both the day and night (Table I and Figure 3). *Eurycercus lamellatus* was found in significantly higher densities in the 10 and 25 m enclosures than at the reference stations (Table I, Figure 4) during both the day and night, mean daytime density of *E. lamellatus* in the 2, 10 and 25 m enclosures being 7, 28 and 16 indiv. l^{-1} , respectively. *Simocephalus vetulus* showed the same, although not as pronounced, tendency as *E. lamellatus*. The mean daytime density in 2, 10 and 25 m macrophyte enclosures was 11, 171 and 92 indiv. l^{-1} , respectively. Moreover, *E. lamellatus* and *S. vetulus* density was higher in the 10 and 25 m enclosures than in the 2 m enclosure, albeit only significant for *E. lamellatus*. For the two species, no day–night change was found. The density at the reference stations was <1 indiv. l^{-1} and both species were absent at the mid-lake station.

Pleuroxus spp. and *Chydorus sphaericus* showed the same diel pattern as *E. lamellatus* and *S. vetulus*, the density of both being higher inside the macrophyte enclosures irrespective of enclosure size and time of sampling (Figure 5). Only during the night were significant variations found in the mean density between the macrophyte beds and the reference stations. Mean density in the macrophyte beds tended to be less at night than during the day, but the difference was not

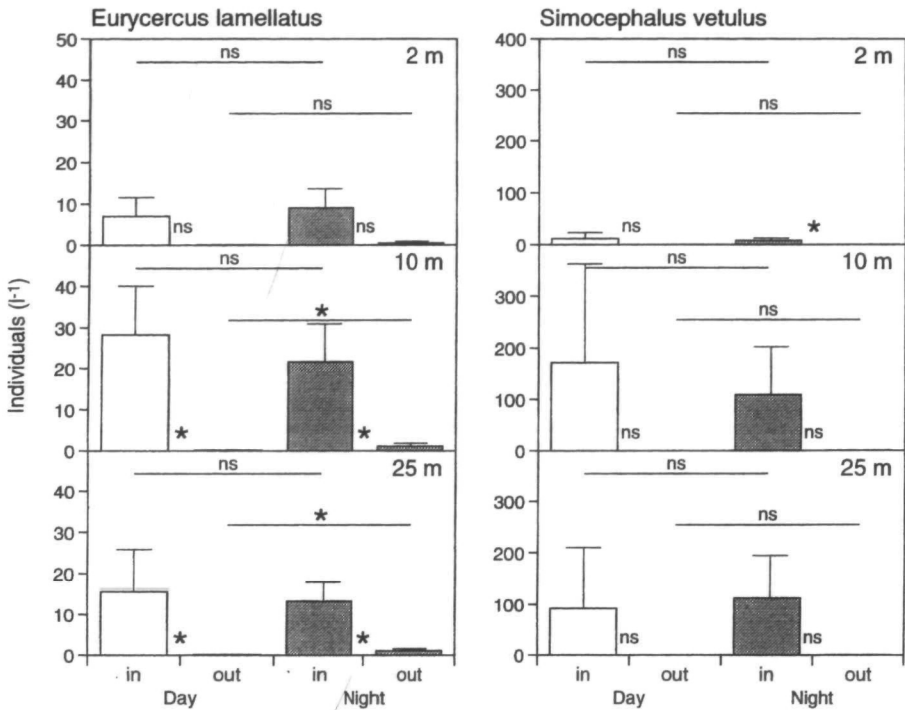


Fig. 4. Mean daytime and night-time density of *Eurycerus lamellatus* and *Simocephalus vetulus* inside and outside macrophyte exclosures of diameter 2, 10 and 25 m. See Figure 2 for further information.

significant. At the reference and mid-lake stations, no consistent day–night pattern was found and the daytime density of *Pleuroxus* spp. and *C.sphaericus* at the mid-lake station was 0 and 2 indiv. l⁻¹, respectively. *Pleuroxus* spp. and *C.sphaericus* density did not differ significantly between the various exclosure sizes.

Discussion

The present study suggests that the macrophyte bed cladoceran community changes in composition depending on bed size. Thus, pelagic and horizontally migrating species dominated in the small macrophyte bed, and littoral non-migrating species in the larger beds. Moreover, diel horizontal migration to and from open water was greatest in the case of a small macrophyte bed.

A reservation about our study, though, is the lack of replicates of the macrophyte bed size because of the accidental, large difference in development of macrophytes within triplicate exclosures. There are nevertheless two good reasons for believing that the conclusion drawn about the impact of macrophyte bed size on cladoceran community composition and diel migration is valid. Firstly, a recent study in the same lake revealed little inter-bed variation in triplicate 5 m macrophyte exclosures, e.g. SE on total abundance for the different species included in

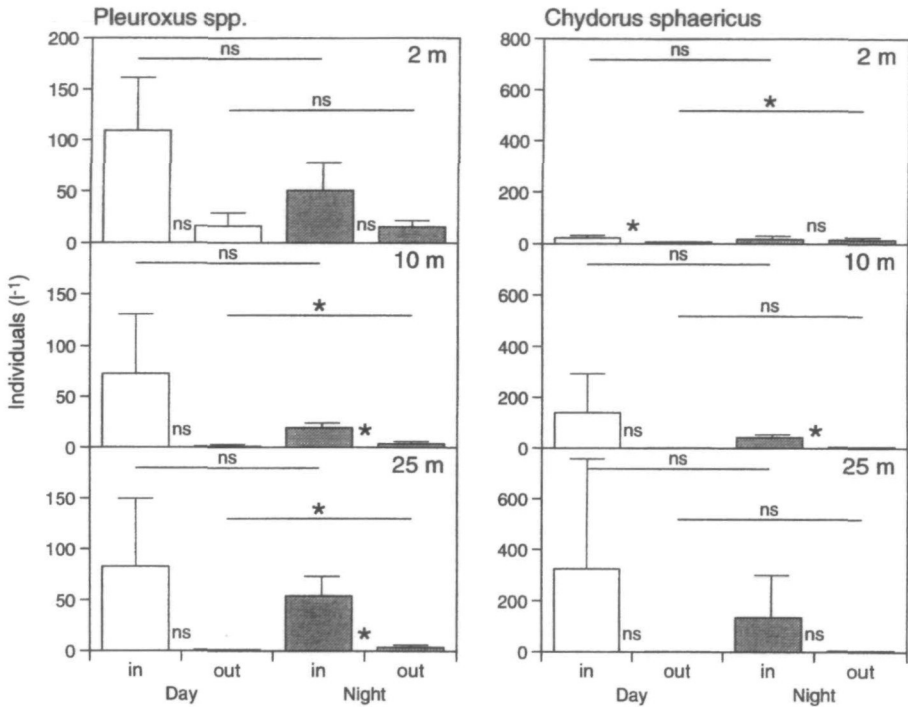


Fig. 5. Mean daytime and night-time density of *Pleuroxus* spp. and *Chydorus sphaericus* inside and outside macrophyte enclosures of diameter 2, 10 and 25 m. See Figure 2 for further information.

the present study averaged 24% (E. Jeppesen, unpublished data), which is substantially lower than the major inter-bed and diel density variations found in the present study for several of the species. Secondly, the 95% CL was low for our reference stations.

Ceriodaphnia spp. and *Bosmina* spp. were both found in very high concentrations in the small macrophyte bed during the day, at which time they totally dominated the cladoceran community. The density of these two species was much less in the larger macrophyte beds, albeit greater than at the reference and the mid-lake stations. At night, the density of both *Bosmina* and *Ceriodaphnia* in the small bed decreased to ~10–20% of the daytime level, and there was a corresponding increase at the reference stations, thus suggesting that both species undergo diel horizontal migration between the macrophyte-covered area and open water. An increase in night-time density of *Bosmina* in open littoral areas has also been reported by DiFonzo and Campbell (1988). *Ceriodaphnia* spp. and *Bosmina* spp. are often found in the pelagic (Lair, 1991; Vuille, 1991; Bast and Seitz, 1993; Paterson, 1993), especially when predation pressure by fish is high. Predation by 0⁺ fish was probably high in Lake Stigsholm, thus *Daphnia* spp. and *Eudiaptomus graciloides*, which were both present in high densities in late spring, disappeared almost completely in mid-June when 0⁺ fish appeared (L. Jensen, unpublished data), and the zooplankton community became dominated by small cladocerans,

cyclopoid copepods and rotifers (Søndergaard *et al.*, 1993). Thus, the substantial diel horizontal migration seen with the 2 m enclosure probably reflects a reaction to high fish predation pressure (Lauridsen and Lodge, 1996).

Diaphanosoma brachyurum was abundant within the two larger macrophyte enclosures. Like *Bosmina* and *Ceriodaphnia*, *D. brachyurum* was observed to migrate from the 2 m enclosure to open water at night. This coincided with the fact that *D. brachyurum* is found in the pelagic zone in many lakes (Jarvis *et al.*, 1987; Vuille, 1991) as well as in Lake Stigsholm (Table I).

Sida crystallina, *E. lamellatus* and *S. vetulus* were found to be closely associated with macrophytes, as has been reported by others (e.g. Quade, 1969; Fairchild, 1981; Lehtovaara and Sarvala, 1994; Paterson, 1994). All three species were present in low density in the small macrophyte enclosure and high density in the large enclosures, but were absent at the mid-lake station. Moreover, for *E. lamellatus* and *S. vetulus* there was no diel variation in density in either the macrophyte enclosures or at the reference stations, indicating that they do not migrate between macrophyte beds and open water. For *S. crystallina*, there was a tendency towards migration from the large macrophyte enclosures as significantly higher density was found in the enclosure than at the reference station during the day, but not during the night. However, there was not any day to night difference in density within the various macrophyte enclosures.

Our study also suggests that *Chydorus sphaericus* and *Pleuroxus* spp. in Lake Stigsholm were mainly macrophyte-associated, showing no diel horizontal migration, although the association is not as close as for *E. lamellatus* and *Simocephalus*. This corresponds well with the fact that *Pleuroxus* spp. is found in surface sediment (DiFonzo and Campbell, 1988) and that *C. sphaericus* occurs in the pelagic zone of many lakes (e.g. Boikova, 1986; Cryer and Townsend, 1988), including Lake Stigsholm (Table I).

Although we registered a major shift from dominance by pelagic species (*Bosmina* spp. and *Ceriodaphnia* spp.) in the small macrophyte enclosure to a higher contribution of macrophyte-associated species in the larger macrophyte enclosures, the density of pelagic species were nevertheless equal to or larger than that of the macrophyte-associated species even in the 25 m enclosures. This may be due to methodological underestimation of macrophyte-associated species. Thus, when comparing open-water samples taken among macrophytes, Vuille (1991) found that *S. crystallina* density was underestimated by a factor of 2–5 in relation to the density in a sample including macrophytes.

The present study thus suggests that per unit area, small-sized macrophyte beds are more important as a daytime refuge for horizontally migrating cladocerans than large-sized beds. This is in concert with the finding of Lauridsen and Buenk (1996) that *Daphnia magna* and *Daphnia hyalina/galeata* favour the edge zone between macrophytes and open water as a daytime refuge rather than the whole bed area. In a parallel study, Jeppesen *et al.* (in press) found that the daytime density in the beds and the migration intensity increased with increasing macrophyte density.

That night-time migration may markedly enhance the density of pelagic cladocerans, even when the macrophyte-covered area is small, can be illustrated by data

from the 2 m enclosure. The reduction in density for *Bosmina* and *Ceriodaphnia* from day to night amounted to 1600 and 2500 l⁻¹, respectively, which is ~35-fold higher than the concentration in mid-lake samples. This means that a 3% coverage of small, dense macrophyte beds (2 m in diameter, 60–70% PVI) may lead to a doubling of cladoceran density in open water during the night. Consequently, a large macrophyte-covered area is not a prerequisite for achieving a significant increase in zooplankton grazing capacity in open water at night.

The establishment of macrophyte refuges protected from waterfowl grazing has been proposed as a restoration measure to supplement loading reductions in shallow lakes (Moss, 1990; Jeppesen *et al.*, 1991). The implication of the present study, therefore, is that establishing numerous small refuges should result in a much higher density of migrating cladocerans than establishing a single or few large refuges. This, in turn, will ensure a greater filtration capacity within the beds during the day and in the open water during the night. Per unit area, small and dense macrophyte refuges may be better able to promote a shift to a clearwater stage than larger ones with low macrophyte density.

Acknowledgements

We thank the technical staff of the National Environmental Research Institute for help with the set-up of this study, Kathe Møgelvang and Juana Jakobsen for drawings, and David I. Barry and Anne Mette Poulsen for editorial assistance. The study was financed in part by the Danish Research Academy, the Centre for Freshwater Environmental Research and the Danish Natural Science Research Council (grant 9501315).

References

- Barko, J.W. and Smart, R.M. (1986) Sediment related mechanisms and growth limitations in submersed macrophytes. *Ecology*, **67**, 1328–1340.
- Bast, S. and Seitz, A. (1993) Differential horizontal distribution during a day-night vertical migration of some cladocerans in a hypereutrophic lake. *Arch. Hydrobiol. Beih.*, **39**, 187–198.
- Boikova, O.S. (1986) Horizontal distribution of crustaceans in Lake Globukoe. *Hydrobiologia*, **141**, 113–123.
- Canfield, D.E., Shireman, J.V., Haller, W.T., Watkins, C.E. and Maccina, M.J. (1984) Prediction of chlorophyll *a* concentrations in Florida lakes: importance of aquatic macrophytes. *Can. J. Fish. Aquat. Sci.*, **41**, 497–501.
- Cryer, M. and Townsend, C.R. (1988) Spatial distribution of zooplankton in a shallow eutrophic lake, with a discussion of its relation to fish predation. *J. Plankton Res.*, **10**, 487–501.
- Davies, J. (1985) Evidence for a diurnal horizontal migration in *Daphnia hyalina lacustris* Sars. *Hydrobiologia*, **120**, 103–105.
- DiFonzo, C.D. and Campbell, J.M. (1988) Spatial partitioning of microhabitats in littoral cladoceran communities. *J. Freshwater Ecol.*, **4**, 303–313.
- Fairchild, G.W. (1981) Movement and microdistribution of *Sida crystallina* and other littoral microcrustacea. *Ecology*, **62**, 1341–1352.
- Gulati, R.D., Lammens, E.H.R.R., Meijer, M.-L. and van Donk, E. (1990) Biomanipulation, tool for water management. *Hydrobiologia*, **200/201**, 1–628.
- Hanson, M.A. and Butler, M.G. (1994) Responses of plankton, turbidity and macrophytes to biomanipulation in a shallow prairie lake. *Can. J. Fish. Aquat. Sci.*, **51**, 1180–1188.
- Jarvis, A.C., Robert, C.H. and Combrink, S. (1987) Cladoceran feeding on size fractioned *Microcystis* colonies and *Chlorella* in a hypertrophic lake (Hartbeespoort Dam, South Africa): implications to resource utilization and cladoceran succession. *J. Plankton Res.*, **9**, 1231–1249.

- Jeppesen, E., Søndergaard, M., Mortensen, E., Kristensen, P., Riemann, B., Jensen, H.J., Muller, J.P., Sortkjaer, O., Jensen, J.P., Christoffersen, K., Bosselmann, S. and Dall, E. (1990) Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes. 1: Cross analysis of three Danish case studies. *Hydrobiologia*, **200/201**, 205–218.
- Jeppesen, E., Kristensen, P., Jensen, J.P., Søndergaard, M., Mortensen, E. and Lauridsen, T. (1991) Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: duration, regulating factors and methods for overcoming resilience. *Mem. Ist. Ital. Idrobiol.*, **48**, 127–148.
- Jeppesen, E., Jensen, J.P., Søndergaard, M., Lauridsen, T., Pedersen, L.J. and Jensen, L. (1996) Top-down control in freshwater lakes: the role of fish, submerged macrophytes and water depth. *Hydrobiologia*, in press.
- Lair, N. (1991) Grazing and assimilation rates of natural populations of planktonic cladocerans in a eutrophic lake. *Hydrobiologia*, **215**, 51–61.
- Lauridsen, T.L. and Buenk, I. (1996) Diel changes in the horizontal distribution of zooplankton in two shallow eutrophic lakes. *Arch. Hydrobiol.*, **137**, 161–176.
- Lauridsen, T.L. and Lodge, D.M. (1996) Avoidance of *Daphnia magna* by fish and macrophytes: chemical cues and predator-mediated use of macrophyte habitat. *Limnol. Oceanogr.*, **41**, 794–798.
- Lauridsen, T.L., Jeppesen, E. and Andersen, F.Ø. (1993) Colonization of submerged macrophytes in shallow manipulated Lake Væng: impact of sediment composition and waterfowl grazing. *Aquat. Bot.*, **46**, 1–15.
- Lehtovaara, A. and Sarvala, J. (1984) Seasonal dynamics of total biomass and species composition of zooplankton in the littoral of an oligotrophic lake. *Verh. Int. Ver. Limnol.*, **22**, 805–810.
- Meijer, M.-L., Jeppesen, E., Van Donk, E., Moss, B., Scheffer, M., Lammens, E., Van Nes, E., Van Berkum, J.A., de Jong, G.J., Faafang, B.A. and Jensen, J.P. (1994) Long-term responses to fish-stock reduction in small shallow lakes: interpretation of five year results of four biomanipulation cases in The Netherlands and Denmark. *Hydrobiologia*, **275/276**, 457–466.
- Moss, B. (1990) Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. *Hydrobiologia*, **200/201**, 367–377.
- Ozimek, T., Gulati, R.D. and Van Donk, E. (1990) Can macrophytes be useful in biomanipulation of lakes? The Lake Zwemlust example. *Hydrobiologia*, **200/201**, 399–407.
- Paterson, M. (1993) The distribution of microcrustacea in the littoral zone of a freshwater lake. *Hydrobiologia*, **263**, 173–183.
- Paterson, M. (1994) Invertebrate predation and the seasonal dynamics of microcrustacea in the littoral zone of a fishless lake. *Arch. Hydrobiol. Suppl.*, **99**, 1–36.
- Quade, H.W. (1969) Cladoceran faunas associated with aquatic macrophytes in some lakes in North-western Minnesota. *Ecology*, **50**, 170–179.
- Ryding, S.O. (1981) Reversibility of man-induced eutrophication. Experience of a lake recovery study in Sweden. *Hydrobiologia*, **66**, 449–503.
- Sas, H. (ed.) (1989) *Lake Restoration by Reduction of Nutrient Loading: Expectations, Experiences, Extrapolations*. Academia Verlag, St Augustin, 497pp.
- Scheffer, M. (1990) Multiplicity of stable states in freshwater systems. *Hydrobiologia*, **200/201**, 475–486.
- Schriver, P., Bøgestrand, J., Jeppesen, E. and Søndergaard, M. (1995) Impact of submerged macrophytes on fish-cladoceran-phytoplankton interactions: large-scale enclosure experiments in a shallow eutrophic lake. *Freshwater Biol.*, **33**, 255–270.
- Søndergaard, M., Bøgestrand, J., Schriver, P., Lauridsen, T., Jeppesen, E., Berg, S. and Hald, P. (1993) Betydningen af fisk, fugle og undervandsplanter for vandkvalitet: biomanipulationsforsøg i Stigsholm Sø. National Environmental Research Institute Technical Report no. **77**, 68 pp. (in Danish).
- Søndergaard, M., Bruun, L., Lauridsen, T.L., Jeppesen, E. and Madsen, T.V. (1996) The impact of grazing waterfowl on submerged macrophytes: In situ experiments in a shallow eutrophic lake. *Aquat. Bot.*, **53**, 73–84.
- Timms, R.M. and Moss, B. (1984) Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. *Limnol. Oceanogr.*, **29**, 472–486.
- Van Donk, E., Gulati, R.D. and Grimm, M.P. (1990) Restoration by biomanipulation in a small hypertrophic lake: first-year results. *Hydrobiologia*, **191**, 285–295.
- Vuille, Th. (1991) Abundance, standing crop and production of microcrustacean populations (Cladocera, Copepoda) in the littoral zone of Lake Biel, Switzerland. *Arch. Hydrobiol.*, **123**, 165–185.

Received on July 24, 1995; accepted on July 11, 1996