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SHALLOW LAKES

Community structure and diel migration of zooplankton in shallow brackish lakes: role of salinity and predators

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Abstract Diel horizontal migration (DHM), where zooplankton moves towards macrophytes during daytime to avoid planktivorous fish, has been reported as a common migration pattern of zooplankton in shallow temperate freshwater lakes. However, in shallow eutrophic brackish lakes, macrophytes seem not to have the same refuge effect, as these lakes may remain turbid even at relatively high macrophyte abundances. To investigate the extent to which macrophytes serve as a refuge for zooplankton at different salinities, we introduced artificial plants mimicking submerged macrophytes in the littoral zone of four shallow lakes, with salinities ranging from almost freshwater (0.3) to oligohaline waters (3.8). Furthermore, we examined the effects of different salinities on the community structure. Diel samples of zooplankton were taken from artificial plants, from areas where macrophytes had been removed (intermediate areas) and, in two of the lakes, also in open water. Fish and macroinvertebrates were sampled amongst the artificial plants and in intermediate areas to investigate their influence on zooplankton migration. Our results indicated that diel vertical migration (DVM) was the most frequent migration pattern of zooplankton groups, suggesting that submerged macrophytes were a poor refuge against predation at all salinities under study. Presumably, this pattern was the result of the relatively high densities of small planktivorous fish and macroinvertebrate predators within the submerged plants. In addition, we found major differences in the composition of zooplankton, fish and macroinvertebrate communities at the different salinities and species richness and diversity of zooplankton decreased with increasing salinity. At low salinities both planktonic/free-swimming and benthic/plant-associated cladocerans occurred, whilst only benthic ones occurred at the highest salinity.

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The low zooplankton biomass and overall smaller-bodied zooplankton specimens may result in a lower grazing capacity on phytoplankton, and enhance the turbid state in nutrient rich shallow brackish lakes.

Keywords Shallow brackish lakes · Zooplankton · Migration patterns · Community structure · Salinity

Introduction

Most studies on restoration and trophic cascades (i.e. downward transmission of top–down effects from fish to phytoplankton, sensu Carpenter & Lodge, 1986) in shallow lakes have focused on freshwater lakes, especially in the temperate regions (e.g. McQueen et al., 1986; Jeppesen et al., 1998), but lately also in the tropics and subtropics (Bachmann et al., 2002; Meerhoff et al., 2007a, b; Iglesias et al., 2007, 2008). The study of zooplankton structure and behaviour is of key importance to elucidate trophic interactions in lakes, with applications for lake restoration (Moss et al., 1996). However, the role of zooplankton in brackish shallow waters is poorly elucidated (Moss & Leah, 1982; Brucet et al., 2005; Brucet et al., 2009), even though these lakes constitute a large proportion of the world's shallow waters (Hammer, 1986).

Salinity per se affects the composition of animal communities (Schallenberg et al., 2003) and thereby alters the trophic interactions in a lake (Jeppesen et al., 2007; Barker et al., 2008; Brucet et al., 2009). Except for truly marine fauna, species richness and the diversity of zooplankton generally decrease with increasing salinity (Boix et al., 2008; Brucet et al., 2009) and are generally lowest at salinities between 5 and 7 (Remane & Schlieper, 1971; Cognetti & Maltagliati, 2000). Most large-bodied cladocerans are restricted to salinities below 3.5 (Lagerspetz, 1958; Frey, 1993), whilst at higher salinities, the zooplankton communities are often dominated by small-bodied, less efficient phytoplankton controllers such as small cladocerans (e.g. *Bosmina* and *Ceriodaphnia*), rotifers and calanoid copepods (Moss & Leah, 1982; Jeppesen et al., 1994; 2007; Brucet et al., 2008, 2009). In temperate brackish lakes, a 2 salinity threshold has been reported for a shift in lake trophic structure and dynamics. At these salinities the efficient phytoplankton controller *Daphnia* disappears (Jeppesen et al., 1994), with the exception of *D. magna* which tolerates salinities up to 8 and 11 in temperate and Mediterranean thalassic lakes, respectively (Brucet et al., 2009; and references therein).

Moreover, brackish lakes react differently to freshwater shallow lakes to changes in nutrient loadings (Moss & Leah, 1982; Hansson et al., 1990). Whilst freshwater lakes can have at least two alternative states: turbid or clear (Irvine et al., 1989; Scheffer et al., 1993). The clear-water state in freshwater temperate lakes is characterised by high submerged macrophyte cover, a high piscivorous:planktivorous fish biomass ratio and a high zooplankton:phytoplankton biomass ratio (Timms & Moss, 1984), and generally high diversity of invertebrates and plants (Declerck et al., 2005). The turbid state is characterised by absence or low coverage of submerged macrophytes and low piscivorous:planktivorous fish and zooplankton:phytoplankton biomass ratios (Scheffer et al., 1993; Jeppesen et al., 2000). In contrast, eutrophic shallow brackish lakes may remain turbid even at a high macrophyte cover (Moss, 1994; Jeppesen et al., 1994). This is normally ascribed to strong top–down control with higher fish and macroinvertebrate predation pressure on zooplankton, especially within the submerged macrophytes, which renders the refuge effect of the macrophytes for the zooplankton small and negligible (Jeppesen et al., 1994). However, experimental evidence is lacking. The abundant planktivorous sticklebacks (i.e. *Gasterosteus aculeatus* and *Pungitius pungitius*) and the predacious shrimp, *Neomysis integer*, can co-exist in European brackish waters because the small sticklebacks prey selectively on smaller stages of mysids, rather than on ovigerous females (Jeppesen et al., 1994; Søndergaard et al., 2000), resulting in a persistently high predation pressure on zooplankton. Presumably, eutrophic shallow brackish lakes resemble some eutrophic subtropical and Mediterranean freshwater lakes in that they are often turbid and the zooplankton is composed mainly of smaller individuals than in temperate freshwater lakes, as a consequence of a high predation pressure (Gyllström et al., 2005; Romo et al., 2005; Meerhoff et al., 2007a; Castro et al., 2007).

Diel horizontal migration (DHM), where pelagic zooplankton seek refuge against fish amongst macrophytes in the littoral zone during daytime, is often seen in shallow freshwater lakes as a predator defence mechanism (Timms & Moss, 1984; reviewed by Burks et al., 2002, 2006). Diel vertical migration (DVM), where the zooplankton migrates to the hypolimnion during the day to avoid visual predators, is a common anti-predator mechanism in deep lakes. However, several studies have shown that the use and type of migration are complex and depend, amongst other aspects, on the fish community structure. Studies by De Stasio (1993), Jeppesen et al. (2002), Castro et al. (2007) and Meerhoff et al. (2007a) showed that cladocerans and copepods also undergo DVM in some shallow freshwater lakes. In shallow brackish lakes, zooplankton migration patterns have not yet been assessed.

Using artificial submerged macrophytes, we investigated the potential effects of salinity on the community structure and migration patterns of littoral zooplankton in four shallow eutrophic lakes, with salinities corresponding to ca. freshwater (0.3) to oligohaline waters (3.8). We hypothesised that zooplankton diversity would decrease with increasing salinity and that submerged macrophytes would not provide an adequate refuge to zooplankton against fish predation. We also expected the zooplankton to alter migration behaviour along the salinity gradient, from DHM to mainly DVM or no migration, due to stronger predation pressure (especially by sticklebacks amongst the submerged plants) at higher salinities.

Materials and methods

Study site

We selected four relatively large shallow lakes with different salinities (0.3–3.8), but with similar total phosphorous (TP) and total nitrogen (TN) concentrations (Table 1). According to their nutrient concentrations, all the lakes can be classified as eutrophic. The lakes are situated in the natural reserve area of Vejlerne, Northern Jutland, Denmark (57°N). Originally, the reserve area consisted of shallow branches of the Limfjord Fiord. In the mid-1870s, farmland was created via land reclamation involving damning and drainage of the area. The resulting brackish lakes are regulated by a central sluice system; and only slight changes in salinity along the year occur in these lakes.

In each lake we introduced eight artificial plant beds (four for night-time samples and four for daytime samples), mimicking submerged plants. The plant beds consisted of 1-m diameter PVC plastic rings with an attached net from which the artificial plants hung (green plastic Christmas' trees garlands, Meerhoff et al., 2007a, b). The beds were attached to two poles placed on both sides to keep the set-up in place. Before introduction, the artificial plants had been disinfected with 1% chlorine solution, rinsed carefully with tap water and wind-dried to avoid the introduction of exotic fauna and to homogenise initial conditions. In each plant bed we used ninety-five 0.75-m long plants with an architecture resembling that of *Ceratophyllum* or *Myriophyllum* spp. (3.5-cm long leaves), leading to a local plant volume inhabited of 44% (PVI, *sensu* Canfield et al., 1984) in each plant bed. In all the lakes, we placed the plant beds at 0.8-m depth in sheltered and plant-free areas in the littoral zone.

The sampling campaign was conducted once in each lake in July 2006, about 3 weeks after introduction of the plant beds, thus allowing colonisation by periphyton and plant-attached invertebrates.

Sampling and processing

We took water samples for the analysis of salinity, TP and TN (DS-Dansk Standardiseringsråd 1975, 1985) and measured the Secchi disk depth in open water near the experimental set up. We compared zooplankton samples from three different habitats (four replicates each): 'submerged plants' ('S': sites where natural plants, if present, were removed prior to introduction of the artificial plant beds), 'intermediate' ('I': sites where the plants present were removed, and no artificial plants were introduced) and 'open water' sites ('O': sites initially without plants). In two of the lakes, Selbjerg Vejle (salinity = 0.5) and Glombak (salinity = 1.2), there were no true open water areas near the experimental set-up. Due to the fact that sampling in a far zone of the lake would likely result in quite different conditions, we decided not to include open water as another habitat in these two lakes. We collected zooplankton during day- and night-time, taking four open water samples at random, whilst 'intermediate' samples were kept constant. Littoral

Table 1 Main limnological characteristics of the four study lakes, and abundance of potentially piscivorous fish (perch and pike-perch, CPUE: abundance per net per night, in multi-mesh sized gillnets)

	Lund Fjord	Selbjerg Vejle	Glombak	Østerild Fjord
Salinity[a]	0.3	0.5	1.2	3.8
Area (ha)	554	446	94	430
Mean depth (m)	0.81	0.5	0.4	0.5
Secchi depth (m)[a]	0.33	0.21	0.47	0.40
TP (mg l^{-1})[a]	0.095	0.159	0.087	0.076
TN (mg l^{-1})[a]	1.81	3.64	2.21	2.2
Chl *a* (μg l^{-1})[b]	20.57	21.59	48.22	88.00
Macrophyte coverage (%)[b]	22	40	25	31
Perca fluviatilis (CPUE)[b]	5.5	13.7	8.6	23.8
Stizostedion lucioperca (CPUE)[b]	1.8	–	–	–

[a] Measured during our sampling campaign

[b] Historical data from NERI, Aarhus University (1999–2003)

zooplankton samples were collected during the day in half of the artificial plant beds, and during the night in the other half. The samples were taken from a small boat to minimise sediment resuspension, using a 1-m long core sampler (diameter 6 cm), quickly collecting a total of 8 l of water from the surface to just above the sediments. The samples were filtered through a 50-μm mesh and preserved with Lugol's solution (4%).

Immediately after collecting the zooplankton samples, we sampled plant-associated macroinvertebrates by carefully removing three plants from each plant bed and preserving them in 70% ethanol. Afterwards, we placed a cylindrical net (1.1 m diameter, mesh size 200–600 μm) on the sediment beneath each plant bed and at each intermediate site. The nets were attached with strings to two poles. After approximately 12 h, we sampled the fish and free-living macroinvertebrates at 'submerged plants' and 'intermediate' sites by quickly pulling the strings and lifting the net up above the water surface. The animals were sieved through a 500-μm mesh sieve and preserved in 70% ethanol. There were no samples of fish and predacious macroinvertebrates from the open water habitat in any of the four lakes.

In the laboratory, we counted crustacean zooplankton (at least 100 individuals of the most abundant taxa per subsample) and identified individuals to genus or, when possible, to species level. Harpaticoid copepods were just identified to order level. When copepod nauplii were not identifiable, species proportions of the adults were assigned. We classified the following cladoceran genera as free-swimming/planktonic: *Bosmina*, *Ceriodaphnia*, *Daphnia* and *Polyphemus*, and *Acroperus*, *Alona*, *Alonella*, *Chydorus*, *Leydigia*, *Macrothrix* and *Sida* as benthic/plant associated. The adult individuals of the cyclopoid copepods were categorised into predatory or non-predatory specimens according to Monakov (2003). We counted fish and macroinvertebrates and identified them to species and to family/genus level, respectively, according to Dall & Lindegaard (1995) and Muus & Dahlstrøm (1990). Fish were categorised as planktivorous or piscivorous, whilst macroinvertebrates were categorised as potentially predatory or non-predatory according to Merrit & Cummins (1996). Due to the lack of piscivorous fish in the samples from this study, we show results of earlier sampling campaigns (1999–2003 data from NERI, Table 1), although we advise caution since these abundances could have changed.

We calculated the Shannon–Wiener index (Shannon & Weaver, 1949 in Pielou 1969) of crustacean zooplankton. The specific richness at each salinity level was calculated as the sum of taxa in intermediate areas and amongst the artificial submerged macrophytes (i.e. not including open water, to avoid bias in the estimations). Since harpaticoid copepods were only identified to order level, they were not included in species richness and diversity calculations.

Dry weight estimations of zooplankton biomasses were obtained from the allometric relationship between the weight and the length of the body following Dumont et al. (1975), Smock (1980) and

Meier (1989). We measured up to 50 individuals of each species, whenever possible.

Statistical analysis

The effects of salinity (as differences in lakes), habitat and time of day on the density of zooplankton, fish and predacious macroinvertebrates were analysed using three-way ANOVA. The factors were: ‘lake’ (with four salinities 0.3, 0.5, 1.2 and 3.8); ‘habitat’ (two levels: I and S) and ‘time’ (two levels: day and night). Zooplankton spatial distribution patterns were analysed using two-way ANOVA for each lake. The factors were: ‘habitat’ (three levels [I, S and O] at 0.3 and 3.8 and two levels [I and S] at 0.5 and 1.2) and ‘time’ (two levels: day and night). We classified the patterns as DVM when zooplankton night-time densities increased in all habitats (a significant effect of ‘time’ in the ANOVA, Meerhoff et al., 2007a), as this suggests that zooplankton stayed in or just above the sediment in the daytime, thus avoiding the sampling device, and migrated upwards in the water column at night. We classified the patterns as DHM when the density amongst the submerged plants decreased during the night with an associated increase in open water (and a significant ‘habitat’ × ‘time’ interaction in the ANOVA). Diel patterns opposed to those described above were classified as ‘reverse’ (RVM, RHM, respectively).

Before the analysis, we tested the data for normal distribution by using the Kolmogorov–Smirnov test and for homoscedasticity by using Cochran’s *C*-test. If necessary, we transformed the data to fulfil the requirements of homogeneity of variance, most frequently by applying the square root. In case of significant differences, we applied Tukey HSD post hoc tests. All statistical tests were conducted using the software Statgraphics Plus ver. 4.1.

Results

Changes in community structure with salinity

We found differences in the structure of the zooplankton communities, both in terms of taxon richness and composition, along the salinity gradient. The specific richness and Shannon–Wiener Index of zooplankton decreased with increasing salinity (Fig. 1). At low salinities both planktonic/free-swimming (hereafter *planktonic*) (e.g. *Daphnia galeata* and *Bosmina coregoni*) and benthic/plant-associated (hereafter *benthic*) (e.g. *Alona rectangula*) cladocerans occurred, whilst only benthic ones occurred at the highest salinity (Fig. 2). Large-sized cladocerans, such as *Daphnia* sp. and the plant-associated *Sida crystalina*, were only present at the lowest salinity.

In the four lakes, the fish communities were characterised by a few species (Table 2) and small-sized individuals (<10 cm standard length), therefore being potentially zooplankton predators (Mittelbach & Persson, 1998). Roach and perch appeared at low salinities (Lund Fjord, Selbjerg and Glombak lakes), whilst sticklebacks appeared at the highest salinity (Lake Østerild). Contrary to our expectation, planktivorous fish abundance was not related to salinity, and significantly higher abundances of planktivorous fish were found at 0.5 (Selbjerg Vejle, Fig. 3, ANOVA, $P < 0.01$, post hoc Tukey’s test, $P < 0.05$). Cladoceran abundance and total zooplankton biomass were negatively related to the densities of planktivorous fish, with the lowest abundance and biomass found in Selbjerg Vejle, together with the highest fish density (Figs. 3, 4, ANOVA, $P < 0.01$, post hoc Tukey’s test, $P < 0.01$) and the lowest Secchi depth (Fig. 4). Free-living macroinvertebrate predators had a tendency to increase with salinity, whilst plant-associated

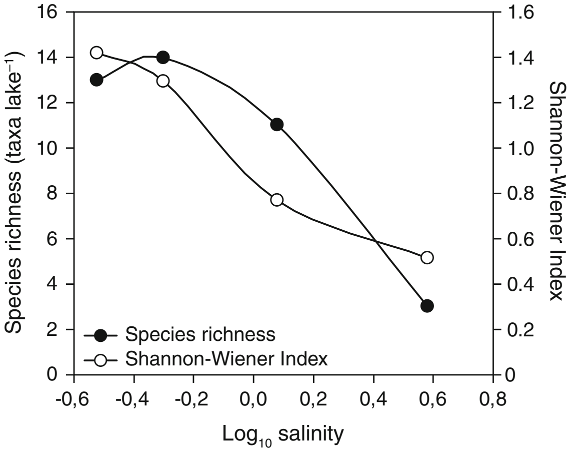
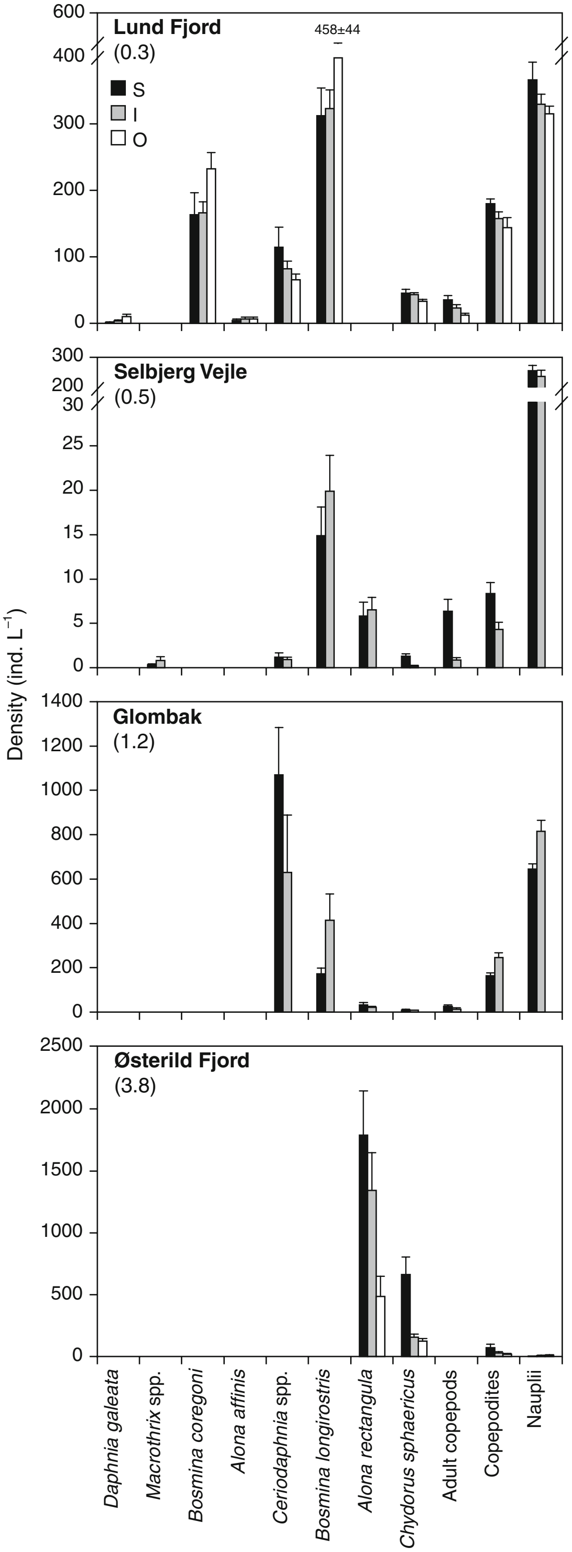


Fig. 1 Specific richness and Shannon–Wiener index of total number of crustacean taxa (cladocerans and cyclopoid and calanoid copepods) in each lake in relation to salinity (each value was calculated as the sum of taxa in intermediate areas and amongst submerged macrophytes)



◀**Fig. 2** Density and distribution of cladocerans and copepods (cyclopoid, calanoid and harpacticoid) at the four salinities (increasing from *top* to *bottom*) amongst submerged macrophytes (S), intermediate areas (I) and open water (O). The cladoceran taxa are ordered by decreasing body size to the right. The data represent the mean densities (day and night average ± SE). Note the different scales in each lake

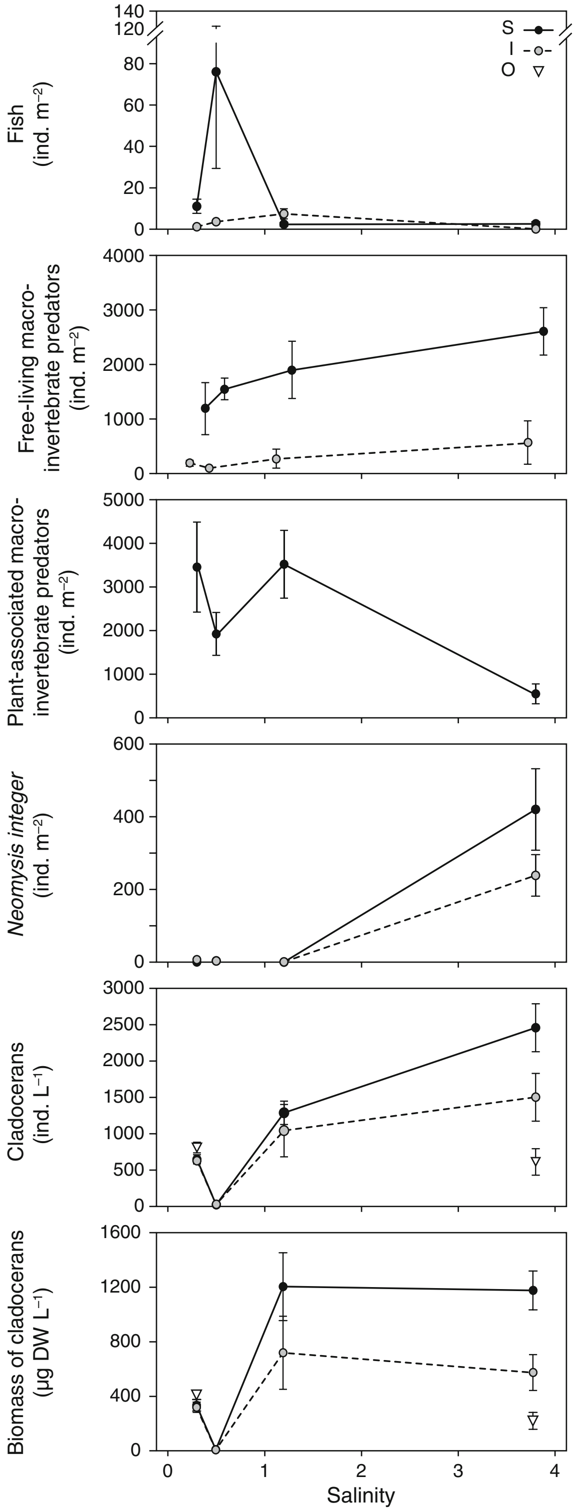
macroinvertebrate predators showed no relationship with salinity or with fish density (Fig. 3; Table 3).

Diel and spatial distribution of organisms along the salinity gradient

The densities of benthic cladocerans and adult predacious cyclopoid copepods were significantly higher amongst the submerged macrophytes than in the other habitats (Table 4). Fish and free-living macroinvertebrate predators also had a tendency to be more numerous amongst the submerged plants, but the significant interaction terms denote that the densities also depended on the lake and, for fish, also on time of the day (Table 4).

At 0.3 (Lund Fjord), *Bosmina longirostris*, *B. coregoni* and nauplii numerically dominated the zooplankton (Fig. 2). The planktonic cladocerans had higher densities in the open water (significant effect of 'habitat'), whereas the benthic cladocerans did not show any differences in density between habitats and time of the day (Table 5; Fig. 5). Whilst adult predacious cyclopoid copepods showed a DVM pattern, with significantly higher night-time densities, copepodites and nauplii exhibited a tendency of reverse vertical migration (RVM) (Fig. 5). In 1999, the piscivorous community was dominated by perch and pikeperch (*Stizostedion lucioperca*) (Table 1), but in low densities: 5.5 and 1.8 CPUE, respectively (catch per unit effort, estimated as individuals per night per net). In our study, we found only two planktivorous fish species (roach, *Rutilus rutilus*, and perch, *Perca fluviatilis*), with dominance of roach (Table 2). Free-living macroinvertebrate predators and planktivorous fish occurred in higher densities amongst the macrophytes, but in the case of fish, the differences disappeared at night-time (significant interaction between 'habitat' and 'time') (Table 5; Fig. 5).

At 0.5 (Selbjerg Vejle), the zooplankton was numerically dominated by nauplii, followed by



◄ **Fig. 3** Changes in mean density (average of day-night densities, ± SE) of fish, potential predacious macroinvertebrates, also showing *Neomysis affinis* separately, and total cladocerans (abundance and biomass) amongst submerged plants (S), intermediate areas (I) and open water (O) with different salinities. There were no samples of fish, predacious macroinvertebrates and *N. affinis* from the open water habitat in any of the four lakes. Note the different scales

B. longirostris but in much lower abundances (Fig. 2). The planktonic cladocerans, as an average, and *B. longirostris* alone, showed diel patterns fitting with reverse vertical migration (RVM), that is, with significantly higher densities during daytime (Fig. 5; Table 6). By contrast, *Ceriodaphnia* apparently underwent DVM (Table 6). The copepodites showed significantly higher densities within the submerged plants, with no changes between sampling times (Table 5; Fig. 5). The free-living macroinvertebrate predators and adult predacious cyclopoid copepods again exhibited a significant association with the submerged plant habitat, the former showing significant DHM and the latter significant DVM (Fig. 5). Whilst the densities of zooplankton were much lower (on average, 35 times lower) than at the other salinities, the density of planktivorous fish was extremely high compared to the other lakes, an average of 16 times higher within the submerged plants (Fig. 5). Similar to Lund Fjord, the planktivorous fish community was dominated (in numbers) by small roach (Table 2), which were more abundant within the plants during the day (Fig. 5). In 2000, the piscivorous fish community was dominated by high densities of perch, 13.7 CPUE (Table 1).

At 1.2 (Glombak), *Ceriodaphnia* spp. and nauplii numerically dominated the zooplankton community (Fig. 2). Benthic cladocerans showed DVM, whilst planktonic cladocerans also had a tendency to DVM (Fig. 5); however, the interaction term in the ANOVA test indicated that this pattern depended on the habitat (Table 5). Contrary to the results at the other salinities, the densities of nauplii and copepodites were significantly higher in the intermediate areas, and no migration pattern could be discerned. Similar to the results at lower salinities, the density of free-living macroinvertebrate predators was highest amongst the submerged macrophytes. The planktivorous fish density did not show any differences between habitats or time of the day. The density of piscivorous fish in year 2000 was 8.6 CPUE, but with exclusive dominance of perch (Table 1).

At 3.8 (Østerild Fjord), the zooplankton was, contrary to the other lakes, dominated by benthic cladocerans (in this case *Chydorus sphaericus* and *Alona rectangula*) (Fig. 2). The planktivorous fish community was dominated by small sticklebacks (Table 2) and the free-living macroinvertebrate predator *Neomysis integer* was highly abundant in comparison to other salinities (Table 3). The density of benthic cladocerans was much higher (from 50 to 300 times higher) whilst that of total nauplii was much lower (from 13 to 45 times lower) than in the other lakes (Fig. 5). As a group, the benthic cladocerans seemed to display significant DVM, but when assessing the two benthic cladoceran species separately, *A. rectangula* showed a spatial pattern fitting with significant DVM, whilst *C. sphaericus* seemingly underwent DHM (Table 6). The copepodites showed a movement pattern fitting with DVM (Fig. 5), but the interaction term in the ANOVA indicated that this night-time increase in density depended on the habitat (the *F*-value being much lower than for the 'time' effect, Table 5). Similar to other salinities, free-living macroinvertebrate predators were more abundant amongst the submerged macrophytes, whilst this was the only lake where the density of plant-associated macroinvertebrate predators increased at night-time (Fig. 5). Earlier studies (in 2003) had shown a high density of piscivorous fish with 23.8 CPUE, also with exclusive perch dominance (Table 1). At this salinity, we found the lowest densities of fish (Fig. 3) and they did not show any differences between habitats and time of the day (Table 5; Fig. 5).

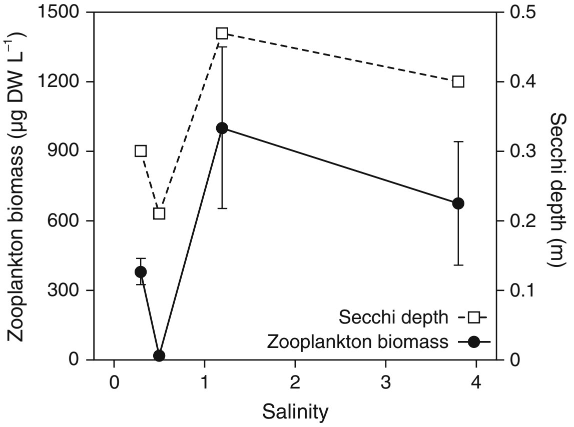


Fig. 4 Changes in mean density of total zooplankton biomass and water transparency as Secchi depth with salinity

Although the type of migration differed amongst the taxa of zooplankton and also varied amongst the lakes, the most frequent migration pattern of main zooplankton groups was DVM (increasing densities at night-time in all habitats) (Table 6; Fig. 5). However, because of the lack of open water samples at 0.5 and 1.2 (due to the high abundance of natural submerged macrophytes), the interpretations for these two lakes are more uncertain.

Discussion

We found major differences in the composition and taxon richness of all studied communities, i.e.

Table 2 Density (individuals m^{-2}) of fish species captured in the four studied lakes (salinities shown in brackets). Average size (standard length in cm) of each fish species is given. Standard error in brackets

Fish species	Lund Fjord (0.3)		Selbjerg (0.5)		Glombak (1.2)		Østerild (3.8)	
	Density	Size	Density	Size	Density	Size	Density	Size
Roach (*Rutilus rutilus*)	4.9 (1.2)	5.5 (0.1)	34.7 (22.9)	2.2 (0.0)	2.3 (0.8)	2.8 (0.2)		
Perch (*Perca fluviatilis*)	0.9 (0.3)	4 (0.2)	2.0 (0.5)	3.0 (0.1)	2.0 (0.9)	3.9 (0.1)		
Smelt (*Osmerus eperlanus*)			0.6 (0.2)	2.9 (0.1)	0.1 (0.1)	3.4 (0.2)		
Three-spined stickleback (*Gasterosteus aculeatus*)			0.1 (0.1)	2.6 (0)	0.1 (0.1)	2.2 (0)	0.9 (0.4)	2.3 (0.2)
Nine-spined stickleback (*Pungitius pungitius*)			0.2 (0.1)	2.1 (0.2)			0.3 (0.1)	1.9 (0.4)
Goby (*Gobius* sp.)							0.1 (0.1)	1.4 (0.1)

Table 3 Density (individuals m^{-2}) of total macroinvertebrate predators and specifically *N. integer* captured in the four studied lakes (salinities in brackets)

	Lund Fjord (0.3)		Selbjerg (0.5)		Glombak (1.2)		Østerild (3.8)	
	Density	*N. integer*	Density	*N. integer*	Density	*N. integer*	Density	*N. integer*
Plant associated	3457 (309)		1924 (147)		3521 (232)		549 (68)	
Free-living	692 (153)	3.7 (1.1)	821 (191)	3.4 (0.6)	1086 (231)	0.5 (0.2)	1585 (282)	329 (65)

Standard error in brackets

Table 4 Results of 3-way ANOVA on the effects of lake (with four salinities: 0.3, 0.5, 1.2 and 3.8), habitat and time on the density of main communities (both potential predators and zooplankton groups)

	d.f.	*F*-values		d.f.	*F*-values	d.f.	*F*-values				
		Fish	Free-living macroinv. predators		Plant-associated macroinv. predators		Adult pred. cyclopoid copepods	Planktonic cladocerans	Benthic cladocerans	Copepodites	Nauplii
Lake (L)	3	14.67***	26.10***	3	67.19***	3	26.04***	703.05***	456.20***	185.77***	659.17***
Habitat (H)	1	17.07**	495.69***		–	2	4.63*	1.18	4.48*	0.81	2.51
Time (T)	1	0.18	0.82	1	0.77	1	12.22**	8.31**	22.47***	13.99**	0.45
L * H	3	8.39**	7.34***		–	4	0.06	6.28**	2.53	13.46***	5.40**
L * T	3	5.70**	0.58	3	7.34**	3	0.19	37.92***	5.02**	5.78**	5.36**
H * T	1	9.00**	1.02		–	2	0.01	1.47	0.39	0.45	2.39
L * H * T	3	7.37**	0.62		–	4	0.77	4.27*	2.10	2.08	0.18
Error	48			24		60					

Note: For Selbjerg Vejle and Glombak, two levels (submerged and intermediate) of habitat occurred due to lack of open water samples; and two levels of habitat (submerged and intermediate) occurred in all lakes in the case of fish and free-living macroinvertebrate predators. Degrees of freedom (d.f.), significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$

zooplankton, fish and macroinvertebrates, amongst the lakes and salinities studied. In accordance with previous findings in other temperate (e.g. Jeppesen et al., 1994), tropical (Attayde & Bozelli, 1998) and Mediterranean (e.g. Brucet et al., 2009) brackish lakes, the species richness and diversity of crustacean zooplankton decreased with increasing salinity (Fig. 1). The zooplankton community changed from being composed of medium-to-large-sized and/or planktonic species, some of them typical for freshwaters (e.g. *Daphnia galeata*, *Macrothrix* spp.) at the lowest salinity, to being composed of smaller and less efficient grazers (Tessier et al., 2001 and references therein, Brucet et al., 2008) at the highest salinity (e.g. *Alona rectangula* and *Chydorus sphaericus*), more typical of brackish waters (Jeppesen et al., 1994; Jeppesen et al., 2007; Brucet et al., 2009). These results agree with the overall low salinity tolerance reported for some cladoceran species (Aladin & Potts, 1995 and references therein). The composition of the fish and macroinvertebrate communities also changed with salinity, with dominance of the salt-tolerant stickleback fish (Wootton, 1976) and the invertebrate *N. integer* at the highest salinity, and a substantial decrease of other fish species. Previous works had already reported an increase in the abundance of the invertebrate predator *Neomysis* at salinities above 0.5 (Jeppesen et al., 1994; Aaser et al., 1995). This seems more pronounced when the fish community changes from dominance of large-bodied roach and perch to small-bodied sticklebacks, which lowers the predation on the mysids (Søndergaard et al., 2000).

Contrary to the hypothesised increase in fish predation along the (although narrow) salinity gradient, neither fish nor zooplankton densities were

Table 5 Results of 2-way ANOVA tests conducted in each lake (salinity in brackets) separately, testing the effects of habitat (thee levels) and time (two levels) on the densities of main communities

Lake	d.f.	*F*-value		d.f.	*F*-value	d.f.	*F*-value				
		Fish	Free-living macroinv. predators		Plant-associated macroinv. predators		Adult pred. cyclopoid copepods	Planktonic cladocerans	Benthic cladocerans	Copepodites	Nauplii
Lund Fjord (0.3)											
Habitat	1	67.77***	80.6***		–	2	8.26**	3.60*	2.28	3.20	6.07**
Time	1	39.14***	0.34	1	0.41	1	34.48***	2.55	0.06	11.35**	35.33***
Habitat * time	1	67.77***	1.03		–	2	0.94	1.59	1.43	4.54*	5.00*
Error	12			6		18					
Selbjerg (0.5)											
Habitat	1	221.39**	1647.62**		–	1	57.16***	2.15	0	8.49*	0.48
Time	1	5.00*	3.49	1	3.93	1	70.82***	18.36**	1.86	2.42	0.08
Habitat * time	1	8.04*	11.57**		–	1	3.23	1.62	1.83	1.83	0.05
Error	12			6		12					
Glombak (1.2)											
Habitat	1	2.37	90.2***		–	1	0.71	6.52*	1.72	14.33**	10.17**
Time	1	4.60	0.32	1	0.11	1	2.44	33.77**	9.30*	4.00	1.85
Habitat * time	1	0.03	0.02		–	1	0.08	5.44*	0.95	0.67	0.42
Error	12			6		12					
Østerild (3.8)											
Habitat	1	2.86	57.7**		–	2	No animals found	No animals found	48.92***	10.55**	1.09
Time	1	0.60	0.94	1	23.32**	1			79.76***	76.68***	13.43**
Habitat * time	1	2.54	0.18		–	2			0.84	4.07*	0.72
Error	12			6		18					

There were no samples of fish and predacious macroinvertebrates from the open water habitat in any of the four lakes and no open water samples in Selbjerg Vejle and Glombak. Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$

related to salinity. Instead, our results suggest that fish predation was the key factor determining zooplankton abundance and biomass, since the lowest values were found in the lakes where fish abundances were highest, and vice versa. Besides, several studies have shown that the pelagic invertebrate *Neomysis* may intensively predate on both cladocerans (e.g. Chigbu, 2004) and copepods (e.g. Aaser et al., 1995). Thus, in our study the high densities of free-living macroinvertebrate predators found at the highest salinity could explain the abundance of benthic cladocerans and the low abundances of copepods compared to the other lakes. Regardless of the predation pressure potentially exerted by micro herbivores, such as ciliates, the consequent lower grazing capacity of mesozooplankton would presumably be responsible for the lower water transparency, since we found a positive relationship between Secchi disk depth and zooplankton biomass (Fig. 3) and abundance. Our results are in accordance with previous empirical (Jeppesen et al., 1994) and experimental (Jakobsen et al., 2004; Jeppesen et al., 2007) studies in brackish lakes showing cascading effects of fish on the phytoplankton community, abundance and size structure as a result of the reduced zooplankton grazing.

Fig. 5 Diel changes in density of main communities amongst submerged macrophytes in (S) intermediate areas (I) and open water (O). There were no samples of fish and predacious macroinvertebrates from the open water habitat in any of the four lakes and no open water samples at 0.5 and 1.2 salinities. Migration patterns with significant results in the two-way ANOVA are indicated. Migration patterns in brackets are interpreted, although were not significant in the statistical tests. Note the different scales ▶

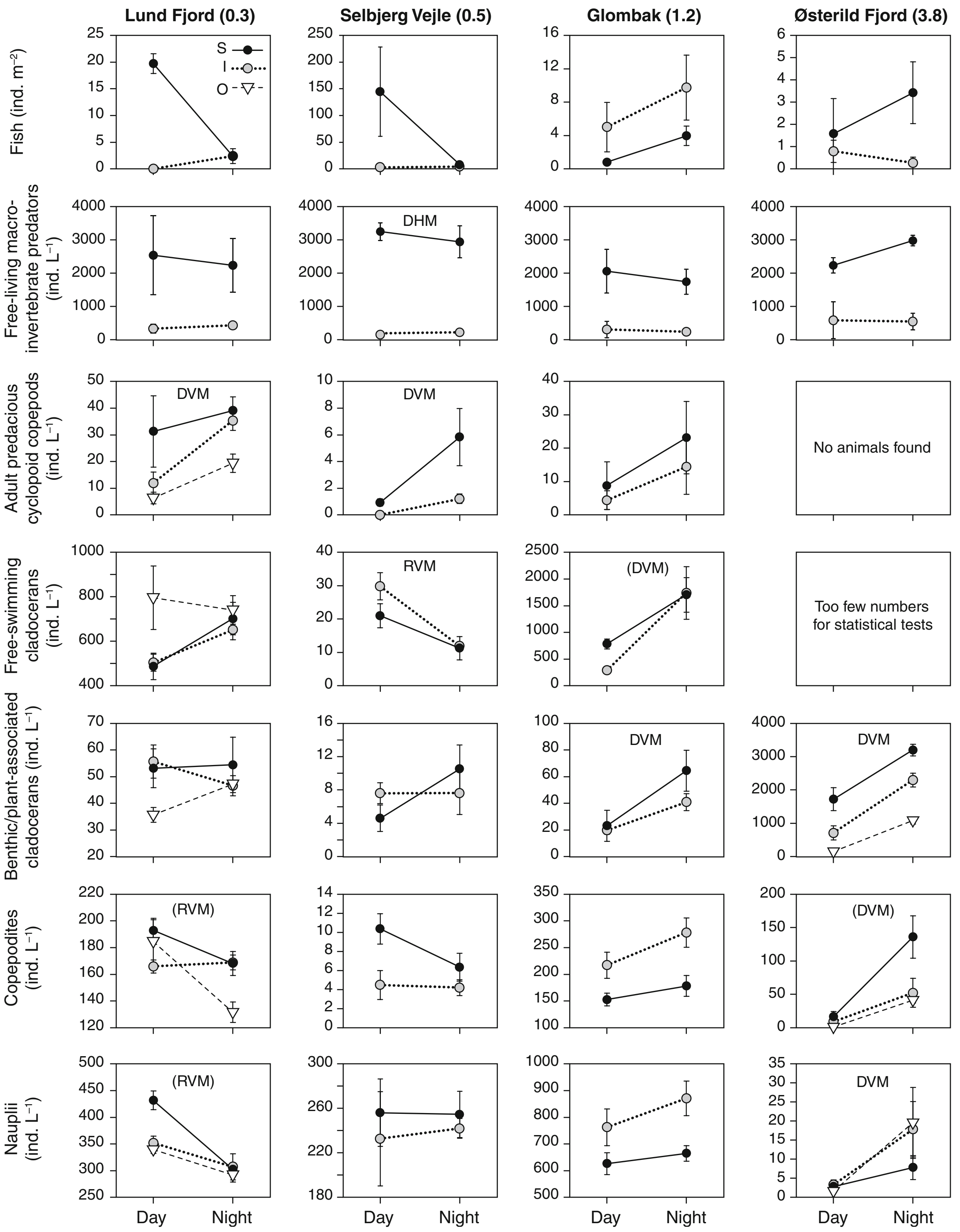

Lund Fjord (0.3)
Selbjerg Vejle (0.5)
Glombak (1.2)
Østerild Fjord (3.8)
S
I
O
Fish (ind. m^{-2})
Free-living macro-invertebrate predators (ind. L^{-1})
DHM
Adult predacious cyclopoid copepods (ind. L^{-1})
DVM
DVM
No animals found
Free-swimming cladocerans (ind. L^{-1})
RVM
(DVM)
Too few numbers for statistical tests
Benthic/plant-associated cladocerans (ind. L^{-1})
DVM
DVM
Copepodites (ind. L^{-1})
(RVM)
(DVM)
Nauplii (ind. L^{-1})
(RVM)
DVM
Day
Night
Day
Night
Day
Night
Day
Night

Table 6 Interpreted patterns of migration for the most abundant cladoceran taxa in the four lakes

	Lund Fjord (0.3)	Selbjerg Vejle (0.5)	Glombak (1.2)	Østerild Fjord (3.8)
Daphnia hyalina/galeata	**DVM**	–	–	–
Bosmina coregoni	**RHM**	–	–	–
Alona affinis	**DVM** (O)	–	Too few numbers	–
Ceriodaphnia sp.	**RVM** (S)	**DVM** (S)	**DVM** (I)	–
Bosmina longirostris	**DVM** (S)	**RVM** (I)	**DVM** (I)	–
Alona rectangula	–	DVM	**DVM** (S)	**DVM** (O, I, S)
Chydorus sphaericus	RVM	DVM	**DVM** (I)	**DHM**

Bold letters indicate significant results in the 2-way ANOVA conducted for each lake separately

The habitats with significantly higher densities identified in the *post hoc* tests are indicated in brackets: O (open water), I (intermediate areas), S (submerged plants)

DVM diel vertical migration, *DHM* diel horizontal migration, *RVM* reverse vertical migration, *RHM* reverse horizontal migration; The genera are ordered from top to bottom by decreasing body size

Note that the patterns in Selbjerg Vejle and Glombak are interpreted from the densities in only two habitat types (due to lack of open water sites, see "Methods")

Our results agree with previous studies showing high water turbidity to be linked with dominance of small-sized zooplankton in eutrophic brackish lakes (Jeppesen et al., 1994; Brucet et al., 2009) and subtropical freshwater lakes (Meerhoff et al., 2007a). In warm shallow, subtropical and Mediterranean lakes, enhanced fish predation pressure, induced directly and indirectly by the higher temperature (higher activity levels, smaller body sizes and higher density of fish, Teixeira de Mello et al., 2009), has been suggested as key factor for the contrasting zooplankton community structure relative to cold-water (temperate) lakes (Romo et al., 2005; Gyllström et al., 2005; Hansson et al., 2007; Meerhoff et al., 2007b).

Contrary to common findings from temperate freshwater lakes (e.g. Burks et al., 2002), evidence of DHM of zooplankton was only recorded for one species (*Chydorus sphaericus*), and only at the highest salinity. DVM was the most pronounced migration pattern of zooplankton groups, resembling the findings by Meerhoff et al. (2007a) for subtropical freshwater lakes and by Castro et al. (2007) in a Mediterranean freshwater lake. The dominance of DVM or no migration rather than DHM indicate that the submerged macrophytes acted as a poor refuge against predation at the macrophyte coverage studied (44%, in each plant bed). This reflects the relatively high daytime planktivorous fish densities amongst the submerged plants, perhaps induced by the presence of the piscivorous perch in open water as reported in previous studies in these lakes (Jeppesen et al., 2002) and in experimental studies (e.g. Snickars et al., 2004). Also, the density of free-living macroinvertebrate predators was higher within the plants than in the cleared-up, intermediate, habitats, further reducing the value of using plants as a daytime refuge for zooplankton. The presence of predacious copepods further complicates the migration patterns in that the organisms function as both prey and predators. The RVM patterns of the small-bodied nauplii and copepodites found in our study, could indicate a mechanism to avoid the predation by adult cyclopoids performing DVM, as has been also observed by Castro et al. (2007).

Obviously, our study has several shortcomings. One is the lack of lake replication at each salinity level, hindering a true test of salinity effects. Another is the lack of replication in time, as we only covered one 24-h period at each site. However, earlier studies in temperate freshwater lakes did not show changes in migration patterns during a 3-day study (Jeppesen et al., unpublished results), but seasonal variations have been very seldom tested (Iglesias et al., 2007). Further studies are therefore needed to fully clarify and generalise migration patterns of zooplankton in brackish lakes.

In conclusion, our results indicate that submerged macrophytes with low–medium coverage constitute a poor refuge for zooplankton against fish and macroinvertebrate predation in shallow eutrophic brackish lakes, giving experimental support for empirically based studies of some shallow brackish lakes (Jeppesen et al., 1994, 2007). Although we did not observe the hypothesised higher frequency of DVM with increasing salinity, our results suggest that low zooplankton biomass and smaller-bodied zooplankton specimens may occur as a consequence of fish predation. This, together with the change in zooplankton composition towards small-bodied and less efficient grazers with increasing salinity (Jeppesen et al., 2007; Brucet et al., 2009) would likely result in a lower grazing capacity on phytoplankton and enhance the phytoplankton-driven turbidity of brackish lakes. The zooplankton community structure in brackish lakes resembles that found in shallow subtropical freshwater lakes, where high densities of small planktivorous fish aggregate within the macrophytes and thereby reduce their refuge capacity for zooplankton and their potential for promoting water transparency (Meerhoff et al., 2007b). As for shallow warm-water freshwater lakes, the chances of clear water in eutrophic temperate brackish lakes would increase when lowering nutrient concentrations to below the limits established for temperate shallow freshwaters (Romo et al., 2004; Beklioglu et al., 2007).

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