

The role of macroinvertebrates and fish in regulating the provision by macrophytes of refugia for zooplankton in a warm temperate shallow lake

MARÍA DE LOS ÁNGELES GONZÁLEZ SAGRARIO^{*‡} AND ESTEBAN BALSEIRO^{†‡}

^{*}Universidad Nacional de Mar del Plata, FCEyN, Dpto. Biología; Mar del Plata, Argentina

[†]INIBIOMA, CONICET-Universidad Nacional del Comahue, Quintral, San Carlos de Bariloche, Argentina

[‡]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)

SUMMARY

1. The zooplankton often undergoes diel horizontal migration (DHM) from the open water to the littoral of shallow lakes, thus avoiding predators in the former. This behaviour has functional impacts within the lake, as it enhances zooplankton survival, increases their control of phytoplankton and tends to stabilise the clear water state. However, most of the evidence supporting this migration pattern comes from cold north temperate lakes, and more evidence from tropical and subtropical areas, as well as from southern temperate areas, is needed.

2. We conducted a field study of the diel horizontal and vertical migration of zooplankton, and the horizontal distribution of potential predatory macroinvertebrates and fish, over two consecutive days in the summer in a temperate lake in the southern hemisphere. We took zooplankton samples at two depths, at three sampling stations (inside beds of aquatic macrophytes, at their edge and in open water) along three transects running from the centre of a bed of *Ceratophyllum demersum* to open water. At each sampling station, we also took samples of macroinvertebrates and fish and measured physical and chemical environmental variables.

3. Zooplankton (pelagic cladocerans, calanoid copepods and rotifers) avoided the shore, probably because of the greater risk from predators there. Larger and more vulnerable cladocerans, such as *Diaphanosoma brachyurum* and *Moina micrura*, were two to four times more abundant in open water than at the edge of or inside beds of macrophytes, respectively, by both day and night. Less vulnerable zooplankton [i.e. of medium body size (*Ceriodaphnia dubia*) or with the ability to swim fast (calanoid copepods)] were distributed evenly between open water and the edge of the plant beds. Small zooplankton, *Bosmina huaronensis* and pelagic rotifers, showed an even distribution among the three sampling stations. Accordingly, no DHM of zooplankton occurred, although larger organisms migrated vertically inside *C. demersum* stands.

4. Macrophytes contained high densities of predatory macroinvertebrates and fish. The predator assemblage, composed of large-bodied macroinvertebrates (including odonates and shrimps) and small littoral fish, was permanently associated with submerged macrophytes. None of these groups moved outside the plant beds or changed their population structure (fish) over the diel cycle.

5. Submerged macrophyte beds do not represent a refuge for zooplankton in lakes where predators are numerous among the plants, implying a weaker top-down control of

Correspondence: María González Sagrario, Universidad Nacional de Mar del Plata, FCEyN. Dpto. Biología; J. B. Justo 2550, (7600) Mar del Plata, Buenos Aires, Argentina. E-mail: gonsagra@mdp.edu.ar or mgonzalezsagrario@conicet.gov.ar

phytoplankton biomass by zooplankton and, consequently, a more turbid lake. The effectiveness of macrophytes as a refuge for zooplankton depends on the associated assemblage of predatory macroinvertebrates and fish among the plants.

Keywords: migration, predation risk, shallow lakes, submerged macrophytes, zooplankton

Introduction

Animal behaviour and life histories reflect many trade-offs between contrasting selection pressures. Both predation and food limitation are density-dependent factors that are responsible for the selection of individual traits. Animals living offshore, such as zooplankton, must find the right trade-off to minimise the risk of falling prey to a predator and to maximise resource intake (Gliwicz, 2003). In deep lakes, diel vertical migration is certainly one of the most apparent examples of a trade-off between minimising predation risk and maximising the rate of growth and reproduction (Gliwicz, 2003; Bezerra-Neto & Pinto-Coelho, 2007). In shallow temperate lakes, migration to habitats where predation risk is low, such as the littoral, may enhance prey survival (Lauridsen & Buenk, 1996; Cazzanelli, Warming & Christoffersen, 2008). In such environments, submerged macrophytes are often used as a daytime refuge by zooplankton when there is a high risk of predation in the open water (Lauridsen *et al.*, 1997; Burks *et al.*, 2002). Thus, diel horizontal migration (DHM) from open water to the littoral zone promotes the survival of large-bodied zooplankton and, consequently, they can exert strong grazing pressure on the phytoplankton. Therefore, DHM can enhance the control of phytoplankton in shallow lakes and, consequently, the dominance of a clear water state (Schou *et al.*, 2009).

Submerged macrophytes can have a dual role, providing refuge not only to zooplankton but also to their potential predators, young-of-the-year fish (YOY-fish) and littoral macroinvertebrates (Burks *et al.*, 2006). Predation is a key process governing many patterns in ecosystems (Sih & Wooster, 1998) that not only has an impact on prey density but can also induce habitat shifts and modify behaviour (Romare & Hansson, 2003). For example, large-bodied zooplankton, such as daphniids, seek refuge in the littoral when YOY-fish are absent there or when the open water is free of piscivores and planktivores, therefore, abundant; however, the appearance of YOY-fish in the

littoral zone induces daphniids to avoid the shore (Gliwicz & Rykowska, 1992; White, 1998; Romare & Hansson, 2003). Moreover, the gradient of predation risk for zooplankton from the littoral to the open water can change seasonally, probably with the recruitment of YOY-fish, leading to seasonal changes in habitat selection by prey (White, 1998).

The occurrence of DHM has been well documented for cold temperate lakes from the Northern Hemisphere (for a review see Burks *et al.*, 2002). However, there is little information from tropical and subtropical lakes, where it has been suggested that vegetation is a poor refuge for large-bodied zooplankton (Jeppesen *et al.*, 2005). Accordingly, Meerhoff *et al.* (2007a) showed that DHM in subtropical lakes is not a feasible antipredator strategy and related the lack of refuge among submerged macrophytes to the permanently abundant and diverse assemblage of small littoral fish in stands of plants. In contrast, in temperate Danish lakes, DHM is an effective antipredator behaviour, probably related to habitat partitioning, with zooplankton in submerged macrophytes and fish in free-floating plants (Meerhoff *et al.*, 2007b). In subtropical lakes, diel vertical migration to avoid predators is more likely but does not suffice to counteract the high predation pressure by littoral fish (Meerhoff *et al.*, 2007a). Moreover, mean fish density, biomass per unit total phosphorus (TP), and fish species richness were several times higher in subtropical than in cool temperate lakes, implying a higher predation risk in submerged macrophytes for zooplankton in subtropical than in Danish lakes (Teixeira-de Mello *et al.*, 2009). The ineffectiveness of macrophytes as a refuge was also observed in a warm Mediterranean lake, probably related to the assemblage of small omnivorous fish (Castro, Marques & Gonçalves, 2007).

Most studies stress that abundant small fish may reduce the effectiveness of macrophytes as a refuge. However, predatory macroinvertebrates such as odonates (Burks, Jeppesen & Lodge, 2001; Van de Meutter, Stoks & De Meester, 2004), flatworms (Trochine, Balseiro & Modenutti, 2008) or notonectids

(Hampton, Gilbert & Burns, 2000) have been recognised as voracious and effective predators of zooplankton and can also induce horizontal migration to littoral or open areas (Van de Meutter, Stoks & De Meester, 2005). Most studies have shown the effect of direct predator–prey interactions; however, zooplankton in the littoral zone must face a diverse assemblage of predatory macroinvertebrates. González Sagrario *et al.* (2009) showed that a wide range littoral predators, with diverse prey capture behaviours, could reduce the large-bodied fraction of the zooplankton in a warm temperate lake by up to a 80% in a 5 day enclosure experiment. Their study suggests that, in warm lakes, the macroinvertebrate assemblage could be important in preventing DHM. The presence of several predators often has emergent effects on prey (Sih & Wooster, 1998) and, if macrophytes host diverse assemblages of invertebrate predators and small fish, then their effectiveness as refuge areas would be reduced. Nevertheless, data from tropical and warm temperate areas are needed to confirm when macrophytes could be used as daytime refuges and to determine what factors might cause their failure as a refuge.

In this study, we focussed on the diel horizontal and vertical migration of zooplankton in a warm temperate lake, and on the habitat selection and diel movements of their potential predators including both macroinvertebrates and fish. We hypothesised that the refuge properties of macrophytes for zooplankton will depend on the diel behaviour and habitat use by macroinvertebrates and fish. Our objectives in this study were as follows: (i) to determine simultaneously the spatial distribution of predatory macroinvertebrates and fish and to relate our findings to the zooplankton distribution, (ii) to assess the effectiveness of macrophytes as refuge areas for zooplankton and (iii) to determine whether diel horizontal and vertical migration occur in a warm temperate lake.

Methods

Study site

Los Padres Lake, in Buenos Aires Province (Pampa Plain, at 55° and 38°02'S and 57°34' and 57°33'W), Argentina, is a medium-small shallow eutrophic lake (area, 2 km²; mean depth, 1.8 m) with a polymictic thermal regime and alkaline water (pH, 8.6). The

transparency is variable, with turbid and clear periods alternating from year to year (Secchi depth ranged from 0.4 to 0.9 m during 1998/2002). The shift observed could be related to changes in rainfall, and also to artificial regulation of the water level (González Sagrario, pers. observation). Chlorophyll *a* (Chl *a*) and TP concentrations showed that both parameters varied between years, ranging from 20–90 µg L⁻¹ for Chl *a* and from 100–400 µg L⁻¹ for TP during 1999–2001 (González Sagrario, unpubl. data).

In the littoral zone of Los Padres Lake, *Schoenoplectus californicus* (Meyer) Steud. forms an outer ring around the whole lake, while within that ring different species of submerged macrophytes dominate, such as *Potamogeton pectinatus* L. and *Ceratophyllum demersum* L. Plant cover has varied between years, covering almost the whole lake bed (1998), distributed in patches (1999–2003) or absent (2004).

In open water, the zooplankton community is composed mainly of medium- to small-bodied cladocerans, such as *Bosmina* (*Neobosmina*) *huaronensis* Delachaux, *Ceriodaphnia dubia* Richard, *Moina micrura* Kurz and *Diaphanosoma brachyurum* (Lievin). The large cladoceran *Daphnia* (*Ctenodaphnia*) *spinulata* Birabén also occurs sporadically. Two species of calanoid copepods are present, (*Notodiaptomus incompositus* (Brian) and *Boeckella bergi* Richard), with *Notodiaptomus* being dominant. *Acanthocyclops robustus* (Sars) is the most numerous of the cyclopoid copepods.

Experimental design and sampling

On 10 and 11 February 2002, we carried out a study on the diel horizontal (DHM) and vertical (DVM) migrations in Los Padres Lake. In that year, discrete patches of the submerged macrophyte *C. demersum* were restricted to the littoral of the lake, occupying a zone 2–5 m wide between the outer ring of the bullrush (*S. californicus*) and the open water (free of macrophytes). We chose three patches of similar size (mean area, 25 m²; length, 6 m; height, 1.10–1.3 m; width, 3–5 m) located along the lake shore, and about 7 m from one another (depth in the littoral: 1.10–1.30 m). Macrophytes occupied almost the whole water column, with a PVI (per cent of volume occupied by plants) (Canfield *et al.*, 1984) of 80%. In that area of the lake, we recorded a mean Secchi depth of 0.4 m. Wind velocity varied during the study, oscillating between 5.3 and 8.5 m s⁻¹ on the first day and <5 m s⁻¹ on the second day.

In each of the three macrophyte stands, we placed a transect from the centre to the open water, including three sampling sites: (i) inside the stand (I) (located 1 m from the edge), (ii) edge (E) and (iii) open water (OW) (6 m from the edge of the stand). We determined physicochemical parameters of the water column (oxygen concentration, pH, conductivity, salinity, turbidity and water temperature) using a HORIBA water analyser (HORIBA Ltd., Kyoto, Japan) at three depths (surface, at 0.50 and 1 m) at the three locations (I, E and OW) over three transects during the first day. At each location, we followed the same sampling protocol; we first sampled zooplankton and littoral microinvertebrates (cladocerans and rotifers), and subsequently macroinvertebrates and small littoral fish during the day (12 : 00–16 : 30) and night (21 : 00–01 : 00; sunset occurred at 20 : 00) on both days.

Samples of zooplankton and littoral cladocerans and rotifers were obtained at two adjacent depth layers that together covered the whole water column: surface water (from 0 to 0.5 m) and deeper water (from 0.5 to 1 m, almost reaching the lake bottom). This sampling design aimed to detect a vertical gradient of cladocerans and rotifers from the surface to the lake bottom. At each sampling location (I, E, OW) and depth, we took three samples (1 L van Dorn bottle) about 0.5 to 1 m apart from each other and combined them into a composite sample (final volume: 3 L). This procedure aimed to avoid over- or underestimation of zooplankton abundances because of aggregation (Lauridsen & Buenk, 1996). We sieved zooplankton and littoral microinvertebrate samples through a 65- μm mesh and fixed the animals in 4% formalin solution. We quantified the zooplankton and littoral cladocerans and rotifers in a 5-mL Bogorov chamber under a stereoscopic microscope; when necessary, subsamples were taken and at least 100 individuals of the dominant species were counted. We identified cladocerans and rotifers to species and counted calanoid copepods (distinguishing females, males and copepodites) and cyclopoid (distinguishing adults and copepodites).

We collected predatory macroinvertebrates and small littoral fish simultaneously using a dip net (with a mouth 35 cm long and 32 cm wide and a net mesh of 150 μm). At each sampling point (OW, E, I), we pulled the dip net through the entire water column 15 times, covering a surface of 1 m². We devoted the same time (2 min) to each surface sample. We fixed

animals with 70% ethanol solution and, in the laboratory, we separated predatory macroinvertebrates through sieves into two fractions: > 1000 μm and 1000–150 μm (the latter included Acari plus the second instar zygopteran larvae). We counted all the predatory macroinvertebrates and subsampled the 1000–150 μm fraction, taking 10 ml of aliquots from a previously homogenised final volume of 35–40 mL. We considered a macroinvertebrate to be a predatory species based on previous descriptions (e.g. Burks *et al.*, 2001; Van de Meutter *et al.*, 2004; Trochine *et al.*, 2008; González Sagrario *et al.*, 2009).

We used a dip net to study the distribution of small fish among locations. This method did not capture large fish, so to do so we employed a gill net (outer mesh size, 5 cm; inner mesh size, 3 cm) (Cailliet, Love & Ebeling, 1996) that was placed in the open water perpendicular to the macrophyte stand on the first sampling day (10 February 2002). Although the gill net was left in the water for 9 h (13 : 00 to 22 : 00), it did not fill up. We narcotised the fish caught using carbonated water and then fixed them with 4% formalin solution. We identified all fish to species, both pelagic and littoral, except for YOY specimens.

Statistical analysis

To test for differences in physicochemical parameters, we performed a two-way ANOVA with depths and horizontal gradient (I, E and OW) as factors. We analysed differences in the densities of pelagic and littoral rotifers, cladocerans and copepods among vegetated areas and open water, performing a four-way analysis of variance (ANOVA). The factors were as follows: (1) lake zones (I, E and OW), (2) depth (0–0.5 m and 0.50–1 m depths), (3) time of day (day and night) and (4) sampling date. We pooled all species of the rotifer genus *Lecane* [*Lecane* sp. 1, *Lecane* sp. 2, *L. bulla* (Gosse) and *L. closterocerca* (Schmarda)] into a single *Lecane* group for the analysis, as their abundances were very low. For each littoral small-bodied fish and predatory macroinvertebrate species, we compared the distribution, performing a three-way ANOVA including sampling points (I, E and OW), time of day and sampling dates as factors. We carried out the analysis for all fish species captured with the dip net and for each macroinvertebrate, with the exception of Zygoptera (*Cyanallagma* spp.) and Acari. *Cyanallagma* abundance corresponds to the sum of

Cyanallagma interruptum (Selys) and *C. bonariense* (Ris) and Acari abundance to the sum of *Koelikea curvipes* Rosso de Ferradás, *Arrenurus oxyurus* Rosso de Ferradás, *Eylais multiespina* Ribaga, *Hydrachna* sp., and *Limnesia* sp. We transformed the data (logarithmic or square root transformations) when necessary to achieve normality and homoscedasticity. When we obtained significant differences, we carried out multiple *post hoc* comparisons using the Student–Newman–Keuls (SNK) test (Underwood, 1997). For each fish species captured with the dip net, we also tested for differences in their size distributions between day and night and between locations (the edge and inner part of macrophyte mats) using a Kolmogorov–Smirnov two sample test (Zar, 1996). For all analyses, the significance level was fixed at $P = 0.05$.

We considered that cladocerans, copepods or rotifers performed a DHM if we found a significant difference at different locations (OW, E and I) at various time of day.

Results

Physicochemical characteristics of the water column

The majority of the physicochemical parameters measured (dissolved O₂, % O₂ saturation, pH and conductivity) showed no difference among locations (OW, I and E) or at different depths (surface, mid-water and at the bottom) (two-way ANOVA, $P > 0.05$ in all cases) (Fig. 1). However, water temperature was lower inside and at the edge of the macrophyte stand than in open water (Fig. 1). Similarly, water temperature at the bottom (26.15 °C) was lower than that at the surface (27.41 °C) (SNK test: $P = 0.018$) or at 0.5 m depth (27.11 °C) in all sampling locations (SNK test: $P = 0.027$) (two-way ANOVA: $F_{2,9} = 6.5$; $P = 0.018$). Turbidity changed with depth depending on the location, increasing near the bottom only at the edge of the macrophytes and in open water (two-way ANOVA: Vertical gradient: $F_{2,8} = 27.84$; $P = 0.0002$; horizontal gradient: $F_{2,8} = 4.86$; $P = 0.042$) (Fig. 1).

Zooplankton distribution in the open water and the littoral zone

Diel horizontal distribution and habitat selection by zooplankton were strongly correlated with body size, as only the larger and medium-bodied zooplankton

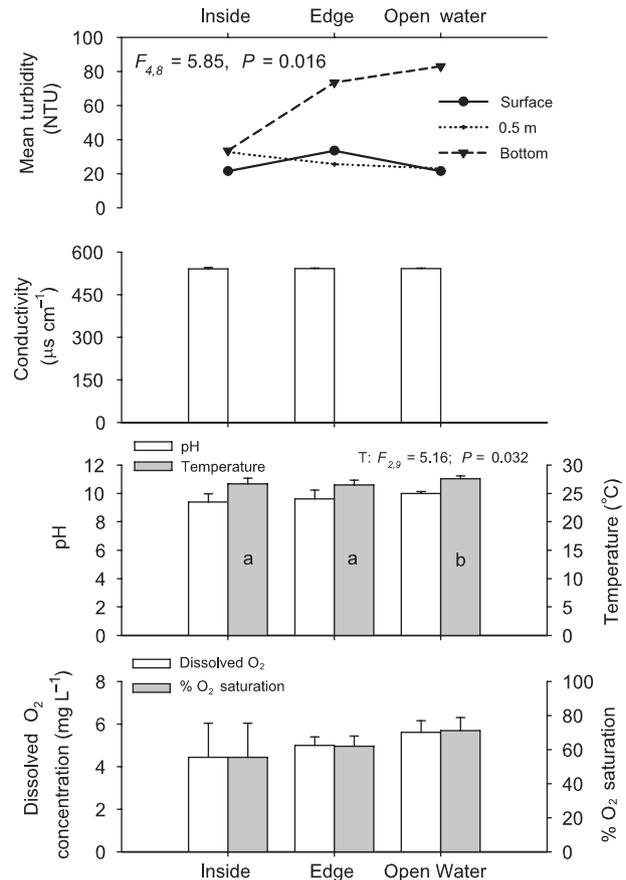


Fig. 1 Mean values (+SE) of the physicochemical parameters measured in submerged macrophyte stands and open water at the surface, 0.50 m and at 1 m of depth. Only significant statistics (F and P -values) for two-way ANOVA are shown and letters represent *post hoc* comparisons performed by Student–Newman–Keuls (SNK) test. Significance level was fixed at 0.05 in all cases. (Sampling points: Inside: inner station 1 m from the edge of macrophyte stand; Edge; Open Water: at 6 m from the macrophyte stand).

selected a particular zone. Larger zooplankton showed differences in their distribution between day and night and/or strong avoidance of macrophytes. The larger- and medium-bodied cladocerans, *Diaphanosoma brachyurum* and *Moina micrura* (0.9–0.7 mm in length), preferred open water to the edge or inner part of the beds of the submerged macrophyte *C. demersum* (Fig. 2; Table 1). *Diaphanosoma brachyurum* and adult calanoids were more numerous inside macrophyte stands at night, although their abundance in open water did not change (SNK test: day/night: $P > 0.2$ in all cases) (Fig. 2; Table 1), presumably indicating a vertical migration inside the stand from the sediment to the water column. Most adult

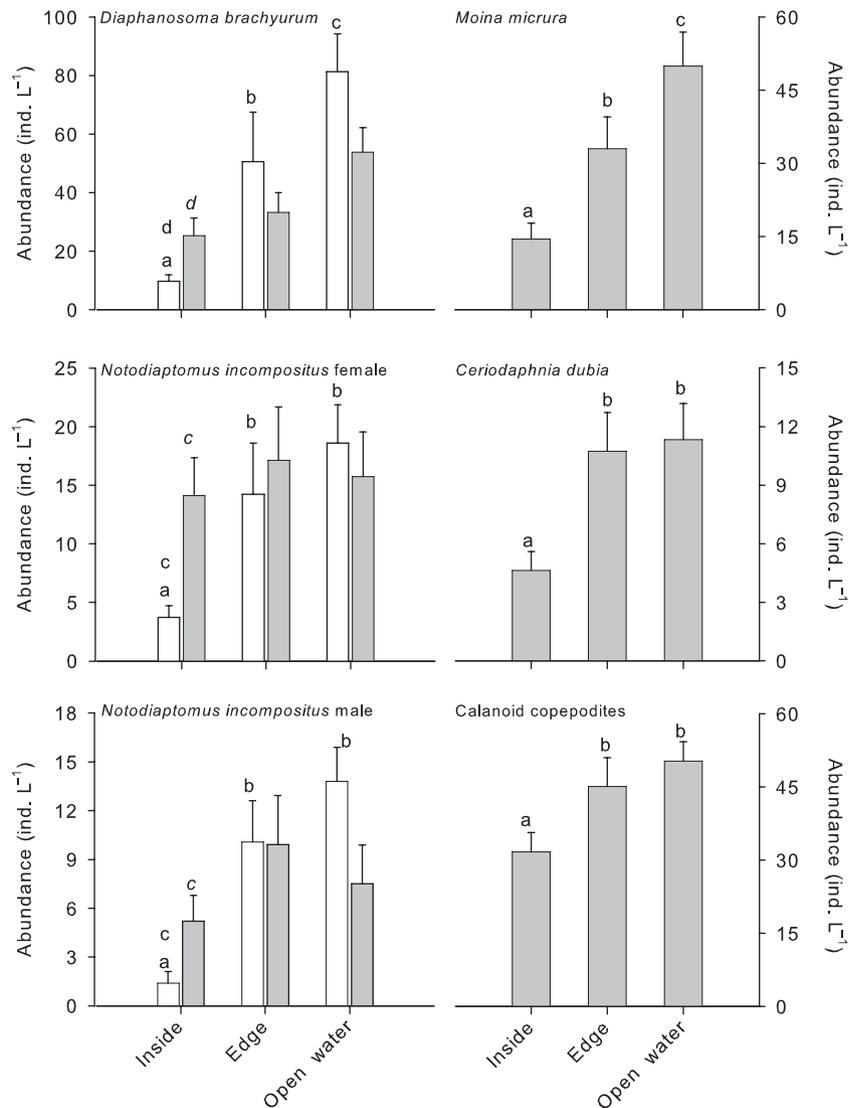


Fig. 2 Mean (+SE) zooplankton abundance across lake zones showing differences (left panel) or not (right panel) in their distributions during the day (white bars) and at night (grey bars). Letters indicate significant differences according to Student–Newman–Keuls (SNK) test after four-way ANOVA. Significance level was fixed at 0.05 in all cases.

calanoids occurred at the edges of the plant beds and in open water (Fig. 2). Medium-bodied zooplankton (*Ceriodaphnia dubia* and calanoid copepodites; Fig. 2; Table 1) were always evenly distributed between open water and the edge of the macrophyte beds but avoided the inner part of the macrophyte stands. In contrast, the smaller zooplankton [*Bosmina huaronensis* and the pelagic rotifers *Hexarthra mira* Scmarda, *Keratella tropica* (Apstein), *K. americana* (Carlin) and *Brachionus caudatus* (Barrois and Daday)] were evenly distributed among the different sampling zones both by day and night (Table 1).

The horizontal distribution of cyclopoid copepods differed depending on body size. Adults occurred evenly between the open water and submerged macrophytes zones, but copepodites were strongly associated with the inner part of the macrophytes stands (Table 1; SNK test: inner/edge: $P = 0.027$; inner/open water: $P = 0.0015$; edge/open water: $P = 0.15$).

There was no evidence of vertical migration for most zooplankton species, and abundance near the surface (0–0.5 m) and in deeper water (0.5 to 1 m, close to the lake bottom) was similar. However, it is

Table 1 *P*-values of four-way ANOVA testing the effect of the lake zone, depth, time of the day and sampling date on the abundance of pelagic and littoral Cladocera, Copepoda and Rotifera for the 72 samples analysed

	Lake zone (1)	Depth (2)	Day/Night (3)	Date (4)	Significant interactions
Zooplankton					
Cladocera					
<i>Diaphanosoma brachyurum</i>	***	0.741	0.631	0.035	1 × 3*
<i>Moina micrura</i>	***	0.882	0.821	***	–
<i>Ceriodaphnia dubia</i>	0.001	0.320	0.08	0.200	–
<i>Bosmina huaronensis</i>	0.12	0.321	0.032	0.007	–
Rotifera					
<i>Keratella americana</i>	0.07	0.967	0.012	0.010	–
<i>Keratella tropica</i>	0.803	0.768	0.998	0.164	1 × 3*
<i>Hexarthra mira</i>	0.141	0.553	0.117	0.008	–
<i>Brachionus caudatus</i>	0.704	0.072	0.941	0.344	–
Calanoid Copepods					
<i>Notodiaptomus incompositus</i> females	0.004	0.451	0.107	0.007	1 × 3*
<i>N. incompositus</i> males	***	0.993	0.935	0.003	1 × 3*
Copepodites	0.006	0.287	0.017	0.005	1 × 4*; 3 × 4**
Cyclopoid Copepods					
Adults	0.597	0.594	0.724	0.007	–
Copepodites	0.002	0.683	0.163	0.015	–
Littoral Cladocera					
<i>Alona pulchella</i>	***	0.604	0.598	0.128	–
<i>Chydorus sphaericus</i>	0.001	0.3090	0.703	0.92	–
<i>Pleuroxus</i> sp.	0.009	0.357	0.432	0.731	–
Littoral Rotifera					
<i>Euchlanis</i> sp.	***	0.02	0.201	0.001	1 × 2*
<i>Brachionus urceolaris</i>	0.004	0.146	0.181	0.005	–
<i>Epiphanes clavula</i>	***	0.669	0.530	***	–
<i>Testudinella patina</i>	0.043	0.974	0.120	0.604	–
<i>Mytilina ventralis</i>	***	0.570	0.630	0.487	–
<i>Lecane</i> spp.	0.001	0.694	0.284	0.465	–

P-values in bold represent $P < 0.05$ and with ***, $P < 0.001$. Significant interactions among factors are denoted by numbers, each number belongs to a factor name and significance level assigned as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Degrees of freedom for each factor: lake zone: 2; depth, time of the day and date: 1.

possible that adult copepods and *D. brachyurum* could have remained hidden in the sediment or in the interstitial inside the plant stands during the day and ascended into the water column by night because their abundances then increased without decreasing in open water or at the edge of macrophytes (Fig. 2). All zooplankton species were more abundant on the second day of sampling (Table 1).

Distribution of littoral microinvertebrates

Littoral microcrustaceans and rotifers were always associated with vegetation and were very abundant inside macrophyte stands. Littoral rotifers were more abundant (329 ± 42 individuals L^{-1} , mean of I and E \pm SE) than littoral cladocerans ($83 \pm 23 L^{-1}$), and

Euchlanis was the most abundant rotifer species recorded ($281 \pm 32 L^{-1}$). Rotifers occupied the inner zone of macrophytes (for example: *Mytilina ventralis* O. F. Müller and *Lecane* spp.) or were distributed homogeneously between the edge and inner parts of macrophyte stands (*Testudinella patina* Hermann, *Brachionus urceolaris* O. F. Müller, *Euchlanis* sp. and *Epiphanes clavula* Ehremerberg) (Table 1) (SNK test: $P < 0.05$ in all cases for each distribution pattern). The littoral cladoceran assemblage was dominated by *Alona pulchella* (De Guerne & Richard), reaching a density of $84 \pm 23 L^{-1}$ in the inner zone of *C. demersum* beds. Littoral cladocerans were distributed along a gradient, reaching the greatest abundance inside the patch (*A. pulchella* and *Pleuroxus* sp.) or homogeneously occupying the inner zone and the edge of macrophyte

stands [*Chydorus sphaericus* (O. F. Müller)] (Table 1) (SNK test: $P < 0.05$ in all cases for each pattern). There was no evidence of horizontal or vertical migrations for littoral rotifers or cladocerans (Table 1). Moreover, their vertical distributions were homogeneous except for *Euchlanis* sp. (horizontal distribution \times depth: $P = 0.002$; Table 1). This rotifer selected the inner zone of macrophyte beds near the surface (0–0.5 m) (SNK test $P < 0.002$ for both comparisons) whereas those in deeper water were distributed homogeneously between the inner zone and the edge of macrophyte stands (0.50–1 m) (SNK test: $P < 0.004$ for both comparisons relative with open water).

Predatory macroinvertebrate and fish distribution

Macroinvertebrates and small fish were permanently associated with the littoral zone, as no diel horizontal migration to open water occurred. Predators differed in their pattern of association with macrophyte stands (Table 2; Figs 3, 4 & 5) but never preferred the open water, as did the large fish *Australoheros facetus* (Jenyns).

The total density of predatory macroinvertebrates was high in macrophyte stands (mean: 329 m^{-2}), and

the damselflies *Cyanallagma bonariense* and *C. interruptum* and the Acari were the most abundant taxa (Table 2). *Koenikea curvipes* dominated the mite assemblage but other species (*Arrenurus oxyurus*, *Eylais multiespina*, *Hydrachna* sp. and *Limnesia* sp) also occurred in small numbers. Macroinvertebrates exhibited three patterns of distribution in the macrophyte stands, with the two most frequent being a gradient (with the highest abundances in the inner zone of the patches and the lowest in the open water) or a preference for the inner part of macrophytes. For example, the zygopterans *C. bonariense* and *C. interruptum* were distributed according to a gradient pattern during the day (Table 2; Fig. 3), while they occurred homogeneously between the inner part and the edge of plant beds at night. Instead, the flatworm *Mesostoma ehrenbergii* Focke (Fig. 3), the anisopteran *Aeshna* sp. and the cnidarian *Hydra* sp. occupied the inner part of the vegetation (Table 2) (SNK test for the inner part relative to the edge and open water: $P < 0.05$ in all cases). Only Acari occurred preferentially at the edge (Table 2; Fig. 4). The third pattern detected, found for adults and juveniles of the grass shrimp (*Palaemonetes argentinus* Nobili), was a homogeneous distribution between the edge and inner part of

Table 2 Mean abundance and P -values of three-way ANOVA testing the effect of the lake zone, time of the day and sampling date on the horizontal distribution of predatory macroinvertebrates and fish

	Inner zone Mean \pm SE	Edge Mean \pm SE	Open water Mean \pm SE	Lake zone	Day/Night	Date
Predatory macroinvertebrates						
<i>Cyanallagma</i> §	142.5 \pm 27.9	70.58 \pm 14.7	2.75 \pm 0.8	***	0.38	0.304
<i>Aeshna</i> sp.	0.5 \pm 0.2	0	0	0.042	0.533	1
<i>Notonecta</i> sp.	0.25 \pm 0.2	0	0	0.186	0.658	0.658
<i>Berosus</i> sp. larvae	1.25 \pm 0.7	1.25 \pm 0.7	0	0.341	0.486	0.690
<i>Belostoma elegans</i>	2.83 \pm 1.3	0.33 \pm 0.33	0	0.053	0.576	0.737
<i>Palaemonetes argentinus</i>	20.58 \pm 6.4	22.67 \pm 7.6	1.83 \pm 0.8	0.004	0.007	0.332
<i>P. argentinus</i> zoea	1.67 \pm 1.7	4.25 \pm 2.5	7.92 \pm 3.4	0.137	0.512	0.029
Acarina ϕ	40.5 \pm 10.2	193.5 \pm 60.3	42.1 \pm 19.9	***	0.007	0.373
<i>Hydra</i> sp.	2 \pm 0.8	0.5 \pm 0.4	0	0.037	0.479	0.120
<i>Mesostoma ehrenbergii</i>	2.5 \pm 1	0.5 \pm 0.3	0	0.010	0.354	0.756
Fish						
<i>Cnesterodon decemmaculatus</i>	11.83 \pm 7.3	0.67 \pm 0.4	0	0.007	0.385	0.907
<i>Jenynsia multidentata</i>	7.41 \pm 2.26	1.08 \pm 0.29	0	***	0.959	0.833
<i>Australoheros facetus</i> (small)	0.33 \pm 0.2	0	0	0.128	0.350	0.422
<i>Astyanax eigenmanniorum</i>	0.33 \pm 0.2	0	0	0.09	1	0.422
young-of-the-year (YOY)-fish	8 \pm 3.3	3.08 \pm 1.1	0.08 \pm 0.08	0.002	0.742	0.245

P -values in bold represent $P < 0.05$ and with ***, $P < 0.001$. Degrees of freedom for each factor: water column structure: 2; depth, day/night and date: 1. §, sum of *C. interruptum* and *C. bonariense*; ϕ , sum of *K. curvipes*, *A. oxyurus*, *E. multiespina*, *Hydrachna* sp. and *Limnesia* sp. All fish and predatory macroinvertebrates included in the analyses were caught with a dip net.

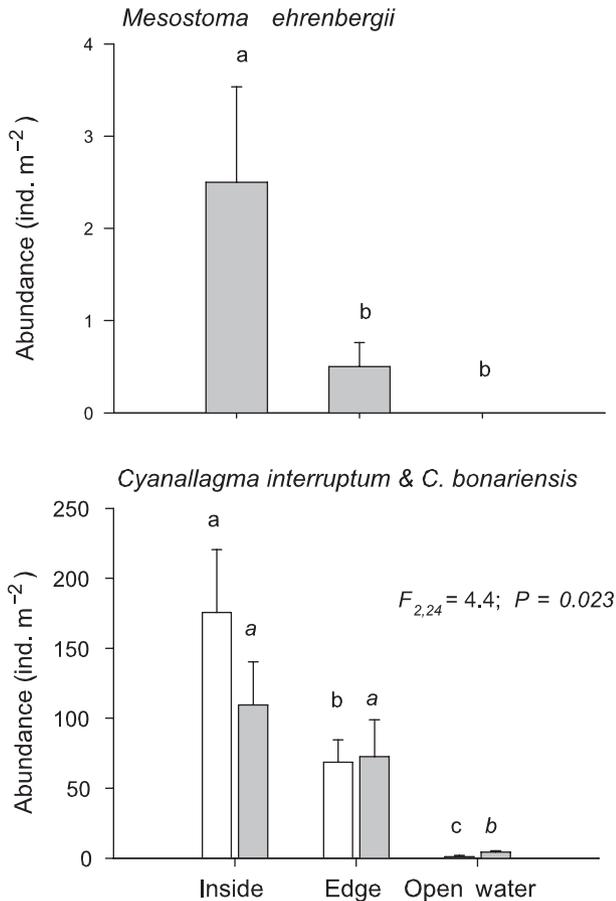


Fig. 3 Mean (+SE) abundance and distribution of two predatory macroinvertebrates: Zygoptera (bottom) and the flatworm, *Mesostoma ehrenbergii*, (top), as examples of a gradient distribution and of selection for the inner part of *Ceratophyllum demersum* stands, respectively. Significant F and P -values for the interaction of time of the day and lake zones (three-way ANOVA) are shown for zygopterans; plain letters represent significant *post hoc* comparisons for the daytime level across lakes zones and italic letters for the comparisons for the night level. For *Mesostoma*, letters represent *post hoc* comparisons performed by Student–Newman–Keuls (SNK) tests among the means. Significance level was fixed at 0.05 in all cases. White bars: day abundance; grey bars: night abundance.

the macrophyte stands and almost absent in open water (Fig. 4). Predatory macroinvertebrates did not change their distribution or preference for any of the macrophyte zones from day to night, except for zygopterans (Table 2). The abundance of Acari and shrimps increased in the macrophyte stands at night (Fig. 4). Some predatory macroinvertebrates, such as the heteropterans *Notonecta* sp. and *Belostoma elegans* (Mayr) and larvae of the coleopteran *Berosus* sp., were poorly represented, which did not allow the detection

of a specific pattern of distribution, although they were always associated with macrophytes (Table 2).

The two sampling methods allowed the characterization of habitat use (littoral or pelagic) by the smaller and larger fish (dip and gill nets, respectively). Fish distribution among littoral areas and open water was related to body size. There was no change in the diel distribution or lake zone preference of any species sampled with the dip net. Large fish, such as the adults of *A. facetus* (15–20 cm body length), occurred only in open water ($n = 20$, caught with a gill net), while small fish (1.25–1.6 cm body length) occurred only in *C. demersum* beds (caught with dip nets) (Table 2). Accordingly, *Cnesterodon decemmaculatus* (Jenyns), *Jenynsia multidentata* (Jenyns), YOY-fish, *Astyanax eigenmanniorum* (Cope) and small *A. facetus* individuals (1.6 cm body length) composed the littoral fish assemblage in the macrophyte stands (Table 2). *Cnesterodon decemmaculatus* and *J. multidentata* were the most abundant fish (Table 2; Fig. 5), and both showed a preference for the inner parts of *C. demersum* stands. The YOY-fish were evenly distributed between the inner part and the edge of macrophyte patches (Fig. 5). *Cnesterodon decemmaculatus* individuals inside plant beds were significantly larger in the daytime than at night (Fig. 5) (mean length: day: 1.7 cm; night 1.4 cm). In contrast, the body length distributions of *J. multidentata* and YOY-fish did not differ inside the macrophytes or at the edge by day or night or in different parts of the macrophyte stands (Fig. 5).

Discussion

Diel horizontal migration of zooplankton implies a change in the abundance of pelagic prey populations on a diel time scale, induced by a horizontal gradient of zooplanktivory (White, 1998). In shallow temperate lakes, submerged macrophytes have been recognised as refuges for zooplankton during the day, thus avoiding predators in the open water (Lauridsen & Buenk, 1996; Burks *et al.*, 2002). In this study, diel horizontal migration did not occur. Rather, we found that zooplankton displayed avoidance of the shore, which was related to body size and the associated risk of predation. Therefore, zooplankton that were highly vulnerable to predation, such as larger- and medium-bodied cladocerans *Diaphanosoma brachyurum* and *Moina micrura* (0.9–0.7 mm in length), showed an avoidance of the littoral during the daytime and at

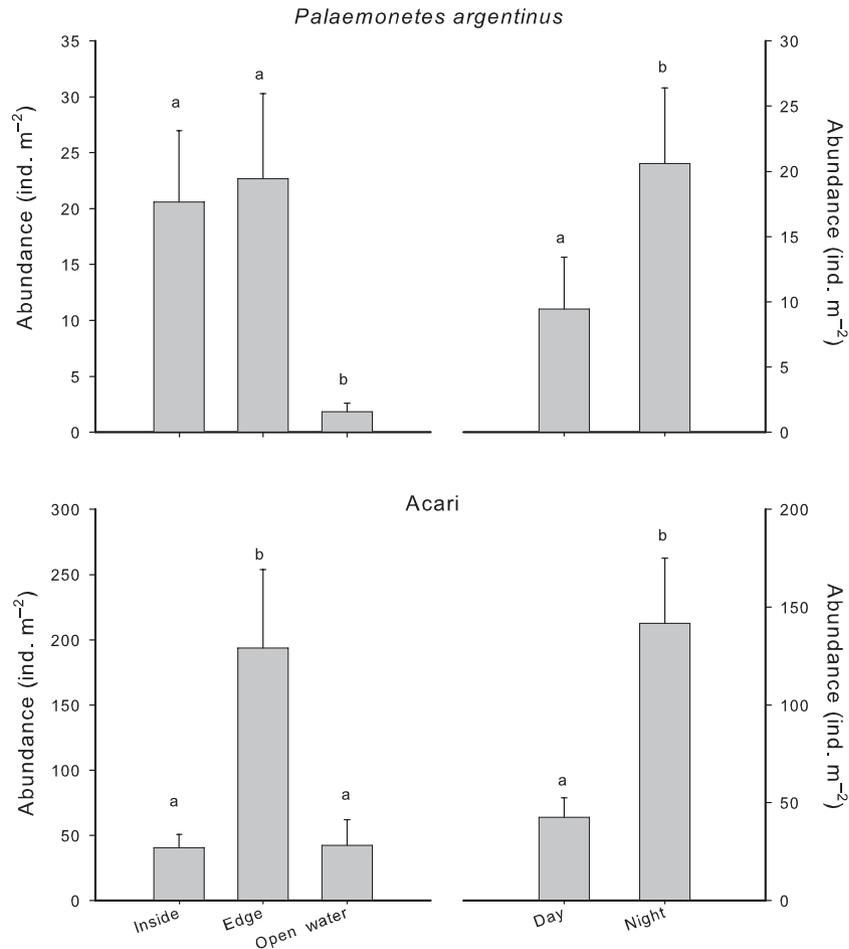


Fig. 4 Mean (+SE) abundance and distribution of the predatory macroinvertebrates *Palaemonetes argentinus* (grass shrimp) and Acari, as examples of a homogeneous distribution, between the inner zone and the edge of *C. demersum* stands, and the selection for the edge of plant beds, respectively. Letters represent *post hoc* comparisons performed by Student–Newman–Keuls (SNK) test. Significance level was fixed at 0.05 in all cases.

night, being up to two to four times more concentrated in open water than at the edge or inner part of *Ceratophyllum demersum* patches, respectively. Conversely, less vulnerable zooplankton of medium body size [*Ceriodaphnia dubia* (0.6 mm)] or with the ability to swim fast (calanoid copepods) were distributed evenly across open water and the edge of the plant beds, while smaller zooplankton were distributed evenly among locations [e.g. *Bosmina* (<0.6 mm) and pelagic rotifers (~0.25 mm)]. In summary, more vulnerable zooplankton selected open water, remaining there by day and night, despite the associated predation pressure in the pelagic.

Several factors can lessen the refuge effect of aquatic plants, such as diel changes in physical and chemical parameters, availability of food resources, allelopathy or plant architecture and density, and the

presence of potential predators (Gliwicz & Rykowska, 1992; Burks *et al.*, 2002, 2006). In our study, the avoidance of the littoral by the zooplankton cannot be explained by the existence of an unfavourable physicochemical environment, as we did not find any difference in the parameters estimated between open water and the macrophyte beds. Moreover, water temperature was almost one degree lower inside the macrophytes during the day (26.66 °C) than in open water (27.57 °C), suggesting that macrophytes are a “cooler environment”. As a consequence, changes or differences in physicochemical parameters (i.e. pH, O₂ concentration and temperature) cannot be a plausible explanation for plant avoidance. However, plant density and design affect prey detection, and refuge efficiency increases with increasing macrophyte density (Dionne, Butler & Folt, 1990; Priyadarshana &

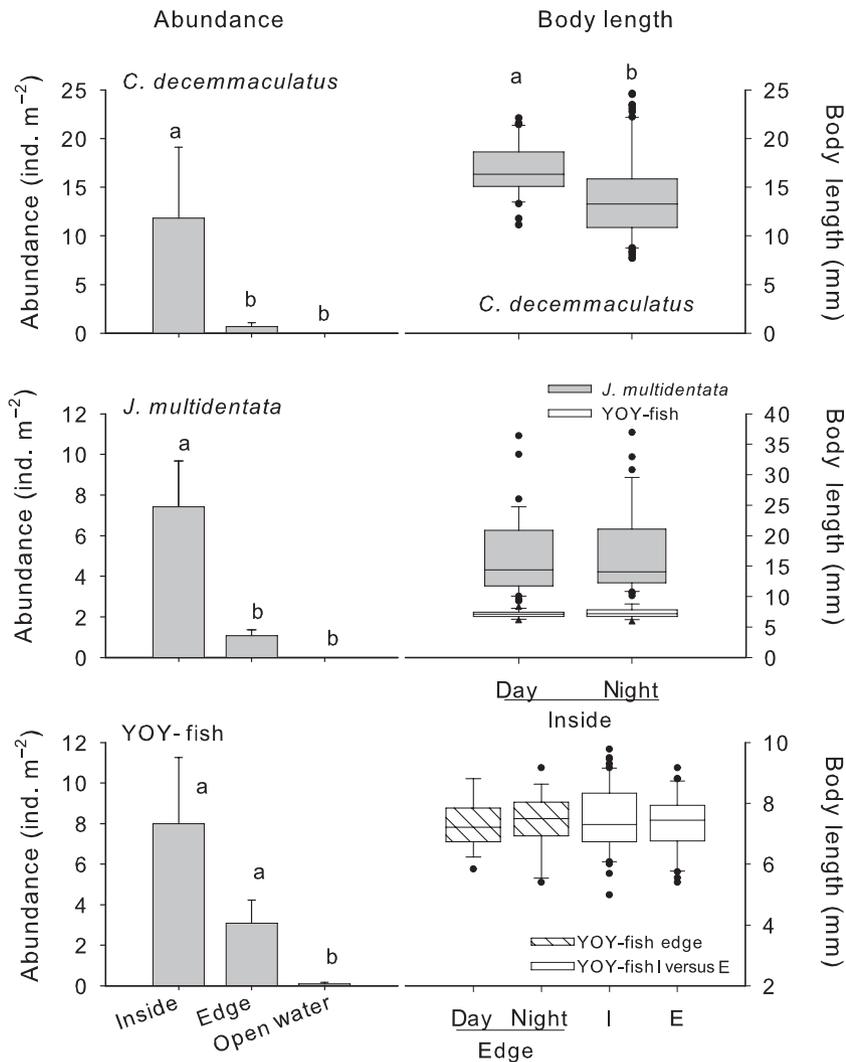


Fig. 5 Mean (+SE) littoral fish abundance (left panel) and body length distribution (right panel) across the lake zones and by day and night. Letters indicate significant differences across the lake zones (Student–Newman–Keuls (SNK) test) for fish abundance and significant body size distributions according to Kolmogorov–Smirnov two sample test. Significance level was fixed at 0.05 in all cases. (I: inner zone, E: edge).

Asaeda, 2007). Accordingly, *C. demersum* stands should represent a good potential refuge in this lake because of its finely dissected form and its high density (PVI: almost 80%).

The avoidance of submerged macrophytes by the larger-bodied zooplankton in this study must be related to the high risk of predation in *C. demersum* stands, as the plants are inhabited by about 300 macroinvertebrate predators m⁻² and small littoral fish plus YOY-fish. Both predatory macroinvertebrates and fish showed a permanent association with plants, indicating a constant high predation pressure in *C. demersum* stands. Our results add evidence that

macrophytes do not act as a safe refuge in warm climate zones. Differences in macrophyte use by zooplankton are reported for cold temperate and warm lakes (subtropical and Mediterranean lakes) and seem related to the fish assemblage and the presence of large-bodied macroinvertebrates (Castro *et al.*, 2007; Meerhoff *et al.*, 2007a,b). The habitat partitioning of fish (in free-floating plants) and zooplankton (submerged plants) in cold temperate lakes (Danish lakes) facilitate a DHM (Meerhoff *et al.*, 2007a,b). In contrast, the presence of the shrimp *P. argentinus*, and a higher species richness, density and biomass of fish inhabiting submerged macro-

phytes in subtropical lakes (Uruguayan lakes), prevent DHM (Meerhoff *et al.*, 2007a,b; Teixeira-de Mello *et al.*, 2009). Littoral fish in these warm shallow lakes are characterised as planktivorous-omnivorous-detritivorous (Rosso, 2006; Teixeira-de Mello *et al.*, 2009), and some species like *J. multidentata* could suppress larger-bodied zooplankton such as *Daphnia* from the system (Iglesias *et al.*, 2008). The fish assemblage of Los Padres Lake is similar to that of subtropical lakes (Teixeira-de Mello *et al.*, 2009). Thus, littoral fish associations and their high potential predation pressure could mediate the shore avoidance recorded by the larger zooplankton, as has been observed for other cold systems (Gliwicz & Rykowska, 1992).

However, we demonstrated that macrophytes were also the refuge of a diverse predatory macroinvertebrate assemblage. The role of macroinvertebrates in preventing DHM has been largely overlooked (Burks *et al.*, 2002), even when their role as predators has been recognised. Most studies showed the direct impacts on zooplankton and the high predation rates and predation risk imposed by predatory macroinvertebrates such as odonates, the flatworm *Mesostoma* or notonectids (Gilbert & Burns, 1999; Hampton *et al.*, 2000; Van de Meutter *et al.*, 2004; Trochine *et al.*, 2008), all of which have been recorded in *C. demersum* stands. The effect of confronting the diverse assemblage of predators reported here was estimated by a combination of field and laboratory experiments by González Sagrario *et al.* (2009). In a field experiment, they showed that the range of invertebrate predators found in *C. demersum* stands could suppress all fractions of the zooplankton (*D. brachyurum*, *M. micrura* and *B. huaronensis* and adult calanoids) by 80%. The invertebrate assemblage combined different types of large-bodied predators (damselflies, notonectids, bellostomatids, shrimps and dytiscids) that display different prey capture techniques (sit and wait strategists, near-surface hunters and divers) and detect prey by both visual and tactile means, which prevented zooplankton escape. The damselfly *Cynallagma interruptum*, the notonectid *Buenoa* and the grass shrimp *P. argentinus* were the most voracious predators (González Sagrario *et al.*, 2009). The results from González Sagrario *et al.* (2009) and the present field study strongly demonstrate that an abundant and diverse assemblage of predatory macroinvertebrates can have a role in preventing DHM patterns in warm lakes and can impose high predation pressure

on a large fraction of the zooplankton. Accordingly, the littoral zone in this warm lake is a dangerous area for zooplankton, as the invertebrate predation risk must be supplemented by the risk of predation from small fish. As for brackish lakes, a combination of invertebrate (*Neomysis*, in this case) and fish predators enhances the risk of predation (Jeppesen *et al.*, 1997).

We found evidence of DVM for the larger cladocerans, *D. brachyurum* and the adult calanoids only inside the submerged macrophytes stands. However, the majority of the zooplankton did not perform DVM. In subtropical lakes, despite the occurrence of DVM patterns, the structure of the zooplankton community indicates that no predator-avoidance behaviour can effectively counteract the high predation pressure in the subtropics (Meerhoff *et al.*, 2007b). Zooplankton body size (medium – small) and community structure in Los Padres Lake indicate a high pressure of planktivory, which is characteristic of this type of warm temperate lake (Quirós *et al.*, 2002; González Sagrario, 2004). Because DHM cannot be an antipredator strategy in this system, as DVM cannot be for most zooplankton, most pelagic prey must find refuge in their reduced body size and in turbidity (González Sagrario, 2004). The importance of the littoral zone as a refuge decreases with turbidity, as low water transparency protects zooplankton in the open water (Estlander, Nurminen & Olin, 2009; Schou *et al.*, 2009). Additionally, at high turbidity, a shift in fish composition and habitat use occurs, increasing fish preference for littoral areas in cold temperate lakes (Jeppesen, Pekcan-Hekim & Lauridsen, 2006; Schou *et al.*, 2009). However, as most macroinvertebrate predators do not depend exclusively on visual prey detection, macrophyte stands in turbid water are much more risky than open water, where turbidity reduces the detection efficiency of large fish.

Considering the overall lake ecosystem, the use of macrophytes by a rich assemblage of littoral predators (macroinvertebrates plus fish) would promote a turbid state in lakes as the zooplankton loses the refuge offered by littoral plants. The clear water state in shallow lakes is promoted by several synergistic mechanisms. Submerged macrophytes are key organisms because they stabilise the water column and reduce sediment resuspension, negatively affect phytoplankton through nutrient competition and allelopathy, and promote large filter feeding zooplankton populations and their control on phytoplankton bio-

mass (van Donk & van de Bund, 2002; Horppila & Nurminen, 2003; Burks *et al.*, 2006; Nurminen & Horppila, 2009). The loss of a macrophyte refuge can have a strong effect at the ecosystem level as large cladocerans, with greater control capacity over phytoplankton, are replaced by medium to small-bodied cladocerans with a lower grazing impact. As a consequence, the pressure from littoral predators will counteract macrophyte refuge provision and promote a turbid lake state. Therefore, clarity or turbidity in shallow lakes is influenced by macrophyte refuge capacity which, in turn, could be affected by the composition, abundance and voraciousness of the predatory assemblage that plants host, making the refuge less effective and driving the system to a less clear state.

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