Effects of *Egeria densa* Planch. beds on a shallow lake without piscivorous fish

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Abstract

Submerged plants are thought to negatively affect phytoplankton crops in the temperate zone by a number of mechanisms, including nutrient and light limitation, and enhancement of top-down control by offering diurnal refuge for zooplankton against visual predation, and by favouring piscivores. In 1997–1998, Lake Blanca (34°54′ S, 54°50′ W), a yellow-brownish shallow lake in Uruguay, suffered a severe water level reduction (associated with El Niño events between 1995–1997) that resulted in a massive fish kill and an extensive colonisation by *Egeria densa*. A clear water phase is established nowadays in the system (Secchi depth > 1 m), despite a fish community restricted to two small omnivorous–planktivorous fish: *Jenynsia multidentata* and *Cnesterodon decemmaculatus*. We studied the effects of *E. densa* on bottom-up and top-down controls on phytoplankton by comparing physical, chemical, and biological characteristics between submerged plant beds and sites without plants, from autumn 2000 to autumn 2001. The water column had low to intermediate nutrient concentrations, and phytoplankton community was highly diverse with a low to moderate biomass (mean Chl-a = 10.6 µg l^{-1}). The water level, recovered during the study, promoted a dilution process that explained the temporal pattern of many chemical variables. Macrophyte PVI represented 28–39% of the lake volume (annual mean biomass = 174 g DW m^{-2}). The zooplankton community was generally dominated by copepods in terms of biomass. Fish and zooplankton were significantly associated with submerged plant beds. In spite of the high biomass and density of omnivorous-planktivorous fish (115 kg ha^{-1}, 13 ind m^{-2}), zooplankton strongly affected phytoplankton spatial and temporal variation. The most important differences of algal biomass between zones coincided with a high herbivorous zooplankton biomass and/or with plants occupying the entire water column during the low level period. Medium-sized zooplankton declined with fish reproduction. The consequent stronger predation of juvenile fish seemed to decrease macrophyte efficiency as a zooplankton refuge in summer. *E. densa* bottom-up mechanisms would also be present, contributing to maintaining clear water. Besides the usually described nutrient and light limitation, the internal production of humic substances could enhance the observed top-down effect.

Introduction

Submerged plants present a series of mechanisms that contribute to the maintenance of low phytoplankton crops (Søndergaard & Moss, 1998). The structuring role of macrophytes in lake ecosystems involves: (a) limnological effects related to changes in physical and chemical conditions in the water and sediments; (b) metabolic effects on production, processing of organic matter and nutrient cycling; and (c) effects on biotic interactions and community structure related to the role of macrophytes in providing a refuge or hab-

itat for zooplankton and small fish (Jeppesen et al., 1998; Søndergaard & Moss, 1998; Ruggiero et al., 2003). However, these last effects are very intricate because macrophytes also influence the mutual interactions between piscivores and prey fish (Persson & Crowder, 1998).

Different morphological types of submerged plants have different impacts on the systems, according to density and the distribution of biomass in the water column (Scheffer, 1998). In turbid, shallow lakes, vegetation is typically dominated by angiosperms that concentrate most of their biomass in a canopy just below water surface, such as *Potamogeton*, *Hydrilla*, *Elodea*, and *Egeria* spp., contrary to the plants in clear water systems, whose biomass is homogeneously distributed along the water column, such as *Chara* and *Myriophyllum* spp. (Scheffer, 1998).

Egeria densa Planch., native to South America, has became a nuisance species in temperate and subtropical places where it is exotic (St. John, 1961), but also in native, disturbed sites (Bini et al., 1999). Despite its wide distribution and high abundance in many shallow lakes, there are relatively few studies on its ecology (Feijoó et al., 1996).

The objective of this paper was to analyse the role of *E. densa* in a shallow subtropical lake that became dominated by this submerged plant after a strong water level decrease, which also resulted in the disappearance of piscivorous fish. The specific objectives were: (a) to determine the modifications of *E. densa* beds on the main physical and chemical attributes of water and sediment; (b) to analyse the differences of plankton composition and biomass between *E. densa* beds and open waters; and (c) to determine the influence of the submerged plants on the spatial distribution of small omnivorous–planktivorous fish and shrimps.

Description of study area

Lake Blanca (34°54′ S; 54°50′ W) is a shallow system (total area = 40.5 ha and Z_{max} = 1.5–3.6 m) located in the main tourist area of Uruguay, and used for water supply (Fig. 1). The eutrophication process started in the late 19th century, due to cattle, forestry, and tourism activities, according to palaeolimnological information (García-Rodríguez et al., 2002). Littoral expansion (ca. 30% of open water area) was observed from 1967 to 1998, including floating mats dominated by *Typha latifolia* L. A severe drought between 1995–1997 related to El Niño events, together with strong

water consumption by the water supply company, resulted in a drastic reduction of the lake volume and the rapid colonisation of *E. densa*. Before this disturbance, the managers had observed cyanobacteria blooms during several summers. The lake volume was recovered during this study.

Materials and methods

The study was carried out from autumn 2000 to autumn 2001. *Egeria densa* biomass was measured monthly (bimonthly during winter) in 16 sampling stations over the entire system (Fig. 1), placing a 0.25 m^2 frame with a net bag by SCUBA diving (one replicate per station). The dry weight (DW) was estimated by drying ten random entire plant samples at 80 °C for 48 hours. After the biomass drying procedure, whole plants were macerated and three random sub-samples were analysed for nutrient concentration. Plant nitrogen (N) concentration was determined by the Kjeldahl method (APHA, 1985) using 0.1 g of plant powder. To analyse phosphorus (P) concentration (0.02 g of plant powder), a digestion with concentrated perchloric–nitric–sulfuric (1:5:0.5) acids was carried out, and the oxidised reactive form was determined according to Murphy & Riley (1962). The percent volume infested of the submerged plants (PVI) was estimated from 109 sites during summer 2001, as the product of percentage cover (estimated by eye) and plant height divided by the water depth (Canfield et al., 1984).

Our knowledge on the structuring role of submerged plants has been drawn from comparisons between macrophyte-free and macrophyte-rich areas (Søndergaard & Moss, 1998). Therefore, we selected two similar zones (distance between zones = 300 m) with and without *E. densa* beds (Fig. 1). We considered fixed beds with active growth to facilitate the analyses of the temporal variation of *E. densa* effects.

Water samples were collected monthly (bimonthly during winter) from the two sampling zones at both surface and bottom, with a water pump (triplicates at random, total $n = 12$). Dissolved oxygen (DO), conductivity (K), pH, and transparency were registered *in situ* using Horiba sensors and Secchi disk (SD). The coefficient of light extinction (k_d) and the euphotic zone depth (1% of incident light) were determined from the photosynthetic active radiation (PAR) in the water column, measured by a radiometer (Licor Model Li-250). Chemical analyses included alkalinity (ALK) and total suspended solids (TSS) (APHA, 1985), sol-
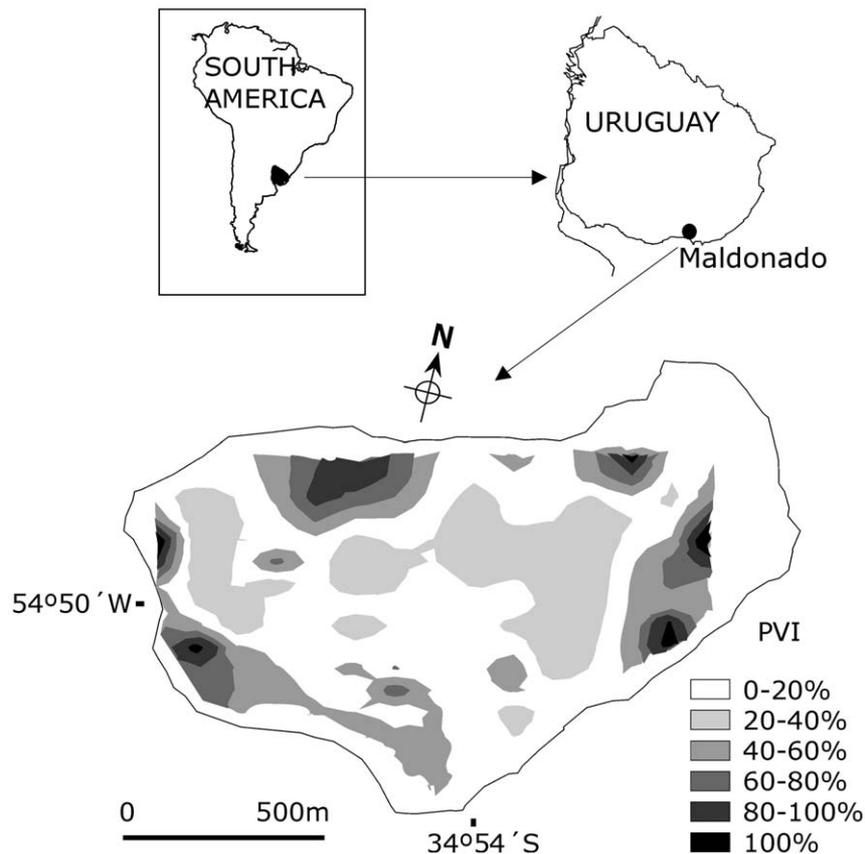
Figure 1. Location of Lake Blanca, and spatial distribution of *E. densa* PVI ('plant volume infested', summer 2001). The zones sampled for water, sediment and plankton analyses included the denser *E. densa* beds in the south part of the lake, and the central zone free of submerged plants. The 16 stations for plant biomass sampling were equally distributed over four transects in SE–NW.

uble reactive phosphorus (SRP) (Murphy & Riley, 1962), nitrate (N-NO$_3^-$) (Müller & Widemann, 1955), ammonium (N-NH$_4^+$) (Koroleff, 1970), total nitrogen (TN) and total phosphorus (TP) (Valderrama, 1981), reactive silicate (RSi) (Müllin & Riley, 1955), and chlorophyll *a* (Chl-*a*) (Nusch, 1980, by hot ethanol). The humic substances in water were estimated indirectly by measuring coloured dissolved organic matter (CDOM) in a spectrofluorometer. The emission at 450 nm was normalized with Raman signal of Milli-Q water and expressed in nm^{-1}. Five random sediment samples were taken by SCUBA diving to determine total nitrogen and phosphorus content, according to Valderrama (1981), and organic matter by gravimetry (Hakanson & Jansson, 1983), every 2 cm up to 10-cm depth.

Phytoplankton-net tows (25-μm mesh size) and integrated water column samples (Ruttner bottle) were collected in triplicate in each zone. Counts were made (Utermöhl, 1958), and biovolume was calculated ac-

cording to Hillebrand et al. (1999). Zooplankton (>68 μm) for qualitative analysis were sampled with a net. For quantitative analysis, three 20-l replicates were collected with a water pump from the surface, middle, and bottom, and then filtered through a 50 μm net (total $n = 18$). Counts were made according to Paggi & de Paggi (1974) in a Sedgwick–Rafter chamber. Biomass was estimated according to Bottrell et al. (1976) and Ruttner-Kolisko (1977). Plankton and water samples were taken simultaneously at midday (10:00–12:00 AM).

The fish and shrimp communities were sampled seasonally by point electric fishing (Perrow et al., 1996), in 80 sites homogeneously distributed in transects located in pelagic and littoral areas. Individuals were counted, measured (total length), and weighed. Fish and shrimp density and biomass were calculated in function of the efficiency of the equipment (Sachs Elektrofischfanggerate GmbH D-88299 Leutkirch) estimated in the field, and as a weighted average of

the corresponding areas of the pelagic and the littoral zones (including zero catches). The point electric fishing was performed at sunset.

Data analysis

Repeated measures of analyses of variance (ANOVA) were performed for physical, chemical, and zooplankton variables, considering three main factors: (a) sampling zones; (b) water column depth; and (c) time; as the study was made on the same sample zones over time (Underwood, 1997). In the case of phytoplankton the factors considered were (a) and (c). Homoscedasticity and the normal distribution of residuals were tested by Cochran's C test and by visual inspection of fitted values, respectively. *Post hoc* comparisons were performed with Tukey's test. Correlations included non-parametric (Spearman, *rs*) and parametric (Pearson, *r*) procedures, depending on type of data available. Zooplankton data were root–root transformed (Field et al., 1982) to satisfy the requirements of the analyses. Chemical data were standardized for correlation analyses.

Results

Egeria densa *biomass and PVI*

The average biomass was 170 g DW m^{-2}, and the highest values were recorded in spring and summer (September and December), without significant differences among most months. The cover of *E. densa*, estimated from the PVI study, was approximately 45% of the lake area without emergent plants, while PVI represented between 28–39% (Fig. 1). Average nutrient content in *E. densa* biomass was 3.5% for nitrogen and 0.2% for phosphorus (dry weight). Nitrogen and phosphorus content were positively correlated (*rs* = 0.78, $p < 0.05$), and a decrease in both was observed with time.

Water and sediment characteristics

Lake Blanca is a warm polymictic system, with low to moderate nutrient concentrations in the water column and generally low turbidity (Table 1). According to the trophic classification of Salas & Martino (1990) (probabilistic model), the phytoplankton biomass corresponded to mesotrophy (52%), but TP levels suggested eutrophic conditions (57%). Following Canfield et al.

(1983) criteria, and including the phosphorus content in submerged plants, the trophic state of Lake Blanca was closer to hypertrophy (54%).

The system presented a notorious yellow-brownish colour associated with important concentrations of CDOM, which were maximal in winter and decreased gradually towards summer. The maximum values of the emission spectra of CDOM were observed between 400 and 470 nm, corresponding to humic substances originated in the aquatic environment (Senesi et al., 1989). Euphotic zone reached generally 2/3 of the water column in the zone without plants ($k_d = 1.63$ m^{-1}), and k_d was 27% lower than in the zone with plants. k_d was directly related to TSS, Chl-a, and indirectly to total zooplankton abundance (ZT) ($k_d = 1.14*TSS + 0.51*Chl$-$a - 0.92*ZT$; $R^2 = 0.79$, $p < 0.05$).

Some physical and chemical variables showed significant differences between the two zones sampled (Table 1). Temperature was higher in *E. densa* beds, but the difference was generally lower than 1 °C. Oxygen concentrations did not differ significantly between zones (Table 1), though the oxygen levels were significantly higher in the *E. densa* zone during April and May. Conversely, the higher DO levels were detected in open waters when the phytoplankton biomass increased, in summer. The photosynthetic activity of plants and microalgae also influenced the spatial pattern of pH. The values were more alkaline within plants in spring, but also more alkaline in the zone without plants during summer. There were higher concentrations of TSS, TP, and TN within *E. densa* beds over time (Table 1). N-NH_4^+ and RSi had higher values in the zone free of plants. The inverse pattern was observed for N-NO_3^- (Table 1).

The study involved two different hydrological conditions the end of a dry and the beginning of a rainy period, which resulted in an important fluctuation of water level. K, ALK, and DO changed strongly in relation to water level (Fig. 2). RSi, SRP, and N-NH_4^+ showed higher concentrations in the low water level period, and SRP and N-NH_4^+ were negatively correlated with DO concentration (water column average) ($r = -0.43$, $p < 0.001$; $r = -0.66$, $p < 0.001$, respectively). The directly available nutrients were inversely correlated with water temperature ($r = -0.25$, $r = -0.61$, $r = -0.55$, and $r = -0.24$, for N-NH_4^+, N-NO_3^-, SRP, and RSi, respectively, with $p < 0.01$ in all cases).

Sediments showed high contents of organic matter, phosphorus, and nitrogen in the top 10 cm, being
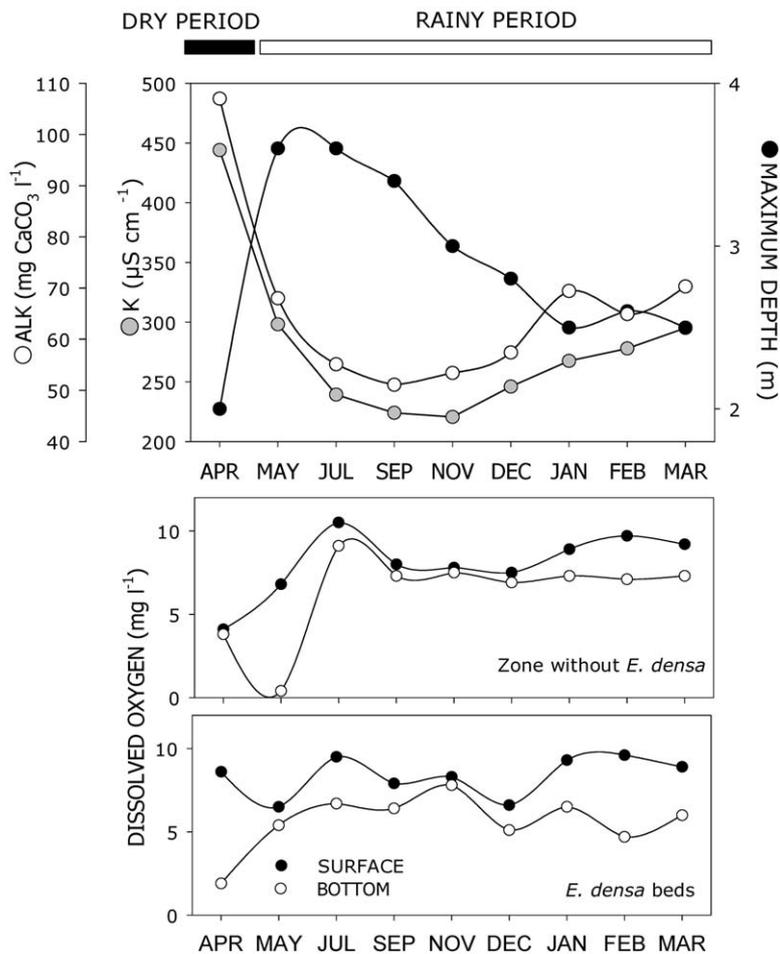
Figure 2. Temporal variation of water level (expressed as maximum depth), ALK, and K, considering the average for the zones with and without *E. densa* (above). Temporal pattern of DO at surface and bottom in each sampling zone (below).
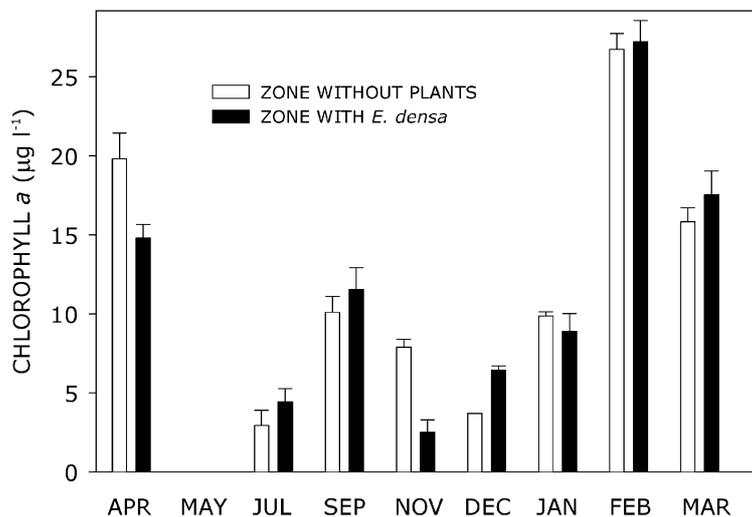

Figure 3. Temporal variation of phytoplankton biomass (Chl-*a*) in open waters and *E. densa* beds.

Table 1. Mean and range values of physical and chemical variables, and 2-way repeated-measures ANOVA results (factors: sites and time), stating *F* values with degrees of freedom, and probability values. The abbreviations E and WE indicate *E. densa* and open water zone, respectively

	WE	E	Sites	Time	Sites × Time
T (°C)	19.7	20.0	$11.4_{(1,8)}$	$1652.0_{(8,64)}$	$8.0_{(8,64)}$
	10–28	10–27.5	$p < 0.01$	$p < 0.001$	$p < 0.001$
			E > WE		
K (μS cm^{-1})	278	279	NS	$8808_{(8,64)}$	$43.3_{(8,64)}$
	214–473	213–437		$p < 0.001$	$p < 0.001$
ALK (mg CaCO$_3$ l^{-1})	66.1	66.2	NS	$6015_{(8,64)}$	$17.7_{(8,64)}$
	50.2–108.4	50–109.4		$p < 0.001$	$p < 0.001$
pH	7.4	7.4	NS	$442.6_{(8,64)}$	$26.4_{(8,64)}$
	6.6–8.4	6.8–8.3		$p < 0.001$	$p < 0.001$
DO (% SATURATION)	81	79	NS	$31.8_{(8,64)}$	$6.3_{(8,64)}$
	2.2–119.9	16.9–176.6		$p < 0.001$	$p < 0.001$
CDOM (nm^{-1})	6.1	6.2	NS	$839.1_{(7,63)}$	$2.6_{(7,63)}$
	3.8–8.6	3.8–8.7		$p < 0.001$	$p < 0.02$
TSS (mg l^{-1})	6.8	10.1	$19.4_{(1,8)}$ $p < 0.01$	$3.6_{(8,64)}$	NS
	1.4–15.0	2.5–40.5	E > WE	$p < 0.01$	
TP (μg l^{-1})	64	76	$19.8_{(1,8)}$ $p < 0.01$	$50.8_{(8,64)}$	$3.5_{(8,64)}$
	25–230	31–215	E > WE	$p < 0.001$	$p < 0.01$
SRP (μg l^{-1})	9	9	NS	NS	NS
	0–34	0–44			
TN (μg l^{-1})	726	766	$6.3_{(1,8)}$ $p < 0.05$	$22.9_{(8,64)}$	$2.5_{(8,64)}$
	278–1273	287–1595	E > WE	$p < 0.001$	$p < 0.02$
N-NH$_4^+$ (μg l^{-1})	40	35	$10.5_{(1,8)}$ $p < 0.01$	$466.9_{(8,64)}$	$24.7_{(8,64)}$
	0–217	0–189	E < WE	$p < 0.001$	$p < 0.001$
N-NO$_3^-$ (μg l^{-1})	76	80	$16.4_{(1,8)}$ $p < 0.01$	$763.4_{(8,64)}$	$5.2_{(8,64)}$
	10–250	33–245	E > WE	$p < 0.001$	$p < 0.001$
RSi (mg l^{-1})	3.1	2.8	$6.2_{(1,8)}$ $p < 0.05$	$1366.2_{(8,64)}$	NS
	1.1–4.5	1.1–4.4	E < WE	$p < 0.001$	
Chl-*a* (μg l^{-1})	11	10	NS	$159.1_{(8,64)}$	$4.8_{(8,32)}$
	0–28	0–29		$p < 0.001$	$p < 0.001$

the mean values 40%, 2.0 and 20.3 mg g^{-1} DW, respectively, in the *E. densa* beds, and 40%, 2.6 and 20.1 mg g^{-1} DW in the open water zone. A significant difference between zones was observed only for phosphorus (ANOVA $F_{(1,8)} = 182$, $p < 0.001$).

Plankton communities

The phytoplankton community was highly diverse and presented low to moderate biomass (as Chl-*a*) (Table 1, Fig. 3), which was linearly correlated with abundance in terms of biovolume. Picoplankton was numerically the most abundant group. Cyanobacteria generally showed the highest biovolume, except during spring when chlorophytes dominated the system.

There were nineteen different functional groups or associations (*sensu* Reynolds et al., 2002) characteristic of different trophic states. Associations from nutrient-poor lakes, such as **Z** (picoplankton) or **A** (*Mallomonas* spp.), to **F** (colonial chlorophytes, such as *Oocystis parva* W. & G.S. West), **X$_2$** (*Monoraphidium contornum* (Thuret) Kom. & Legn.), **H** (nitrogen-fixer cyanobacteria, such as *Aphanizomenon gracile* Lemmermann), or **L$_M$** (*Microcystis* spp.), typical of eutrophic conditions, were found. Despite the important temporal variation, there were non-significant differences in the composition and abundance of taxa or associations between zones. Chl-*a* presented statistically significant differences between sampling zones in some months (Table 1, Fig. 3), especially in April
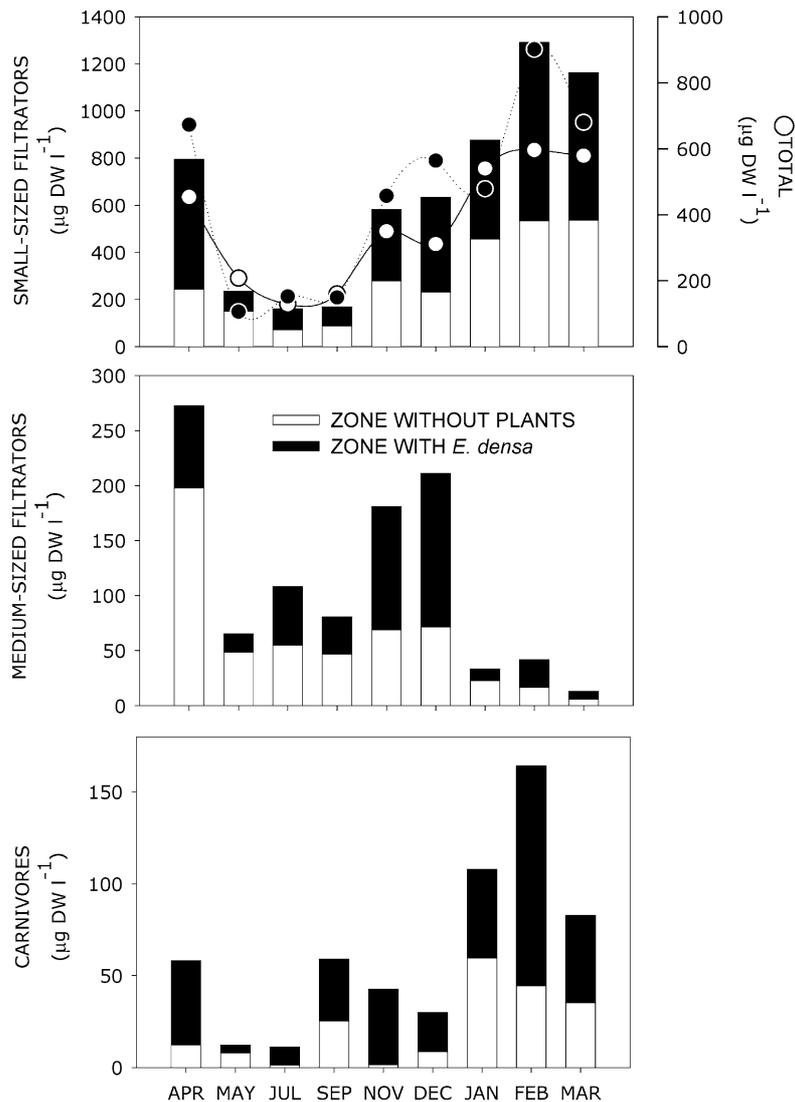
Figure 4. Spatial and temporal distribution of the biomass of total and main zooplankton groups, according to size and feeding behaviour: small-sized filtrators (rotifers + nauplii, above), medium-sized filtrators (calanoid copepods + cladocerans, middle), carnivores (cyclopoid copepods, below). Total zooplankton biomass in dots (above).

and November when the lowest values were found within *E. densa* beds.

Zooplankton community comprised 25 taxa of rotifers, three of copepods, and five of cladocerans. Only three species were collected exclusively within *E. densa* beds; *Platyias quadricornis* Ehrenberg, *Euchlanis dilatata* Ehrenberg, and *Trichotria tetractis* Ehrenberg (all rotifers). The minimum and maximum biomasses (Fig. 4) and abundances were registered in July and February, respectively. Copepods (*Notodiaptomus incompositus* Brian, *Mesocyclops longisetus* Thiébaud, and *Metacyclops mendocinus* Wierzejski)

generally dominated zooplankton community in terms of biomass, except in March 2001 when rotifers predominated. Cladocerans (*Bosmina longirostris* Müller, *Dunhevedia odontoplax* Sars, *Pleuroxus quasidenticulatus* Birge, *P. similes* Vávra, *Ceriodaphnia dubia* Richard, *Moina micrura* Kurz, *Diaphanosoma birgei* Korineck, and *Chydorus spp.*) were the second group in terms of biomass from May to December, but the abundance decreased drastically in summer. Biomass differed significantly between zones in the case of rotifers, cyclopoids, nauplii, and total zooplankton, all with higher values within submerged plants
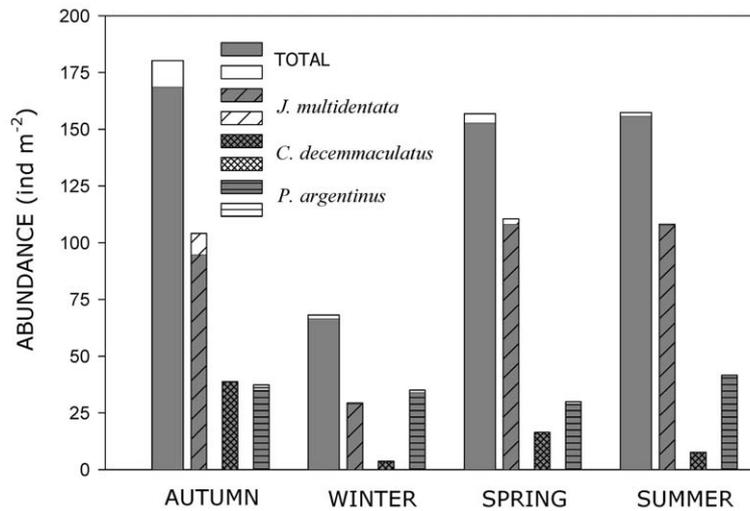
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Figure 5. Spatial distribution and seasonal variation of the abundance of fish and shrimp. Littoral zone (including *E. densa* beds) data are shaded, and open water data are clear patterns on top of each bar.

(Table 2). The medium-sized herbivores (calanoids and cladocerans) showed significant differences when the interactions site × time were considered. Calonoids presented higher biomass in *E. densa* beds during late spring (November and December), the same for cladocerans during autumn and summer (April and December). The vertical distribution of all groups and taxa (except nauplii) indicated a preference for middle and bottom depths during midday (Table 2).

Nekton communities

Lake Blanca presented only two fish species of Cyprinodontiforms, *Cnesterodon decemmaculatus* Jenyns (Poecilidae) and *Jenynsia multidentata* Jenyns (Anablepidae). Besides, one shrimp (*Palaemonetes argentinus* Nobili) species was also collected (Fig. 5). The average biomass and density of the fish community were 115 kg ha^{-1} and 13 ind m^{-2}, while the shrimp biomass and density were 13 kg ha^{-1} and 5 ind m^{-2}. The highest and lowest fish biomasses were collected in spring and winter, respectively. Despite the fish biomass difference between spring and summer, total abundance did not differ (Fig. 5). Open water and littoral area differed importantly, as the highest abundance was registered for both total fish (98.6%) and total shrimp biomass (95.3%) in the littoral zones, preferentially associated with *E. densa*. Temporal analysis of fish size showed that *J. multidentata* had various reproductive events between spring and autumn.

Juvenile *C. decemmaculatus* individuals (<2 cm TL) were observed in summer and autumn, while the reproductive period of *P. argentinus* occurred only in summer.

Interactions

The most important differences of algal biomass between zones coincided with a high herbivorous zooplankton biomass in November (principally of calanoids) and April (principally of cladocerans). During April, in addition, the plants occupied the entire water column. Temporal changes in phytoplankton biomass were positively correlated with the biomass of rotifers and cyclopoids ($rs = 0.72$, $p < 0.05$; $rs = 0.85$, $p < 0.01$, respectively). The temporal pattern of cladocerans and calanoids was very similar ($rs = 0.71$, $p < 0.05$). In the zone without *E. densa*, these relationships were either not significant or with weaker correlations. The decrease of herbivorous zooplankton biomass during summer (Fig. 5) coincided with the appearance of 0^+ fish and juveniles of shrimp *P. argentinus*, and with the predominance of cyanobacteria within the phytoplankton community.

Table 2. Results of 3-way repeated-measures ANOVA on main zooplankton group biomasses for site, depth, and time effects, stating F values with degrees of freedom, and probability, of main factors and interactions

	Sites (S)	Depth (D)	Time (T)	S × D	S × T	D × T	S × D × T
Rotifers	$101.6_{(1,12)}$ $p<0.001$ E>WE	$41.8_{(2,12)}$ $p<0.001$ B>M>S	$1178.1_{(8,96)}$ $p<0.001$	$16.2_{(2,12)}$ $p<0.001$	$21.7_{(8,96)}$ $p<0.001$	$8.8_{(16,96)}$ $p<0.001$	$7.3_{(16,96)}$ $p<0.001$
Cyclopoids	$51.9_{(1,12)}$ $p < 0.001$ E>WE	$254.7_{(2,12)}$ $p < 0.001$ B>M>S	$83.2_{(8,96)}$ $p < 0.001$	$37.6_{(2,12)}$ $p < 0.001$	$12.1_{(8,96)}$ $p < 0.001$	11.5 $_{(16,96)}$ $p < 0.001$	$6.6_{(16,96)}$ $p < 0.001$
Calanoids	NS	$50.0_{(2,12)}$ $p < 0.001$ B>M>S	$59.6_{(8,96)}$ $p < 0.001$	NS	$4.9_{(8,96)}$ $p < 0.001$	15.5 $_{(16,96)}$ $p < 0.001$	$3.9_{(16,96)}$ $p < 0.001$
Nauplii	$23.5_{(1,12)}$ $p < 0.001$ E>WE	NS	$37.2_{(8,96)}$ $p < 0.001$	$42.3_{(2,12)}$ $p < 0.001$	$9.3_{(8,96)}$ $p < 0.001$	$5.1_{(16,96)}$ $p < 0.001$	$11.0_{(16,96)}$ $p < 0.001$
Cladocerans	NS	$33.8_{(2,12)}$ $p < 0.001$ (BM)>S	$44.9_{(8,96)}$ $p < 0.001$	NS	$5.3_{(8,96)}$ $p < 0.001$	$9.4_{(16,96)}$ $p < 0.001$	$4.0_{(16,96)}$ $p < 0.001$
Total Zooplankton	$10.5_{(1,12)}$ $p<0.01$ E>WE	$25.5_{(2,12)}$ $p < 0.001$ (BM)>S	$94.4_{(8,96)}$ $p < 0.001$	$20.4_{(2,12)}$ $p < 0.001$	$4.8_{(8,96)}$ $p < 0.001$	$8.2_{(16,96)}$ $p < 0.001$	$3.9_{(16,96)}$ $p < 0.001$

Abbreviations: E and WE indicate *E. densa* beds and open water zone, respectively; B, M, S indicate water depth (bottom, middle, and surface); NS= not significant difference. Sites and depths are ranked by the higher mean values, according to *post hoc* tests

Discussion

Temporal variation and spatial distribution of Egeria densa

Egeria densa shows active growth phases within a temperature range between 10 to 30 °C (Getsinger & Dillon, 1984). In the subtropical and tropical latitudes, *E. densa* biomass would not have a bimodal pattern as in temperate regions (Haramoto & Ikusima, 1988), but the active growth would be maintained all year, with maximum biomass values in summer (Feijoó et al., 1996). We found the same pattern and the morphological attributes corresponding with the summer type described for the temperate zones.

The euphotic zone depth suggested that light did not limit the occurrence and growth of *E. densa* in Lake Blanca. The dense canopy of *E. densa* on the surface (during autumn 2000), and its associated effects, were promoted mainly by water level decrease and not by light availability in the water column. Nutrient limitation would play a secondary role in eutrophic systems (Barko & Smart, 1980), such as Lake Blanca, as the high nutrient load, in this case associated with the sediment, can support a very high plant biomass.

The continuous mixing of the water column, the fluffy sediment, and the poor root system of *E. densa*, caused its drifting and the spatial pattern directed by strong or predominant winds.

Effects of Egeria densa on physical and chemical features of water and sediment

The nutrient uptake by the submerged plants and their associated epiphytes can explain the lower $N\text{-}NH_4^+$ and RSi in *E. densa* beds. We calculated that nutrients stored in macrophyte tissues represented an equivalent to 64% of total phosphorus and 75% of total nitrogen in the water column, excluding the sediment load. Similar values were found during the rapid growth period of *Elodea* in Lake Zwemlust (van Donk & Gulati, 1995).

The higher amount of suspended matter within *E. densa* beds seemed to be associated with a major retention of particulate matter on submerged plants that were collected by the water pump during the sampling process, therefore producing the higher TN and TP detected within *E. densa* zone.

Sediment phosphorus concentration was lower beneath *E. densa*. Evidence indicates that rooted submerged macrophytes, even with relatively tiny root systems, can lead to significant depletion of pools of P in the sediment (Barko & James, 1998). Canopy-forming macrophyte types, such as *Elodea* or *Egeria* spp., may generate more or less anoxic conditions at the bottom. Therefore, the potential for phosphorus release from the sediment is increased, particularly where iron-bound and redox-sensitive phos-

phorus constitute a significant part of the TP in the sediment (Søndergaard & Moss, 1998). The negative relationships between SRP and DO observed in Lake Blanca confirm the occurrence of this mechanism. This was evident when *E. densa* reached the surface and an oxygen deficit in the water column was promoted, even at midday. In addition, phosphorus release can occur at high pH, under aerobic conditions, by replacement of $PO4^{-3}$ with OH^- on iron or aluminium oxides (Barko & James, 1998). In low water level periods, before our study, the water supply company registered pH values near 9.0. We did not observe the lower nitrogen concentrations expected in the sediment of *E. densa* beds, determined by plant uptake and enhanced denitrification. We recorded an increase of nitrogen content in the sediment (both sites analysed), suggesting on the contrary the occurrence of nitrification process. The higher concentrations of $N-NO_3^-$ during the high water level, compared with $N-NH_4^+$, are in close agreement with this hypothesis.

There were considerable changes associated with the water level fluctuation, which even overcame differences promoted by the presence of *E. densa* beds. The increased level led to a dilution process that explained the temporal pattern of ALK and K. This dilution process conditioned also the decrease of SRP, $N-NH_4^-$, $N-NO_3^-$, RSi, and CDOM and the increase of the oxygen reserve.

Effects of Egeria densa *on plankton and nekton*

The effects of macrophytes on phytoplankton extend to biomass, species size, and composition (Søndergaard & Moss, 1998). The general tendency, also found in Lake Blanca during the first part of this study, is a predominance of picoplankton and flagellates in the presence of macrophytes and/or of large-sized zooplankton (Søndergaard & Moss, 1998). Small organisms with low sinking rates are favoured in shallow waters (Balls et al., 1989), while flagellates are better adapted to exploit a heterogeneous and structured environment with respect to nutrient patches, such as that created by macrophytes (Sommer, 1988). The increase and predominance of cyanobacteria during the second part of the study coincided with higher temperatures, lower availability of SRP, and lower abundance of herbivorous mesozooplankton, which does not allow us to identify the main mechanism behind this pattern.

Two processes could explain the lack of differences in the phytoplankton community between zones: (a) the area colonised by *E. densa* was very extensive and the effects were observed in the whole system, but not at the scale analysed; and (b) the water exchange (wind-induced and convective circulation) between zones with and without plants decreased otherwise larger differences.

Considering the spatial distribution of zooplankton and differences in algal biomass between zones, we hypothesise that *E. densa* acted as a refuge, and also as a feeding zone. Timms & Moss (1984) suggested submerged plants promote the horizontal heterogeneity of zooplankton and changes in their specific composition. The refuge effect for zooplankton seems to be higher in small, dense areas of submerged plants than in large, low-density areas (Lauridsen et al., 1996). The distribution of *E. densa* in Lake Blanca determined different vegetation patches, in terms of size and density, promoting a diverse zooplankton community and a differential use of the space. Evidence from temperate lakes indicates that submerged plants with 15–20% PVI allow large-sized zooplankton to reach high abundance despite fish presence (Schriver et al., 1995). However, the refuge capacity of aquatic plants depends on their abundance and also on the density of planktivorous fish (Wojtal et al., 2003). Schriver et al. (1995) and Jacobsen et al. (1997) demonstrated experimentally that submerged plants lose the refuge capacity when planktivorous fish density is higher than 2–5 ind m^{-2}. For natural systems, Perrow et al. (1999) suggested that the density of submerged plants capable of offering refuge for zooplankton depends strongly on the food regimen of the most abundant fish, and a PVI higher than 70% may sometimes be necessary for the refuge effect to occur. The fish and shrimp found in Lake Blanca are omnivorous species that predate actively on medium and large zooplankton (Collins, 1999; Mazzeo et al., unpubl. data). The abundance, food preferences, and spatial use of fish and shrimps, as well as the PVI of *E. densa*, determined that the refuge capacity for calanoids and cladocerans was not enough during summer, when most 0^+ fish appeared. The preference of fish and shrimps for *E. densa* beds and littoral areas in the absence of piscivorous fish, suggest this habitat use was mainly determined by food availability.

Final remarks

Lake Blanca is a hypertrophic system in a clear water phase (DS > 1 m), with lower phytoplankton biomass than expected according to the nutrient con-

centrations in the water. The water colour, CDOM levels, sediment characteristics, and some biological indicators, suggest a tendency to dystrophy, especially during low water level periods. The predominance of flagellates and picoplankton, and the occurrence of *Bosmina longirostris*, *Trichocerca similis* Wierzejski, and *Aneuropsis fissa* Gosse in this lake, are frequent attributes of humic systems (Arvola et al., 1999; Sarvala, 1999). Besides the usually described nutrient and light limitation of algae by submerged plants, the internal production of humic substances could enhance the observed top-down effects on phytoplankton, as these substances affect nutrient and light availability in the water column (Hessen & Tranvik, 1998).

Considering the main purpose of this system, the El Niño event of 1995–1997 can be regarded as a positive switch that promoted the dominance of submerged plants (see: Coops et al., 2003). However, the lack of piscivorous fish and the high internal nutrient load could be key factors in the re-establishment of a turbid phase. The control of both factors therefore acquires great importance for Lake Blanca management.

Acknowledgements

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