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Biomass, composition and size structure of invertebrate communities associated to different types of aquatic vegetation during summer in Lago di Candia (Italy)

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ABSTRACT

*We compared the biomass, taxonomic composition, and size distribution of invertebrates associated to emergent (*Schoenoplectus lacustris*), submerged (*Myriophyllum spicatum*), and floating leaved (*Trapa natans*) vegetation at two depths (surface and water column) during summer in Lago di Candia, Italy. Invertebrate biomass was positively related to epiphyton biomass (Chl-*a*).* M. spicatum *supported higher invertebrate biomass per unit of plant weight than* S. lacustris *whereas* T. natans *was somewhat intermediate. Depth did not affect invertebrate biomass significatively. Surface sections of* M. spicatum *and* T. natans *supported invertebrate communities with similar taxonomic composition dominated by oligochaetes and ostracods. Large hirudineans and gastropods characterized the communities on the water column sections of* M. spicatum. S. lacustris *and the water column sections of* T. natans *(composed of stems and aquatic roots) were supporting invertebrate communities dominated by copepod nauplii and lacking large organisms. Changes in aquatic vegetation in Lago di Candia following harvesting of* T. natans *and removal of submerged vegetation by the invasion of the rodent coypu (*Miocastor coypus*) may affect the invertebrate biomass of its littoral zone.*

Key words: phytophilous invertebrates, epiphyton, Trapa natans*,* Schoenoplectus lacustris*,* Myriophyllum spicatum

1. INTRODUCTION

Aquatic vegetation in lake littoral zone represents a complex habitat, which offers support, protection and food to aquatic fauna. High invertebrate densities and biomasses are often associated to extensive and diversified aquatic vegetation (Crowder & Cooper 1982; Gilinsky 1984; Diehl 1992).

Because of their differing architecture, aquatic plants can support invertebrate communities varying in biomass, size structure and taxonomic composition (Dvořak & Best 1982; Cyr & Downing 1988; Hanson 1990; Feldman 2001; Cheruvelil *et al*. 2002). Plants with dissected leaves may favour invertebrates by offering support and protection against predators. Furthermore, a dissected substratum may represent a better food source for invertebrates than morphologically simple plants because of its larger surface colonized by epiphyton. Plant architecture can also influence the phytophilous invertebrates by affecting light penetration and dissolved oxygen in the water column (Caraco & Cole 2002).

Several fish species live among the littoral vegetation where they can reduce their risk of predation by piscivorous fish and feed on phytophilous invertebrates (Crowder & Cooper 1982; Gilinsky 1984; Mittlebach 1988). Because littoral zone invertebrates play a key role in the energy transfer from primary producers to fish (Boisclair & Leggett 1985) it is important to study their response to vegetation alterations.

During summer, three types of vegetation grow side by side in the littoral zone of Lago di Candia, a small lake in northern Italy: the emergent *Schoenoplectus lacustris*, the submerged *Myriophyllum spicatum*, and the floating-leaved *Trapa natans* (water chestnut). While *S. lacustris* is constituted of a unique stem, the architecture of *M. spicatum* is much more complex with secondary ramifications that increase the plant surface/mass ratio. *T. natans* morphology varies with depth. Leaf rosettes form a dense canopy at the water surface hindering light penetration. Underneath the canopy, in the water column, *T. natans* presents stems with much dissected aquatic roots.

The composition of the aquatic vegetation of Lago di Candia underwent important modifications during the past two decades. A selective harvest of *T. natans* was initiated in 1986 as part of a biomanipulation project to counteract eutrophication by reducing internal nutrient loading (Galanti *et al*. 1990). Following this harvest and in consequence of a marked increase in water transparency, submerged macrophytes, particularly *Ceratophyllum demersum* and *Najas marina*, colonized some space previously occupied by *Trapa natans* and expanded their presence to deeper sites (Giussani *et al*. 1997; Cattaneo *et al*. 1998). Submerged vegetation reached its maximum expansion in 1995 and then started to decrease dramatically in coincidence with the invasion of the lakeshore by the rodent *Miocastor coypus* (coypu) and, possibly, with the increase of grazing water fowls. At the time of our study, *C. demer-*

sum and *N. marina* were absent whereas the cover of *M. spicatum* and *T. natans* was considerably reduced. On the contrary, emergent (*S. lacustris*) and other floating-leaved plants (*Nymphaea alba*, *Nymphoides peltata* and *Nuphar luteum*) were not affected, probably because less palatable to this rodent and to water fowl.

If invertebrate communities colonizing different types of macrophytes vary in quantity and quality, previous and future changes in the littoral vegetation of Lago di Candia, may have important impacts on the lake littoral food webs. Thus, better assessment of changes in phytophilous invertebrate in response to variations in littoral vegetation is needed. This study aims to test if phytophilous invertebrates were affected by the architecture of the host plants co-occurring in Lago di Candia during summer in which macrophytes reach their highest biomass. To this end, we compared biomass, size structure and taxonomic composition of the invertebrate communities associated to emergent, submerged and floating-leaved plants. We also measured epiphyton biomass associated to these three types of vegetation because epiphyton is an important resource for phytophilous invertebrates and thus likely to explain a significant part of their variation.

2. METHODS

2.1. Study site

Lago di Candia is a small (1.52 km^2) eutrophic lake of Northern Italy (45°19'N, 7°54'E). The limnological characteristics of Lago di Candia vary very little spatially and are indicative of a lightly alkaline system, well mineralized and rich in nutrients (phosphorus and nitrogen) (Giussani *et al.* 1997 and Tab. 1). At sampling, we measured water physical and chemical characteristics near each vegetation type. Subsurface water samples were collected for laboratory measurements of pH, conductivity (reference temperature 20 °C), total nitrogen (TN; Valderrama 1981), total phosphorus (TP; Valderrama 1981), and phytoplankton chlorophyll a (Chl-*a*). Temperature was measured *in situ* with a temperature probe LAB90. Light extinction profiles were obtained by measuring light intensity between 400 and 700 nm (PAR radiation) at different depths using a LI-COR LI-192 SB.

Tab. 1. Limnological characteristics of Lago di Candia. Chemical and biological variables were measured near the three types of vegetation on July 17th, 2001.

Variable	*S. lacustris*	*M. spicatum*	*T. natans*
Temperature (°C)	26.1	26.1	27.0
pH	7.58	7.83	7.78
Conductivity (µS cm^{-1})	113.9	113.9	114.2
Total N (mg l^{-1})	0.71	0.68	0.78
Total P (µg l^{-1})	32	32	44
Phytoplankton Chl-*a* (µg l^{-1})	11.8	11.3	11.7

2.2. Experimental design

Sampling occurred on July 17th and 18th, 2001, coinciding with the period of maximum plant biomass. *S. lacustris* and *M. spicatum* are perennials, while *T. natans* is an annual that germinates by seeds in late April and completely disappears in November (Galanti *et al.* 1990). The three types of vegetation were sampled in three pure stands that were located at a distance of about 40 m from each other. A previous study (Cattaneo *et al.* 1998) found that spatial differences in algal and invertebrate littoral communities are small around this lake. *M. spicatum* and *T. natans* were sampled near the surface (surface) and in the water column at an approximate depth of 1.5 m (deep). The emergent *S. lacustris*, present only in shallow water, could be sampled only near the surface. The depth comparison was particularly relevant for *T. natans* because its morphology near the surface, mainly composed of leaf rosettes, differs greatly from its morphology below the canopy characterized by stems and aquatic roots.

2.3. Sampling of vegetation for epiphyton analyses

Five sections (replicates) of plant, chosen haphazardly, were cut underwater with scissors and gently brought to the surface taking care not to disturb the biofilm on the plants. Epiphyton was separated from the plant by vigorously shaking the plant fragments for 1 min in a 2-l plastic bottle containing 1.2 l of tap water. A volume of the epiphyton suspension, varying between 25 and 70 ml, was filtered through Whatman GF/C glass fiber filters for Chl-*a* determination. Chl-*a* was analyzed by spectrophotometry after overnight extraction with 95% ethanol in the dark. Chl-*a* calculations were performed as in Bergman & Peters (1980). The plants were dried at 105 °C for 24 h in an oven for dry mass determination. Epiphyton biomass is expressed as Chl-*a* per substratum dry weight (µg g^{-1} d.w. vegetation).

2.4. Sampling of vegetation for invertebrate analyses

For each vegetation type and depth, a diver collected five replicate samples by closing a Plexiglas box (5.7 liters) around the vegetation (Downing & Cyr 1985). This device allowed to sample quantitatively all invertebrates including those loosely associated with the vegetation. The entire content of the sampler was emptied in a 10-l plastic container and vigorously agitated for 1 min to dislodge the invertebrates. The water was then filtered on a 63 µm mesh sieve to retain invertebrates and plant fragments. The invertebrates were preserved in 70% ethanol for taxonomic analyses. The plants were dried in an oven at 105 °C for 24 h for dry mass determination.

Tab. 2. Light extinction profiles in the three macrophyte stands for July 17th and 18th, 2001. [a]: Light underneath leaf canopy; [b]: Light outside macrophyte stand; *: % of incident light was measured immediately below the surface of the water.

Depth (m)	July 17th, 2001			July 18th, 2001		
	S. lacustris	*M. spicatum*	*T. natans*	*S. lacustris*	*M. spicatum*	*T. natans*
Surface*	0.773	0.649	0.127[a]	0.174	0.675	0.614[b]
0.5	0.032	0.127	0.021	0.025	0.068	0.052
1.0		0.027	0.014		0.020	0.014

2.5. *Invertebrate taxonomic analyses and biomass determination*

In the laboratory, invertebrates were separated by sieving into two size fractions (63-400 µm and >400 µm) to facilitate sorting. Invertebrates were counted, measured and identified to major groups or family under a binocular at 16, 40 or 50× magnification. When invertebrate samples were very rich (>500 individuals), we analyzed sub-samples. The size of these sub-samples was established so that at least 150 individuals of the most abundant taxonomic groups were counted. Individual dry weight was estimated from body length, using various length-weight equations from the literature (Eckblad 1971; Dumont *et al.* 1975; Mason 1977; Tudorancea *et al.* 1979; Smock 1980; Rosen 1981; Peters & Downing 1984; Burgherr & Meyer; 1997; Benke *et al.* 1999). Besides expressing invertebrate biomass per plant dry weight (mg g^{-1} d.w.), we expressed it per water volume (mg l^{-1}) to better compare among samples the invertebrates that are not directly attached to the vegetation.

2.6. *Statistical analyses*

One-way analyses of variance, followed by Tukey multiple comparison tests, were conducted to compare total invertebrate biomass and epiphyton Chl-*a* among the three types of vegetation and the two depths (surface and water column). A simple regression analysis was performed to evaluate the relationship between epiphyton Chl-*a* and total invertebrate biomass. Prior to analyses, invertebrate biomass and epiphyton Chl-*a* were log-transformed to stabilize the variance. Statistical analyses were performed using the analytical software Statistix for Windows version 2.0 (Analytical Software, Tallahassee, Fl.).

To examine differences in invertebrate taxonomic composition among vegetation types and depth, we used ordinary principal components analysis with centering by species (CANOCO for Windows, version 4; ter Braak & Šmilauer 1998). Prior to analysis, values of invertebrate biomass were transformed to Hellinger distances to make them usable in linear analyses as suggested in Legendre & Gallagher (2001).

Invertebrates were grouped in logarithmically (Log_2) increasing size classes to examine the size distribution of the communities.

3. RESULTS

3.1. *Physical and chemical characteristics*

Physical and chemical characteristics measured near the three types of vegetation were similar (Tab. 1) but light extinction varied (Tab. 2). Light penetration below the leaf rosettes of *T. natans* was lower than in free water among stands of *M. spicatum* or *S. lacustris*. This difference is likely related to the denser canopy formed by the thick floating leaves of *T. natans*. The low light penetration observed in stands of *S. lacustris* could be a consequence of shading by the emergent portion of this plant.

3.2. *Epiphyton and total invertebrate biomass*

Epiphyton biomass (as Chl-*a*) was significantly higher on *M. spicatum* than on *S. lacustris* and *T. natans*, which were not significantly different (Fig. 1). On *T. natans*, epiphyton Chl-*a* was significantly higher on the stems and aquatic roots in the water column than on the floating leaves at the water surface. *M. spicatum* showed no significant depth variation in epiphyton Chl-*a*.

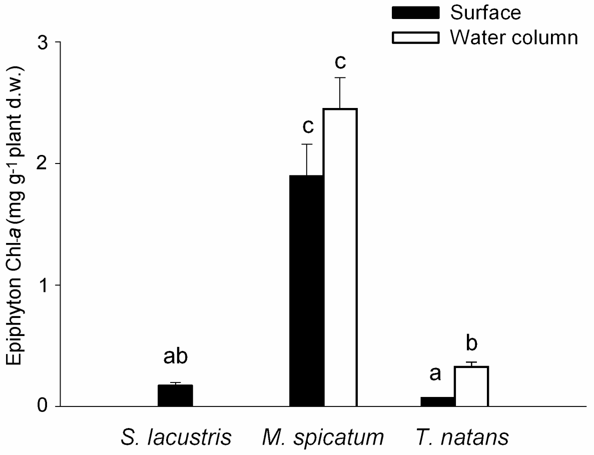

Fig. 1. Epiphyton Chl-*a* associated to the three macrophytes, at the water surface and in the water column. Bars represent mean values (n = 5) with standard errors. Bars marked with different lower-case letters are significantly different from each other (ANOVA followed by Tukey multiple comparison tests, $p < 0.01$).

In general, variation patterns in total invertebrate biomass (mg g^{-1} plant d.w.) agreed with those observed

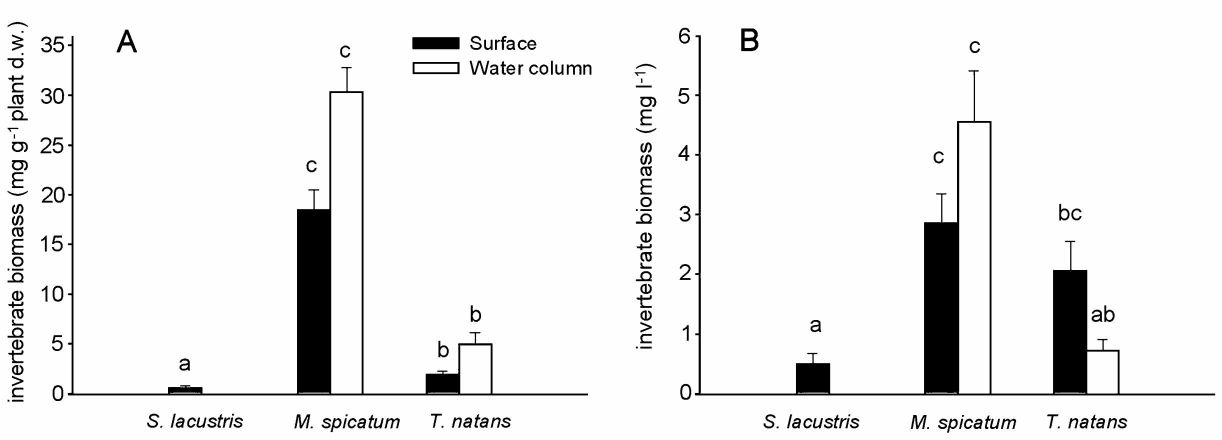

Fig. 2. Invertebrate biomass associated to the three macrophytes, at the water surface and in the water column. Values are expressed as mg g^{-1} plant d.w. (panel **A**) and as mg l^{-1} (panel **B**). Bars represent mean values (n = 5) with standard errors. Bars marked with different lower-case letters are significantly different from each other (ANOVA followed by Tukey multiple comparison tests, $p < 0.01$).

for epiphyton Chl-*a* (Fig. 2A). *M. spicatum* supported about 30 times more invertebrate biomass than *S. lacustris*. Biomass on *T. natans* was significantly higher than on *S. lacustris* but represented less than 1/7 of the biomass on *M. spicatum*. For both *M. spicatum* and *T. natans*, depth had no significant effect on total invertebrate biomass. When data were expressed per liter of water (Fig. 2B), the differences among vegetation were somewhat less striking but still significant. Highest biomass was on *M. spicatum* and lowest on *S. lacustris*. Biomass on *T. natans* was intermediate: values at the surface were not significantly lower than on *M. spicatum* and values in the water column were not significantly higher than on *S. lacustris*.

When all type of vegetation were considered, there was a close coupling between epiphyton Chl-*a* and invertebrate biomass that were significantly positively correlated (Fig. 3A, equation 1). Inspection of the scatter plot suggested that invertebrate biomass observed on *S. lacustris* were lower than expected from this general relationship. An analysis of the residuals (ANOVA followed by Tukey multiple comparisons) of the regression between epiphyton and invertebrate biomass confirmed that residuals for *S. lacustris* were significantly different from residuals for the other plants (Fig. 3B). Omitting these outlier values, we recalculated the regression between epiphyton chlorophyll and invertebrate biomass (Fig. 3A, equation 2), which presented less scatter than the regression calculated using all data (Fig. 3A, equation 1).

3.3. Invertebrate taxonomic composition

Typical macrobenthic taxa like ostracods, annelids, gastropods, and several insect larvae, with the predominance of chironomids, were abundant in the phytophilous invertebrate communities. However, a significant portion of the biomass was represented by microcrustaceans, mostly copepods but also cladocerans, that are more loosely associated to the vegetation. The dominant invertebrate groups varied depending on macrophyte type and depth (Tab. 3). Copepod nauplii dominated the communities on *S. lacustris* (33% of total biomass) and on *T. natans*-deep (31%). Samples collected on *M. spicatum*-surface and *T. natans*-surface were dominated by Oligochaeta (34% and 32% respectively), whereas Hirudinea were prevalent (34%) in *M. spicatum*-deep samples collected in the water column. A principal components analysis (PCA) showed that invertebrate samples could be differentiated on the basis of their composition (Fig. 4). The first axis of the PCA explaining 40% of the total variance separated the invertebrate samples collected on *S. lacustris* and on the stems and aquatic roots of *T. natans* (right size on Axis I) from all the others (left side on Axis I). These samples were characterized by high percentages of nauplii, Sididae, and chironomids. The second axis, which explained further 18% of the total variance in invertebrate assemblages, separated *M. spicatum*-deep samples characterized by high percentages of Hirudinea and Valvatidae gastropods from samples collected near the surface on *M. spicatum* and *T. natans* dominated by Oligochaeta, and Ostracoda. Some groups are restricted to few samples and separate them from the other replicates. It is the case of a sample of *Trapa*-surface characterized by high percentage of Odonata.

3.4. Invertebrate size distribution

Invertebrate biomass was differently partitioned among size classes depending on the vegetation type (Fig. 5). The smallest size classes (<0.25 µg) were mainly represented by Rotatoria, which, although numerous, constituted <2% of the total biomass everywhere. Invertebrates in the size class 0.5–1.0 µg represented more than 30% of the total biomass of samples of *S. lacustris* and *T. natans*-deep. On the samples at the surface of *M. spicatum* and *T. natans*, the dominant size classes were 2-4 µg and 4–8 µg respectively, which represented close to 30% of the total biomass.

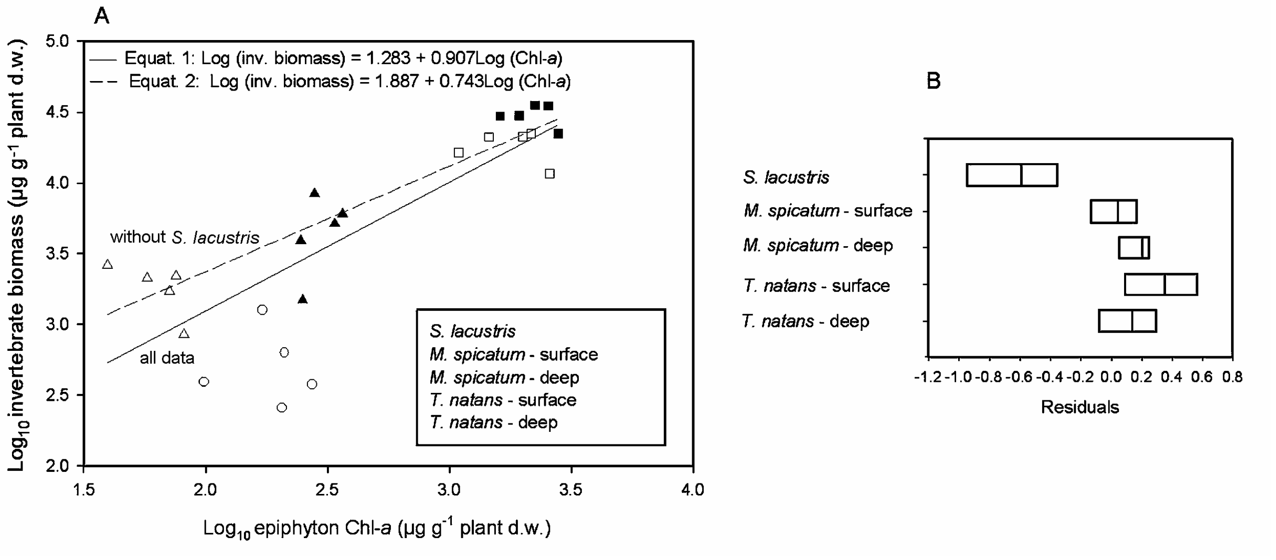

Fig. 3. **A**) Relation between epiphyton Chl-*a* and total invertebrate biomass observed in the three types of vegetation. Regression calculated with all data is represented by the solid line (equation 1: $n = 25$, $r^2 = 0.64$, $F = 42.9$, $p < 0.0001$, residual variance = 0.17). Broken line represents regression calculated excluding the samples collected on *S. lacustris* (equation 2: $n = 20$, $r^2 = 0.83$, $F = 0.96.2$, $p < 0.0001$, residual variance = 0.05). **B**) Box plot of the residuals of above equation 1 observed for the different types of vegetation. The median value for each vegetation type is marked by the central vertical line; 25 and 75-percentile values form the ends of the box.

Tab. 3. Percentage of the total invertebrate biomass represented by the taxa observed on three types of vegetation at different depths in Lago di Candia. Values represent the average, and standard errors are in brackets where n = 5. -: not present; +: percentage <0.1.

Taxon	Code	*S. lacustris*	*M. spicatum*		*T. natans*	
			Surface	Deep	Surface	Deep
Rotatoria	roti	2.4 (0.7)	0.6 (0.1)	1.0 (0.2)	0.6 (0.1)	1.0 (0.3)
Copepoda						
Calanoïda	cala	-	+	+	0.1 (0.1)	2.9 (1.2)
Cyclopoïda	cycl	1.9 (0.2)	4.5 (0.7)	3.2 (0.7)	1.6 (0.4)	4.4 (0.8)
Nauplii	naup	32.9 (13.5)	2.5 (0.8)	1.9 (0.3)	2.6 (1.5)	30.8 (8.5)
Cladocera						
Chydoridae	chyd	1.7 (0.5)	2.3 (0.2)	0.9 (0.2)	2.9 (0.6)	1.9 (0.5)
Daphnidae	daph	-	0.2 (0.2)	+	+	0.3 (0.1)
Sididae	sida	3.1 (1.4)	1.2 (0.4)	0.7 (0.5)	3.2 (1.5)	5.6 (1.7)
Ostracoda	ostr	9.7 (3.0)	26.2 (3.1)	14.3 (3.0)	21.1 (4.5)	10.7 (3.5)
Hydracarina	hydr	4.6 (4.0)	2.6 (1.2)	2.9 (1.0)	0.6 (0.4)	2.1 (0.9)
Annelida						
Hirudinea	hyru	-	11.8 (6.4)	34.1 (9.0)	8.6 (2.8)	2.4 (1.8)
Oligochaeta	olig	19.7 (6.2)	33.9 (2.9)	29.1 (7.7)	32.2 (6.7)	15.7 (3.0)
Gastropoda						
Valvatidae	valv	-	0.7 (0.5)	5.2 (2.6)	0.5 (0.5)	-
Diptera						
Ceratopogonidae	cera	-	-	-	7.2 (2.4)	+
Chironomidae	chir	14.3 (4.6)	4.9 (1.6)	2.3 (0.7)	3.9 (0.4)	5.8 (2.0)
Ephemeroptera	ephe	+	-	-	+	4.2 (3.8)
Hemiptera	hemi	0.1 (0.1)	-	-	0.3 (0.2)	-
Odonata	odon	0.2 (0.1)	-	-	12.3 (8.8)	1.9 (1.2)
Plecoptera	plec	-	4.7 (4.3)	0.1 (0.1)	1.4 (1.3)	0.1 (0.1)
Trichoptera	tric	8.8 (5.0)	3.9 (1.5)	4.0 (3.3)	0.9 (0.3)	10.3 (3.2)
Total biomass (mg g^{-1} plant d.w.)		0.58 (0.18)	18.48 (1.98)	30.35 (2.38)	1.90 (0.30)	4.98 (1.14)
Total biomass (mg l^{-1})		0.49 (0.17)	2.85 (0.49)	4.55 (0.85)	2.06 (0.72)	0.72 (0.18)

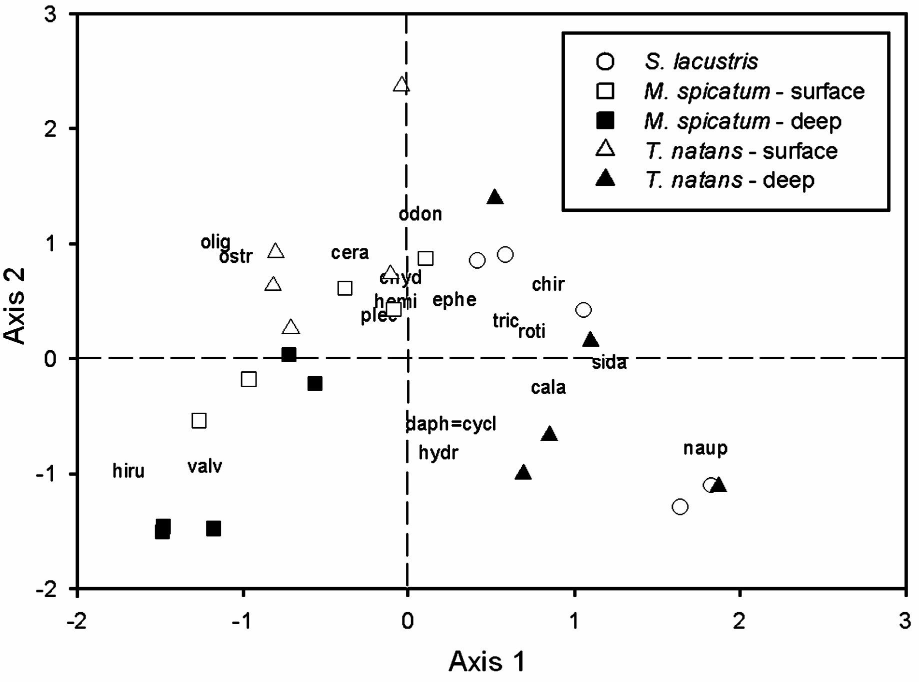

Fig. 4. Positions of samples and invertebrate taxa (codes as in table 3) along the first two axes defined by a principal components analysis.

On the *M. spicatum*-deep samples, there was a peak in percent biomass (30%) corresponding to the size class 125-250 µg. Another major difference in the size structure among vegetation types was the absence of invertebrates in the largest size class (>1 mg) in samples of *S. lacustris* and *T. natans*-deep. While the largest size class of invertebrates associated to *S. lacustris* was 125-250 µg (Hydracarina), surface samples on *M. spicatum* and *T. natans* supported invertebrates in size classes 2000-4000 µg (Plecoptera) and 8000-16000 µg (Odonata), respectively.

4. DISCUSSION

The three types of aquatic vegetation sampled in Lago di Candia had strongly different invertebrate biomass g^{-1} plant d.w. These differences could partly arise from the fact that these plants vary in morphology and thickness and thus offer widely different amount of colonizable surface per unit of plant weight. The simple and thick stems of the emergent *S. lacustris* have a low surface/weight ratio of ~70 cm^2 g^{-1} plant d.w. (G. Galanti, unpublished data). In *T. natans*, surface/weight ratio is low for the leaf rosettes at the surface (160 cm^2 g^{-1}) but very high for stems and aquatic roots found in the water column (1210 cm^2 g^{-1}) (Galanti & Romo 1997). Surface/weight ratios reported in the literature for *M. spicatum* range widely (300-1200 cm^2 g^{-1}) depending on the amount of ramification and possibly on the methods (Cattaneo & Kalff 1980; Sher-Kaul *et al.* 1995; Gosselain *et al.* 2004). These disparities in surface/weight ratios among plant types, although large, are not sufficient to offset the 30-fold difference in invertebrate biomass observed between *M. spicatum* and *S. lacustris*. They could substantially decrease the 9-fold difference between *M. spicatum* and the surface rosettes of *T. natans*, however. Results of quantitative studies of vegetation distribution in aquatic systems are usually expressed as g plant d.w. m^{-2} (e.g. Chambers & Kalff 1985; Duarte *et al.* 1986; Hudon 1997). Consequently, expression of invertebrate biomass per unit of plant d.w. facilitates estimates of areal biomass allowing an assessment of the impact of vegetation modifications on invertebrates.

Because several invertebrates are not directly attached to the substratum, it is meaningful to express invertebrate biomass also per unit of water volume. This alternative expression of the results keeps in account the three dimensional environment in which most aquatic organisms live, including fish. The pattern of highest biomass on *M. spicatum*, lowest on *S. lacustris* and intermediate on *T. natans* observed when expressing data g^{-1} plant d.w. persisted when data were expressed l^{-1}. Our sampling method, which enclosed the plant as well as the surrounding water, and the use of a fine mesh (0.63 µm) allowed including microcrustaceans and rotifers in our study. Meiofauna is not generally considered in studies of phytophilous communities, which address mostly the macroinvertebrates. Nauplii were the most important organisms in this meiofauna reaching similar biomass per unit of volume in all types of vegetation. However, their percentage contribution to total biomass varied from over 30% on *S. lacustris* to 2% on *M. spicatum*.

Taxonomic composition and size structure differentiated samples of *S. lacustris* and *T. natans*-deep from

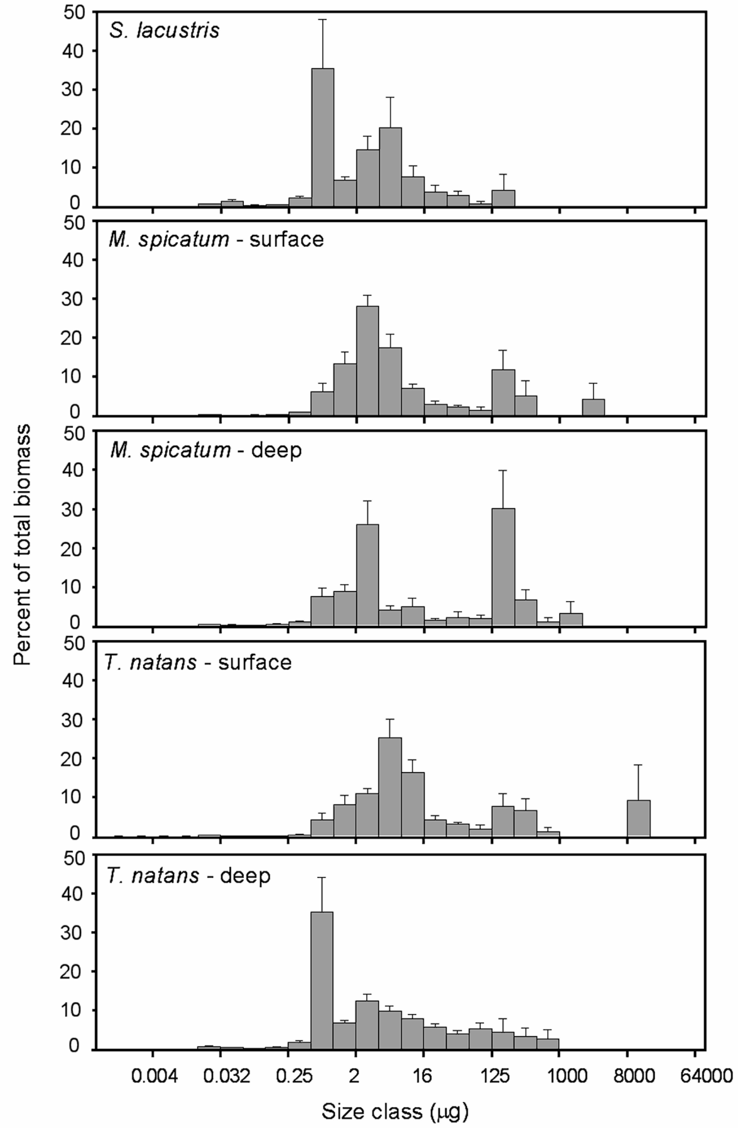

Fig. 5. Percent of total biomass observed in Log_2 size classes of individual d.w. on the three types of vegetation at the surface and in the water column. Bars represent mean values (n = 5) with standard errors.

all the others. Nauplii were the dominant group in these samples whereas the typical and larger benthic invertebrates were much reduced. This similarity is intriguing because the morphology of the simple stems of *S. lacustris* differs from the highly dissected aquatic roots observed in *T. natans*. Reduction of large invertebrates is usually considered as an indication of fish predation (Blumenshine *et al.* 2000). Indeed, on emergent macrophytes, lacking ramifications, leaves, and clumps, large invertebrates may not benefit of sufficient support and refuge against predation. This explanation for the scarcity of large invertebrates, however, applies less well to the relatively complex morphology of *T. natans*-deep. Furthermore, low light penetration under the surface canopy may represent a defense against visual predators like fish. This hypothesis was advanced to explain a slight shift towards large invertebrates observed on *Trapa* but not on *Vallisneria* in the Hudson River (Feldman 2001). Low light levels may limit epiphyton production in *T. natans* and therefore the resources to maintain large invertebrates. On the other hand, invertebrates were not likely to be resource limited on *S. lacustris* because invertebrate biomass was lower than expected from the epiphyton biomass. Different mechanisms, predation, and resource limitation, appear to lead invertebrate communities on *S. lacustris* and *T. natans*-deep towards similar taxonomic composition and size structure.

The effect of depth on the invertebrate communities differed depending on the vegetation. On *M. spicatum*, epiphyton and invertebrate biomass was higher, but not significantly, in the water column than near the surface.

A similar vertical pattern in invertebrate density has been observed on submerged macrophytes in a Sweden lake (Marklund *et al.* 2001). Epiphyte and invertebrate biomass on *T. natans* was lower at the surface than in the water column when results were expressed per unit of plant d.w., but the opposite trend was found when biomass l^{-1} was considered. This divergence is a consequence of the strikingly different vertical morphology of *T. natans*. The sampler included a much higher plant weight when closed around the thick leaf rosettes than when the thin stems and aquatic roots were collected. Similarly, in a previous work on epiphyton on *T. natans* in this lake (Galanti & Romo 1997), epiphyton was highest on aquatic roots when expressed per unit plant weight but it was highest on leaf rosettes when expressed per unit of plant surface.

Samples collected near the water surface on *M. spicatum* and *T. natans* had similarities in invertebrate taxonomic composition and size structure. Ostracoda and Oligochaeta were dominant in both communities. Sections of *M. spicatum*-deep were instead characterized by the dominance of large Hirudinea as well as by a higher biomass of Valvatidae gastropods than in the other samples. Large invertebrates were more important at the surface on *T. natans* but in the water column on *M. spicatum*.

Gastropods and chironomids were the dominant macroinvertebrates on *T. natans* and on submerged plants in a previous study in this lake, which was also conducted in mid-summer (Cattaneo *et al.* 1998). The discrepancy in invertebrate taxonomic composition between the two studies may partly be explained by the different mesh size (300 *versus* 63 µm) altering the relative emphasis on large organisms. Nevertheless, we cannot exclude that the fauna may have changed in the 6-year lapse between the two studies, in which the lake has been perturbed by the invasion of the rodent coypu. Because sampling extended over only a few days in both studies, annual differences in invertebrate seasonal succession may have biased the comparison.

T. natans is a successful invader, which is able to displace the native submerged vegetation (Caraco & Cole 2002). Invertebrate density on this invader was much lower than on nearby submerged vegetation in previous comparisons in the Hudson River (Feldman 2001) and in Lago di Candia (Cattaneo *et al.* 1998). Submerged plants harbored more invertebrate biomass per unit of plant d.w. than the emergent *Typha* both in a Dutch lake (Dvořak & Best 1982) and in a fluvial lake of the St. Lawrence River (Tessier 2002). To our knowledge, this is the first study to compare invertebrate communities on *T. natans* to both submerged and emergent vegetation. Our results confirm that submerged vegetation is a superior host for invertebrates and suggest that *T. natans* is somewhat intermediate between submerged and emergent plants.

Changes in aquatic vegetation in Lago di Candia may affect the secondary production of its littoral zone. Typical standing crop of *S. lacustris* is 700 g m^{-2} (G. Galanti, unpublished data) whereas that of *T. natans* is 400 g m^{-2} (Galanti & Romo 1997). These values together with our estimates of invertebrate biomass g^{-1} plant d.w. allow at least a rough estimate of the areal invertebrate biomass on different vegetation beds. According to these calculations, *T. natans* would harbour twice more areal biomass (1062 mg m^{-2}) than *S. lacustris* (420 mg m^{-2}). Even a small standing crop of *M. spicatum* (50 g m^{-2}) could provide as much invertebrate biomass (1200 mg m^{-2}) as a *T. natans* bed. Dense beds of *M. spicatum* (>250 g m^{-2}) may reach an areal invertebrate biomass (6000 mg m^{-2}) that is an order of magnitude higher than on *S. lacustris*. A previous study in Lago di Candia (Cattaneo *et al.* 1998) indicated that other submerged species, now completely absent, like *C. demersum* and *N. marina* are even better substrata than *M. spicatum* for epiphyton and macroinvertebrates. Therefore, the loss of submerged plants following coypu grazing may have seriously decreased the invertebrate production in the lake. On the other hand, an increase of submerged vegetation, promoted by mechanical harvesting of *T. natans* is auspicable. An increased development of emergent macrophytes and of *T. natans*, would scarcely affect the microcrustaceans living in loose association with the vegetation but would strongly reduce large invertebrates, which likely represent an important source of food for fish. Nevertheless, *S. lacustris*, by being present year round, can have an important ecological role providing substratum for phytophilous invertebrates over a more extended period than the other more seasonal plants.

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