Early succession of the macroinvertebrate community in a shallow lake: Response to changes in the habitat condition

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ABSTRACT

In the present study the initial succession of the aquatic macroinvertebrate communities of a newly created shallow lake in a wetland area was monitored during 15 months. Three different types of macroinvertebrate samples (multihabitat, associated to the *Phragmites australis* stands and associated to the sediment) were collected monthly from May 2004 to July 2005. Additional samples were collected in the reed stand in 2007, when the reed belt had become much taller and thicker. Colonization of the lake was fast, and the colonization sequence was mainly related to the dispersal abilities of the taxa. Habitat-specific changes in the assemblage's structure and composition were registered. The communities associated to the sediment showed a decrease in overall biomass, density and species richness along time. The density of the gastropod *Physella acuta* and the chironomid species *Dicrotendipes pallidicornis*, *Polypedilum nubifer* and *Tanytarsus horni* decreased significantly, after *Chara* stands declined; while the chironomid *Chironomus riparius* became dominant. The epiphytic macroinvertebrate communities associated with the reed stands followed a seasonal pattern, with a warm-period community dominated by the chironomid species *Ablabesmyia monilis* and *Psectrocladius sordidellus*-group, and a cold-period community dominated by the chironomid species *Cricotopus ornatus* and *D. pallidicornis*.

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Introduction

During recent decades, a high percentage of natural wetlands and their associated water bodies have disappeared as a result of land reclamation (Sharitz and Batzer 1999; Oertli et al. 2005; Marchetti et al. 2008). This constitutes a great potential threat for the populations of aquatic organisms. The configuration of wetlands along the landscape acts as a network, which plays an important role at the metapopulation and metacommunity levels by creating ecological corridors or providing refugee areas for many endemic and/or endangered species (De Meester et al. 2005). Local and regional administrations, increasingly aware of the loss of animal and plant biodiversity that reclamation produces, have sought to create wetlands to balance the process (Gilbert and Anderson 1998). Aquatic macroinvertebrates are usually among the first colonizing organisms when a new wetland or lake is created. When geographical barriers are not present (Milner 1994) and sources of potential colonists are widely available, colonization can be expected to be fast, with large macroinvertebrate populations established within the first year of lake's creation (Barnes 1983; Wrubleski 1999).

The results from the available studies suggest that the initial colonization sequence is mainly related to the dispersal abilities of the taxa (Bilton et al. 2001), while the further changes that take place in the community composition and structure are mainly ruled by the changes that take place in the habitat condition, e.g.: the shift from macrophyte-dominated to phytoplankton-dominated lakes (Scheffer et al. 1993; Jeppesen et al. 1999; Jones and Sayer 2003). Barnes (1983) compared the macroinvertebrate communities of ball-clay ponds of different ages, ranging from 6 months to 15 years, and established a successional sequence according to changes in the habitat. Overall, the information concerning the process of primary succession of aquatic macroinvertebrate communities is still scarce.

In the present study, the early succession of the aquatic macroinvertebrate communities of a newly created shallow lake in a wetland area was monitored along 15 months. The colonization process was explored simultaneously in different habitats of the lake in order to detect habitat-specific patterns. Our hypothesis were that: (i) the colonization of the lake by aquatic macroinvertebrates would be fast and mainly linked to the dispersal abilities of the different taxa; (ii) the changes in the community composition along time would be habitat-specific.

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Fig. 1. Study site location. On the left, the Iberian Peninsula with the Llobregat Delta marked with a white spot. On the right, a satellite image of Cal Tet lagoon (longitude: 2°7′20.96″; latitude: 41°18′9.276″). Sampling sites are marked with the following symbols: water samples (physico-chemical analyses) = cross; multihabitat samples = squares, Phragmites samples = stars; sediment samples = circles. Satellite image source: Institut Cartogràfic de Catalunya.

Methods

Study site

The Llobregat Delta wetlands occupy a total area of 97 km^2 and they are located in the right side of the city of Barcelona (41°16′–41°25′N latitude and 1°58′–°10′E longitude), in Spain. In 2001, a major infrastructure development project began within the area. As compensation for the loss of natural habitats that this project entailed, the area management consortium (a joint committee of local, regional and national public administration entities) promoted the creation of a new coastal shallow lake, Cal Tet (Fig. 1). The lake was created in winter 2003. It is relatively small (surface area 13 ha), is completely confined (separated from the coastline by a sand barrier), and is fed exclusively by rain and groundwater coming from the superficial aquifer. Maximum depth of the lake during the study period was 1.80 m, but during maximum inundation periods it has been reported to reach 2.40 m of maximum depth (Seguí and Pérez 2006).

Water physico-chemical analysis

To characterize the lake, several physico-chemical variables were recorded in its central area (Fig. 1), which was the deepest area in the lake (maximum depth 1.80 m). Water transparency (Secchi depth), conductivity, pH, water temperature and dissolved oxygen were measured *in situ* using a multiparametric sensor (WTW, multiparameter model 197i). Surface water was collected for dissolved inorganic nutrient analysis (NH_4^+, NO_3^-, NO_2^-, DIN, SRP, Si^{2+}), as well as for analyses of total organic carbon (TOC), phytoplanktonic chlorophyll-a, and suspended solids. All variables were measured monthly from June 2004 to July 2005 and again in July and October 2007. All the analyses employed standard methods (Greenberg et al. 1999).

Biological samples

Macroinvertebrates were collected monthly from June 2004 to July 2005. To obtain a general overview of the macroinvertebrate

biodiversity dynamics, three replicates of semi-quantitative samples (from now on multihabitat samples) were collected along the shoreline. A dip net of 250 μm mesh size was used during a standardized effort time of 60 s trying to integrate all the habitats by kicking the emergent helophytes and the bottom substrate, including sediment, gravel and macrophytes. When the study started, available habitat included mainly the very newly developed emergent helophyte vegetation, completely dominated by *Phragmites australis* (Cav.) Trin. ex Steudel; while in the central areas of the lake, the soft sediments were covered by a *Chara* bed, mainly *Chara globularis* Thuiller and *Chara vulgaris* var. *longibracteata* (Kütz.) (Seguí and Pérez 2006).

To monitor habitat specific changes, quantitative samples were collected during the same study period in the two dominant habitats: the sediment and the *Phragmites* stands. Three sediment samples were collected monthly in the deepest part of the lake using a Van Veen grab sampler (total area = 299 cm^2) and filtered through a 250 μm mesh. Similarly, three samples of epiphytic macroinvertebrates attached to *Phragmites australis* were collected monthly following Kornijów and Kairesalo (1994). A plastic tube 6 cm wide and 50 cm long was lowered over the *Phragmites* stems. The stems were then cut by shears so that they floated up into the tube. Water was then drained through 250 μm mesh. Macroinvertebrates were removed carefully from the stems by hand. Stem surface was measured (diameter × height × 3.14) for density calculation (individuals m^{-2}). Complementary samples were collected in July and October 2007 in recognition of the habitat changes occurring there (the *Phragmites* belt was much taller and denser).

All samples were fixed for preservation in 4% formaldehyde. All taxa were identified to species level when possible, except for the oligochaetes and the non-chironomidae diptera, which were identified at family level.

Mean individual biomass of epiphytic macroinvertebrates was determined by measuring ash-free dry mass (550 °C, 4 h) of representative individuals of each taxon. For chironomids the different instar biomasses (instars 2–4) were determined due to the high abundance registered by this family. We used literature data (Prat and Rieradevall 1995) when less than 10 specimens were available to be weighted.

For the measurement of epiphytic algae biomass (denoted EAB) and epiphytic particulate organic matter (EPOM) on *Phragmites australis*, two submerged reed pieces (immediately below the water surface) of two different stems were cut off. The pieces were washed into a vial with the aid of a toothbrush and measured to estimate the amount of colonizable surface. Epiphytic chlorophyll-a concentration was measured using spectrophotometric techniques according to standard methods (Greenberg et al. 1999). For the conversion of chlorophyll a to carbon, we used the chlorophyll:carbon ratio of 50 proposed by Reynolds (1984).

Epiphytic particulate organic matter samples were filtered through previously combusted Whatman GF/C filters of 0.45 μm pore size. Organic matter was then calculated as the difference of the dry mass (60 °C, 24 h) and the ash-free dry mass (550 °C, 4 h). Since they were registered separately, the sum of algal (EAB) and macroinvertebrate biomasses was then subtracted from that difference. The weight resulting from this subtraction served to measure the amount of epiphytic particulate organic matter (EPOM), which was mainly composed by detritus.

Data analysis

General descriptors of community structure were calculated, including taxa richness (*S*), Shannon diversity (*H′*), sample abundances and biomasses (for qualitative samples) and densities (for quantitative samples), Colonization time, defined as the time elapsed (in months) until a taxon was recorded for the first time

in a habitat, was plotted for each taxon in each habitat. For a general overview, we showed the results of taxa grouped by order, since members of the same order are expected to have similar dispersal abilities (Bilton et al. 2001). The dipterans were split between Chironomidae and other dipterans because of the relative abundance and species richness of the former. The colonization time of each group (i.e.: chironomids) was expressed as the mean and the standard deviation of all taxa included in that group (i.e.: all the chironomid species) for the different sample types (multihabitat, *Phragmites* and sediment samples). It is generally assumed that, as succession proceeds, density-dependent processes increase the stability of the system (Southwood et al. 1977, 1988; Lu and Wu 2000). Because macroinvertebrate communities are highly dynamic, β-diversity was used to ascertain whether a given community tended to be more stable over time (low β-diversity values for successive samples would indicate a lack of stability). β-Diversity was expressed as $\beta = S/\alpha - 1$, where S is the total number of taxa in two consecutive samples in time and α is the number of taxa that the samples share (Whittaker 1960).

Differences among sample types in terms of the composition of their associated macroinvertebrate community were assessed using ANOSIM analysis (Warwick and Clarke 2006). This method determines whether the differences between *a priori* defined groups are statistically significant when compared with corresponding differences within groups. Significant species for each habitat were identified based on their frequencies and their relative abundances (Dufrêne and Legendre 1997) using IndVal analysis (McCune and Mefford 1999). A further exploration of the macroinvertebrate communities and their relation with the environmental variables and the lake's age was performed through a redundancy analysis (RDA) using CANOCO 4.5 (Lepš and Šmilauer 2003). To reduce the number of explanatory variables to those best suited to model the response variable, a forward selection was carried out with a stopping significance level of 0.05 (Legendre and Legendre 1998; Blanchet et al. 2008).

Three types of responses in physico-chemical and biological data were explored: progressive changes (associated to the aging of the lake), seasonal changes and drastic changes (associated with the change in aquatic vegetation dominance). Progressive changes were explored by Spearman correlation tests of each variable with the variable age (months elapsed from the beginning of the study) and by the β-diversity spectrum, which showed taxa composition changes over time. Seasonal differences were tested with Mann–Whitney test between two groups: warm months (water temperature higher than the mean) and cold months (water temperature lower than the mean). In both cases results with a level of significance between 0.05 and 0.01 were considered significant (*) and below 0.01 highly significant (**). Drastic changes were explored by change-point analysis, using Change-Point Analyzer 2.0 (Taylor 2000). This analysis serves to detect significant changes in the mean of the variables under study or changes in the autocorrelation structure of the set of variables (Taylor 2000; Khaliq et al. 2007). All the physico-chemical variables were included in the change-point analysis. For the macroinvertebrate data set only total density and biomass, taxa richness and Shannon's diversity were tested. All the analyses were performed for each habitat type separately.

Results

Macroinvertebrate colonization times

Colonization by some macroinvertebrates was fast (Fig. 2). The gastropod *Physella acuta* was recorded in all habitats from the first month of study. The dipterans were also among the pioneer taxa,
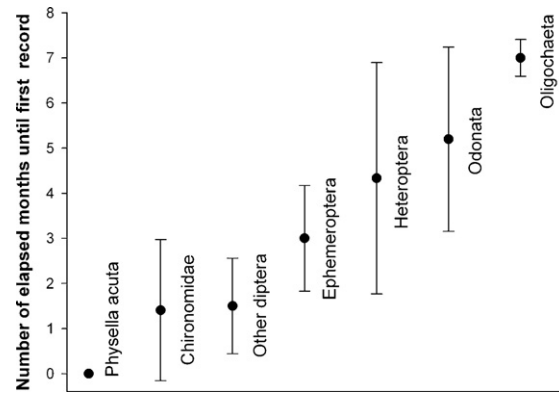

Fig. 2. Months elapsed until the first record of each taxon (grouped by order, except for dipterans) during the study period (starting in June 2004), with chironomids distinguished from the rest. Mean values (black circles) and standard deviations (black lines), considering all the habitats in which each taxon was registered and all the different colonization times for each taxon within a given order, are plotted.

with many chironomids (78% of species) being registered in at least some of the habitats from the first month of study. The remaining actively dispersing taxa were recorded in at least one habitat within the first nine months of study (except for the chironomid *Parakiefferiella*, first recorded in 2007). The oligochaetes exhibited the longest colonization times.

Differences between habitat assemblages

We found significant between-habitat differences in macroinvertebrate composition (ANOSIM: $R = 0.61$; $p = 0.001$). Only 10 (31%) of 32 macroinvertebrate taxa were present in all the habitats (Table 1). Chironomids were the most abundant taxon and represented the largest number of species in all habitats (above 50% of total taxa richness). The multihabitat samples contained the highest number of taxa ($S = 24$), with the odonates *Ischnura elegans* and *Sympetrum fonscolombii* as indicator species. According to IndVal analysis, the indicator species of the *Phragmites*-associated communities were the chironomids *Cricotopus ornatus* and *Dicrotendipes pallidicornis*, as well as the *Psectrocladius sordidellus* group. In the sediment samples, the indicator species were the chironomids *Chironomus riparius*, *Microchironomus deribae*, *Procladius choreus*, *Polypedilum nubifer* and *Tanytarsus horni*.

Changes in the environmental conditions

Surface water temperatures ranged between 9 and 25 °C. The lake was alkaline (pH = 8.92 ± 2.4) and oxygen-saturated (DO = 109 ± 25%). Mean dissolved nutrient concentrations were: SRP = 0.04 ± 0.025 mg l^{-1}, DIN = 1.31 ± 1.2 mg l^{-1}. Total organic carbon (TOC) was the only environmental variable significantly correlated with the lake's age ($r^2 = 0.76$; $p < 0.0001$). Phytoplanktonic chlorophyll-a concentration tended to be low in cold months (temperature lower than the mean) and high in warm months (temperature higher than the mean). The highest concentrations of phytoplanktonic chlorophyll-a were registered in the warm months of 2005 and 2007 (Fig. 3). Secchi depth (Fig. 3) was significantly lower in warm months than in the cold months ($T = 7.5$, $p = 0.039$). Conversely, conductivity was significantly higher in the warm months than in the cold months ($T = 6.0$, $p = 0.011$). Based on available data (Seguí and Pérez 2006, and present study), warm-month conductivity increased with time in successive years (significant linear trend, $r^2 = 0.85$, $p = 0.0001$).

Change-point analysis detected two significant changes in environmental conditions. These changes were (1) epiphytic

Table 1
Mean macroinvertebrate densities, associated to the *Phragmites australis* (individuals per square meter of stem) and the sediment (individual per square meter of sediment), and abundances, multi-habitat samples (individuals sample-1), registered in each habitat along the study period (2004, 2005 and 2007). Standard deviation in parentheses. Codes for Chironomidae follow Schnell et al. (1999).

	Code	Phragmites (ind m^{-2})		Sediment (ind m^{-2})	Multihabitat (ind sample $^{-1}$)
		2004–2005	2007	2004–2005	2004–2005
Oligochaeta					
Naididae	Naid	8 (±8)	–	35 (±62)	3 (±4)
Tubificidae	Tubi	–	–	–	31 (±56)
Gasteropoda					
Physella acuta (Draparnaud, 1805)	Phys acu	21 (±27)	–	56 (±88)	10 (±11)
Crustacea					
Palaemon longirostris H. Milne Edwards, 1837	Pala lon	–	–	–	1 (±1)
Ephemeroptera					
Caenis macrura Stephens, 1835	Caen mac	1 (±3)	–	5 (±6)	2 (±1)
Cloeon cognatum Stephens, 1835	Cloe cog	2 (±2)	25 (±36)	–	2 (±1)
Odonata					
Crocothemis erythraea (Brullé, 1832)	Croc ery	–	–	–	2 (±1)
Ischnura elegans (V. d. Lind., 1820);	Isch ele	30 (±31)	38 (±54)	1 (±1)	36 (±19)
Orthetrum cancellatum (Linnaeus, 1758)	Orth can	–	–	–	1 (±1)
Sympetrum fonscolombii (Selys, 1841)	Symp fons	–	–	–	3 (±3)
Heteroptera					
Micronecta scholtzi (Fieber, 1860)	Micr sch	–	–	–	2 (±2)
Naucoris maculatus Fabricius, 1798	Nauc mac	–	–	–	1 (±1)
Coleoptera					
Enochrus bicolor (Fabricius, 1792)	Enoc bic	–	15 (±21)	–	–
Diptera					
Crambidae	Cramb	–	–	–	2 (±2)
Ceratopogonidae	Cera	–	–	–	1 (±1)
Empididae	Empi	1 (±1)	–	–	–
Ephydridae	Ephy	1 (±1)	–	–	–
Tipulidae	Tipu	-	60 (±84)	–	–
Chironomidae					
Ablabesmyia monilis (Linnaeus, 1758)	Abla mon	63 (±54)	1163 (±1644)	67 (±90)	19 (±13)
Chironomus riparius Meigen, 1804	Chir rip	20 (±21)	–	265 (±215)	7 (±10)
Chironomus salinarius Kieffer in Thienemann, 1915	Chir sal	–	–	1 (±2)	–
Cricotopus (Isocladius) ornatus (Meigen, 1818)	Cric orn	184 (±184)	268 (±379)	–	8 (±6)
Cricotopus (Isocladius) sylvestris (Fabricius, 1794)	Cric syl	20 (±37)	134 (±190)	3 (±3)	4 (±4)
Cryptochironomus cf. *obreptans* Walker, 1856	Cryp	–	–	–	1 (±1)
Dicrotendipes pallidicornis (Goetghebuer, 1934)	Dicro pal	696 (±287)	291 (±411)	34 (±34)	89 (±78)
Microchironomus deribae (Freeman, 1957)	Micc der	–	–	470 (±613)	-
Parakiefferiella indet.	Parakind	–	1270 (±903)	–	–
Paratanytarsus grimmi	Para gri	25 (±33)	324 (±78)	–	–
Polypedilum nubifer (Skuse, 1889)	Poly nub	–	–	421 (±302)	2 (±2)
Procladius choreus (Meigen, 1804);	Proc cho	–	–	167 (±107)	26 (±29)
Psectrocladius sordidellus (Zetterstedt, 1838)	Psec sor	433 (±178)	1104 (±1348)	86 (±64)	201 (±170)
Tanytarsus formosanus Goetghebuer, 1934	Tany for	6 (±11)	–	542 (±325)	94 (±54)
Total macroinvertebrates		1510 (±878)	4691 (±198)	2153 (±1915)	541 (±467)
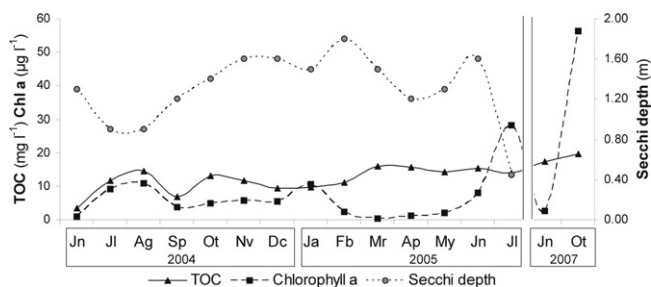
Fig. 3. Dissolved total organic carbon (TOC) and phytoplanktonic chlorophyll-concentrations (first *Y*-axis) and Secchi depth (second *Y*-axis) for the study period (2004, 2005 and 2007). Concentrations measured in 2004 and 2005 are separated using a blank box.

algae biomass (EAB) in December 2004 (confidence interval = 96%; mean value before change = 3.94 g m^{-2}, mean value after change = 1.52 g m^{-2}) and (2) Secchi depth in July 2005 (confidence interval = 96%; mean value before change = 1.36 m, mean value after change = 0.45 m).

Changes in macroinvertebrate communities

In the multihabitat samples, the variables water temperature ($F = 3.32$, $p = 0.02$) and age ($F = 2.12$, $p = 0.04$) were forward selected and explained 27.8% of total variance. The ordination trajectories of the samples tended to disperse from the first sample up to sample 035 (March 2005), when assemblages seemed to respond to water temperature (Fig. 4). The invertebrate predators and the gastropod *P. acuta* characterized the warmer months. Lake age was positively related to the presence of oligochaetes, odonates, Crambidae, the chironomids *C. riparius* and *P. sordidellus*-group.

Although the semi-quantitative nature of the multihabitat samples does not allow analyzing the data in terms of species densities, some results can be drawn from the species relative abundances. In the multihabitat samples the relative abundances of *D. pallidicornis* and *T. horni* declined significantly over the study period (Table 2), while *Ischnura elegans* and the *P. sordidellus*-group became dominant in 2005 (Fig. 5).

In the *Phragmites* samples, EAB ($F = 2.75$, $p = 0.009$) and water temperature ($F = 2.25$, $p = 0.013$) were forward selected in the RDA. Together, these two variables explained 33% of total variance. Presence of ephemeropterans and of the chirono-
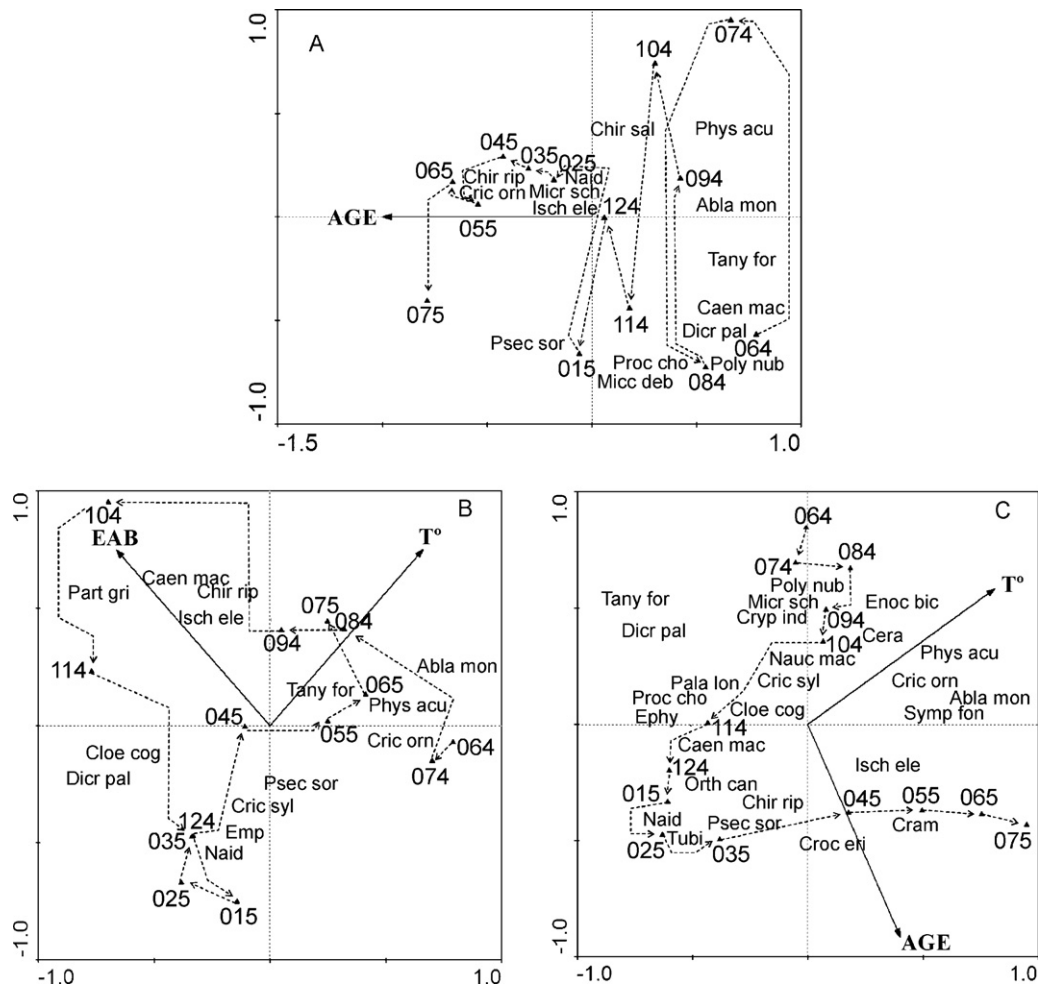
Fig. 4. Triplots (samples, species and environmental variables) of the results of the redundancy analyses (RDA) using the macroinvertebrate assemblages associated to the sediment (A. upper graphic), the *Phragmites australis* (B. lower left) and the multi-habitat (C. lower right) samples. Explanatory variables are marked with and arrow and were forward selected using a stopping significance level of 0.05. T° = temperature. EAB = Epiphytic algae biomass. Samples are marked with a triangle and codified following month + year (i.e.: 064 = June 2004). See Table 1 for species abbreviations.

mids *Paratanytarsus grimmi* and *C. riparius* was related to high biomasses of epiphytic algae. No clear trend was observed over time (Fig. 5). However, in summer 2007 mean total macroinvertebrate density $(4692 \pm 1995$ individuals m$^{-2})$ was 3.8 times higher than the mean for the warm periods of 2004 and 2005 $(1238 \pm 1995$ individuals m$^{-2})$. The chironomid genus *Parakiefferiella* (not recorded in any habitat during 2004 and 2005) exhibited relatively high abundances (Fig. 5). The ordination trajectories of the samples formed a seasonal sequence (Fig. 4). The predator *Ablabesmyia monilis* and the scraper *P. acuta* were associated with warmer months, while a cold-period community was dominated by the chironomid species *C. ornatus* and *D. pallidicornis*. In the sediment samples, lake age ($F = 2.78$, $p = 0.016$) was the only variable selected. Lake age explained 19% of total variance. The ordination trajectories of the samples spread progressively farther from the first sample on the first axis and exhibited large fluctuations on the second axis (Fig. 4). The invertebrate predators *Ischnura elegans* and *Micronecta scholtzi*, the naidid oligochaetes and the chironomids *C. riparius* and *C. ornatus* were positively correlated with lake age. The rest of the species were negatively correlated with lake age. Total density, total biomass and species richness of the macroinvertebrate community associated with the sediment decreased significantly over time (Table 2). Presence of the chironomids *A. monilis*, *D. pallidicornis*, *P. nubifer* and *T. horni*

also decreased significantly (Table 2). *P. acuta* and *P. nubifer* disappeared by February 2005. The chironomid *T. horni* exhibited far lower densities beginning in November 2004. However, the relative abundances of *C. riparius* and of the *P. sordidellus*-group increased (Fig. 5).

Change-point analysis detected no significant change-points (drastic changes) in structural parameters (total density and biomass and taxa richness). This result does not reflect the significance of the density relations for some taxa, nor does it reflect progressive changes in overall structural parameters with lake age in the multihabitat and the sediment samples indicated by Spearman correlations. Differences between cold and warm season communities were not significant (Mann–Whitney test).

Compared to the reed and to the sediment samples, the macroinvertebrate multihabitat samples exhibited a lower rate of change during the study. Their lower β-diversity values (Fig. 6) reflected this lower rate. Summer was a time of change for the epiphytic macroinvertebrate community associated with *Phragmites*. The β-diversity values for this community were higher in summer than in the rest of the year, and they were higher in the summer of 2004 than in the following summers (2005 and 2007). Higher β-diversity values were recorded for the macroinvertebrate community associated with sediment in spring and summer 2005 than for the rest of the months (Fig. 6).

Table 2
Results from Spearman correlation analyses of lake age and macroinvertebrate structural parameters for each habitat. Analyses were also performed for each species separately, but only statistically significant results are shown. Multihabitat samples refer to semi-quantitative samples collected along the shoreline using a dip-net of 250 μm mesh size and trying to integrate all the habitats by kicking the emergent helophytes and the sediment.

	Time	
	rs	ρ
Phragmites		
Density	−0.18	ns
Biomass	−0.07	ns
Diversity	0.21	ns
S	−0.16	ns
Sediment		
Density	−0.56	*
Biomass	−0.59	*
Diversity	−0.39	ns
S	−0.49	*
Ablabesmyia monilis	−0.58	*
Dicrotendipes pallidicornis	−0.64	**
Polypedilum nubifer	−0.58	*
Tanytarsus horni	−0.71	**
Multihabitat		
Abundance	−0.24	ns
Biomass	−0.23	ns
Diversity	−0.14	ns
S	−0.01	ns
Dicrotendipes pallidicornis	−0.52	*
Tanytarsus horni	−0.64	*
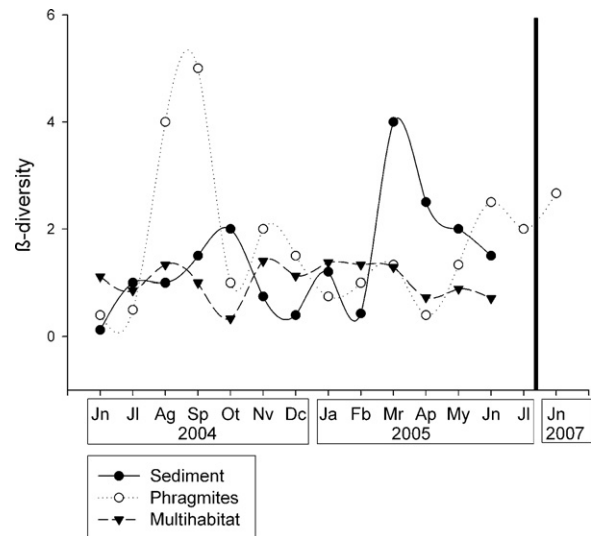
Fig. 6. Change rate of the macroinvertebrate assemblage associated with each habitat, expressed as β-diversity values over time (low β-diversity values mean high resemblance between time successive samples). Sediment = black circles. Phragmites = white circles. Multi-habitat = black triangles.
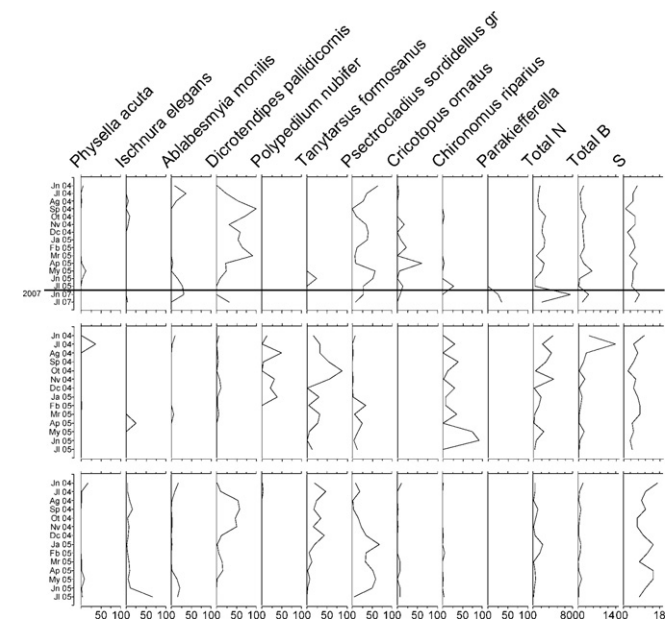
Fig. 5. Relative abundances (%) of selected taxa (according to their density and the significance of their correlations with explanatory variables) and mean total abundance, biomass and taxon richness for each habitat. Total N = mean total density in individuals per square meter (Phragmites and sediment habitats) and mean total abundance in individuals per sample (multi-habitat). Total B = total biomass (mg m^{-2}). Total S = total taxon richness. The black line indicates time discontinuity in sampling.

Discussion

Colonization of the lake by macroinvertebrates was fast. Several insect species were registered in high densities during the first month of study, meaning that they were able to establish large populations within the first year after the creation of the lake. Fast colonization was possible because the area contained numerous sources of potentially colonizing organisms (Cañedo-Argüelles and

Rieradevall 2009; Sànchez-Millaruelo et al. 2009). Furthermore, no geographical barriers existed. Potentially, such barriers can limit the establishment of aquatic macroinvertebrate communities. For example, Milner (1994) reported a time scale of 13 years of colonization of invertebrates in receding glaciers, and Brady et al. (2002) registered an absence of non-aerial invertebrates in natural wetlands that could host high snail abundances when colonization was facilitated. The successional sequence resembled that previously reported from the few available studies of macroinvertebrate primary succession (e.g., Layton and Voshell 1991; Velasco et al. 1993a, for different sets of experimental ponds; Batzer and Resh 1992, for a newly flooded marsh). As previously reported from other colonization studies (Barnes 1983; Christman and Voshell 1993; Velasco et al. 1993b; Frantzen et al. 1994; Levin et al. 1996; Ruhí et al. 2009) chironomids dominated the assemblage in the first months, probably because of their high dispersal abilities and their short life cycles (Armitage et al. 1995; Bilton et al. 2001). Although, the gastropod P. acuta lacks active dispersal mechanisms, it was also a fast colonizer. This observation could result from avian dispersal of eggs and of mature individuals. P. acuta could have adhered directly to the birds or to the fragments of vegetation that birds transport (Barnes 1983; Fairchild et al. 1999). Colonization by P. acuta could also have resulted if mature snails were already attached to the reeds before transplanting. As the system matured, the invertebrate predators became more abundant and began to regulate herbivore abundances. This trend usually characterizes recovery processes in temporary ponds (Lake et al. 1989; Williams 1997; Boix et al. 2000).

Seasonality was the chief determinant of composition and abundance for the epiphytic macroinvertebrate communities associated with Phragmites australis, although no significant differences were registered between the warm and cold period communities. Significantly higher macroinvertebrate densities occurred during summer 2007, when the reed belt was taller and denser. This finding could be a consequence of higher carrying capacity of the old stems (Oertli and Lachavanne 1995), formation of new microhabitats (Szalay and Resh 2000) and accumulation of decomposed material in the reed bed (Varga 2001; Bedford and Powell 2005).

The community associated to the sediment registered a progressive impoverishment in total density, biomass and species richness as the lake aged. This probably resulted from the loss of Chara that took place during the study period, in the Autumn of 2004

(Seguí and Pérez 2006). Charophytes furnish suitable habitat conditions for diverse invertebrate communities (van den Berg et al. 1997, 1998). This is related to the fact that they provide winter substrate (Hargeby 1990; Pieczyńska et al. 1999) and refuge against predators (Hanson 1990; Diehl and Kornijów 1998). Evidence for the suitable habitat conditions provided by *Chara* are available from Lake Krankesjön (Sweden), where the total biomass of macroinvertebrates was found to be much greater in *Chara* beds than in *P. pectinatus* stands or in bare sediment (Hargeby et al. 1994), and from Søbygaard Lake (Denmark), where chironomid stratigraphy revealed higher species richness and diversity in the *Chara*-dominated period (Brodersen et al. 2001). In the present study the chironomid *C. riparius* dominated the sediment assemblage (up to 91% of relative abundance) after *Chara* disappeared. This dominance of *C. riparius* (a collector – suspension feeder species) must have been favored by loss of *Chara*, whose presence can reduce the supply of fresh and dead planktonic algae to the bottom (Diehl and Kornijów 1998; Kornijów and Moss 1998). At the same time, *C. riparius* could have promoted turbidity by mobilizing the sediment while burrowing and searching for food. The chironomids *A. monilis*, *D. pallidicornis*, *P. nubifer* and *T. horni* exhibited a contrasting tendency to that showed by *C. riparius*, decreasing in abundance and biomass in the sediment along time. This is also probably related to their habitat preferences, since they tend to occur in association with *Chara* vegetation (Velasco et al. 1993a; Brodersen et al. 2001; Smiljkov and Slavevska-Stamenkovic 2006; Halkiewicz 2008).

The differences in the changes of the community associated to each habitat along time were also evidenced by the β-diversity analysis. The higher β-diversity values for the sediment occurred in the final months. This means that the main changes in sediment-associated macroinvertebrate community composition occurred at the end of the study period, when *Chara* had almost disappeared from the lake (Seguí and Pérez 2006). The macroinvertebrate community associated to *P. australis* registered a different pattern. In this case the higher β-diversity values were registered during the summer periods, when most insects are more active and reproduce more rapidly (Armitage et al. 1995; Batzer and Wissinger 1996; MacKenzie 2005). However, higher β-diversity values occurred in summer 2004 than in summer 2005. This decline could reflect the organization of the system (as a result of the growing and maturation of the reed stands) and the greater importance of density dependent processes (Southwood et al. 1977, 1988; Koskenniemi 1994; Lu and Wu 2000).

Conclusions

As we hypothesized, the absence of dispersal barriers and the wide availability of colonizing sources led to a fast colonization of the lake. The colonization sequence was similar to that reported by previous studies and it was mainly linked to the dispersal abilities of the different taxa. Habitat specific changes in the assemblage's structure and composition were registered. The assemblages associated to *Phragmites australis* were mainly shaped by the seasonal changes and the food availability in the form of epiphytic algae while the assemblages associated to the sediment showed a significant relation with the lake's age and seemed to be influenced by the loss of *Chara* stands.

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