



# Succession of microconsumers in waterlogged pampean soils (Buenos aires, Argentina) and its significance for nearby wetlands

Lía C. Solari<sup>1</sup> · Karina P. Quaini<sup>2</sup> · Néstor A. Gabellone<sup>1</sup>

Received: 12 October 2017 / Accepted: 31 August 2018  
© Springer Nature Switzerland AG 2018

## Abstract

In floodplains, the passive dispersal by drift occurs when water bodies become connected, and is a key feature offering pathways for the recolonization of periodically flooded habitats. Mesocosms with experimental flooding were used to document the succession of small invertebrates under differing hydrologic regimes with the intent of identifying which animals were capable of moving among habitats. The mesocosm experiments were performed in soils in sandy areas of the Salado-River basin including a mixed-use plot, a plot for breeding livestock, and a plot currently without any use located in different topographic positions (upper, middle, lower). Forty-seven taxa were found including ciliates, amoebae, rotifers, and microcrustaceans. The maximum total specific richness was recorded in middle soil and the minimum in upper soil because of a shorter colonization time. Higher mean densities occurred in middle and lower topographies, while the upper exhibited lower values. The ciliates and rotifers were the dominant. During the intermediate stage of flooding, the high density and biomass of the primary producers resulted in high concentration of dissolved oxygen (photosynthesis exceeded respiration). In contrast, in the final stage, low densities of microalgae led to low concentrations of dissolved oxygen and a high density of consumers (preponderance of respiration over photosynthesis). These flooded areas are significant as sources of microorganism inocula into the river. An abundance of microbiota arising from temporary wetlands and floodplains is fundamental for a successful recruitment of native-fish species.

**Keywords** In-situ-soil-flooding simulation · Colonization and succession of microconsumers · Agricultural land · Salado-River basin

## Introduction

The dynamic interaction between water and land connects components of floodplains and affects the adaptations of the biota evolving in those environments (Bayley 1995). Variation in water flow facilitates high productivity, drives species distributions, and facilitates enhanced biodiversity in river-floodplain systems (Shiel et al. 1998; Górski et al. 2013). In such floodplains, passive dispersal by drift may occur upon the connection of water bodies during the aquatic phase (Junk and Robertson 1997; Havel et al.

2000). This typically seasonal joining of water bodies in floodplains is a key feature enabling pathways for the recolonization of periodically flooded habitats (Frisch 2002). It is significant to highlight the importance of early stages of the organisms in the succession for the maintenance of biodiversity (Prach and Walker 2011). Rotifers, small cladocerans, and copepods are usually more abundant and diverse in floodplain wetlands and riverine lakes where a high physical and chemical heterogeneity provides a range of microhabitats compared to the main river channel (Aoyagui and Bonecker 2004; Górski et al. 2013). Ciliates are widely distributed over a range of environments including soil (Foissner 1997, 2002; Foissner et al. 2002). Field studies need first to explore which species colonize only the inundated floodplains and are not found in the plankton of the permanent waters and then investigate whether certain of those species colonize the flooded areas but also use the permanent oxbows and backwaters as refuges during the terrestrial phase (Schröder 2001). Resting

✉ Lía C. Solari  
solari@ilpla.edu.ar

<sup>1</sup> Instituto de Limnología “Dr. Raúl A. Ringuelet” CCT CONICET La Plata, Boulevard 120 y 62, 1900 La Plata, Buenos Aires, Argentina

<sup>2</sup> Ministerio de Ambiente y Desarrollo Sustentable, Buenos Aires, Argentina

eggs furthermore might serve as propagules transported by water currents from temporary to permanent waters, thus surviving the terrestrial phase (Schröder 2001, 2005). In addition, resting eggs in sediments provide an important source of biodiversity, thus contributing to the recolonization of the environment (Palazzo et al. 2008; Catlin et al. 2017). In lakes and other aquatic systems, diapause prevails over other strategies for dormancy and results in the production of such resting eggs (Santangelo et al. 2015). Since most of the species that colonize floodplains are typical denizens of aquatic environments, the presence of those taxa in floodwater could indicate their prior residence in the soil in a latent stage and subsequent development in times of flooding. Several reports suggest that the disturbance of flooding is a characteristic element in the development of the humid-pampas ecosystem (Ameghino 1884; Gabellone et al. 2003; Chaneton 2006). In systems of high fluctuation, certain organisms become adapted either to flooding or to drought conditions, others not only can subsist in both phases (Neiff 1996) but also depend on stressful conditions in order to continue their life cycle (Reddy and DeLaune 2008; Mitsch and Gosselink 2015).

Rotifers are constantly and obligatorily connected to aquatic environments in all biologically active states except when in the resistant structures that are resilient to drought (Segers 2008; Devetter and Schöll 2014). Dormancy is common among rotifers: bdelloids easily produce dormant propagules in the face of unfavorable periods and long-distance dispersal (Bohonak and Jenkins 2003; Santangelo et al. 2015). Crustaceans, however, can reestablish larger populations and biomasses only when lentic conditions prevail over longer periods.

In the Salado-River basin, several investigations on plankton have been carried out during the last decades (Claps et al. 2009; Gabellone et al. 2014). When the plankton in a backwater pond was recorded monthly in the lower basin (Gabellone et al. 2001; Solari et al. 2002), an input of biota from that pond was detected in the river; and the zooplankton structure downstream from that lentic environment was found to be similar to that recorded in the pond itself suggesting a close linkage amongst habitats.

The Salado River is a typical lowland river with a watershed of 150,000 km<sup>2</sup> and articulating with a large number of lentic water bodies that may reach an area of 10,000 km<sup>2</sup> (Gabellone et al. 2013). The constant floods that the Salado-River basin has undergone over time are a key element in the structure of the ecosystem and the configuration of the basin's landscape. The ecological influence of these floods seems to have become essential in the evolution of the ecosystem, with the latter's very existence apparently depending on the continuity of these events since certain attributes of the system are invariably disrupted by the absence of such perturbations.

Variations in the topography of a given environment determine the differences in frequency, intensity, and length of the stages of flooding and drought, as well as the habitat offered for micro- and macroorganisms. Different land use, for its part, will directly affect the nutrient concentration, while the biologic activity of the resident organisms will influence the dynamics of nutrient availability within the environment.

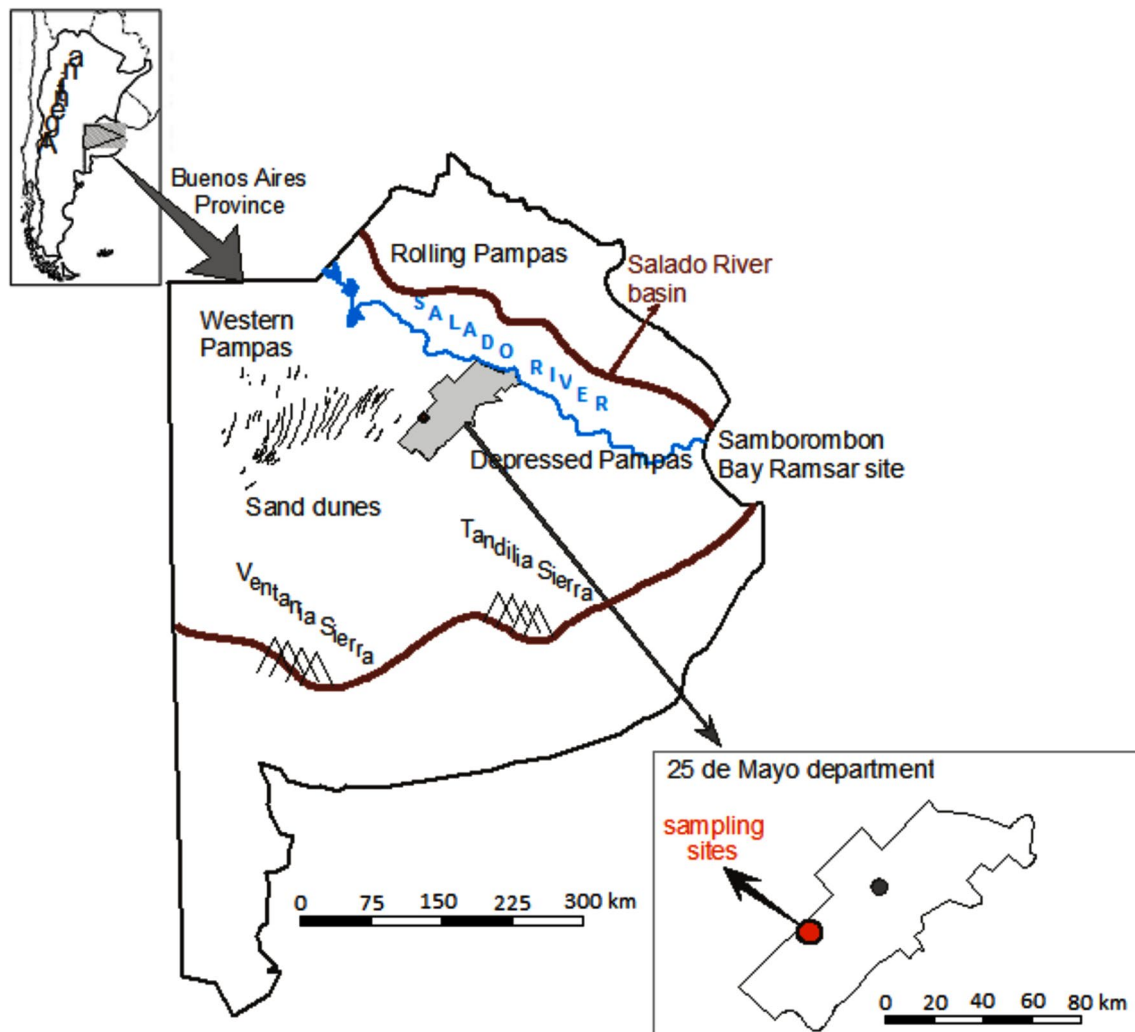
Here we describe the colonization and succession of microconsumers in historically agricultural land through a simulation of different periods of soil flooding by in-situ experiments. The experiments were performed in soils located in sandy areas of the Salado-River basin that varied in topography and land use. Our central question was to determine the effects of the characteristics of the soil and the topographic position with respect to the runoff after flooding on the development of colonizing organisms.

## Materials and methods

### Study area

The Salado—a typical lowland river whose watershed includes endorheic areas, at present joined by canals—has a length of approximately 600 km, and a low slope (mean 0.107 m km<sup>-1</sup>; Gabellone et al. 2005; Fig. 1). The agricultural soils in this area are one of the most productive in the country, and both the cultivation of crops and the pasturing of livestock have completely altered the landscape and habitat (Neschuk 2001; Neschuk et al. 2002). The flow regime of the Salado River is quite variable: the flow does not exceed 100 m<sup>3</sup> s<sup>-1</sup> in dry periods but can reach 1500 m<sup>3</sup> s<sup>-1</sup> at the mouth in times of flooding, with consequent variations in the conductivity and the transport of dissolved materials and particulates. Large areas may be inundated for weeks or even months (Gabellone et al. 2005).

The study area is part of the Salado-River basin, which watershed is in the ecoregion of the Argentine pampas or pampas plain (Viglizzo et al. 2006) and the neotropical region of Chaco Domain (La Pampa province; Cabrera 1971). The basin is characterized by flat relief; a humid, temperate climate; an undeveloped hydrologic network; poorly drained soils; dominant grasses; and a relatively high biotic diversity as a result of the presence of shallow lakes and easily flooded areas historically subject to regular seasonal flooding and drought cycles (Ameghino 1884). The annual precipitation during the sampling period was 1012 mm and the rain accumulated during the sampling months (*i. e.*, June through November) 356 mm. The maximum historical rainfall (period 1972–2014) of this area is recorded in summer and spring, with the highest average monthly rainfall in March (summer 148 mm) and in October (spring 106 mm).



**Fig. 1** Location of the sampling site in the Salado-River basin

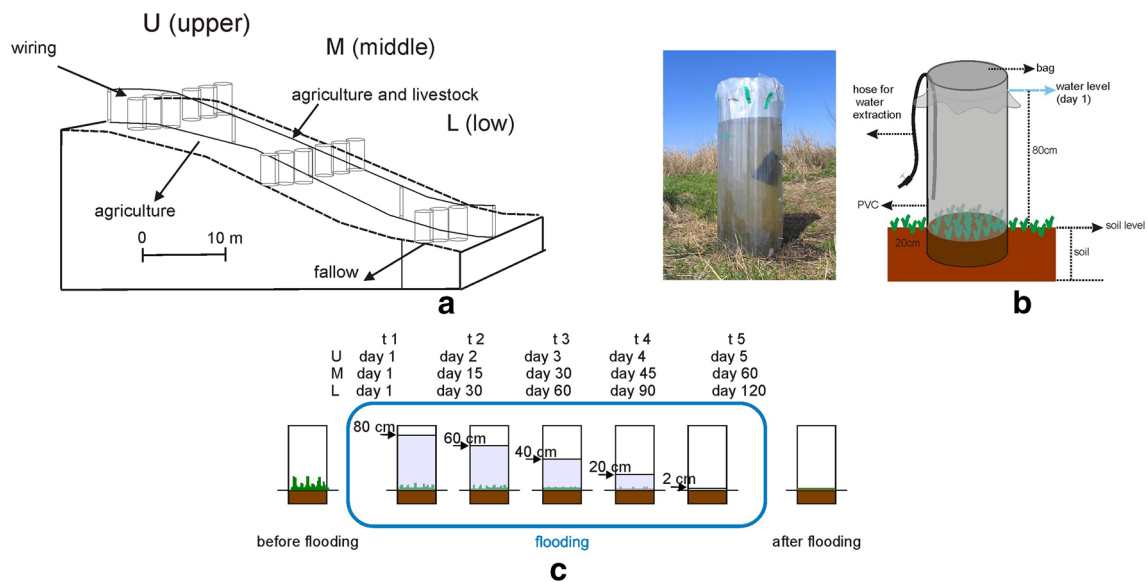
The lowest average monthly rainfall (37 mm) occurs in winter (August). At times of low rainfall frequency and intensity, the lower elevation accumulated water for some time; while the middle became infiltrated but drained quickly, leaving the soil damp though not flooded.

October was the month of maximum rainfall at 208 mm. The mean annual temperature during the sampling period was 15.2 °C and the mean temperature during the sampling months 12.9 °C, with the minimum occurring in June at 10.0 °C and the maximum in November at 18.6 °C.

The in-situ investigations were undertaken in an experimental field at María Cruz and Manuel Inchausti, an agrotechnical school of the La Plata National University (35°39'00"S, 60°29'00"W, near the town of Valdés, County of 25 de Mayo, Buenos Aires province). The study site was located in the region called Sandy Pampa at 61 km within the main course of the Salado River. The landscape is characterized by the presence of longitudinal dunes and small interdunal shallow

lakes. We selected an area having the topographic gradient U (upper), M (middle) and L (lower) as indicated in Fig. 2a with a northwest-to-southeast orientation, a total transect length of 40.3 m, and a slope of 3.5%.

The soils were classified as Entic Hapludolls (Soil Survey Staff 2003) with a predominance of fine sand in the upper and an increase in the percentage of silt in the lower (Ventimiglia et al. 2000). The plant species for each sampling site were *Glycine max* (soybean) for agricultural use in upper and middle, *Festuca arundinacea*, *Bromus unioloides*, and *Trifolium repens* for mixed use in upper and middle, and *Distichlis spicata*, *Sorghum halepense*, and *Bromus secalinus* in the lower.



**Fig. 2** **a** Scheme of topographic gradient, **b** photograph and scheme of the enclosures used in the “in-situ” experiment. The water removal was in only the upper, **c** scheme of water residence in the enclosures at different times according to the topography

## In-situ experiment

### Enclosure construction

We built cylindrical enclosures 1 m in height and 35 cm in diameter with a 96-L capacity made of 0.8-mm-thick biaxially oriented ultraviolet-protection polyvinylchloride (PVC) (Ondex™ plates). Two uncovered bags of transparent so-called crystal nylon (100  $\mu\text{m}$  thick, 1.20 m high, 0.70 m wide) were placed inside the PVC cylinder along with a sample of soil at the bottom (25 cm deep, 35 cm in diameter) containing the original vegetation (Fig. 2b). Then the bags were filled with groundwater up to a height of 0.80 m above the soil to simulate a flooding. The addition of the water was very slow in order to minimize the disturbance to the soil. Once the enclosures were filled, they were left untouched for 24 h to stabilize.

### Sampling design

The soils used in the treatments—selected according to current land-use conditions—included a mixed-use plot for agriculture and breeding livestock, a plot for agriculture alone, and a fallow plot (Fig. 2a). The soils of mixed and of agricultural uses were located in the upper and middle, whereas the fallow soil was located in the lower; and since the soil in that sector was of a single type of use, only three replicates were made. For the sectors containing mixed-use and agriculture soils (the upper and middle), three land-use replicates were performed for both those topographies (Fig. 2a). Therefore to these three sectors, five treatments

were designated according to the topography (U, M, and L) and to the land use (a, agriculture; m, mixed—*i. e.*, agriculture and livestock) resulting in treatments Ua, Um, Ma, Mm, and L (fallow). Three replicates were used for each treatment, resulting in a total of 15 enclosures (Fig. 2a). Furthermore, an enclosure was included as a control with water but without soil.

The physicochemical characteristics of the groundwater were: conductivity, 701  $\mu\text{S cm}^{-1}$ ; pH, 6.9; concentration of dissolved oxygen (DO) at 58.4% saturation, 5.65  $\text{mg L}^{-1}$ ;  $\text{N-NO}_3^-$ , 6.3  $\text{mg L}^{-1}$ ; and total phosphorus, 98  $\mu\text{g L}^{-1}$ .

Because the water flowed faster in U than in the other topographies (Fig. 2b), the excess water was removed through a drainage hose (0.5 cm in diameter with a valve to regulate the flow; Fig. 2b). In each topography, the sampling was performed in accordance with the length of time that would have been required to dry the soil at a given topography through realistic evaporation, infiltration, and percolation. Therefore, we estimated that the residence time of the water on the soil would be 5 days in U, 60 days in M, and 120 days in L.

Five samplings (t1–t5) were taken at each site from June 15 through November 21, 2006, but at different frequencies for the three the topographies—*i. e.*, U every day, M, every 15 days, and L every 30 days (Fig. 2c).

### Measurement of biologic and physicochemical parameters

Water samples were taken from the entire water column of each enclosure, from the bottom to the surface, by means of a hose and a manual pump, for qualitative and quantitative

analysis of the consumer microorganisms. Between 3 and 7.5 L of water were filtered through a net of 35  $\mu\text{m}$  and the resulting concentrate (250 ml) was fixed with 5% (v/v) aqueous formaldehyde. Protozoans and rotifers were counted in (1-mL) Sedgwick-Rafter and crustaceans in (10-mL) Bogorov chambers. The coefficient of variation (maximum 20%) was used for abundance comparisons between dominant species in paired samples. The organisms were identified taxonomically down to the genus and/or species level according to the relevant literature (Elster and Ohle 1972; Darwin Project Nematodes (2018); Koste and Jose de Paggi 1982; Reid 1985; Koste and Shiel 1987; Segers 1995; De Smet 1996; Foissner 1997, 2002; Foissner et al. 1999; Frutos 1998; Lynn 2008). In the water, measurements of temperature, pH, conductivity, and turbidity were made with a Horiba Multimeter U-10; the DO concentration with an YSI sensor; and the oxidation–reduction potential with a redox electrode. The total phosphorus (TP) was determined by the ascorbic-acid method after digestion with acidic persulfate (method 4500-PB, APHA 1995) and the soluble-reactive phosphorus (SRP) without digestion. Whatman GF/C filters were used to collect material for spectrophotometric analysis of the chlorophyll “a” (chl “a”) concentration (method 10,200 H, APHA 1995). The nitrate and nitrite levels were measured by the hydrazine-reduction method (4500 H, APHA 1995) and the ammonium-ion concentration by the phenate technique (4500 F, APHA 1995). The concentration of suspended solids (in  $\text{g L}^{-1}$ ), as determined according to method 2540 D of APHA (1995) and the concentrations of particulate organic matter (OM) estimated as the material retained in the filter by weight loss on ignition at 550  $^{\circ}\text{C}$  (method 2540 E, APHA 1995). The dissolved polyphenols and ammonium-ion concentrations were measured according to the respective procedures 5550 B and 4500 F of APHA (1995).

### Statistical analysis

The statistical analyses performed were the Student *t* test, the two-way analysis of variance (ANOVA), and the correlation analysis, all with a confidence level of 0.05 ( $p < 0.05$ ). In the “Results” section, the probability is shown as  $p < 0.05$  (when of lower confidence level) and as  $p < 0.01$  (when the confidence level is markedly high; Sokal and Rohlf 1979; Montgomery 2005). The diversity index was calculated according to Shannon and Weaver (1949).

## Results

### In-situ experiment

#### Water chemistry

Before the filling of the enclosures, the soil pH was moderately acid (5.8–6.5), whereas the pH of the original water was 6.9. The pH of the water decreased for the first 5 days after the flooding simulation—to 5.7 in L, 6.5 in M, and 6.3 in U—but then increased until day 45, reaching a value of 7.4 in Ma. The differences between the soils exposed to agriculture and mixed usage was not significant ( $p = 0.98$  n.s.) (Fig. 3a, left ordinate).

The minimum DO levels were registered in topography U on Day 5 after flooding, at values of  $1.3 \text{ mg L}^{-1}$  in Ua and  $2.6 \text{ mg L}^{-1}$  in Um. The maximum concentration of DO was reached in topography M on Day 45 at  $17 \text{ mg L}^{-1}$  in Mm and  $14 \text{ mg L}^{-1}$  in Ma. This parameter was not significantly different among the fallow soils and those exposed to agricultural and mixed use (univariate ANOVA  $p = 0.59$ ; d.f., 2; 24) (Fig. 3a, right ordinate).

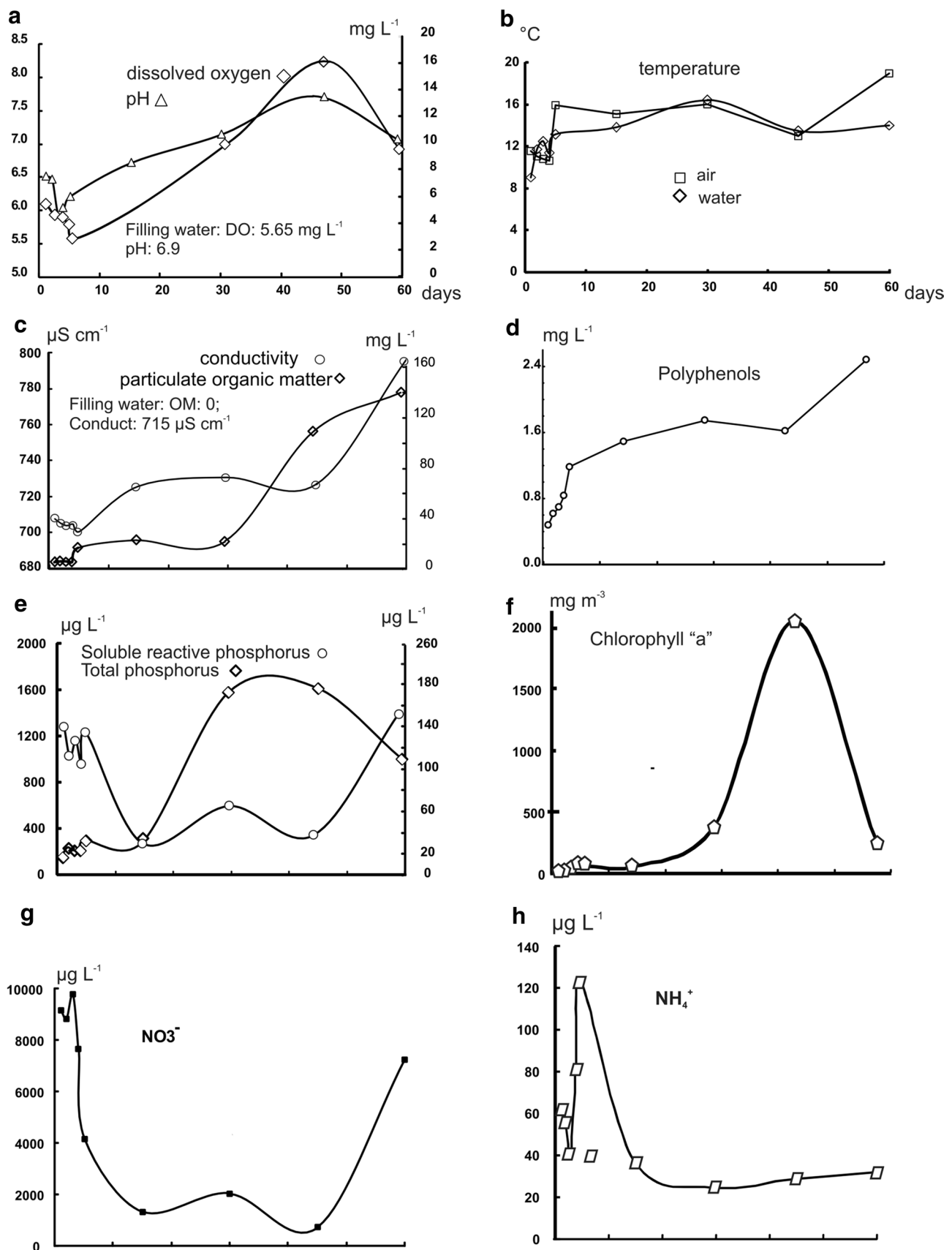
The differences between the air and water temperatures were not significant (paired Student *t* test,  $p > 0.09$  for all treatments) (Fig. 3b).

The conductivity decreased during the first 5 days of flooding down to  $692 \mu\text{S cm}^{-1}$  in Ua, though the average value shown in the figure was about  $700 \mu\text{S cm}^{-1}$ . The conductivity then increased to reach a maximum—at the low site at  $853 \mu\text{S cm}^{-1}$ —at the moment of desiccation at 60 days after the start of the experiment (Fig. 3c, left ordinate).

The concentration of organic matter was used instead of turbidity measurements because that parameter was more sensitive in detecting the presence of particles. Furthermore, the concentrations of OM exhibited a high correlation with suspended solids ( $r = 0.92$ ;  $p < 0.05$ ). The OM levels underwent two pronounced increases, one beginning at 5 days and another at 30 days after the start of the in-situ experiment, thereafter rising progressively until Day 60. The minimum values were estimated in Ua at  $1.3 \text{ mg L}^{-1}$  and the maximum in L at  $259 \text{ mg L}^{-1}$  on Day 60 and in Mm at  $165 \text{ mg L}^{-1}$  on Day 45. The differences between the enclosures exposed to agriculture or mixed use were not significant (Student *t* test;  $p = 0.15$ ; n, 12) (Fig. 3c, right ordinate).

The dissolved polyphenols displayed a clear pattern of increasing concentrations (except for between days 30 and 40) from the time of groundwater addition up to the point of the soils’ drying out, with that increase being especially steep during the first 5 days. The minimum values were registered in Um at  $0.26 \text{ mg L}^{-1}$  and the maximum in L at





**Fig. 3** Variations in the mean values of selected physicochemical parameters and nutrient concentrations for all the experimental topographies during the time of flooding. **a** pH and dissolved oxygen; **b** temperature; **c** conductivity and particulate organic matter; **d** polyphenols; **e** soluble reactive phosphorus and total phosphorus; **f** chlorophyll “a”; **g** nitrates; **h** ammonium ion

3.05 mg L<sup>-1</sup> on Day 60. The differences between soil use were significant in either U (Student t test;  $p < 0.05$ ;  $n$ , 15) or M (Student t test;  $p < 0.05$ ;  $n$ , 14) (Fig. 3d).

The concentration range of TP for all the treatments was between 145 and 2190  $\mu\text{g L}^{-1}$ , with the TP concentration for the initial groundwater being 98  $\mu\text{g L}^{-1}$ . On the day after flooding, the water contained an average concentration of 217  $\mu\text{g L}^{-1}$ , but with the values being significantly higher in the mixed-use (m) than in agricultural-use (a) treatment (Student t test:  $p = 0.04$ ;  $n$ , 6) but similar to those in L (Student t test:  $p > 0.05$ ;  $n$ , 6). The concentrations of TP always remained higher than the initial groundwater levels. The TP concentrations were significantly correlated with the water–chlorophyll-“a” concentrations (Mm:  $r$ , 0.61;  $p = 0.03$ ;  $n$ , 15; Ma:  $r$ , 0.65;  $p = 0.03$ ;  $n$ , 15; and L:  $r$ , 0.96;  $p = 0.03$ ;  $n$ , 9) (Fig. 3e, left ordinate).

The SRP for the initial groundwater was 55  $\mu\text{g L}^{-1}$ . After flooding, the average SRP values increased to 154  $\mu\text{g L}^{-1}$  in all the treatments. The elevation in SRP concentration was 3.5-fold in Um, threefold in Mm, and almost fourfold in L. The profile of the SRP concentration consisted of a decrease until Day 15 (as a result of algal consumption) and then an overall increase up to Day 60 (Fig. 3e, right ordinate).

The chl “a” concentration exhibited a progressive increase from Day 15 until Day 45 of the experiment. In Ua, the range of chl “a” varied between 0  $\mu\text{g L}^{-1}$  on the first day to 87  $\mu\text{g L}^{-1}$  on the fifth day. The maximum values were reached in Mm at 3190  $\mu\text{g L}^{-1}$  (Fig. 3f). The values of chl “a” were significantly greater in Mm than in Ma. The chl-“a” concentration became elevated at this time as a result of the high number of free-living algae in the enclosure.

At the beginning of the experiment, the nitrate concentration first increased abruptly, by about 30% with respect to the groundwater added (at a level of 6.62 mg L<sup>-1</sup>), until Day 3 and then began to decrease as evidence of the algal growth. The soils with different use exhibited similar values during the experiment. The minimum concentration was measured in Mm at 0.305 mg L<sup>-1</sup> on Day 15 and the maximum in L at 14.6 mg L<sup>-1</sup> on Day 60 (Fig. 3g).

The ammonium-ion concentration was two orders of magnitude lower than that of the nitrate. Those values increased from the time of filling—from 60 to 125  $\mu\text{g L}^{-1}$ , after the 5th day, and then decreased abruptly and markedly. The maximum value registered was in Um at 175  $\mu\text{g L}^{-1}$  on Day 5 and the minimum in Ma on Day 45 at 18  $\mu\text{g L}^{-1}$  (Fig. 3h).

## Microconsumers: species composition, specific richness and diversity

The taxa collected (Table 1) were: 20 Rotifera, 19 Ciliophora, 4 Amoebozoa, 1 Rhizaria and various Crustacea (2 Cladocera, 1 Copepoda, and ostracods)—in addition to oligochaetes, nematodes, acarids, collembolans, and insect larvae (Ephydriidae and Chironomidae). The presence of aquatic microconsumers was not detected in the control enclosure (without soil) during the course of the experiment.

The maximum total species richness (SR) was recorded in M and the minimum in U because of a shorter time for colonization (Fig. 4a). The differences between the enclosures containing soils of different land use were not significant (Fig. 4b–d).

The succession of species in Ma and Mm (Fig. 4c) exhibited a similar pattern, characterized by a overall increase in SR and diversity until the end of the experiment. The average SR was significantly higher in the soil having received mixed use at 15, 30, and 60 days. Several genera of ciliates in particular contributed to this increase (Table 2).

In topography L (Fig. 4d), the SR increased during the first 30 days and then stabilized between then and Day 60.

In U the mean species-diversity index ( $H'$ ) displayed a similar pattern to that of SR, and both decreased their values on Day 5 (Fig. 4b). In M the diversity exhibited an overall increase, reaching the highest mean value for soils of both land use types within 60 days (Fig. 4c). The differences between the two types of soils were not significant. In topography L, as with the SR, the diversity index increased at 30 days, but then stabilized between then and Day 60 (Fig. 4d).

## Species abundance

Higher mean densities occurred in topographies M and L, while U exhibited lower values (Fig. 5a). The soil exposed to agriculture exhibited higher density in U compared to mixed use (Fig. 5b–d).

The most abundant microorganisms were the ciliates and rotifers in both types of soil in the middle topography, these taxa were followed in abundance by the testate amoebae and the crustaceans, to the end of experiment (Fig. 6a–e).

The mean maximum density of the ciliates occurred in topography Mm (Fig. 7c) for *Urocentrum turbo* at 15 days (at 5710 ind L<sup>-1</sup>) and in L (Fig. 7d) for *Didinium* sp., *Euplotes* sp., *Prorodon* sp., and *U. turbo* at 30 days; whereas in topography Ma (Fig. 7b) at 15 days, *Didinium* sp., *Euplotes* sp., *U. turbo*, and *Halteria* sp. dominated. In Ua and Um (Fig. 7a), on the fourth to fifth day, the hypotrichs and gymnostome ciliates were prevalent.

The rotifers reached a maximum mean density in L on Day 60 (at 12,400 ind L<sup>-1</sup>), with *Brachionus quadridentatus*, *Lepadella ovalis*, *Cephalodella* sp., *Proales* sp.

**Table 1** Microconsumer taxa in the floodwater in the five topographies

Ciliophora	Rotifera	Nemata
<i>Aspidisca</i> sp.	Bdelloidea	Annelida
<i>Colpidium</i> sp.	<i>Brachionus quadridentatus</i> Hermann	
<i>Didinium</i> sp.	<i>Brachionus caudatus</i> Barrois & Daday	
<i>Dileptus</i> sp.	<i>Plationus patulus</i> Müller	Arthropoda
<i>Epistylis</i> sp.	<i>Cephalodella</i> sp1	<i>Coronatella</i> sp.
		<i>Chydorus</i> sp.
<i>Euplotes</i> sp.	<i>Cephalodella</i> sp2	Copepoda
<i>Frontonia</i> sp.	<i>Euchlanis dilatata</i> Ehr.	Ostracoda
<i>Halteria</i> sp.	<i>Keratella tropica</i> Apstein	Acari
<i>Lacrymaria</i> sp.	<i>Lecane bulla</i> Gosse	Diptera
<i>Podophrya fixa</i> Müller	<i>Lecane hornemanni</i> Ehrb.	Ephydriidae
<i>Vorticella</i> sp.	<i>Lecane pyriformis</i> Daday	Chironomidae
<i>Vorticella</i> sp1	<i>Lepadella ovalis</i> Müller	Collembola
<i>Vorticella</i> sp2	<i>Lophocharis salpina</i> Ehr.	
<i>Vorticella</i> sp3	<i>Monomata</i> sp.	
Hypotrichida	<i>Notommata</i> sp	
Gymnostomatida	<i>Polyarthra vulgaris</i> Carlin	
	<i>Proales</i> sp.	
Amoebozoa	<i>Ptygura</i> sp.	
<i>Arcella vulgaris</i> Ehr.	<i>Taphrocampa</i> sp.	
<i>Diffugia</i> sp.	Undetermined rotifer	
<i>Cyclopyxis</i> sp.		
<i>Centropyxis</i> sp.		
Rhizaria		
<i>Euglypha</i> sp.		

and bdelloids dominating (Fig. 8c). In Mm (Fig. 8b), the mean abundance of rotifers was greater than in Ma (3193 ind L<sup>-1</sup>; Fig. 8a), reaching a value of 6310 ind L<sup>-1</sup> on Day 60. *Notommata* sp. only was found in Ma on days 15 and 30 whereas *Lepadella ovalis* in L, on days 30 and 60. In all topographies the bdelloids became prevalent to the beginning of the experiments and Monogononta *Lecane pyriformis* in Mm. The early appearance of these rotifers may be due to the fact that they belong to the soil.

## Succession and feeding habitats of consuming organisms

### Topography U

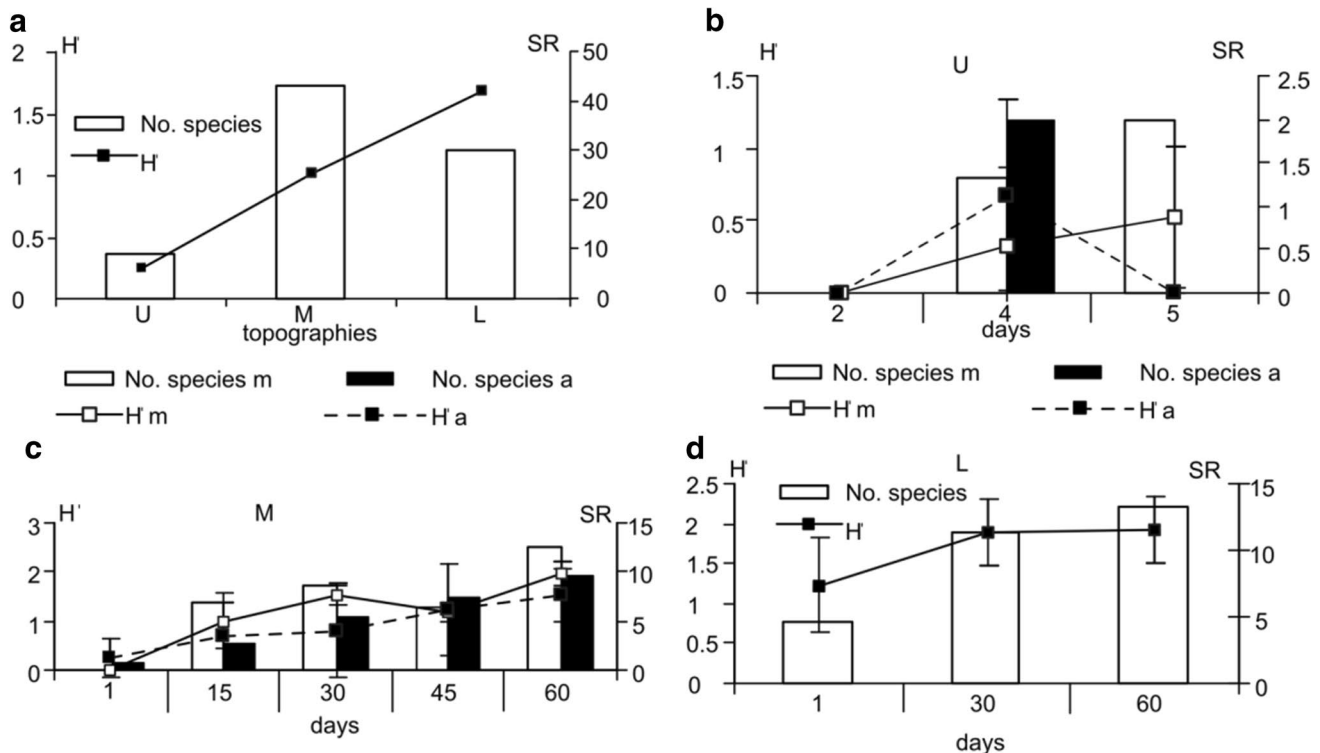
A few species were recorded in U, mainly bacteriophages and filter feeders, protozoa, and organic particles and debris. The most abundant organisms were ciliates followed by rotifers. Nematodes and acari were recorded occasionally, while most of the organisms identified did not remain present over time (Fig. 6a, b; Table 2a).

### Topography M with mixed-use soil (Mm)

Some resistance structures were recorded in Mm on the first day of flooding. The succession started on Day 15 with the appearance of free-living ciliates that feed on bacteria (*e. g.*, *Urocentrum turbo*, *Halteria* sp., and *Colpidium* sp.)—some creeping, such as *Euplotes* sp.; others attaching; both ciliate types being bacteriophagic—along with filtering (*e. g.*, bdelloids, *B. quadridentatus*) and predatory (*Cephalodella* sp.) rotifers. In addition, two ciliate-eating gymnostomes (*Lacrymaria* sp. and *Trachelophyllum* sp.) were registered in only the M topography.

On Day 30, the free-living ciliates declined, while the substrate-attached bacteriophagic ciliates such as *Vorticella* spp. increased. On Day 45, the filter-feeding rotifers *B. quadridentatus*, *Brachionus patulus*, *Brachionus caudatus*, and *Lophocaris salpina* dominated and increased in abundance up to Day 60. The attached ciliates were still remaining on Day 60, while the crawling ciliates such as *Euplotes* sp.—after diminishing substantially between days 30 and 45—increased remarkably at this time to feed on the bacteria, other ciliates, and flagellates. The succession at Mm





**Fig. 4** The mean species diversity and the total species richness of microorganism consumers in different topographies and land uses during the period of flooding. In the figure, species diversity ( $H'$ , squares) on the left ordinates and richness (SR, bars) on the right ordinates are plotted in Panel **a** for the three different topographies

(U, upper; M, middle, L, lower) designated on the *abscissa* and in Panels **b** (upper), **c** (middle), and **d** (lower) for the different days of the experiment indicated on the *abscissas*. In **b** and **c**, white squares (whole line) and bars represent mixed land use (m) and black squares (broken line) and bars, agriculture (a)

thus followed the sequence: ciliates (initial stage), rotifers (at intermediate stages), and rotifers plus other taxa (final stage). The succession of feeding-habit organisms was: none present (initial stage); bacteriophagic, predatory, and grazing (intermediate stage); and filtering, predatory, and grazing (final stage) microconsumers (Figs. 7c, 8b; Table 2b).

#### Topography M with agricultural soil (Ma)

In Ma, *Urocentrum turbo* was present on the first day of flooding (Fig. 7b). On Day 15, *Halteria* sp. and some creeping feeders, such as *Euplotes* sp., appeared. *Didinium* sp.—a free-living ciliate that is predatory especially on *Colpidium* sp. was also recorded. On Day 30 a testate amoeba, *Centropyxis* sp., was present, but was then replaced by *Euglypha* sp. (Fig. 6c). *Frontonia* sp.—free-living ciliate that feed on fungi, algae, and ciliates—and *Podophrya fixa*, a suctorian predator on ciliates, was also registered at this time. On Day 45, predator rotifers, such as *Cephalodella* sp., along with filter feeders, such as *Keratella tropica* and *L. salpina*, appeared as well as nematodes—with the latter being present only at this stage (Fig. 8a). On Day 60, free-living ciliates,

numerous testate amoebae, and filter-feeder rotifers were recorded.

The succession of feeding-habit organisms in Ma followed the sequence (Table 2b): bacteriophagic and filter-feeding (early stage); bacteriophagic, predatory, and filter-feeding (intermediate stage); and scavenging, predatory, and filter-feeding (final stage) microconsumers.

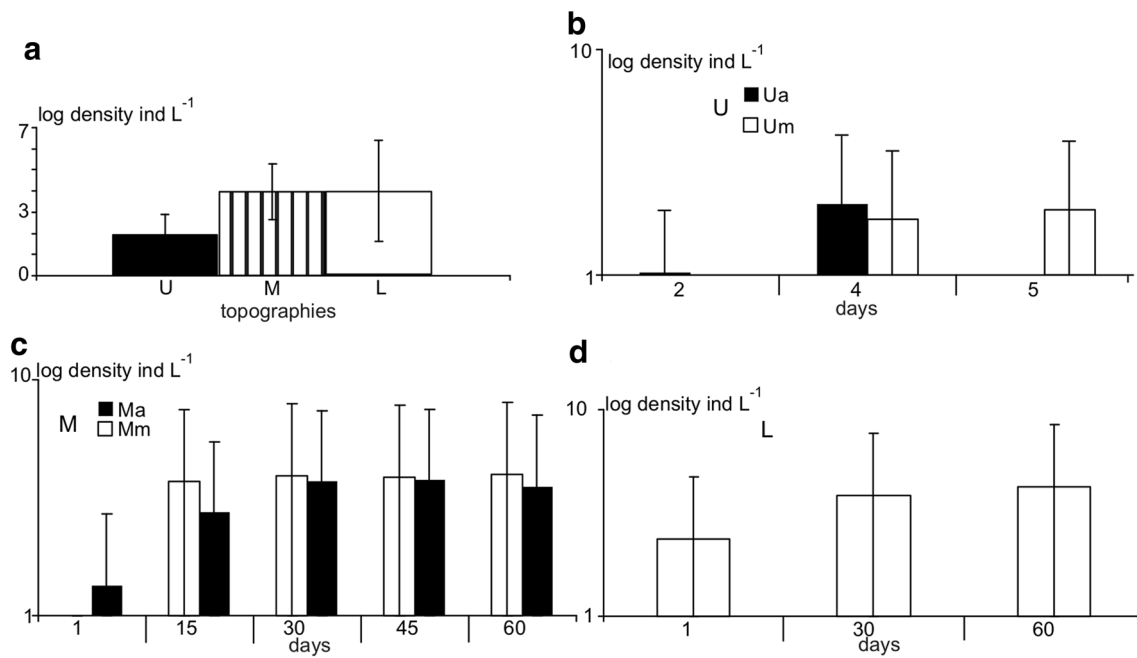
#### Topography L

In L, at the initial stage, free-living organisms such as *Aspidisca* sp. and *U. turbo* as well as periphytic ciliates such as *Vorticella* sp.—all of which taxa feed on bacteria—were recorded (Fig. 7d). Moreover, a predatory ciliate (*Dileptus* sp.), filter-feeder rotifers (bdelloids), ostracods, and nematodes were also present (Fig. 6e). On Day 30, bacteriophagic ciliate (*Euplotes* sp., *Vorticella* sp.), and filter feeders rotifers (*B. quadridentatus*, *L. salpina*, *L. ovalis*, and *K. tropica*) remained in abundance; while predator species (*Cephalodella* sp.) also appeared (Figs. 7d, 8c). On Day 60, filter feeders (*L. ovalis*) and predatory species (*Cephalodella* sp.) were dominant (Fig. 8c), while nematodes were also found in abundance (Fig. 6e). The

**Table 2** Stages in the succession of microorganisms within different topographies and land uses: (a) upper; (b) middle; (c) lower

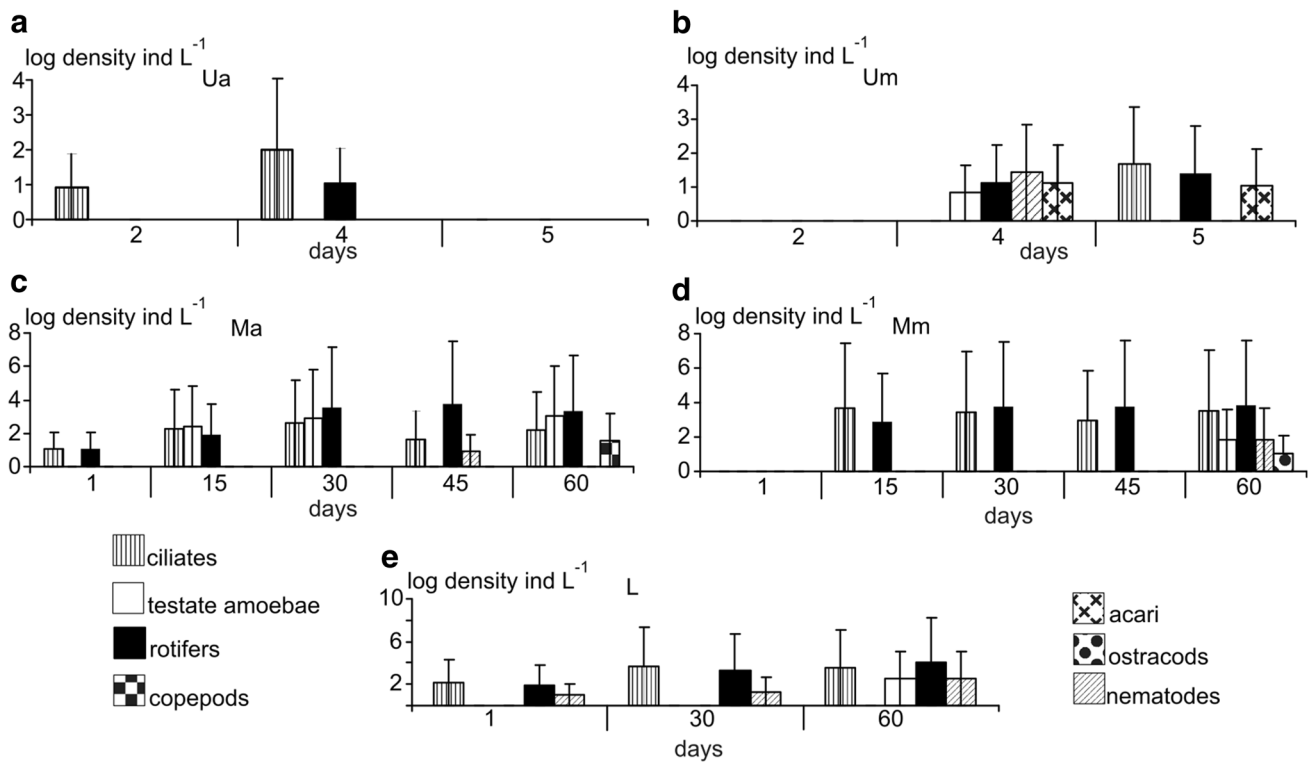
(a)		
Topography	Upper	
Land use	Mixed	Agriculture
Initial period	Day 2 (74 cm): organisms not recorded	Day 2 (76 cm): <i>Urocentrum turbo</i>
Intermediate period	Day 4 (33 cm): <i>Cyclopyxis</i> , and bdelloid rotifers. The nematodes present at only this stage	Day 4 (50 cm): ciliates such as <i>Vorticella</i> spp., and one of gymnostome. <i>Lecane pyriformis</i> was registered once
Final period	Day 5 (20 cm): one hypotrich, one gymnostome, and bdelloids	Day 5 (29 cm): organisms not recorded
Species habitat	Of the organisms, 83% were attached to a substrate such as hypotrich ciliates, testate amoebae ( <i>Cyclopyxis</i> ), bdelloid rotifers, and nematodes	Of the organisms, 80% were associated with a substrate such as peritrich ciliates ( <i>Vorticella</i> spp.), and rotifers of the genus <i>Lecane</i>
(b)		
Topography	Middle	
Land use	Mixed	Agriculture
Initial period	Day 2 (78 cm): organisms not recorded	Day 2 (78 cm): ciliate <i>Urocentrum turbo</i> , and bdelloid rotifers
Intermediate period	Day 15 (71 cm): ciliates <i>Urocentrum turbo</i> , <i>Didinium</i> sp., <i>Euplotes</i> sp., <i>Halteria</i> sp., <i>Trachelophyllum</i> sp., <i>Vorticella</i> spp., <i>Lacrymaria</i> . Rotifers began to appear with <i>Proales</i> sp., bdelloids, <i>Brachionus quadridentatus</i> , and <i>Cephalodella</i> sp	Day 15 (71 cm): ciliates such as <i>Euplotes</i> sp., <i>Didinium</i> sp., <i>Halteria</i> sp., and <i>Lacrymaria</i> sp. Rotifers such as <i>Brachionus quadridentatus</i> , and <i>Notommata</i> sp. Testate amoebae <i>Centropyxis</i> sp. were present
Final period	Day 30 (43 cm): ciliates such as <i>Vorticella</i> spp. Rotifers such as <i>Proales</i> sp., and <i>Cephalodella</i> sp	Day 30 (43 cm): <i>Euglypha</i> sp. Ciliates such as <i>Frontonia</i> sp., and <i>Podophrya fixa</i>
	Day 45 (36 cm): <i>B. quadridentatus</i> , <i>Lophocaris salpina</i>	Day 45 (37 cm): rotifers such as <i>Cephalodella</i> , <i>Keratella tropica</i> , and <i>Lophocaris salpina</i> . Nematodes were present
	Day 60 (8 cm): ciliates such as <i>Euplotes</i> sp. <i>Euglypha</i> among testate amoebae. Among the 13 species of rotifers, the most abundant found were <i>Lophocaris salpina</i> , <i>Lepadella ovalis</i> , and <i>Cephalodella</i> sp. Ostracods were found	Day 60 (8 cm): there ciliates, and testate amoebae were found such as <i>Arcella vulgaris</i> and <i>Diffugia</i> sp. Rotifers as <i>Polyarthra vulgaris</i> , <i>Keratella tropica</i> , <i>Lecane bulla</i> , <i>Lecane hornemanni</i> , <i>Lepadella ovalis</i> Chironomid larvae, nauplii larvae, and adults of crustaceans ( <i>Coronatella</i> sp.)
Species habitat	53% of species were free-living. The rest were for periphytic forms. <i>Lacrymaria</i> sp., and <i>Tracheophyllum</i> sp. are predatory ciliates swimmers, and is also associated with substrates	57% of species were periphytic forms including several species of testate amoebae, and rotifers such as species of <i>Cephalodella</i> , and <i>Lecane</i>
(c)		
Topography	Lower	
Land use	Fallow	
Initial period	Day 3 (73 cm): only 9 species were registered: <i>Aspidisca</i> sp., <i>Urocentrum turbo</i> , and <i>Vorticella</i> spp. Also <i>Proales</i> sp., and bdelloid rotifers, ostracods, and nematodes were found	
Intermediate period	Day 30 (60 cm): 17 species were found: ciliates such as <i>Euplotes</i> sp., and <i>Vorticella</i> sp., rotifers such as <i>Brachionus quadridentatus</i> , <i>Keratella tropica</i> , <i>Proales</i> sp., <i>Cephalodella</i> sp., <i>Lepadella ovalis</i> , and <i>Lophocaris salpina</i>	
Final period	Day 60 (7 cm): ciliates density decreased slightly, and rotifers increased an order of magnitude due to <i>Lepadella ovalis</i> , and <i>Cephalodella</i> sp. <i>Euglypha</i> spp., and nematodes were present	
Species habitat	54% of species were associated with substrates such as ciliates <i>Aspidisca</i> sp., <i>Euplotes</i> sp., <i>Podophrya fixa</i> , <i>Vorticella</i> spp. such as rotifers <i>Cephalodella</i> spp., <i>Euchlanis dilatata</i> , and <i>Lepadella ovalis</i> 46% were free-living organisms such as <i>Didinium</i> sp., <i>Halteria</i> sp., <i>Brachionus</i> spp., <i>L. salpina</i> , <i>K. tropica</i> , and <i>Proales</i> sp. <i>Dileptus</i> sp. is a predatory ciliated swimmer, and its feeding habit is found associated with substrates	

Detail of the water level in parentheses



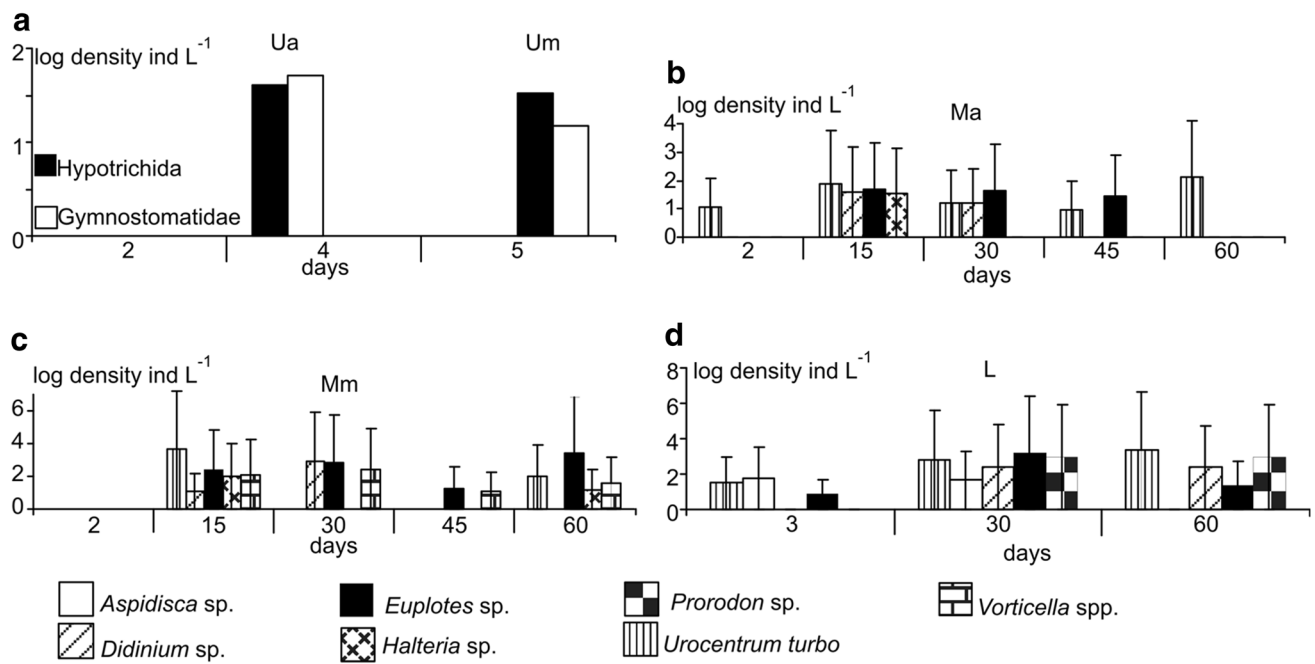
**Fig. 5** The mean total density plus the standard error of consumer microorganisms, expressed as the logarithm of the number of individuals L<sup>-1</sup>, is plotted on the ordinates in Panel **a** for the different topographies (U, upper; M, middle, L, lower) (**a**) and in Panel **b** (upper:

black bars, agriculture; white bars, mixed land use), Panel **c** (middle: black bars, agriculture; white bars, mixed land use), and Panel **d** (lower) for the different days of the experiment indicated on the abscissa



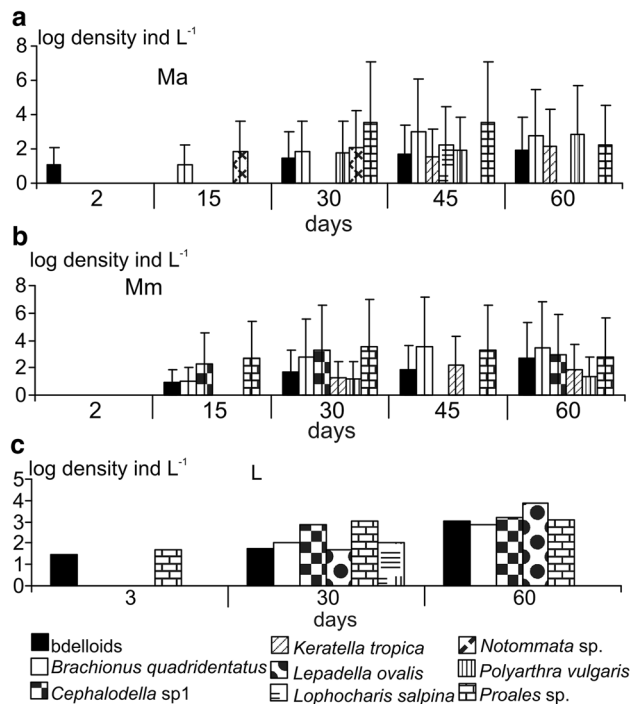
**Fig. 6** The mean total density plus the standard error of taxa of consumer microorganisms, expressed as the logarithm of the number of individuals L<sup>-1</sup>, is plotted on the ordinates for the different days of the experiment indicated on the abscissas. Panel [please change the

rest] **a** upper, agriculture soil (Ua); **b** upper, mixed-use soil (Um); **c** middle, agriculture soil (Ma); **d** middle, mixed-use soil (Mm); **e** lower (L)



**Fig. 7** The mean total density plus the standard error of the most abundant ciliates in different topographies and land uses, expressed as the logarithm of the number of individuals  $L^{-1}$ , is plotted on the ordi-

nates for the different days of the experiment indicated on the abscissas. **a** upper, agriculture soil (Ua), mixed-use soil (Um); **b** middle, agriculture soil (Ma); **c** middle, mixed-use soil (Mm); **d** lower



**Fig. 8** The mean density plus the standard error of the most abundant species of rotifers in topographies M (Ma, Mm) and L, expressed as the logarithm of the number of individuals  $L^{-1}$ , is plotted on the ordinates for the different days of the experiment indicated on the abscissas. **a** middle, agriculture soil (Ma); **b** middle, mixed-use soil (Mm); **c** lower

sequence of feeding-habit organisms in L was: bacteriophagic, filter-feeding, and predatory (initial and intermediate stage) and filter-feeding and predatory (final stage) microconsumers (Table 2c).

## Discussion

The colonization of a new environment by consumer organisms can occur within days or weeks (Ward and Stanford 1995). Colonizing over short distances has been demonstrated to be effective through different means, though most species do so mainly by wind. Even if distance is not a limiting condition for colonization, water chemistry or the geomorphologic features of the environment can be (Cohen and Shurin 2003). Nevertheless, many species arise from resistant structures that remain in the soil after a flooding, or originate in soil communities that can reside within the moisture prevailing in between sporadic rains.

After the flooding, colonization was initiated by opportunistic species that did not persist over time. Subsequently, species of ciliates and rotifers with different feeding behavior were dominant during the whole flooding period. The crustaceans appear in both types of land use in the middle topography at the end of the experiment. The highest species richness and diversity was recorded at the middle topography, with mixed use.

## Dominant groups and quiescence strategies

Ciliate and rotifer species with different eating habits were the dominant groups during the whole period of flooding, right from the initial stages on. Both groups are ubiquitous owing to the ability of many of those biota to produce resistant stages that allow them to remain viable during developmentally unfavorable periods and in so doing adapt to survival in environments with a total lack of water (Foissner 1997; Ricci 2001; Brock et al. 2003; Cohen and Shurin 2003; Segers 2008). Furthermore, in the production of resistant structures, ciliates are considered to be ‘r’ strategists, since that tactic gives those species an additional adaptive advantage to exploit temporary environments (Foissner et al. 1999). *Urocentrum turbo* represents a good example of strategist “r” in our experiment for its behavior at the beginning of the flood (Fig. 7b–d). Indeed, to complete their life cycle, the success of certain species depends on changing environmental conditions. Since many “r” strategists have evolved to live in only temporarily humid environments, droughts do not constitute adversities or disasters (Reddy and DeLaune 2008). The bdelloids rotifers resist drought for long periods in cryptobiosis while the monogononta do it by means of resting eggs. The bdelloid rotifers appeared on topographies M and L immediately after flooding the closures. This suggests that these organisms are from the soil as they emerged quickly as the Monogononta *Lecane pyriformis* (Koste 1996). The resting eggs mainly serve as dormant stages to bridge the terrestrial phase in places where those dormant forms have been produced during the aquatic phase (Schröder 2001, 2005).

*Brachionus quadridentatus*, *Keratella tropica*, *Lecane bulla*, *Lepadella ovalis*, and *Lophocaris salpina* are opportunistic strategists that colonize the floodplain during the transition between the aquatic and terrestrial phases. These rotifers take advantage in an adverse period because there are more available food resources (Schröder 2001, 2005). The increase in the abundance of *B. quadridentatus* in the present experiments would be associated with its tolerance to abiotic conditions in sites rich in nutrients and is favored as a result of the algae that develop in those locations as a food source (Angeler et al. 2010). The microcrustaceans were at low abundance only in the final period in Ma with nauplii larvae, adult copepods and a cladoceran *Coronatella* sp. Copepods need a longer water-residence time in order to develop a critical biomass and size (Schöll and Kiss 2008; Santangelo et al. 2015).

Several species of nematodes that live in the water film surrounding soil particles are able to survive desiccation through the ability to hide in cryptobiosis (Pilato 1979; Boulton and Lloyd 1992). In the experiment they occurred from day 30 at L and from day 45 at M. The flooding must remain for some time so that the quiescent states can develop

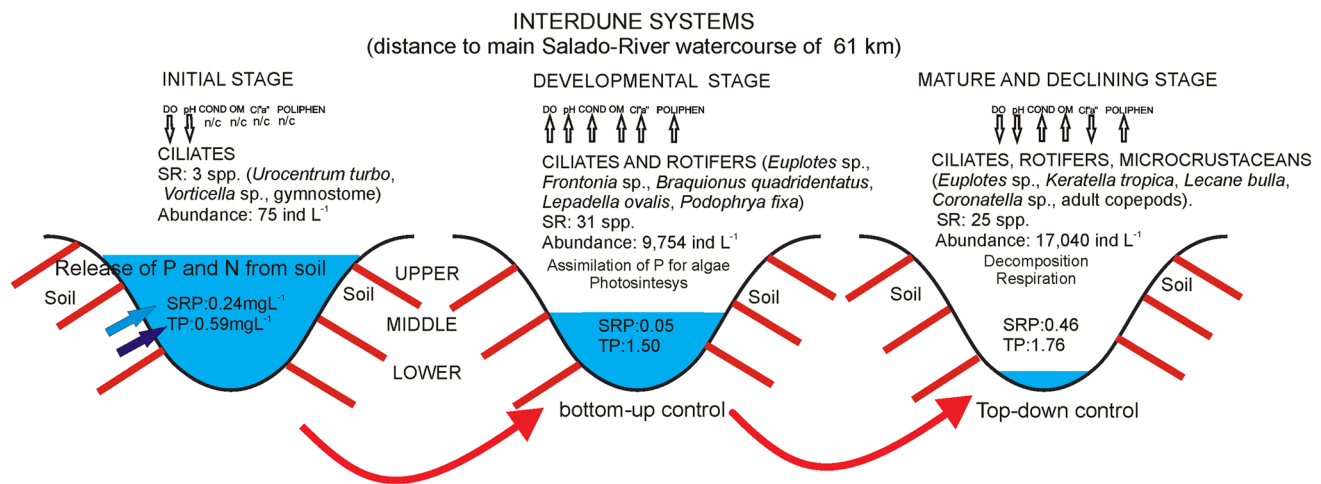
resting eggs that are stored in floodplain soils and may remain viable for many years (Catlin et al. 2017).

## Succession and feeding habitats

In the present experiment, colonization, just 5 days after flooding, was performed by opportunistic species (*e. g.*, ciliates, testate amoebae, and bdelloid rotifers) at very low densities, but did not persist over time. The variety of feeding habits at this early time point—*i. e.*, detritivory and bacteriophagy, those being characteristic of early stages in the succession—was very narrow (Foissner et al. 1999). Species richness increased at lower elevations, with a higher richness and abundance of the earliest consuming species being found in the lower. This apparent distribution probably resulted because the initial sampling in the upper- and middle topographies was done two days after the flooding; whereas the lower samples were taken on the third day, thus affording an extra day of colonization time for that topography. Moreover, because the lower remained wet over time, even when not flooded, through proximity to the groundwater level and the basin’s geomorphology; the soil community remained in a more constant environment over time.

An eventual high algal development (chlorophyll “a”, Fig. 3f) with a few species is characteristic of an early succession stage (Odum 1969), resulted in such a depletion of the nutrients (SRP,  $\text{NO}_3^-$ , Fig. 3e, g), and later the producer community became accordingly reduced. Thus, in the lower, the additional control of producer populations by the consumers seems to have led to a community with a high degree of self-regulation—*i. e.*, an initial consumption of nutrients allowed the microalgae to increase in density, and thus the consumer population could do so as well. There may be mentioned at this stage filtering rotifers as *Brachionus quadridentatus*, *Keratella tropica* and *Lophocaris salpina* (Fig. 8). In this scenario, a so-called top-down control occurred in which the producer community was regulated by the consumers. Furthermore, in the middle topography, the rapid consumption of nutrients by the producers (both the free-water and the periphytic algae) during the initial and intermediate time periods caused a decrease in the producers’ biomass that resulted in a subsequent decrease in the consumers—here occurring an example of what is referred to as bottom-up control (Scheffer 1998). Moreover, another difference between the two topographies was with respect to their energy processes. During the flooding in the middle, the high density and biomass of the primary producer community resulted in high levels of DO (Fig. 3a) in the water, leading to a dynamic where photosynthesis exceeded respiration (*i. e.*, an autotrophic system). In contrast, in the lower topography, low densities of microalgae led to low concentrations of DO and a high density of consumers, thus





**Fig. 9** Three-stage succession scheme of the in-situ experiment, with mean values for the dynamics of water-phosphorus concentrations indicated. DO dissolved oxygen; CONDUC conductivity; OM par-

ticulate organic matter; POLYPHEN dissolved polyphenols; Chl "a" chlorophyll "a"; pH and the main characteristics of the microconsumers: SR specific richness; dominant species; and abundance

indicating the preponderance of respiration over photosynthesis (*i. e.*, a heterotrophic system, Fig. 9).

The presence of resistant structures facilitates the ability of an ecosystem to recover by means of a flooding after a drought, as those structures allow species to develop quickly once the dormancy period ends (Brock et al. 2003). Thus, considering the frequency of the recurrence of floods in the study area and recognizing the ecological role of those occasions in the evolution of the ecosystem (Gabellone et al. 2003; Chaneton 2006), we expected that the soil would be provided with forms of resistance that would develop when the moisture conditions became adequate.

### Microorganisms in the floodwater and in the Salado River basin

In less mature ecosystems large fluctuation in population can be expected. These fluctuations can represent an export of organisms to other communities (Margalef 1963). The species of consumer microorganisms we identified in the soil during the flooding are common to many different lotic environments of the Salado-River basin (Claps et al. 2009). Of the most abundant rotifer, ciliate, and testate-amoeba species recorded in the flooded soil; 75%, 84%, and 47%, respectively, have been registered previously in the river (Claps et al. 2009). The Danube, Matjulu, and Murray rivers also share more than 30% of the ciliates that are in the associated floodplains (Foissner et al. 2008). These data reveal the significance of such flooded areas as sources of microorganisms for inoculation into a river. Certain species of rotifers found in floodwaters but not registered in the Salado-River, such as some of the Brachionidae members such as *Platyonus patulus*. Certain ciliates, such as *Prorodon* sp., that are not

common to the river are found in temporary environments; while others, such as *Trachelophyllum* sp., live in the sediments (Foissner et al. 1999) and still others, such as *Dileptus* sp., have been recorded in sandy soils or—in the example of *Urocentrum turbo* and *Frontonia* sp.—in streams (Foissner et al. 2008).

The complete role of the microbiota (*i. e.*, protists, rotifers, microcrustaceans) arising from temporary wetlands and floodplains in the reproductive success of native-fish species is not completely known; but those microconsumers, when carried into the Salado River by floodings, must certainly constitute the vital first link in the trophic chain by serving as food for that river's resident fish since hydrologic occurrences have been shown to trigger responses in fish spawning, and certain hydroecological processes result in an increased recruitment of larvae and fry (Bunn and Arthington 2002). Therefore, measures dictating the formation and management of policies determining anthropogenic alterations in the Salado-floodplain landscape, such as canalization, need improvement in order to take into account the impact of such interventions on these natural processes and on the biota in this region that would necessarily be affected. Despite the intensive agricultural use of soil, and the loss of the ecological integrity of the natural grasslands, that environment still maintains its bank of propagules.

**Acknowledgements** We thank to the managers, teachers, professionals, and staff of the María Cruz and Manuel Inchausti School for allowing us to stay at the School during the sampling in the school's field and for their unconditional support of this investigation. We are grateful to Dr. Gabriela Küppers for characterizing the ciliates. We are very grateful to the reviewers and the editors for the careful reading of our manuscript and the constructive and valuable comments. Dr. Donald F. Haggerty, a retired academic career investigator and native English

speaker, edited the final version of the manuscript. This work was partially funded by the Argentine Agency for Science and Technology promotion (ANPCyT), National Council of Sciences and Technology (CONICET; PIP 5612) and by the La Plata National University (Grant N484). Scientific contribution no. 1140 of the La Plata Ringuelet Limnology Institute.

## References

- Ameghino F (1884) Las secas y las inundaciones en la provincia de Buenos Aires. Obras de retención y no de desagüe. Publicaciones del Ministerio de Asuntos Agrarios de la Provincia de Buenos Aires, La Plata
- Angeler DG, Alvarez-Cobelas M, Sánchez-Carrillo S (2010) Evaluating environmental conditions of a temporary pond complex using rotifer emergence from dry soils. *Ecol Indic* 10:545–549
- Aoyagui ASM, Bonecker CC (2004) The art status of rotifer studies in natural environments of South America: floodplains. *Acta Sci Biol Sci* 26:385–406. <https://doi.org/10.4025/actascibiolsoci.v26i4.1521>
- APHA (1995) Standard methods for the examination of waters and wastewaters, 19th edn. APHA/AWWA/WPCF, Washington DC
- Bayley PB (1995) Understanding large river: floodplain ecosystems. *Bioscience* 45:153–158
- Bohonak AJ, Jenkins DG (2003) Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecol Lett* 6:783–796
- Boulton AJ, Lloyd LN (1992) Flooding frequency and invertebrate emergence from dry floodplain sediments of the River Murray, Australia. *River Res Appl* 7(2):137–151
- Brock MA, Nielsen DL, Shiel RJ, Green JD, Langley JD (2003) Drought and aquatic community resilience: the role of eggs and seeds in sediments of temporary wetlands. *Freshw Biol* 48:1207–1218
- Bunn SE, Arthington AH (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environ Manag* 30(4):492–507
- Cabrera AL (1971) Fitogeografía de la República Argentina. *Boletín de la Sociedad Argentina de Botánica* 14:1–42
- Catlin AK, Collier KJ, Duggan IC (2017) Zooplankton generation following inundation of floodplain soils: effects of vegetation type and riverine connectivity. *Mar Freshw Res* 68:76–86
- Chaneton EJ (2006) Las inundaciones en pastizales pampeanos. Impacto ecológico de las perturbaciones naturales. *Ciencia Hoy* 16(92):18–32
- Claps MC, Gabellone NA, Neschuk NC (2009) Influence of regional factors on zooplankton structure in a Author: Kindly provide accessed date for the references (Darwin Project Nematodes 2018; Lynn 2008). saline lowland river: the Salado River (Buenos Aires province, Argentina). *River Res Appl* 25(4):453–471
- Cohen GM, Shurin JB (2003) Scale-dependence and mechanisms of dispersal in freshwater zooplankton. *Oikos* 103:603–617
- Darwin Project Nematodes (2009). <http://pml.ac.uk/nematode/tech/nemid.htm>
- De Smet W (1996) Rotifera: the Proalidae (Monogononta). In: Dumont H (ed) Guides to the identification of the microinvertebrates of the continental waters of the world, vol 4
- Devetter M, Schöll K (2014) Hydrobiont animals in floodplain soil: are they positively or negatively affected by flooding? *Soil Biol Biochem* 69:393–397
- Elster H-J, Ohle W (1972) Das Zooplankton der Binnengewässer. 1. Teil. E. Schweizerbart'sche Verlagsbuchhandlung (Nägele u. Obermiller), Stuttgart
- Foissner W (1997) Soil ciliates (Protozoa: Ciliophora) from evergreen rain forests of Australia, South America and Costa Rica: diversity and description of new species. *Biol Fertil Soils* 25:317–339
- Foissner W (2002) Neotypification of protests, especially ciliates (Protozoa, Ciliophora). *Bull Zool Nomencl* 59(3):165–169
- Foissner W, Berger H, Schaumburg J (1999) Identification and ecology of limnetic plankton ciliates. Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft, Heft 3/99:1–799
- Foissner W, Agatha S, Berger H (2002) Soil ciliates (Protozoa, Ciliophora) from Namibia (Southwest Africa), with emphasis on two contrasting environments, the Etosha Region and the Namib Desert. *Denisia* 5:1–1459
- Foissner W, Chao A, Katz LA (2008) Diversity and geographic distribution of ciliates (Protista: Ciliophora). *Biodivers Conserv* 17:345–363
- Frisch D (2002) Dormancy, dispersal and the survival of cyclopoid copepods (Cyclopoida, Copepoda) in a lowland floodplain. *Freshw Biol* 47:1269–1281
- Frutos SM (1998) Densidad y diversidad del zooplancton en los ríos Salado y Negro— planicie del río Paraná—Argentina. *Rev Bras Biol* 58(3):431–444
- Gabellone NA, Solari LC, Claps MC (2001) Planktonic and physico-chemical dynamics of a markedly fluctuating backwater pond associated with a lowland river (Salado River, Buenos Aires, Argentina). *Lakes Reserv Res Manag* 6:133–142
- Gabellone NA, Sarandón R, Claps MC (2003) Caracterización y zonificación ecológica de la cuenca del río Salado. In: Maiola O, Gabellone NA, Hernández M (eds) Inundaciones en la región pampeana. Editorial Universidad Nacional de La Plata, La Plata, pp 87–122
- Gabellone NA, Claps MC, Solari LC, Neschuk NC (2005) Nutrients, conductivity and plankton in a landscape approach to a Pampean saline lowland river (Salado River, Argentina). *Biogeochemistry* 75:455–477
- Gabellone NA, Claps MC, Solari LC, Neschuk NC, Ardohain DM (2013) Spatial and temporal distribution pattern of phosphorus fractions in a saline lowland river with agricultural land use (Salado River, Buenos Aires, Argentina). *Fundam Appl Limnol* 183/4:271–286
- Gabellone NA, Claps MC, Ardohain DM, Dippolito A, Bazzuri ME, Solari LC (2014) Relationship between the zoo- and phytoplankton biomasses in a saline lowland river (Argentina): a short-time-scale analysis. *Fundam Appl Limnol* 184/4:307–327
- Górski K, Collier K, Duggan IC, Taylor CM, Hamilton DP (2013) Connectivity and complexity of floodplain habitats govern zooplankton dynamics in a large temperate river system. *Freshw Biol* 58:1458–1470
- Havel JE, Matt Eisenbacher E, Black AA (2000) Diversity of crustacean zooplankton in riparian wetlands: colonization and egg banks. *Aquat Ecol* 34:63–76
- Junk WJ, Robertson BA (1997) Aquatic invertebrates. In: Junk WJ (ed) The central amazon floodplain ecology of a pulsing system. Springer, Berlin, pp 279–298
- Koste W (1996) On soil Rotatoria from a Lithotelma near Halali Lodge in Etosha National Park in N-Namibia, South Africa. *Internationale Revue der gesamten Hydrobiologie Hydrographie* 81:353–365
- Koste W, Shiel RJ (1987) Rotifera from Australian inland waters. II. Epiphanidae and Brachionidae (Rotifera: Monogononta). *Invertebr Syst* 1:949–1021. <https://doi.org/10.1071/IT9870949>
- Koste W, José de Paggi S (1982) Rotifera of the Superorder Monogononta recorded from Neotropis. *Gewässer Abwässer* 68:71–102
- Lynn DH (2008) The ciliated protozoa: characterization, classification, and guide to the literature. Springer Science & Business Media, Canada. [https://books.google.com.ar/books?id=Hd3jKGBDR48C&lr=&hl=es&source=gb\\_s\\_navlinks\\_s](https://books.google.com.ar/books?id=Hd3jKGBDR48C&lr=&hl=es&source=gb_s_navlinks_s)

- Margalef R (1963) On certain unifying principles in ecology. *Am Nat* 897:357–374
- Mitsch WJ, Gosselink JG (2015) *Wetlands*, 5th edn. Wiley, New Jersey, p 736
- Montgomery D (2005) *Design and analysis of experiments*, 6th edn. John Wiley, New York
- Nieff JJ (1996) Large rivers of South America: toward the new approach. *Verh Int Ver Theoret Angew Limnol* 26:167–180
- Neschuk NC (2001) *Limnología del río Salado (Buenos Aires) y el uso de la tierra en su cuenca*. Tesis Doctoral 767. Facultad Ciencias Naturales y Museo, Universidad Nacional de La Plata
- Neschuk N, Gabellone NA, Solari LC (2002) Plankton characterisation of a lowland river (Salado River, Argentina). *Verh Int Ver Theoret Angew Limnol* 28:1336–1339
- Odum E (1969) The strategy of ecosystem development. *Science* 164:262–270
- Palazzo F, Bonecker CC, Negae M (2008) Zooplankton dormancy forms in two environments of the upper Paraná River floodplain (Brazil). *Acta Limnol Bras* 20:55–62
- Pilato G (1979) Correlations between cryptobiosis and other biological characteristics in some soil animals. *Ital J Zool* 46(4):319–332
- Prach K, Walker LR (2011) Four opportunities for studies of ecological succession. *Trends Ecol evol* 26(3):119–123
- Reddy KR, DeLaune RD (2008) *Biogeochemistry of wetlands*. Science and applications. EUA, New York
- Reid J (1985) Clave de identificação e lista de referências bibliográficas para as espécies continentais sulamericanas de vida livre da ordem Cyclopoidea (Crustacea, Copepoda). *Boletim de zoologia Universidade Sao Paulo* 9:17–143
- Ricci C (2001) Dormancy patterns in rotifers. In: *Rotifera IX* 1–11. Springer, Netherlands
- Santangelo JM, Lopes PM, Nascimento MO, Fernandes APC, Bartole S, Figueiredo-Barros MP, Leal JFF, Esteves FA, Farjalla VF, Bonecker CC, Bozelli RL (2015) Community structure of resting egg banks and concordance patterns between dormant and active zooplankters in tropical lakes. *Hydrobiologia* 758(1):183–195
- Scheffer M (1998) *Ecology of shallow lakes*. Chapman and Hall, London, p 357
- Schöll K, Kiss A (2008) Spatial and temporal distribution patterns of zooplankton assemblages (Rotifera, Cladocera, Copepoda) in the water bodies of the Gemenc Floodplain (Duna-Dráva National Park, Hungary). *Opuscula Zool Budapest* 39:65–76
- Schröder T (2001) Colonising strategies and diapause of planktonic rotifers (Monogononta Rotifers) during aquatic and terrestrial phases in a floodplain (Lower Oder Valley, Germany). *Int Rev Hydrobiol* 86(6):635–660
- Schröder T (2005) Diapause in monogonont rotifers. *Hydrobiologia* 546:291–306
- Segers H (1995) Rotifera: the Lecanidae (Monogononta). In: Dumont H (ed) *Guides to the identification of the microinvertebrates of the continental waters of the world*, vol 6. SPB Academic Publishing, The Hague
- Segers H (2008) Global diversity of rotifers (Rotifera) in freshwater. *Hydrobiologia* 595:49–59
- Shannon CE, Weaver W (1949) *The mathematical theory of communication*. University of Illinois Press, Urbana
- Shiel RJ, Green JD, Nielsen DL (1998) Floodplain biodiversity: why are there so many species? *Hydrobiologia* 387/388:39–46
- Soil Survey Staff (2003) *Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys*, 9th edn. Natural Resources Conservation Service. US Department of Agriculture Handbook, Washington DC, p 325
- Sokal RR, Rohlf FJ (1979) *Biometria: principios y métodos estadísticos en la investigación biológica*. H. Blume, Madrid
- Solari LC, Claps MC, Gabellone NA (2002) River backwater pond interactions in the lower basin of the Salado River (Buenos Aires, Argentina). *Arch Hydrobiol* 141(1/2):99–119
- Ventimiglia LA, Carta HG, Rillo SN (2000) Soja: nutrición nitrogenada. *Revista de tecnología agropecuaria*. INTA 5(14):45–48
- Viglizzo EF, Frank FC, Carreño L (2006) Situación ambiental en las ecorregiones Pampa y Campos y Malezas. In: Brown A, Martinez O, Acari M, Corchera J (eds) *La Situación Ambiental Argentina 2005*, 1st edn. Fundación Vida Silvestre Argentina, Buenos Aires, pp 262–278
- Ward JV, Stanford JA (1995) Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *River Res Appl* 11(1):105–119