

# Zooplankton biomass and community structure in a Danube River floodplain system: effects of hydrology

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## SUMMARY

1. Zooplankton density and biomass was examined in a Danube River floodplain section with highly variable hydrological dynamics. Temporal patterns were analysed to assess the effects of hydrological conditions on zooplankton community structure and the differential response of the two major zooplankton taxa, rotifers and crustaceans.
2. Calculated floodplain water age was used as an integrated parameter describing hydrological conditions and connectivity.
3. Total zooplankton biomass, crustacean biomass and crustacean species number were significantly positively related to water age. Rotifer biomass followed a hump-shaped relationship with water age, and rotifer species number decreased with increasing water age.
4. Rotifers dominated the community in periods of low to medium water ages. In periods of higher water ages the community was dominated by crustaceans.
5. We propose that the hydrological regime of floodplains is crucial for zooplankton biomass patterns and succession, through the alternation of washing-out effects, taxon-specific potential of reproduction and biological interactions. Flood events and high water levels reset the community to an early successional phase.

*Keywords:* hydrology, large river, restoration, water age, zooplankton succession

## Introduction

A growing number of studies have focused on factors regulating plankton development in large rivers (e.g. Thorp, Black & Haag, 1994; Basu & Pick, 1996; Reckendorfer *et al.*, 1999). The hydrological regime of running waters proves to be a major factor determining riverine plankton dynamics (Basu & Pick, 1997), and there is consensus that zooplankton assemblages in rivers are mainly physically controlled (Hynes, 1970).

The significance of inshore retention for zooplankton dynamics was recently demonstrated by Reckendorfer *et al.* (1999) and Schiemer *et al.* (2001). These authors analysed the importance of storage zones with

slow-moving or still water and found a positive correlation between the availability of such zones and the zooplankton abundance in the river. The temporal availability of storage zones depends on both the water level and the morphology of the river margins.

Besides the significance of inshore habitats for the population and community dynamics of riverine invertebrates (Hildrew, 1996; Robertson *et al.*, 1997; Reckendorfer *et al.*, 1999), the importance of adjacent water bodies such as floodplain habitats for the zooplankton production of large rivers was pointed out by Vranovsky (1974) and Saunders & Lewis (1989). Depending on hydrological connectivity with the river, the hydrological regime within the floodplain areas can range from lotic to lentic conditions. Therefore the hydrology of floodplain water bodies may be as important for the zooplankton community as it is in the main channel of large rivers. Flood events cause major changes in physical

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environmental conditions (Tockner *et al.*, 1999) as well as high zooplankton mortality or removal (washing-out), and are followed by a gradual re-establishment of lentic environmental conditions and population re-colonisation. Floods are thus disturbance events for the zooplankton community. Townsend, Doleddec & Scarsbrook (1997) suggested that faced with disturbance, populations may exhibit the capacity of rapid return towards the predisturbance densities (resilience) or the capacity to withstand the disturbance without dramatic loss of individuals (resistance). The latter is unlikely for pelagic zooplankton organisms.

Rotifers should be more successful than crustaceans under lotic conditions because of their shorter development time (Ecker & Walz, 1998), a life history trait which confers resilience (Townsend *et al.*, 1997). Crustaceans should re-establish larger population sizes and biomasses only when lentic conditions prevail over longer periods. As rotifers and crustaceans are known to compete exploitatively for many of the same phytoplankton food resources (Kirk, 1991), and larger cladocerans also interfere mechanically with rotifers (Gilbert, 1988), biological interactions are likely to gain importance with increasing retention time and crustacean biomass. Thus the alternation of biotic interactions and physical features may be crucial for interpreting zooplankton community dynamics in large river floodplains.

Although the Danube River, like all large rivers in Europe and North America (Petts, Moller & Roux, 1989; Ward, 1998), has been considerably affected by regulation schemes, the 50 km river reach downstream of Vienna represents one of the last remnants of river floodplain systems where the key attributes of integrated floodplains like hydrological dynamics and flood pulses are still partially operative (Schiemer, Baumgartner & Tockner, 1999). This river section offers a broad spectrum of river-floodplain connections ranging from strongly dammed sites to areas, albeit regulated, exhibiting a high degree of hydrological connectivity.

The present study was conducted in a floodplain area of the Danube River (Regelsbrunn) 30 km downstream of Vienna which was part of the 'Danube River Restoration Project'. The main restoration target was to enhance the intensity as well as the frequency of surface connectivity with the Danube River. Thus the floodplain flow regime is to a large extent exposed to

stochastic flow patterns of the river (Schiemer *et al.*, 1999). A hydrological model was developed (A. Steel, personal communication) to calculate water age for each pool of the floodplain. The present work describes zooplankton biomass and community structure patterns along a hydrological gradient expressed as water age and quantifies the significance of water age for the zooplankton community in this floodplain area.

## Methods

### Study site

The flow regime of the Danube River is characterised by high fluctuations in water level and discharge ( $800\text{--}6000\text{ m}^3\text{ s}^{-1}$ ) (Hein *et al.*, 1999) with an average annual discharge of about  $1900\text{ m}^3\text{ s}^{-1}$  and marked seasonality (Tockner *et al.*, 1999). The sampling point was located on the downstream end of the Regelsbrunn floodplain.

The Regelsbrunn floodplain is connected with the Danube River via the surface when the Danube River water level reaches approximately mean water – 0.5 m. The sidearm is therefore integrated in the river's flow regime for approximately 220 days year<sup>-1</sup>. This leads to changing hydrological conditions within the floodplain area ranging from lotic to lentic. We expressed this abiotic environmental factor by calculating water age at the sampling point for each sampling date.

### Sampling

A total of 44 samples were taken at weekly to biweekly intervals from 4 March to 4 November 1997 (24 samples) and from 12 May to 15 September 1998 (20 samples). Samples were taken with a 10-L Schindler trap, passed through a 37- $\mu\text{m}$  mesh plankton net, and preserved with 4% formalin. For comparison, Danube River zooplankton abundance data were used from samples taken at weekly to monthly intervals between May and August 1994 at river kilometre 1910, which is approximately 5 km upstream of the uppermost floodplain inflow area (Reckendorfer *et al.*, 1999).

### Calculation of water age

Here, age is defined as how long the water has been contained in the respective water body system, up to

any position within the system and at any point in time.

For example, if Danube River water is taken as having age 0 (i.e. the water has spent no time within the system) then the age of the water as defined above is some inverse measure of the lotic 'River-like' character of the waters within the pools. Thus low age implies very 'River-like', whereas high age means lentic and not very 'River-like'. This is because the implied long time in the pools will have allowed physical and biological processes significantly to alter the quality characteristics of the waters. Hence, water age is also some inverse measure of the connectivity to the river, with low age indicating high connectivity.

The software program 'Regels 3.2' (A. Steel, unpublished data) was used to calculate water age at our sampling point for each sampling date. The program uses the volume (derived from pool depths and bathymetric survey data), the inflow (bank overflows, bank weirs, bank culverts and ground water infiltration) and the outflow through the bottom of the pool to calculate water age at different pools. The water age at the outlet of the backwater cascade (sampling point) was calculated considering the water age in the preceding pools and the water input from the main river in the respective flow contribution.

#### *Sediment loading*

The concentration of small suspended particles ( $<3\ \mu\text{m}$ ) was determined by separating the  $<3\ \mu\text{m}$  size fraction of 5 L water samples using a Nitex screen. About 1–2 L of the screened water was filtered through weighted Millipore APF/F filters. The organic fraction was determined as loss upon combustion (2 h at  $490\ ^\circ\text{C}$ ).

#### *Zooplankton species composition, biomass and size*

Zooplankton abundance was assessed by enumerating either whole samples or counting at least 100 individuals in subsamples using an inverted microscope.

Adult individuals were identified to species level in nearly all cases following Koste (1978) (rotifers) and Kiefer (1978) (crustaceans). Species which could not be distinguished in routine counting were treated as

one category (e.g. *Synchaeta oblonga/tremula*). Juvenile stages were treated as one category.

The dry weight of rotifers was estimated by biovolume calculation of each species assuming a specific weight of 1 and a wet weight:dry weight ratio of 10:1. The dry weight of crustaceans was assessed from size to dry weight relations for all species (Holarek, 1999). Carbon content was calculated assuming a dry weight:carbon relation of 10:4 (Gorsky *et al.*, 1988).

For each sampling date the average body size of the plankton community was estimated as the weighted mean.

#### *Sample similarity*

To analyse changes in species composition along the hydrological gradient (water age), the Morisita Horn (MH) sample similarity index (Magurran, 1988) was calculated using the EstimateS (5.0.1) software package. Results were pooled according to water age as follows (abbreviations used are given in parentheses): Danube River samples (D); Regelsbrunn samples at water ages between  $>0$  and  $\leq 2$  days (RI); Regelsbrunn samples at water ages between  $>2$  and  $\leq 5$  days (RII); Regelsbrunn samples at water ages between  $>5$  and  $\leq 17$  days (RIII); and Regelsbrunn samples at water ages between  $>17$  and  $\leq 39$  days (RIV). The mean values of within-group similarity were calculated as well as the sample similarity between the Danube River samples and the Regelsbrunn samples.

#### *Data analysis*

All data except species numbers, crustacean body size and particle concentrations were transformed to the natural logarithm  $[\ln(1 + x)]$  prior to regression analysis.

Different regression equations were derived in order to predict the values of the dependent variables (zooplankton biomass, crustacean biomass, rotifer biomass, crustacean species number, rotifer species number, suspended particles) by the independent variable water age. Polynomial (linear; quadratic), sigmoid, hump-shaped (Gaussian, Lorentzian) and exponential regression models were tested. The best regression equations were defined as those having the highest  $r^2$  and being significant ( $P < 0.05$ ) for all parameters as well as for the total model.

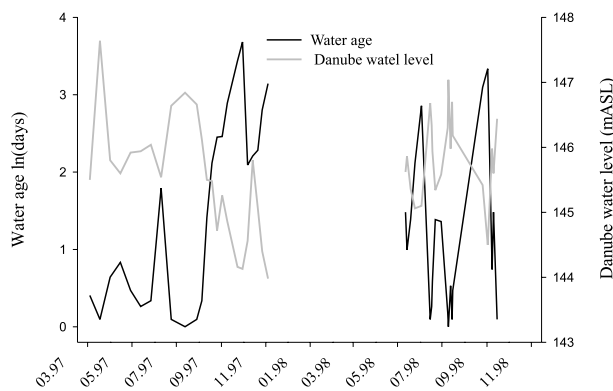
## Results

### Water age

Calculated water ages showed striking variation during the study period. They ranged from a few hours in the case of flood events up to 39 days at low water periods. The seasonal pattern depended on water level fluctuations of the river (Fig. 1). The average water level fluctuation ( $\pm$ SD) of the Danube River during the investigation period was about  $23 \text{ cm day}^{-1}$  ( $\pm 27 \text{ cm day}^{-1}$ ), with a maximum of  $264 \text{ cm day}^{-1}$ .

### Suspended inorganic particles

The mean concentration of small ( $<3 \mu\text{m}$ ) suspended inorganic particles was  $12.3 \text{ mg L}^{-1}$  ( $\pm 9.7$ ), although values showed considerable variation ranging



**Fig. 1** Danube River water level and floodplain water age (mean water level = 145.89 m a.s.l., location of the hydrograph = Orth, 1901.83 km).

between  $1.0$  and  $38.6 \text{ mg L}^{-1}$ . Particle loadings were highest at periods of low water age as a result of the high sediment input from the Danube River. Concentrations above  $20 \text{ mg L}^{-1}$  were reached only at ages under 2 days. Particle loadings decreased exponentially with increasing water age (Table 1, Fig. 2).

### Zooplankton species composition, biomass

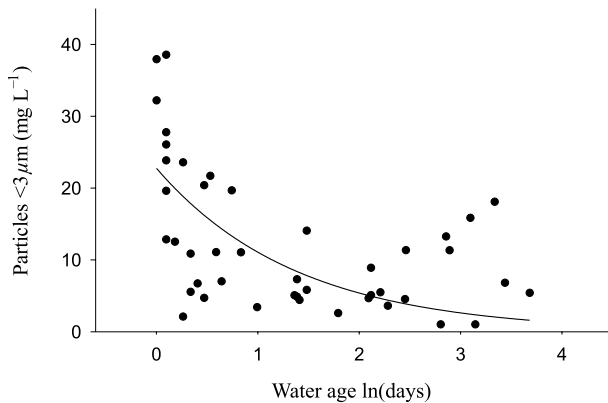
A total of 63 zooplankton taxa were recorded in the total 44 samples. Rotifers dominated the community in terms of species and individual abundances. The total number of rotifer taxa was 43, with a sample average of  $15.3 (\pm 4.4)$  and a range between 8 and 27. On average they comprised 84.4% of zooplankton individual numbers, showing a mean density of  $847.5 \text{ individuals L}^{-1}$  ( $\pm 1387.7$ ) and peaking at more than  $7000 \text{ individuals L}^{-1}$  (Table 2). Among the rotifers, *Polyarthra dolichoptera/vulgaris* (Idelson, 1985/Carlin, 1943), *S. oblonga/tremula* (Ehrenberg, 1831/O.F. Müller, 1786), *Keratella cochlearis* versus *tecta* (Lauterborn, 1900), *K. cochlearis cochlearis* (Gosse, 1851), *Asplanchna priodonata/girodi* (De Gurne 1888/Gosse 1851) and *Brachionus angularis* (Pallas, 1766) were the most abundant taxa, contributing about  $81.6\% (\pm 8.9)$  to the total rotifer number (Table 2). These taxa also showed the highest relative occurrence, ranging between 70% for *A. priodonata/girodi* and 100% for the rotifers *P. dolichoptera/vulgaris* and *S. oblonga/tremula*. All other taxa occurred only occasionally and in low abundances.

In terms of biomass ( $\mu\text{g carbon L}^{-1}$ ), rotifers contributed an average sample percentage of  $60.1\% (\pm 29.7)$ . The most abundant taxa dominated again, accounting

**Table 1** The independent (x) and dependent (y) variables used for regression analysis and the regression equations

x	y	Equation	$r^2$	P
Water age ln(days)	Particles $<3 \mu\text{m}$ ( $\text{mg L}^{-1}$ )	$y = 22.76 \exp(-0.72x)$	0.36	$<0.001$
Water age ln(days)	Zp. biomass ln( $\mu\text{g C L}^{-1}$ )	$y = 5.34/[1 + \exp(-(x - 1.06)/0.69)]$	0.66	$<0.001$
Water age ln(days)	Cr. biomass ln( $\mu\text{g C L}^{-1}$ )	$y = \exp(0.48x)$	0.61	$<0.001$
Water age ln(days)	Ro. biomass ln( $\mu\text{g C L}^{-1}$ )	$y = 3.72 \exp[-0.5[(x - 2.28)/1.29]^2]$	0.45	$<0.001$
Cr biomass ln( $\mu\text{g C L}^{-1}$ )	Ro. biomass ln( $\mu\text{g C L}^{-1}$ )	$y = 3.97 \exp[-0.5[(x - 3.90)/2.26]^2]$	0.45	$<0.001$
Water age ln(days)	Ro. biomass (%)	$y = 72.15/[1 + \exp(-(x - 2.74)/-0.41)]$	0.43	$<0.001$
Water age ln(days)	Ro. species number (n)	$y = 17.40 - 1.54x$	0.16	0.007
Water age ln(days)	Cr. species number (n)	$y = \exp(0.60x)$	0.47	$<0.001$
Cr. biomass ln( $\mu\text{g C L}^{-1}$ )	Cr. body size ( $\mu\text{m}$ )	$y = 188.53 - 18.78x$	0.36	$<0.001$

Units of measurement are given in parentheses. Variables were abbreviated as follows: Zp. = total zooplankton; Ro. = rotifers; Cr. = crustaceans.



**Fig. 2** Relationship between water age and the concentration of suspended particles  $<3 \mu\text{m}$ . The equation of the non-linear regression is given in Table 1.

for a sample average of 71.9% ( $\pm 21.4$ ) of the rotifer biomass (Table 2).

The crustacean community was dominated by the cladoceran *Bosmina longirostris* (O. F. Müller, 1785), which on average contributed 70.5% ( $\pm 35.8$ ) to the adult crustacean individual abundances and 54.8% ( $\pm 39.2$ ) to the biomass. *Bosmina longirostris* was also

the taxon with the highest relative occurrence (63.6%). Other cladoceran and copepod species like *Chydorus sphaericus* (O.F. Müller, 1786), *Daphnia cucullata* (Sars, 1862), *Acanthocyclops robustus/vernalis* (Sars, 1863/ Fischer, 1853) and *Cyclops vicinus* (Uljanin, 1875) occurred only occasionally (11.4–22.7%) (Table 2). In periods of high water age, however, these species dominated in terms of biomass.

#### Water age, zooplankton biomass and species richness

Total zooplankton biomass was best predicted by water age following a sigmoid regression (Fig. 3, Table 1). Values were generally low ( $4.4 \pm 5.9 \mu\text{g C L}^{-1}$ ) at periods of high hydrological dynamics. Total biomass increased continuously with water age up to approximately 10 days and showed relatively stable values at higher ages.

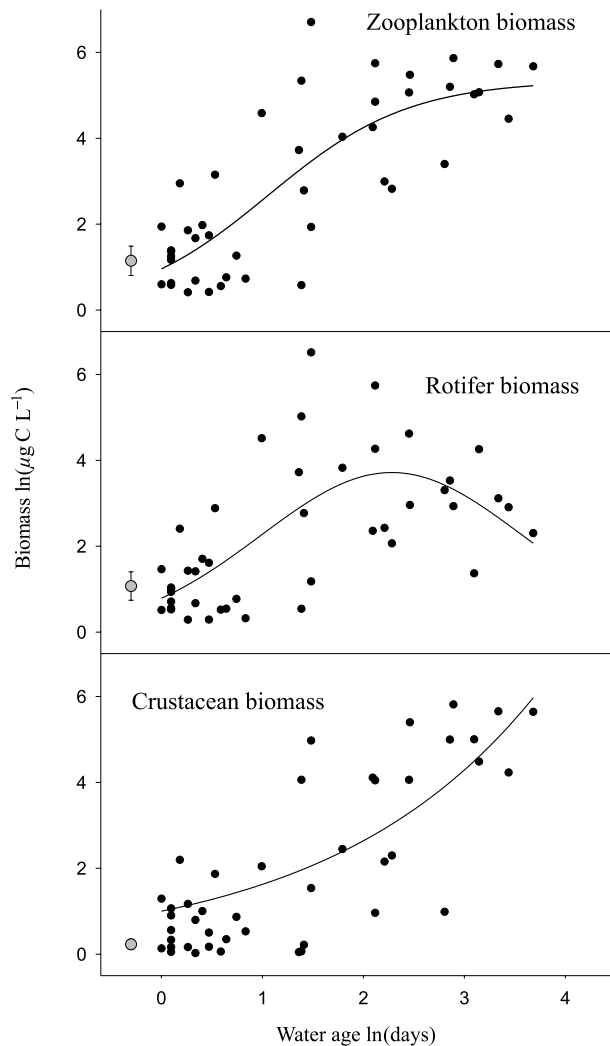
The crustacean fraction showed similar patterns but could be better described by exponential regression (Fig. 3, Table 1).

In contrast to the crustaceans, rotifers followed a hump-shaped relationship (Fig. 3, Table 1). Values

**Table 2** Absolute and relative abundances and biomasses (carbon) for the total zooplankton and the most abundant taxa averaged over the entire sampling time

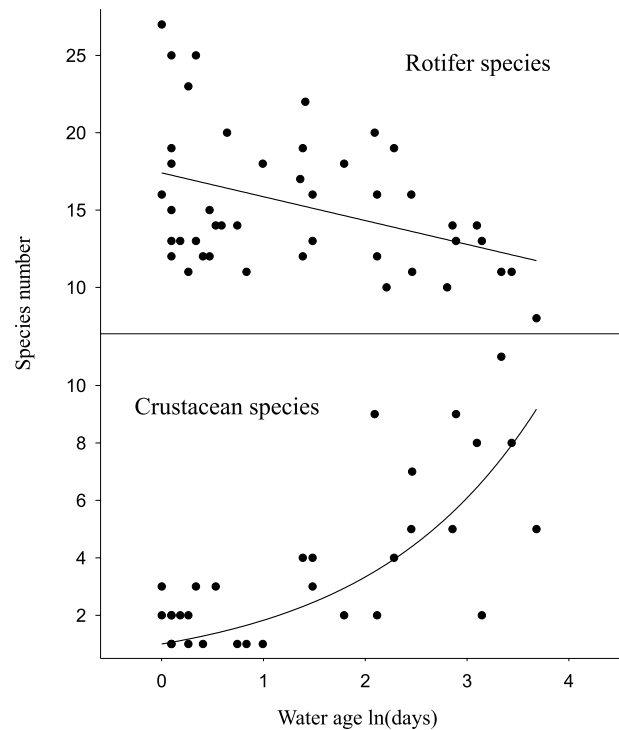
Taxon	Abundance (individuals $\text{L}^{-1}$ )	Mean/ range	Percentage	Mean/ range	Biomass carbon ( $\mu\text{g L}^{-1}$ )	Mean/ range	Percentage	Mean/ range
<b>Total zooplankton</b>	1022.9 (1494.8)	15.2/7112	100		87.7 (152.4)	0.5/823.2	100	
Crustaceans total	175.4 (322.9)	0.4/551.3	15.6 (17.1)	0.1/66.6	45.9 (86.0)	<0.1/334.4	39.9 (29.7)	0.1/67.5
Crustaceans adult	55.9 (169.9)	0.0/1011.3	3.4 (7.4)	0.0/33.4	28.5 (55.8)	0.0/247.6	21.8 (23.4)	0.0/78.2
Crustaceans juvenil	119.5 (198.6)	0.0/965.0	12.1 (13.0)	0.0/61.6	17.4 (35.5)	0.0/167.1	18.1 (14.2)	0.0/56.5
Rotifers	847.5 (1387.7)	14.2/7044	84.4 (17.1)	30.4/99.9	41.8 (112.4)	0.3/679.8	60.1 (29.7)	2.5/99.9
<b>Rotifers</b>								
<i>Polyarthra dolichoptera/vulgaris</i>	176.8 (395.6)	0.9/1974.7	16.5 (11.9)	1.1/42.6	2.2 (4.4)	<0.1/20.4	10.8 (10.9)	0.2/43.9
<i>Synchaeta oblonga/tremula</i>	155.1 (321.6)	1.3/1820	28.1 (21.5)	<0.1/67.8	1.7 (3.5)	<0.1/20.0	20.0 (18.0)	<0.1/53.1
<i>Keratella cochlearis cochlearis</i>	54.4 (102.7)	0.0/380.0	5.5 (6.4)	0.0/30.0	0.2 (0.3)	0.0/1.2	0.9 (1.2)	0.0/6.0
<i>Keratella cochlearis tecta</i>	220.4 (435.0)	0.0/2384.0	24.7 (16.3)	0.0/60.7	0.2 (0.4)	0.0/2.1	1.3 (1.6)	0.0/9.1
<i>Asplanchna</i> sp.	59.9 (164.9)	0.0/836.6	4.8 (9.0)	0.0/45.8	30.6 (98.9)	0.0/622.8	35.6 (33.9)	0.0/97.2
<i>Brachionus angularis</i>	31.8 (92.6)	0.0/534.6	2.0 (2.8)	0.0/10.9	0.3 (1.1)	0.0/5.9	0.7 (1.2)	0.0/6.3
<b>Total</b>	698.4 (1114.7)	8.9/5504	81.6 (8.9)	62.7/96.3	35.2 (102.6)	0.1/643.5	71.9 (21.4)	9.1/97.9
<b>Adult crustaceans</b>								
<i>Bosmina longirostris</i>	47.6 (161.8)	0.0/964.0	70.5 (35.8)	0.0/100	11.57 (31.8)	0.0/169	54.8 (39.2)	0.0/1
<i>Chydorus sphaericus</i>	1.7 (10.5)	0.0/70.0	3.8 (14.5)	0.0/77.7	1.8 (11.5)	0.0/23.8	5.1 (17.9)	0.0/29.1
<i>Daphnia cucullata</i>	1.9 (7.6)	0.0/50.0	5.7 (14.5)	0.0/71.4	1.2 (4.9)	0.0/32.1	2.7 (6.7)	0.0/28.0
<i>Acanthocyclops</i> sp.	1.2 (4.0)	0.0/23.3	3.0 (9.8)	0.0/39.7	5.2 (17.9)	0.0/103.4	6.6 (16.6)	0.0/58.2
<i>Cyclops vicinus</i>	0.2 (0.5)	0.0/2.0	0.5 (1.6)	0.0/6.7	2.0 (5.9)	0.0/23.8	2.6 (7.2)	0.0/29.1
<b>Total</b>	52.5 (163.8)	0.0/978.7	81.3 (26.0)	0.0/100.0	21.8 (45.7)	0.0/215.8	71.8 (32.7)	0.0/100

Standard deviations are given in parentheses.



**Fig. 3** Relationship between water age and zooplankton biomass, rotifer biomass and crustacean biomass. Reference samples from the Danube River are given as mean and standard deviation (open circles with error bars) but were not included in the regression analysis. The regression equations are given in Table 1.

increased up to water ages of approximately 10 days but decreased afterwards. A similar pattern emerged when rotifer biomass was plotted against crustacean biomass (Table 1). When crustacean biomass exceeded ca.  $55 \mu\text{g C L}^{-1}$  the rotifers decreased. This was also demonstrated by plotting the relative rotifer biomass (percentage of the total zooplankton biomass) against water age. Relative biomass ranged between 35% and more than 90% up to water ages of approximately 7 days; it declined to minimum values of 3% when lentic conditions prevailed and



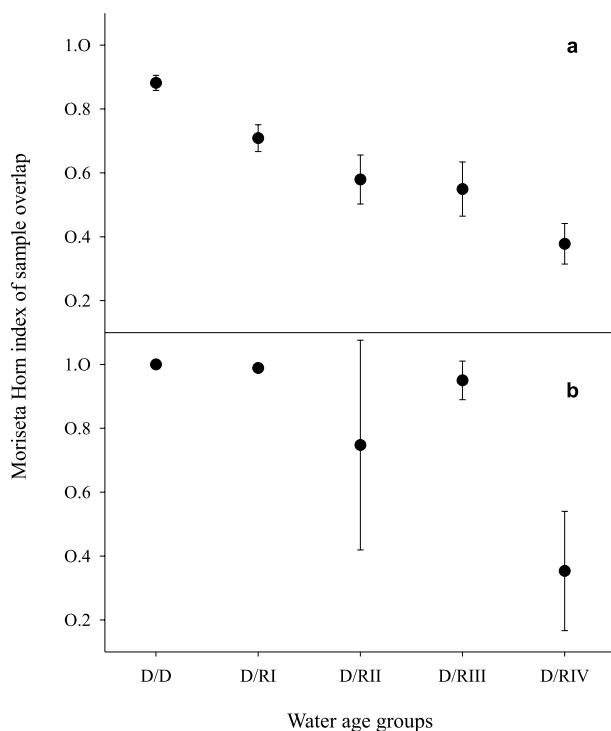
**Fig. 4** Relationship between water age and rotifer and crustacean species number. The regression equations are given in Table 1.

crustaceans dominated the zooplankton community. A sigmoid function was fitted to describe this relationship (Table 1).

Species richness of the rotifers and crustaceans showed contrasting patterns along the water age gradient. Rotifer species number decreased linearly (Fig. 4, Table 1) while crustacean species number increased exponentially at water ages above 2 weeks (Fig. 4, Table 1). Larger species like *D. cucullata*, *Ceriodaphnia pulchella*, *Eurytemora velox* and *Acanthocyclops* sp. became abundant, whereas the relative abundance of *B. longirostris* decreased.

#### *Species similarity patterns*

Samples of each water age group were compared with Danube River samples. Rotifer samples showed continuously decreasing sample overlaps, indicating a constant change in species composition (Fig. 5a). Crustaceans sample overlaps remained quite uniform over a wider water age range but changed dramatically above 20 days (Fig. 5b).



**Fig. 5** Mean ( $\pm$ SD) sample overlaps (Morisita Horn index) between Danube samples and the floodplain samples, for (a) rotifers and (b) crustaceans. Samples were pooled according to water age the following way: (D) Danube River samples; (RI) Regelsbrunn samples at water ages between  $>0$  and  $\leq 2$  days; (RII) Regelsbrunn samples at water ages between  $>2$  and  $\leq 5$  days; (RIII) Regelsbrunn samples at water ages between  $>5$  and  $\leq 17$  days; (RIV) Regelsbrunn samples at water ages between  $>17$  and  $\leq 39$  days.

## Discussion

### Abiotic environmental conditions

Water age varied considerably during the two sampling periods (Fig. 1). It provides an integrated descriptive variable of those abiotic environmental factors likely to have differential effects on various freshwater zooplankton taxa and, to influence zooplankton community structure and population dynamics (Rzoska, 1978). Current velocities at the sampling point ranged from 0 to ca.  $1 \text{ m s}^{-1}$ . Besides washing-out effects, high current velocities are known to inhibit zooplankton population growth rates. Zooplankton reproduction and thus population growth is rarely observed at velocities higher than  $0.4 \text{ m s}^{-1}$  (Rzoska, 1978). Saunders & Lewis (1989) reported an inverse relationship between egg ratios and water velocity.

The concentrations of small-sized ( $<3 \mu\text{m}$ ) inorganic suspended particles at the sampling site were controlled by hydrology and could be predicted by water age (Table 1, Fig. 2). High inorganic particle concentrations of this size are known to have differential effects on rotifers and cladocerans (Kirk & Gilbert, 1990; Kirk, 1991) and thus are likely to alter the competitive outcome between these two groups.

### Biomass patterns

The present study underlines the high colonisation capacity of rotifers. They contributed up to 90% of total zooplankton biomass when lotic conditions prevailed (water age  $<7$  days) (Table 2). Rotifer biomass increased rapidly with water age, peaking at ages between 4 and 10 days (Fig. 3, Table 1), after which the curve dropped. They are more successful than crustaceans under lotic conditions because of their short embryonic development time, which is a life history trait conferring resilience (Townsend *et al.*, 1997). Ecker & Walz (1998) observed rotifer embryonic development times at  $20^\circ\text{C}$  of less than 1 day for *S. oblonga*, and approximately 2 days for *K. cochlearis*. Embryonic development of *B. longirostris* takes 3 days at  $20^\circ\text{C}$  (Kwick & Carter, 1975). When water age was very low (0–1.7 days) the observed biomasses were similar to those found by Reckendorfer *et al.* (1999) in the main channel of the Danube River a few kilometres (river kilometre 1910–1909) upstream of the Regelsbrunn floodplain in 1994.

Because of their longer development times (Herzig, 1983), crustaceans re-establish substantial populations much slower than rotifers. We found that their biomass increased exponentially with water age (Fig. 3, Table 1). Highest values ( $334 \mu\text{g C L}^{-1}$ ) were reached at periods of maximal water age (20–39 days). These values are even higher than the maximum crustacean biomass of  $186 \mu\text{g C L}^{-1}$  at an isolated floodplain system of the Danube River at Vienna (Hein *et al.*, 1999).

Our results show that water age had a major influence on both the abiotic and biological mechanisms regulating zooplankton biomass. When plotted against water age, the total zooplankton biomass showed a sigmoid relationship (Fig. 3, Table 1). Values were low during periods of low water age up to 2 days. Mean zooplankton biomass was  $16.7 \mu\text{g L}^{-1}$ . This was 3.5 times higher than the values found by Reckendorfer



et al. (1999) in the Danube River ( $4.6 \mu\text{g L}^{-1}$ ) and within the range reported by Basu & Pick (1996) ( $11.3 \mu\text{g L}^{-1}$ ) who sampled 31 North American large, temperate rivers. As illustrated in Fig. 3, biomass increased rapidly with increasing water age and reached a mean value of  $330 \mu\text{g L}^{-1}$  under lentic environmental conditions (water age <7 days).

#### Evidence for biological interactions (competition)

Crustacean biomass exceeded rotifer biomass at water ages of approximately 14 days (Table 2, Fig. 6). Afterwards rotifer biomass declined whereas crustacean biomass increased exponentially.

Rotifers are suppressed and often excluded by large cladocerans (Gilbert, 1988). Exploitative competition for the same phytoplankton food resources (Kirk, 1991) and mechanical interference of rotifers by crustaceans (Gilbert & Stemberger, 1985; Burns & Gilbert, 1986) are possible explanations for the asymmetrical interactions between the two groups. The competitive outcome between crustaceans and rotifers is known to depend on the zooplankton size structure, because larger species feed more efficiently (Brooks & Dodson, 1965).

Our data indicate that the suppression of rotifers is at least partly because of the competitive superiority of the crustacean community. The mean body size (weighted mean) of the crustaceans was small and not significantly correlated (Spearman rank correlation

$r = 0.10$ ;  $P = 0.66$ ) with water age up to 14 days. The crustacean plankton in this period consisted nearly exclusively of *B. longirostris*.

In laboratory experiments, MacIsaac & Gilbert (1989) demonstrated that *B. longirostris* failed to exclude *K. cochlearis* and *S. oblonga* but coexisted with those rotifers for 8 weeks although the authors used food levels and population densities which ensured that competition would take place between these species, between these species. We found larger species nearly exclusively at older water ages (>20 days). The average body size in the crustacean community increased significantly at ages above 2 weeks (Spearman  $r = 0.83$ ;  $P = 0.003$ ), indicating that larger and thus more 'efficient' species with longer development times became abundant. The average size of the crustaceans was also positively correlated to crustacean biomass (Table 2). S. Keckeis (personal communication) found maximal values for the relative daily grazing rates of the cladoceran community at water ages of approximately 17 days at the same study site. Thus competition for food resources is likely and may act together with mechanical interference.

Although large-size zooplankton also occurred at low water ages, the abiotic characteristic of the lotic environment made exploitative competition unlikely because of the high concentrations of small-sized (<3  $\mu\text{m}$ ) inorganic particles. Kirk & Gilbert (1990) showed that high particle concentrations strongly reduced the population growth of cladocerans while rotifers were not affected. Kirk (1991) provided a mechanistic explanation based on the different feeding modes of the two taxa. In the present study, hydrology expressed as water age turned out to be crucial for zooplankton biomass patterns and succession, because of the alternation of flood-caused mortality (e.g. washing-out effects), taxon-specific reproduction and biological interactions. Flood events and high water levels reset the community.

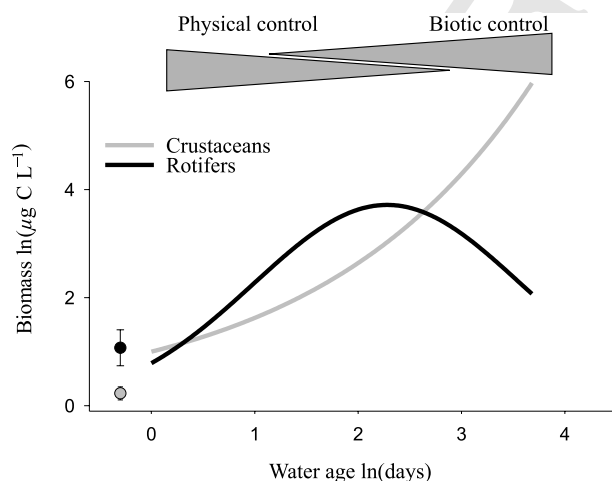


Fig. 6 Predicted relationship (Table 1) between water age and rotifer and crustacean biomass. The relative importance of physical features and biotic interactions of zooplankton dynamics is represented by bars.

#### Species composition

In the pooled data of our study, rotifers clearly dominated the zooplankton community, contributing more than 80% to total abundance and 60% to total biomass. The most abundant rotifer taxa included *Synchaeta*, *Polyathra*, *Keratella*, *Asplanchna* and *Brachionus* (Table 2). Rotifers were followed by the



small cladoceran species *B. longirostris* and juvenile crustaceans. Larger cladocerans (e.g. *C. sphaericus* and *D. cucullata*) and copepods (e.g. *Acanthocyclops* sp. and *C. vicinus*) were much less abundant. Generally, the species composition and community structure resembled those found by Basu & Pick (1996) for 31 North American large temperate rivers and Reckendorfer *et al.* (1999), who reported a rotifer-dominated zooplankton community for inshore areas of the Danube River.

In our study, however, species composition varied considerably between sampling dates (Table 2, Fig. 5a,b) and included samples in which rotifers were rare and they were clearly dominated by larger crustacean species.

Rotifer species composition and similarity with the Danube River reference sample changed gradually with water age (Fig. 5a). Rotifer communities of the Danube River were very uniform, with a mean sample overlap of approximately 90%. *Synchaeta oblonga/tremula* clearly dominated, indicating their ability to develop substantial populations under lotic environmental conditions. Zoufal (1991) described *Synchaeta* as the dominant rotifer taxon in the Danube River over a 3-year period (1985–87) and Heinbockel *et al.* (1988) concluded that their short development times even at low temperatures should favour them above other rotifer species in lotic habitats. Rotifer species composition in periods of very low water ages ( $\leq 2$  days RI) were also quite similar to the Danube River community (Morisita Horn = 0.75) because *Synchaeta* dominated in the floodplain too. The decreasing similarity with the Danube River (Fig. 5a) was because of both the linear decrease in total species number (Fig. 4) and the changes in the relative abundance of the taxa *S. oblonga/tremula* and *K. cochlearis*. *Keratella* tended to increase, whereas the relative abundance of *Synchaeta* decreased. When water age exceeded 21 days the rotifer community showed a 40% overlap with the Danube River.

The crustacean community showed quite different patterns (Fig. 5b). Danube River samples exclusively contained *B. longirostris* and juvenile stages, as did floodplain samples. *Bosmina* dominated crustacean plankton up to water ages of 20 days, and species composition was uniform. When lentic conditions prevailed for longer periods, larger species like *D. cucullata*, *C. pulchella*, *E. velox* and *Acanthocyclops* sp. became abundant and similarity decreased sharply to approximately 40%.

We conclude that water age in the investigated floodplain area is an important determinant of both zooplankton biomass and species composition. When water age was low, species with short development times like rotifers and small cladocerans were favoured and abiotic environmental conditions were likely to alter the competitive outcome between rotifers and larger crustacean species. At higher water ages, crustacean biomass and average size increased and biological interactions gained importance (Fig. 6). Thus, hydrological conditions (i.e. water age) determined the switch from physical features to biotic interactions as the main factor governing zooplankton community structure.

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