The significance of zooplankton grazing in a floodplain system of the River Danube

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Floodplain systems along rivers are influenced by the hydrological regime of the river to an extent which depends on the degree of connectivity. As a result, the age of water within the system varies widely. Zooplankton development is restricted to areas and periods of higher water age and thus the role of zooplankton in planktonic carbon flow is strongly influenced by the hydrological dynamics. In 1997 and 1998 the plankton community was examined in the floodplain system along the River Danube, at two sections differing in connectivity to the main river. Zooplankton grazing rates and consumption were calculated, using filtration rates from the literature, based on qualitative and quantitative phyto- and zooplankton data. A succession in grazing dominance from rotifers to cladocerans and copepods was found with increasing water age. Maximal carbon flow and impact on algae by grazing rates of >100% (mean 40.5%) were observed at intermediate connectivity, when zooplankton biomass peaked. Mean grazing impact at high connectivity amounted to 2.5%, and at low connectivity 8.8%, of the total phytoplankton biomass. The main grazers were Synchaeta spp., Polyarthra spp., and the small cladoceran, Bosmina longirostris. Herbivory dominated carbon transfer in the planktonic food webs during dynamic conditions. When conditions are stable, additional food pathways (bacterivory, predation) increase in significance and result in an increased biotic control.

INTRODUCTION

Floodplains along large rivers are heterogeneous systems dependent on both surface water and groundwater seepage (Junk *et al.*, 1989; Galat *et al.*, 1997; Schiemer *et al.*, 1999; Ward *et al.*, 1999). The water level fluctuations in the river influence the hydrological regime of the floodplain backwaters according to the intensity of connectivity, resulting in changes between lotic and lentic conditions.

Intense research in the floodplain system of the River Danube near Vienna has revealed the structuring effect of hydrological connectivity on plankton dynamics (Heiler *et al.*, 1994, 1995; Hein *et al.*, 1999a). Zooplankton biomass in any quantity is restricted to sections and periods of higher residence times, since colonization and reproduction require time (Baranyi *et al.*, 2002.).

In food webs, organisms of the zooplankton represent a link from autochthonous material to higher trophic levels, e.g. juvenile riverine fish, which use backwaters as feeding grounds (Kurmayer *et al.*, 1996). Hence the grazing activity of zooplankton is an important mechanism in the material flow which opens the carbon pool to the aquatic community. Zooplankton grazing is widely discussed in the literature [reviews see (Gulati, 1975; Sterner, 1989)]. The PEG model (Sommer *et al.*, 1986) demonstrates the potential influence of zooplankton grazing on phytoplankton structure and density along the time course of seasonal succession in lakes. Cladocerans, especially, can influence the structure of the planktonic food web by efficient feeding on picoplankton, thus shortening the transfer of carbon to higher trophic levels in the food web (Hart and Jarvis, 1993; Juergens, 1994).

The zooplankton community in river-floodplain systems and slow-flowing lowland rivers is characterized by rotifers and small cladocerans, which can reach considerable numbers (Admiraal *et al.*, 1994; Garnier *et al.*, 1995; Viroux, 1997; Gosselain *et al.*, 1998; Kobayashi *et al.*, 1998; May and Bass, 1998). Even in the Austrian Danube, high zooplankton production has been observed

along the shoreline (Reckendorfer *et al.*, 1999). In back-waters, the alternation of physical features caused by hydrology and biotic interactions determines the composition of plankton community. Flood pulses not only wash out plankton organisms but also the nutrient inputs which stimulate phytoplankton production (Riedler and Schagerl, 1998; Hein *et al.*, 1999a) and thus provide a considerable food resource during periods of decreasing connectivity, particularly since river phytoplankton consists mainly of centric diatoms (Reynolds and Descy, 1996), which represent food of high quality.

In this context, the functional role of zooplankton is examined in relation to hydrological connectivity, defined by water age, a more precise measure than retention time. Highest carbon flow is expected in intermediate conditions, when the proportion of autochthonous carbon is high (Hein *et al.*, 1999a). During plankton succession we suggest that there will be a shift from a predominance of herbivory to a food web of multiple pathways, including omnivory, bacterivory and predation, reflecting a stabilized plankton community controlled by internal mechanisms. In this context, daily carbon flows from phyto- to zooplankton were analysed in a floodplain system of the River Danube in order to understand the controlling mechanisms and the functional role of different zooplankton organisms.

Several methods have been developed to measure clearance and filtration rates, mainly by cell counts or radiotracer techniques [for review, see (Peters, 1984)]. An empirical analysis of zooplankton grazing and feeding rates has been done by Peters and Downing (Peters and Downing, 1984) in regression equations for cladocerans, marine calanoid copepods and all zooplankton. For this study, grazing was estimated using appropriate clearance and filtration rates at genus or species level from the literature.

Study area

The River Danube downstream of Vienna was originally a braided river section with large floodplains. River regulation and damming in the last century drastically changed the hydrological conditions: the Danube was channelized and the floodplain areas were reduced to narrow strips along the river except in a small area which still remains free-flowing downstream of Vienna. This area is part of a National Park founded in 1996. Here, restoration projects aim to re-establish the dynamic characteristics underlying the high diversity and productivity of river–floodplain systems (Schiemer *et al.*, 1999; Hein *et al.*, 1999b). Within this area, two sites were identified with differing hydrological conditions. Regelsbrunn represents a dynamic section of interconnected pools with high connectivity to the river (Figure 1). The Lobau is a back-water system of low connectivity with the Danube (Figure 1) which is only influenced by the river at high floods by back-flowing water from a downstream opening.

METHOD

Calculation of water age at Regelsbrunn was derived from a software program 'REGELS 3.2' adapted to the Regelsbrunn section (Figure 1) (A. Steel, unpublished). Here, age is defined as the length of time the water has been contained in the waterbody system. The program calculated the age of water using the volume, derived from survey data, the inflow (bank overflows, bank weirs, bank culverts and ground water infiltration) and the outflow of different pools. Thus, for the actual sampling point the water age is calculated at the outlet of the pool, taking into account the age in the preceding pools and the water from the main river in proportion to their respective flow contributions. Danube water is taken as having age 0, which means that the water has spent no time within the floodplain system. The age of the water, as defined above, is therefore some inverse measure of the 'Danube-like' character of the water within the pools. The implied length of time in the pools will have allowed physical and biological processes to alter significantly 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.

Three situations of different water age were recognized in relation to the times required for categories of zooplankton to colonize and reproduce within the system. A water age of ≤10 days was defined as high connectivity (H), a period allowing the rotifer community to reach high population densities (Ruttner-Kollisko, 1972). From water age >10 days onwards, crustaceans become components of the zooplankton community and we defined situations >10 days at Regelsbrunn as intermediate connectivity (M). In fact, the highest water age in the dynamic section was 27 days. With low connectivity (L), isolated from the river, the water age was assumed to be >200 days, a situation found only at Lobau.

We sampled at weekly to biweekly intervals from March 4 to November 4 1997 at both sections and on May 25, June 3, August 26 and September 2 1998 at Regelsbrunn. Phytoplankton samples were fixed in Lugol's solution, counted and measured to the highest possible taxonomic level, using an inverted microscope. Results on the phytoplankton composition will be presented by Riedler *et al.* (in preparation). Biomass was calculated by converting biovolume (1 μm^3 = 10^{-9} mg FW) to algal fresh weight (FW). Carbon content was derived by multiplying fresh weight by 0.1 (Lundstedt and Brett, 1991). For zooplankton sampling we used a 10 l
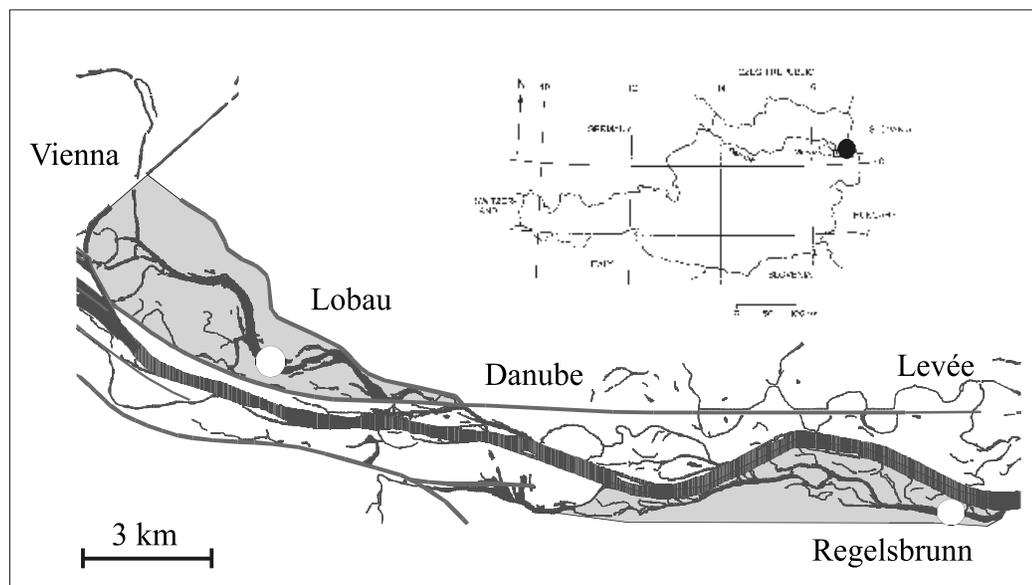
Fig. 1. The River Danube floodplain system downstream of Vienna. Shaded areas indicate investigated floodplain segments, white circles mark the sampling stations.

Schindler trap in the first meter of the water column. After filtration (37 μm mesh), samples were fixed in 4% formalin. Determination to species level and counts were done using an inverted microscope (Nikon TE200, magnification ×100). From length measurements of a maximum of 20 individuals per species, for every season, we estimated biomass. Fresh weight of rotifers was determined by converting biovolumes for rotifers (Ruttner-Kollisko, 1977) assuming a specific weight of 1 (Dumont *et al.*, 1975). For crustacean fresh weight we used published length–weight relationships (Dumont *et al.*, 1975; Bottrell *et al.*, 1976; Vuille, 1991). Dry weight was taken to be 0.1 × fresh weight (Bottrell *et al.*, 1976) and carbon content was assumed to be 0.5 × dry weight (Herzig, 1984).

For the calculation of grazing rates we applied clearance rates from literature for the most abundant planktonic species with filtering or raptorial feeding modes (Table I). Since most of the relevant species are known for size selective feeding (Table I), these preferences were considered in the application of clearance rates to the actual supply of algal food. The theoretical carbon consumption thus resulted from multiplying clearance rates (μl day^{-1} ind^{-1}) with zooplankton species abundance, and the biomass of edible algal cells of the preferred size class. Phytoplankton was separated into five size classes: <5 μm, 5–10 μm, 11–20 μm, 21–50 μm and >50 μm greatest axial linear dimension (GALD). Additionally, edible and non-edible algae were distin-guished on the basis of grazing-resistant shapes and adaptations (e.g. spines, colony). All algae >50 μm were also regarded as non-edible. Since temperature influences physiological rates, clearance rates were corrected for the prevailing temperature in the field using the exponential function: $\log(CR) = \log(CR_0) + \log Q_{10}(t - t_0)/10$ (Hansen *et al.*, 1997). For rotifers a Q_{10} value of 2.4 was taken (Gilbert and Bogdan, 1985), for cladocerans and copepods 2.8 [mean value of (Hansen *et al.*, 1997)]. For *Keratella cochlearis cochlearis* and *Bosmina longirostris* temperature was already considered in the formula given for clearance rate (Bogdan and Gilbert, 1982).

Finally we calculated the relative grazing rate (% grazing rate day^{-1}) of algal standing stock by comparing consumed carbon with available phytoplankton biomass of a particular size class, or total biomass. At high grazing pressure this rate can exceed 100%, indicating complete depletion of food algae.

Statistical analyses on differences in plankton biomass and grazing activity between the three different hydrological situations (H, M and L) were tested with the Kruskal–Wallis test. Pairwise tests were done using the Mann–Whitney U test. Herbivorous grazing activity was calculated as the ratio of consumed algal carbon per total metazooplankton biomass. For analyses of correlation between relative grazing rates and water age at Regelsbrunn we applied polynomial functions to the first and to the second order. Significance was tested by analysis of variance.

Table I: Filtration rates used to calculate relative grazing rates and daily carbon consumption

Taxon measured	Clearance rate (μl l^{-1} h^{-1})	Food type	Temperature (°C)	Source	Applied to algal size (μm)	Applied to
Brachionus calyciflorus	5.61	*Rhodotorula glutinis*	20	(1)	5–10	*Brachionus calyciflorus, B. angularis, B. urceolaris*
Filinia longiseta	0.179	bacteria	19	(2)	<5	*F. longiseta longiseta, F. longiseta limnetica*
Keratella cochlearis cochlearis	0.173T–0.119	*Chlamydomonas reinhardtii*	3.5–25	(3)	5–10	*Keratella cochlearis cochlearis K. cochlearis var. tecta f. micracantha K. cochlearis var. tecta f. typica, K. quadrata*
Kellicottia bostoniensis	0.74	*Chlamydomonas reinhardtii*	24	(4)	5–10	*Kellicottia longispina*
Polyarthra vulgaris	4	*Cryptomonas phaseolus*	3.1	(4)	11–20	*Polyarthra vulgaris, P. dolichoptera*
Synchaeta pectinata	14.84	*Cryptomonas phaseolus*	3.8	(4)	11–20	*Synchaeta pectinata, S. oblonga, S. stylata*
Bosmina longirostris	0.132T + 0.999	*Chlamydomonas reinhardtii*	3.5–25	(3)	5–10	*Bosmina longirostris*
Ceriodaphnia reticulata	100	*Chlorella* sp.	–21	(5)	5–10	*Ceriodaphnia pulchella*
Daphnia sp. juv.	118	*in situ*	–15	(6)	<5	*Daphnia cucculata, D. hyalina, D. obtusa*
Diphanosoma birgei lacustris	60	*in situ*	–15	(6)	<5	*Diaphanosoma brachyurum*
Moina micrura	110	*Chlorella* sp.	–21	(5)	5–10	*Moina micrura*
Naupliar stage	4.17	*in situ*	–15	(6)	11–20	Cyclopoid and calanoid nauplii
Cyclops sp. copepodite	38.75	*in situ*	–15	(6)	11–20	Cyclopoid copepodites
Cyclops sp.	72.9	*in situ*	~15	(6)	21–50	*Acanthocyclops robustus, Cyclops vivinus, Eucyclops serrulatus*
Eudiaptomus sp. copepodite	63.75	*in situ*	~15	(6)	11–20	Calanoid copepodites
Eudiaptomus gracilis	127	*in situ*	~15	(6)	11–20	*Eudiaptomus gracilis, Eurytemora velox*
Mesocyclops leukarti	75.58	*In situ*	~15	(6)	21–50	*Mesocyclops leukartii, Thermocyclops crassus, T. oithonoides*

T, temperature in °C. Sources in parenthesis: (1) Starkweather and Gilbert, 1978; (2) Ooms-Wilms *et al.*, 1993; (3) Bogdan and Gilbert, 1982; (4) Gilbert and Bogdan, 1985; (5) Hart and Jarvis, 1993; (6) Zánkai and Ponyi, 1986

RESULTS

Plankton biomass

The highest algal biomasses occurred during periods of intermediate connectivity (M) in a range between 40 and 1290 μg C l^{-1} (Table II). At high connectivity (H) mean phytoplankton biomass dropped to 364 μg C l^{-1} (17–1094) and differed significantly (Mann–Whitney U test, $P <$ 0.05) from the isolated site (L) which had the lowest mean algal biomass (155) and a range of 20–404 μg C l^{-1}.

Zooplankton biomasses differed significantly between all the hydrological situations (Kruskal–Wallis test, $P <$ 0.0001) (Table II). We found the highest mean biomass with intermediate conditions (231 μg C l^{-1}) and the lowest value (37 μg C l^{-1}) during high connectivity. At high water age mean zooplankton biomass was 76 μg C l^{-1}.

Grazing rates

Seasonal variation in relative community grazing rates of the total phytoplankton biomass turned out to be generally negligible at the dynamic site (Figure 2B). Only during a low water period, caused by low water levels in the Danube (Figure 2A), could substantial consumption rates be determined at that site, with maximal theoretical depletion of >100% of algal biomass. At the isolated section we found a relatively even seasonal grazing impact with a maximal rate of 50% of algal biomass (Figure 2C).

Table II: Mean zooplankton and phytoplankton biomass (mg C l^{-1})

		Regelsbrunn Dynamic section		Lobau Isolated section	Kruskal–Wallis test (Mann–Whitney *U* test)
		H	M	L	
Phytoplankton	mean (SD)	364	489	155	*
		(300)	(508)	(143)	(H/L)
Zooplankton	mean (SD)	37	231	76	***
		(79)	(83)	(63)	(H/M)
					(H/L)
					(M/L)

Differences between hydrological situations are tested with Kruskal–Wallis test (*$P < 0.05$, ***$P < 0.001$). Pairwise significant differences by Mann–Whitney *U* test in parentheses

The grazing impact of zooplankton community differed significantly (Kruskal–Wallis test, $P < 0.01$) in the different hydrological situations (Figure 3). At high connectivity, relative grazing rates of total algal biomass ranged between 0 and 13% (Figure 3). At intermediate
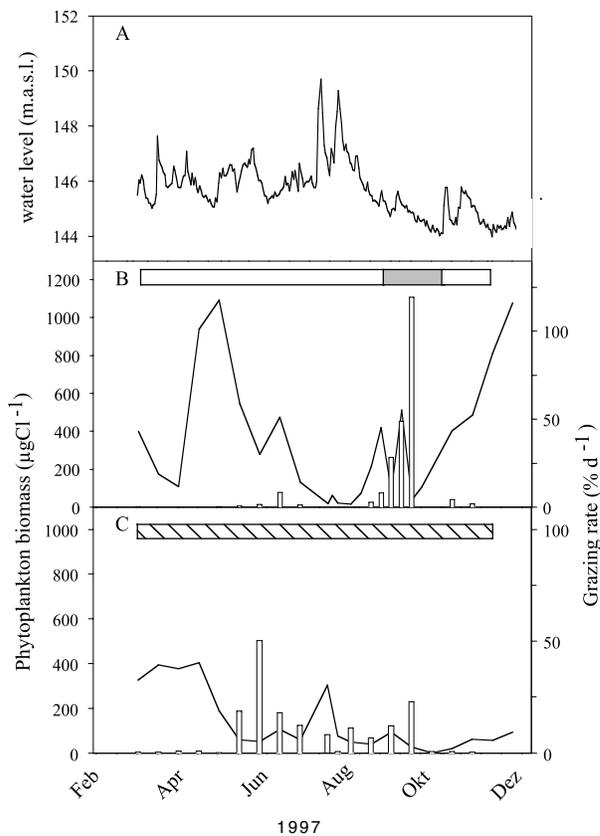
Fig. 3. Mean relative community grazing rates with standard deviations of total phytoplankton biomass (% day^{-1}) at different water age classes. Arrows indicate significant differences by Mann–Whitney *U* test.

Fig. 2. Seasonal course of water level in the River Danube (**A**). Relative community grazing rates of total phytoplankton biomass (open columns) at (**B**) Regelsbrunn and (**C**) Lobau, algal biomass (solid line) and temperature (dashed line). The bars represent different situations of water age, white <10 days, shaded >10 days, hatched >200 days.
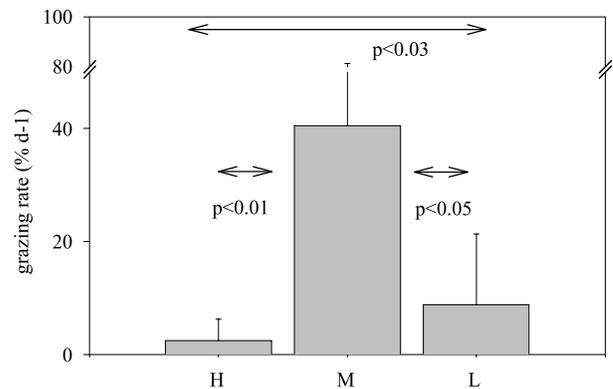
connectivity, we found a much wider range of grazing rates from 3 to a maximum of 115% of algal standing stock. When connectivity was low mean relative grazing pressure on the algae amounted to 9%, with a range of 0.3–50% (Figure 3).

In terms of size selective grazing impact, rotifers dominated the grazing activity, taking primarily algae of 11–20 μm GALD with a mean rate of 23% during high connectivity. The main grazers were *Synchaeta oblonga* and *S. pectinata*. Brachionids (e.g. *Brachionus angularis*, *B. calyciflorus*, *Keratella cochlearis cochlearis*, *K. cochlearis var. tecta f. micracantha*, *K. cochlearis var. tecta f. typica* and *K. quadrata*) had little impact on algae of 5–10 μm size, with mean grazing rates of only 3% (Table III) at high connectivity when the grazing activity of cladocerans and copepods was also negligible. In respect of total phytoplankton biomass, relative grazing rates were very low (<2%) on all categories.

Table III: Mean (SD) relative grazing rates (% day^{-1}) of different food size classes at the different hydrological situations

Food size (µm)	Regelsbrunn dynamic section H			M			Lobau isolated section L		
	rot	clad	cop	rot	clad	cop	rot	clad	cop
<5	0.0	0.1	–	0.0	3.2	–	0.0	2.5	–
	±0.0	±0.3	–	±0.1	±1.9	–	±0.0	±5.2	–
5–10	3.4	1.4	–	7.0	83.2	–	0.8	12.5	–
	±10.6	±3.9	–	±9.0	±96.4	–	±1.0	±22.3	–
11–20	23.3	–	0.6	30.3	–	15.1	28.2	–	9.9
	±36.4	–	±1.2	±39.3	–	±5.6	±25.0	–	±12.0
21–50	–	–	0.1	–	–	6.9	–	–	4.2
	–	–	±0.2	–	–	±3.9	–	–	±6.4
Total	1.5	0.9	0.0	5.1	33.4	1.9	2.3	5.8	0.7
	±2.2	±2.4	±0.1	±6.5	±40.5	±0.7	±2.5	±10.6	±1.2

rot, rotifers; clad, cladocerans; cop, copepods.

The highest consumption rates were recorded at intermediate connectivity (Table III) for all types of grazers. Cladocerans especially had a considerable impact on algae of 5–10 µm with a mean rate of 83%. Maximal consumption rates, dominated by *B. longirostris*, amounted to 250% of available algal cells. The same rotifer species as mentioned above, removed 7% of the 5–10 µm algae but the impact of rotifers on algae of 11–20 µm turned out to be much higher. Mainly *Polyarthra vulgaris* and *P. dolichoptera*, and to a lesser extent *Synchaeta* spp., removed these algae at relatively high rates with a mean value of 30% and maximum of 99.8% (Table III). Copepods too consumed this size class (11–20 µm) with a mean daily consumption of 15% due to the feeding of nauplii and young copepodite stages (Table III). Considering the total algal biomass, cladocerans had the greatest impact with a mean relative grazing rate of 33% (Table III) at intermediate connectivity.

At low connectivity the highest grazing impact (mean rate 28%) was again exerted on algae of 11–20 µm by rotifers, mostly *P. vulgaris* and *P. dolichoptera* (Table III). The cladoceran feeding impact turned out to be lower, with a mean grazing rate of 13% of algae of 5–10 µm size, but again *B. longirostris* dominated. Copepod consumption rates on individual algal size classes did not exceed 10%. In terms of total phytoplankton biomass, the grazing impact of all grazers was relatively low at the low connectivity site; cladocera dominated with a mean rate of 6% (Table III).

In maximal relative grazing rates on distinct algal sizes we found a succession from rotifers to crustaceans with increasing water age. Maximal grazing rates of >90% of particles of 11–20 µm were exerted by Synchaetidae (*S. oblonga*, *S. pectinata*, *P. vulgaris*, *P. dolichoptera*) at water ages of 3 and 10 days. The highest theoretical daily removal potential was that by *B. longirostris* with 250% in water of 17 days old. Other species or functional groups did not exceed a relative grazing rate of 40%. Large bodied cladocerans and copepods had maximal impacts even at high water age.

The relationship between grazing impact and water age showed an increasing linear trend for copepods and a unimodal trend for rotifers and cladocerans (Figure 4). For rotifers, regression analysis of relative grazing rates on total phytoplankton biomass and water age in the dynamic section showed a second order polynomial relationship ($y = -0.12 + 1.1x - 0.04x^2$, $r^2 = 0.47$, $P < 0.01$, n = 24) (Figure 4A). A similar trend was determined for cladocerans, with a slight shift of the maximal peak to higher water age ($y = 2.25 - 4.68.-4.68x + 0.65x^2$, $r^2 = 0.94$, $P < 0.001$, $n = 24$, Figure 4B). Copepod grazing impact on total algal biomass followed a linear relationship ($y = -0.13 + 0.09x$, $r^2 = 0.7$, $P < 0.001$, $n = 24$) (Figure 4C) and showed a constant increase of relative grazing rate with pool age. Rates never reached those of rotifers or cladocerans. No relationship was found for total phytoplankton biomass and water age (Figure 4D). However, peaks in grazing impact corresponded with low values of standing stock.

Table IV: Mean (SD) theoretical daily carbon consumption in $\mu g\ C\ l^{-1}\ day^{-1}$

		Regelsbrunn dynamic section		Lobau isolated section	
		H	M	L	Kruskal–Wallis test
Rotifers	mean (SD)	6 (9)	10 (6)	3 (6)	*
Cladocerans	mean (SD)	4 (10)	63 (83)	4 (6)	**
Copepods	mean (SD)	0.4 (1)	20 (22)	0.4 (1)	**

Differences between hydrological situations are tested with Kruskal–Wallis test (*$P = 0.05$, **$P = 0.001$).

Daily carbon flow

In terms of theoretical daily carbon flow, mean consumption by the zooplankton community was significantly higher at intermediate connectivity (93 $\mu g\ C\ l^{-1}\ day^{-1}$) than in the other two hydrological situations (10 and 7 $\mu g\ C\ l^{-1}\ day^{-1}$) (Kruskal–Wallis test, $P < 0.05$) (Figure 5).

Considering the different grazer categories, cladocerans had the highest carbon consumption (mean 63 $\mu g\ C\ l^{-1}\ day^{-1}$) at intermediate connectivity with a maximal value of 224 $\mu g\ C\ l^{-1}\ day^{-1}$ (Table IV) mainly due to *B. longirostris*. During high and low connectivity, cladocerans showed a similar, but lower, mean daily carbon uptake (mean 4 $\mu g\ C\ l^{-1}\ day^{-1}$). Mean daily algal consumption by rotifers was highest at the intermediate situation (10 $\mu g\ C\ l^{-1}\ day^{-1}$) and lowest under isolated conditions (3 $\mu g\ C\ l^{-1}\ day^{-1}$) (Table IV). Copepod consumption differed widely between intermediate, with mean rates of 20 $\mu g\ C\ l^{-1}\ day^{-1}$, and high as well as low connectivity (0.4 $\mu g\ C\ l^{-1}\ day^{-1}$) (Table IV). High carbon consumption figures at intermediate water ages are primarily produced by an abundance of nauplii and young copepodite stages. The Kruskal–Wallis test revealed significant differences between intermediate and the other hydrological situations, for all categories.

Herbivory, expressed as a ratio of algal consumption to zooplankton biomass, showed higher values in dynamic conditions (high and intermediate connectivity) (Figure 6). The ratio at low connectivity was significantly lower (Mann–Whitney U test, $P < 0.01$).

DISCUSSION

The role of the zooplankton community in carbon flow varies widely in the different components of the river–floodplain system examined (Figures 2 and 3). The limiting effect of flowing water on population development is clearly demonstrated, e.g. zooplankton is washed out at periods of high connectivity to the River Danube.

Consequently, its ecological contribution to carbon dynamics is negligible under hydrologically dynamic conditions. Considerable grazing impact takes place with increasing residence time of the water, peaking at intermediate ages of the water (17 days) (Figure 4). In fact, this strong grazing pressure (maximal >100% of total algal biomass) leads to a collapse of the phytoplankton standing stock. At greater water ages (>200 days) community grazing (Figures 2 and 3) fluctuated within a range comparable with measurements found in shallow eutrophic lakes [Vechten (Gulati *et al.*, 1982); Tjeukemeer (Gulati, 1975); Balaton (Zánkai and Ponyi, 1986)]. The observed zooplankton communities in these lakes show a similar species composition to those we observed, with dominance of rotifers and Bosminidae.

Along the gradient of water age, the grazing pressure on phytoplankton changes with various grazer categories (Figure 4). Rotifers reach their maximal grazing pressure at a water age of 10 days. They profit by their fast reproduction cycle which allows fast colonization. Comparable high rotifer abundances have been observed in summer during low discharge periods in slow flowing lowland rivers (Viroux, 1997; Kobayashi *et al.*, 1998; May and Bass, 1998) and, in the River Meuse for example, a perceptible impact by rotifers on algae smaller than 20μm was determined at a constant grazing rate of 20% per day (Gosselain *et al.*, 1998). Additionally, rotifers have proved to be less susceptible to suspended sediment than cladocerans (Kirk and Gilbert, 1990). This implies that rotifers are at an advantage in riverine situations with high loads of suspended solids. Cladocerans show maximum grazing activity at a water age of 17 days and replace rotifers in grazing dominance. Herbivory by copepods, on the other hand, increases continuously with water age, but never reaches grazing rates comparable with those of rotifers and cladocerans.

This observation implies a functional succession in the grazing impact of various taxonomic groups in dynamic floodplains, with highest impact by cladocerans, which
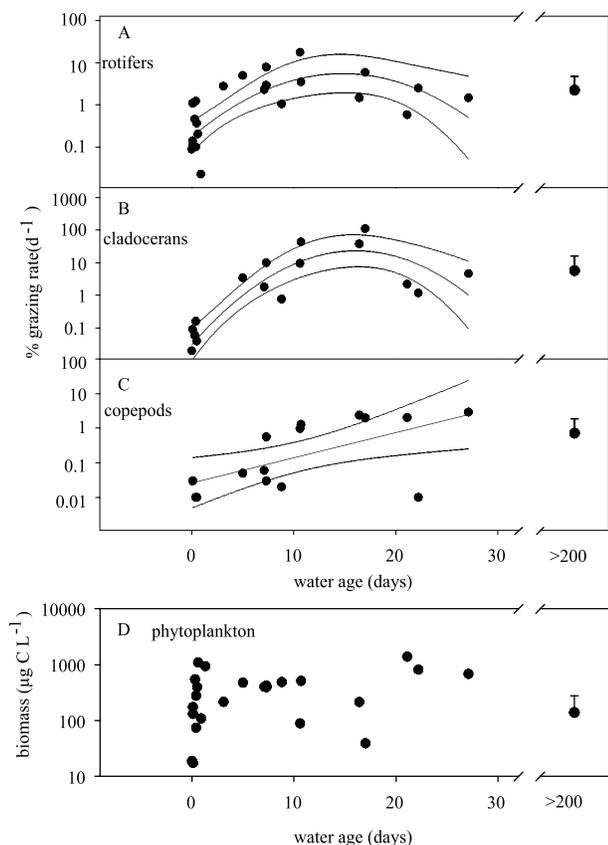
Fig. 4. Relationships of theoretical daily relative grazing rates on total algal biomass (% day^{-1}) by (**A**) rotifers, (**B**) cladocerans and (**C**) copepods to water age Regelsbrunhn. (**D**) Phytoplankton biomass (μg C l^{-1}) versus water age. A reference mean and standard deviation at the isolated section is shown on the right side in each panel.

can lead to a total depletion of available algae. At high water age top–down interactions start to control primary producers.

Finally, the complexity of planktonic interactions is increased by the addition of omnivory and bacterivory, adult copepods and some cladocerans. The grazing pressure on algae decreases. Biotic interactions control abundance and prevent the high population densities observed during the early period of succession. A relatively stable plankton community, characterized by lower fluctuations in grazing potential, becomes established.

Despite the high species diversity of floodplain zooplankton (Baranyi *et al.*, 2002) only a few species are significant. Within the early 'rotifer' period *Synchaeta oblonga* and *S. pectinata* colonize the water body first and exert grazing pressure on algae of a distinct size class. In the later rotifer phase, *Polyarthra vulgaris* and *P. dolichoptera*, which have a similar, particle-grasping feeding method as synchaetids, continue the high grazing impact on these

algae. The brachionids (*Brachionus angularis*, *B. calyciflorus*, *Keratella cochlearis*), which as filter feeders affect smaller cells, never reach these high removal rates. However, despite high population densities and intense grazing activity, there is a good supply of preferred algal food and rotifers cannot deplete this food resource.

The most important grazer is *B. longirostris* because of its high population densities and high grazing rates. This species has proved to be a most important cladoceran in floodplain systems (Bothár, 1972; Vranovsky, 1972; Heiler *et al.*, 1994). Probably they are able to cope with the heterogeneous environment better than daphnids, which might need open water conditions, and hence low predation pressure by fish, to reach high numbers (Juergens, 1994).

Copepods require much more stable conditions to pass through their ontogenetic development. Therefore their adult stages are present only at high water ages. This supports results from earlier studies on the Danube floodplain system (Bothár, 1972; Vranovsky, 1972; Heiler *et al.*, 1994). In the early periods only nauplii and young copepodite stages contribute to grazing. Generally the role of copepods in herbivory proves to be low, and efficient grazers such as calanoid species occur only in small numbers. Cyclopoids, such as *Acanthocyclops* spp. and *Thermocyclops* spp. dominate; they are omnivorous species which are even able to ingest prey of their own body size (Dussart and Defaye, 1995). An experiment set up at a period of long disconnection from the river (30 days water age) confirmed the increasing significance of large copepodite stages and adult copepods in biotic interactions (unpublished data).

In terms of daily carbon flow, periods of intermediate residence time (>10–27 days water age) showed the highest turnover (Figure 5). Phytoplankton biomass is channelled to higher trophic levels by strong herbivory, which is demonstrated quite clearly by the ratio of consumed algal and zooplankton carbon (Figure 6). Absolute daily carbon transfer at low water age (≤10 days) is much lower, but efficiency in consumption of autochthonous carbon by zooplankton is similar. The degree of herbivory is completely different at periods of high water age (Figure 6). These results demonstrate, moreover, the decreasing dominance of phytoplankton with decreasing hydrological connectivity and increasing degree of succession. Dynamic floodplains are characterized by high algal productivity and biomass (Hein *et al.*, 1999a). Consequently, carbon flow via herbivory is dominant in the planktonic food web. With depletion by grazing, phytoplankton finally loses predominance. Planktonic interactions become more complex, complemented by internal predatory regulation and stronger links from metazoans to micro-organisms (Arndt, 1993).
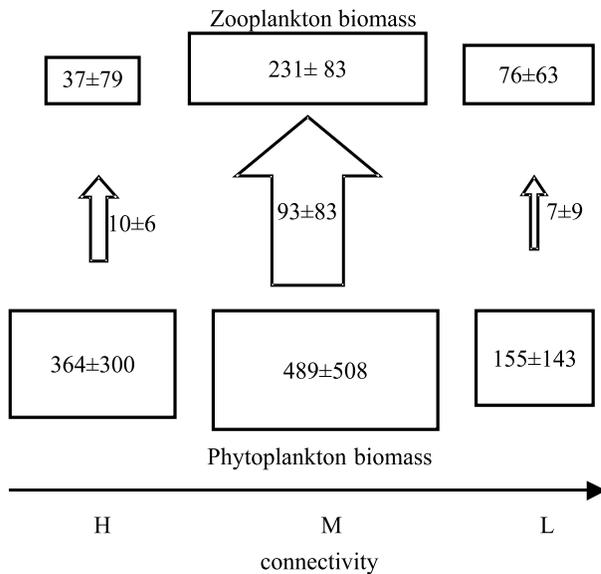
Fig. 5. Mean (+SD) theoretical daily carbon flow by community grazing for three different classes of water age. Arrows indicate carbon flow (μg C l^{-1} day^{-1}). Phyto- and zooplankton biomass in boxes (μg C l^{-1}).
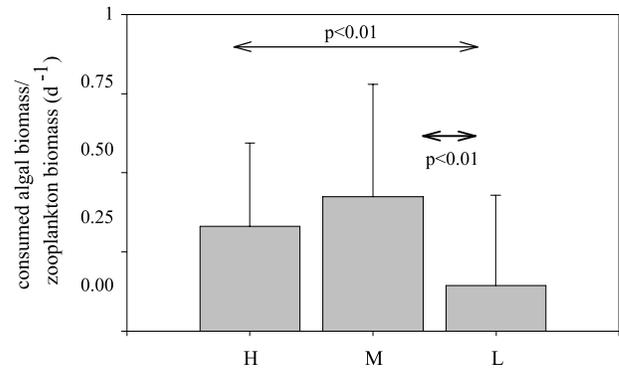

Fig. 6. Mean ratio of consumed algal biomass to zooplankton biomass at different classes of water age. Arrows indicate significant differences by Mann–Whitney U test.

The potential carbon flow demonstrated confirms the importance of river–floodplain systems as zones of storage and turnover of organic matter. Flood controlled disturbances in backwaters have a stimulating effect on the succeeding plankton development and carbon transfer and consequently on the whole aquatic community. For river biota, such as riverine fish, which use backwaters as feeding and nursery grounds (Schiemer and Zalewski, 1992; Schiemer and Waidbacher, 1992; Kurmayer *et al.*, 1996), this organic matter pool represents an important food resource.

In this regard our results support the efforts to restore river–floodplain systems, which mainly focus on conservation of biodiversity (Schiemer and Waidbacher, 1992; Tockner and Ward, 1999; Tockner *et al.*, 1998; Schiemer, 1999; Ward *et al.*, 1999), by demonstrating their importance for carbon dynamics as well.

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REFERENCES

Admiraal, W., Breebaart, L., Tubbing, G. M. J., Van Zanten, B., De Ruijter van Steveninck, E. D. and Bijkerk, R. (1994) Seasonal variation in composition and production of planktonic communities in the lower River Rhine. *Freshwater Biol.*, **32**, 519–531.

Arndt, H. (1993) Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates)—a review. *Hydrobiologia*, **255/256**, 231–246.

Baranyi, C., Hein, T., Holarek, C., Keckeis, S. and Schiemer, F. (2002) Zooplankton biomass and community structure in a Danube River floodplain. *Freshwater Biology*, **47**, 473–482.

Bogdan, K. G. and Gilbert, J. J. (1982) Seasonal patterns of feeding by natural populations of Keratella, Polyarthra, and Bosmina: clearance rates, selectivities and contributions to community grazing. *Limnol. Oceanogr.*, **27**, 918–934.

Bothár, A. (1972) Hydrobiologische Untersuchungen im Nebenarm der Donau bei God. Danub. Hung. LXII, Ann. Univ. Sci. Budapest, *Sect. Biol.*, **14**, 9–23.

Bottrell, H .H., Duncan, A., Gliwicz, Z. M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P. and Weglenska, T. (1976) A review of some problems in zooplankton production studies. *Norw. J. Zool.*, **24**, 419–456.

Dumont, J. D., Van de Velde, I. and Dumont, S. (1975) The dry weight estimate of biomass in a selection of cladocera, copepoda and rotifera from the plankton, periphyton and benthos of continental waters. Oecologia, **19**, 75–97.

Dussart, B. H. and Defaye, D. (1995) Copepoda—introduction to the copepoda. In Dumont, H. J. F. (ed.), *Guides to the Identification of the*

Macroinvertebrates of the Continental Waters of the World. SPB Academic Publishing. The Hague, The Netherlands.

Galat, D. L., Kubisiak, J. F., Hooker, J. B. and Sowa, L. M. (1997) Geomorphology, distribution and connectivity of lower Missouri River floodplain waterbodies scoured by the flood of 1993. *Verh. Internat. Verein. Limnol.*, **26**, 869–878.

Garnier, J., Billen, G. and Coste, M. (1995) Seasonal succession of diatoms and chlorophyceae in a drainage network of the Seine River: observations and modelling. *Limnol. Oceanogr.*, **40**, 750–765.

Gilbert, J. J. and Bogdan, K. G. (1985) Rotifer grazing: in situ studies on selectivity and rates. In Meyers, D. G. and Strickler, J. R. (ed.), *Trophic Interactions Within Aquatic Ecosystems*. AAAS Selected Symposium 85, Westview press, Boulder, Colorado.

Gosselain, V., Descy, J.-P., Joaquim-Justo, C., Hammer, A., Métens, A. and Schweitzer, S. (1998) Grazing by large river zooplankton: a key to summer potamoplankton decline? The case of the Meuse and Moselle rivers in 1994 and 1995. *Hydrobiologia*, **369**, 199–216.

Gulati, R. D. (1975) A study on the role of herbivorous zooplankton community as primary consumers in Dutch lakes. *Verh. Int. Ver. Limnol.*, **20**, 1202–1210.

Gulati, R. D., Siewertsen, K. and Postema, G. (1982) The zooplankton: its community structure, food and feeding, and the role in the ecosystem of Lake Vechten. *Hydrobiologia*, **95**, 127–163.

Hansen, P. J., Bjørnsen, P. K. and Hansen, B. W. (1997) Zooplankton grazing and growth: scaling within the 2–2000-mm body size range. *Limnol. Oceanogr.*, **42**, 687–704.

Hart, R. C. and Jarvis, A. C. (1993) In situ determinations of bacterial selectivity and filtration rates by five cladoceran zooplankters in a hypertrophic subtropical reservoir. *J. Plankton Res.*, **15**, 295–315.

Heiler, G., Hein, T. and Schiemer, F. (1994) The significance of hydrological connectivity for limnological processes in Danubian backwaters. *Verh. Internat. Verein. Limnol.*, **25**, 1674–1679.

Heiler, G., Hein, T. and Schiemer, F. (1995) Hydrological connectivity and flood pulses as the central aspects for the integrity of a river-floodplain system. *Regul. Rivers: Res. Mgmt.*, **11**, 351–361.

Hein, T., Baranyi, C., Heiler, G., Holarek, C., Riedler, P. and Schiemer, F. (1999a) Hydrology as a major factor determining plankton development in two floodplain segments and the River Danube, Austria. *Arch. Hydrobiol. Suppl.*, **115**, 439–452.

Hein, T., Heiler, G., Pennetzdorfer, D., Riedler, P., Schagerl, M. and Schiemer, F. (1999b) The Danube Restoration Project: functional aspects and planktonic productivity in the floodplain system. *Regul. Rivers: Res. Mgmt.*, **15**, 259–270.

Herzig, A. (1984) Fundamental requirements of zooplankton. *Production studies*. Limnol. Institute of Austrian Academy of Science, 83 pp.

Juergens, K. (1994) The impact of Daphnia on microbial food webs. *Mar. Microb. Food Webs*, **8**, 295–324.

Junk, W. J., Bayley, P. B. and Sparks, R. E. (1989) The flood pulse concept in river-floodplain systems. In Dodge, D. P. (ed.), *Internat. Large River Symp. Canad. Spec. Pub. Fish. Aquat. Sci.*, **106**, 110–127.

Kirk, K. L. and Gilbert, J. J. (1990) Suspended clay and the population dynamics of planktonic rotifers and cladocerans. *Ecology*, **71**, 1741–1755.

Kobayashi, T., Shiel, R. J., Gibbs, P. and Dixon, P. I. (1998) Freshwater zooplankton in the Hawkesbury-Nepean River: comparison of community structure with other rivers. *Hydrobiologia*, **377**, 133–145.

Kurmayer, R., Keckeis, H., Schrutka, S. and Zweimueller, I. (1996) Macro- and microhabitat used by 0+ fish in a side-arm of the River Danube *Arch. Hyrobiol. Suppl.*, **113**, 425–432.

Lundstedt, L. and Brett, M. T. (1991) Differential growth rates of three cladoceran species in response to mono- and mixed-algal cultures. *Limnol. Oceanogr.*, **36**, 159–165.

May, L. and Bass, J. A. B. (1998) A study of rotifers in the River Thames, England, April-October, 1996. *Hydrobiologia*, **387/388**, 251–257.

Ooms-Wilms, A. L., Postema, G. and Gulati, R. D. (1993) Clearance rates of bacteria by the rotifer Filinia longiseta (Ehrb.) measured using three tracers. *Hydrobiologia*, **255/256**, 255–260.

Peters, R. H. (1984) Methods for the study of feeding, filtering and assimilation by zooplankton. In Downing, J. A. and Rigler, F. H. (ed.), *A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters*. IBP Handbook 17, Blackwell Scientific Publications. pp. 336–412.

Peters, R. H. and Downing, J. A. (1984) Empirical analysis of zooplankton filtering and feeding rates. *Limnol. Oceanogr.*, **29**, 763–784.

Reckendorfer, W., Keckeis, H., Winkler, G. and Schiemer, F. (1999) Zooplankton abundance in the River Danube, Austria: the significance of inshore retention. *Freshwater Biol.*, **41**, 583–591.

Reynolds, C. S. and Descy, J.-P. (1996) The production, biomass and structure of phytoplankton in large rivers. *Arch. Hydrobiol. Suppl.*, **113**, 161–187.

Riedler, P. and Schagerl, M. (1998) Pelagic primary production and related parameters in the River Danube near Vienna (Austria). *Arch. Hydrobiol. Suppl.*, **115**, 139–151.

Ruttner-Kollisko, A (1972) III. Rotatoria. Das Zooplankton der Binnengewaesser. 1. *Die Binnengewaesser*, **26**, 99–234.

Ruttner-Kollisko, A. (1977) Suggestions for biomass calculation of plankton rotifers. *Arch. Hydrobiol. Suppl.*, **8**, 71–76.

Schiemer, F. (1999) Conservation of biodiversity in floodplain rivers. *Arch. Hydrobiol. Suppl.*, **115**, 423–438.

Schiemer, F. and Waidbacher, H. (1992) Strategies for conservation of a Danubian fish fauna. In Boon, P. J., Calow, P. and Petts, G. E. (ed.), *River Conservation and Management*. Wiley and Sons Ltd., Chichester, pp. 364–382.

Schiemer, F. and Zalewski, M. (1992) The importance of riparian ecotones for diversity and productivity of riverine fish communities. *Neth. J. Zoology*, **42**, 323–335.

Schiemer, F, Baumgartner, C. and Tockner, C. (1999) Restoration of floodplain rivers: the Danube Restoration project. *Reg. Rivers: Res. Mgmt.*, **15**, 231–244.

Sommer, U., Gliwicz, Z. M., Lampert, W. and Duncan, A. (1986) The PEG-model of seasonal succession of planktonic events in fresh waters. *Arch. Hydrobiol.*, **106**, 433–471.

Starkweather, P. L. and Gilbert, J. J. (1978) Feeding in the rotifer Brachionus calyciflorus IV. Selective feeding on tracer particles as a factor in trophic ecology and in situ technique. *Verh. Internat. Verein. Limnol.*, **20**, 2389–2394.

Sterner, R. W. (1989) The role of grazers in phytoplankton succession. In Sommer, U. (ed.), *Plankton Ecology, Succession in Plankton Communities*, Brock/Springer Series in Contemporary Bioscience. pp. 107–171.

Tockner, K. and Ward, J. V. (1999) Biodiversity along riparian corridors. *Arch. Hydrobiol. Suppl.*, **115**, 293–310.

Tockner, K., Schiemer, F. and Ward, J. V. (1998) Conservation by restoration: the management concept for a river-floodplain system on the River Danube in Austria. *Aquat. Conserv.*, **8**, 71–86.

Viroux, L. (1997) Zooplankton development in two large lowland rivers, the Moselle (France) and the Meuse (Belgium), in 1993. *J. Plankton Res.*, **19**, 1743–1762.

Vranovsky, M. (1972) Einige weitere Ergebnisse der Zooplanktonunter-

suchungen im tschechoslowakisch-ungarischen Donauabschnitt. *Biológia (Bratislava)*, **27**, 821–827.

Vranovsky, M. (1995) The effect of current velocity upon the biomass of zooplankton in the River Danube side arms. *Biológia (Bratislava)*, **50**, 461–464.

Vuille, T. (1991) Abundance, standing crop and production of micro-crustacean populations (cladocera, copepoda) in the littoral zone of Lake Biel, Switzerland. *Arch. Hydrobiol.*, **123**, 165–185.

Ward, J. V., Tockner, K. and Schiemer, F. (1999) Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regul. Rivers: Res. Mgmt.*, **15**, 125–139.

Zánkai, P. N. and Ponyi, J. E. (1986) Composition, density and feeding of crustacean zooplankton community in a shallow, temperate lake (Lake Balaton, Hungary). *Hydrobiologia*, **135**, 131–147.