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ADVANCES IN ROTIFIER RESEARCH

Spatial dynamics of rotifers in a large lowland river, the Elbe, Germany: How important are retentive shoreline habitats for the plankton community?

Heike Zimmermann-Timm · Henry Holst · Hartmut Kausch

Abstract The longitudinal dynamics of Rotifers in the Potamal region of the River Elbe between Dresden, km 46, and Geesthacht, km 583, was investigated on a Lagrangian survey in 2000 which included transversal sampling (left bank, main channel, right bank) and sampling of five major tributaries and backwaters to evaluate lateral impacts on the zooplankton community. A simple model of longitudinal development for the dominant species *Trichocerca pusilla* was calculated, based on the results of an in situ incubation in Dresden and on literature data and compared with the dynamics observed on the Lagrangian survey. To characterize the influence of groyne fields on the main channel zooplankton community, an additional lateral sampling was conducted in August 2000 at Havelberg, km 423. Zooplankton community was clearly dominated by rotifers. A distinct downstream-directed increase of rotifers was observed. Longitudinal development of rotifers could be explained predominantly by reproduction during downstream transport.

Keywords Potamoplankton · Large river · Retentive shoreline habitat · Transport · Growth rates

Introduction

Confirming earliest river concepts such as the River Continuum Concept (Vannote et al., 1980) a downstream directed plankton development has been observed in many larger rivers (De Ruyter van Steveninck et al., 1992; Meister, 1994; Viroux, 1997, 2002; Kim & Joo, 2000). Nevertheless, this simplified view of longitudinal potamoplankton development excludes hydromorphological channel diversity and has therefore been criticized (Reckendorfer et al., 1999). Longitudinal discontinuities, such as lateral dams and reservoirs, as well as fluvial lakes, could constitute a source of plankton (Thorp et al., 1994; Pourriot et al., 1997; Akopain et al., 1999; Welker & Walz, 1999; Basu et al., 2000a, b. Since Reynolds et al. (1991) and Reynolds & Glaister (1993) demonstrated the importance of retentive inshore habitats ("storage zones") for the growth and abundance of lotic phytoplankton, several authors emphasized the effect of these structures on zooplankton dynamics in larger rivers as well. In the River Danube higher

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Advances in Rotifer Research

This paper is dedicated to Alois Herzig, a colleague and friend, on the occasion of his 60th birthday on May 24th, 2006.

H. Zimmermann-Timm (✉)
Potsdam-Institute for Climate Impact Research, Telegrafenberg A31, 14467 Potsdam, Germany
e-mail: Heike.Zimmermann-Timm@pik-potsdam.de

H. Zimmermann-Timm · H. Holst · H. Kausch
Institute of Hydrobiology and Fishery Science, University Hamburg, Zeiseweg 9, 22765 Hamburg, Germany

zooplankton abundances were detected within slow flowing inshore habitats (Reckendorfer et al., 1999; Baranyi et al., 2002), a phenomenon which supported the "inshore retention concept" (Schiemer et al., 2001). Lair & Reyes-Marchant (1997) discussed the capacity of side shore habitats as inocula for mainstream zooplankton populations. In contrast to slow flowing side channels, the relative small retentive capacity of constructed shore habitats consisting of groyne fields inhibits significant lateral gradients in zooplankton abundance (Spaink et al., 1998; Holst et al., 2002), although a cumulative effect of these structures has not been evaluated. The quantitative and qualitative influence of tributaries on the potamoplankton community depends on the abiotic (temperature, residence time) and biotic (competition, predation) characteristics of each tributary as well as its contribution to the overall discharge of the main river and is therefore highly variable (Thorp et al., 1994; Wehr & Thorp, 1997; Kim & Joo, 2000; Lair, 2005).

With a free flowing section of about 600 km, eutrophic conditions and a substantial growth of autotrophic and heterotrophic food organisms, the Potamal of the river Elbe provides potential favorable conditions for a distinct longitudinal zooplankton development (Meister, 1994; Holst et al., 2002). The aim was to evaluate differences between the riverine population development with special attention on the utilization of lateral retentive inshore habitats (groyne fields). The latter aspect was deepened by an additionary lateral sampling investigation, performed at a single station. A simple model for the mainstream population growth of *Trichocerca pusilla* was calculated and compared with field data to give an impression of the impact of retentive side habitats on this dominant zooplankton species. Quantitative and qualitative sampling of rotifers in tributaries and connected side arms reveals baseline information about the rotifer community and its influence on the mainstream populations.

Method

Study site

With a length of 1,091 km and a catchment area of about 14,8261 km^2, the Elbe is one of the largest rivers in Western Europe. Mean annual discharge is about 327 m^3 s^{-1} at Dresden (km 55.6 at which German river km start with km 0 at the Czech-German border), 720 m^3 s^{-1} at Neu Darchau (km 536.4) and 870 m^3 s^{-1} at the river mouth (km 725.2). Major tributaries in the German Potamal region are the Mulde (km 251) with 75 m^3 s^{-1}, the Saale (km 291) with 116 m^3 s^{-1} and the Havel (km 438) with 115 m^3 s^{-1} mean annual discharge (Fig. 1). In the Czech part of the River, several navigation dams disrupt longitudinal continuity, whereas in the German stretch of the River only one weir, located at Geesthacht, km 586 exists. Average water transport time at MQ is about 8 days from the German border to the weir Geesthacht (ARGE Elbe).

Increased sewage plant capacity reduced the organic pollution, since the reunification of Germany in 1990, but the Elbe is still one of the most polluted rivers in Central Europe (Adams et al., 1996; Guhr et al., 1996), with high nutrient concentrations and high conductivities, caused by salt mining in the middle reaches of the Potamal. Although the Potamal of the River Elbe reveals a near-natural floodplain system, compared to other large lowland rivers, the channel morphology at low water levels, apparent during the summer months, shows little diversity characterized by groyne fields. In the upper part of the investigated river stretch gravel sediments and flow velocities above 1 m s^{-1} are prevalent whereas the lower parts are characterized by sandy sediments and lower flow velocities and a higher overall retention by larger groyne fields. Macrophytes are almost absent and flows through side branches are rare.

Longitudinal survey

In July 2000, a longitudinal survey was performed by successive sampling the same water parcel during its downstream passage at 16 stations (Lagrangian sampling). Calculation of water transport time based on the model QSIM from the Bundesanstalt für Gewässerkunde, BfG, Koblenz (Eidner, BfG Berlin pers. comm.) was fed by the actual discharge data. At each station left bank (L), mainstream (MS) and right bank (R) was sampled. Additionally, five major tributaries, three channels and nine connected backwaters were investigated. Surface samples were taken from the mainstream at each station. Rotifer samples were taken using a 2.25 l horizontal tube (HYDROBIOS, Kiel, Germany). Organisms were concentrated on a

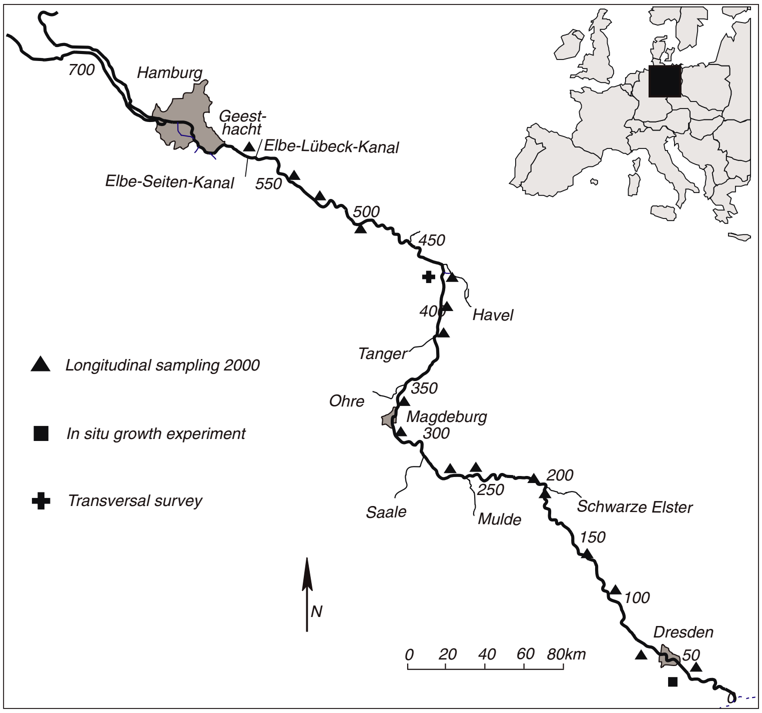

Fig. 1 Location of the sampling stations on the River Elbe, Germany. Symbols indicate the different sampling surveys and the location of the in situ growth experiment in July 2000

30-µm mesh, narcotized with carbonated water and fixed in 5% formaldehyde solution. All samples were stained in the laboratory with bengal red to facilitate detection. Samples were counted either completely or divided into subsamples containing at least 300 individuals using a plunger HENSEN—pipette. The specimens were identified according to Koste (1978) and counted in sedimentation chambers at 60–600× magnification using an inverted microscope. Crustacean samples were counted completely under a stereo microscope at 22–66× magnification. For determination and counting phytoplankton, 200 ml samples were fixed with Lugol's solution and the organisms examined under an inverted microscope (Utermöhl, 1958). For chlorophyll *a* determinations, 150–500 ml samples were concentrated on glass fiber filters (WHATMAN GF/F) and analyzed photometrically after hot ethanol extraction (Nusch, 1980). The physico-chemical parameters were measured with a portable multiprobe (HORIBA, Japan).

In situ growth experiments

From 20th to 23rd of July 2000 an in situ incubation experiment was carried out simultaneously with the Lagrangian survey in order to compare rotifer growth rates at with the observed longitudinal dynamics. At the beginning of the survey, at station km 49 (Fig. 1), untreated water from the mainstream was gently filled in nine transparent cylinders (Vol. 9 l) and incubated at 0.3 m depth under rotating conditions to simulate turbulence (approx. 10 r.p.m.). After 24, 48, and 72 h three containers at a time were put out of the rotating device and rotifers were concentrated on a 30-µm mesh and processed as described above.

Transverse survey

From 12th to 13th of August 2000 eight transects were repeatedly sampled in 4 h intervals at Havelberg, km 423 (Fig. 1). Sampling started at 8.00 pm and ended at 12.00 pm at the next day. Each transect consisted of three transverse stations, left groyne field, mainstream and right groyne field. Physico-chemical parameters were measured with a portable multiprobe (HORIBA, Japan) and rotifers and crustaceans were processed as described above.

Data analysis

Plankton abundances obtained from the Lagrangian survey in July 2000 and of the transverse survey at

Havelberg in August 2000 were tested to detect differences between mainstream and groyne fields using unpaired non-parametric ANOVA (Kruskall–Wallis test).

Based on the given discharge rates, the water transport time and population growth rates the downstream developments for *Trichocerca pusilla* was calculated and compared with the observed dynamics. Instantaneous population growth rate for *T. pusilla* (r = 0,51) was developed by linear regression of ln-transformed abundance versus time, using the dataset of the in situ incubation in Dresden (Fig. 2). Discharge values based on the mean discharge from July 20th to July 28th were obtained from the ARGE Elbe. The water transport time is based on QSIM calculation (Eidner, BfG Berlin pers. comm.). Possible influences by predation and food limitation were neglected as well as temperature effects. Dilution effects of tributaries that contained no individuals of the observed species were covered by the increase of mainstream discharge. Tributaries that included *T. pusilla* (Mulde and Havel) were fitted separately into each calculation. The formula for the development within river stretches without tributary influence was given by

$$C_{tx} = C_{t0} * e^{r*\Delta t} * (Q_{t0}/Q_{tx}) \quad (1)$$

where C_{tx} represents the abundance (ind l^{-1}) at the time x (km x), C_{t0} is the abundance at $t = 0$ (for *T. pusilla* = 184.44 ind. l^{-1}). r is the given exponential growth rate (h^{-1}) and Δt (h) reflects the water transport time between t_0 and t_x. Q_{t0} is the discharge (m^3 s^{-1}) at t_0 and Q_{tx} reflects the discharge at t_x.

Tributary influence is definable as:

$$C_b = (C_a * e^{r*\Delta ta} * Q_a + C_{tr} * e^{r*\Delta ttr} * Q_{tr})/(Q_a + Q_{tr}) \quad (2)$$

where C_b is the calculated abundance at the closest station below the confluence of the tributary with the mainstream. C_a is the abundance at the closest station above the tributary and C_{tr} reflects the abundance within the tributary. Δta is the transport time between upper and lower mainstream station, whereas Δttr is the transport time between confluence and lower mainstream station. Q_a and Q_{tr} are the discharge values at the upper mainstream station and the tributary, respectively.

Development from Dresden (km 49) to the upper station of tributary and river stretches below tributaries were calculated by formula (1), whereas the alteration in abundance between upper and lower station of the confluence of a tributary was calculated by formula (2).

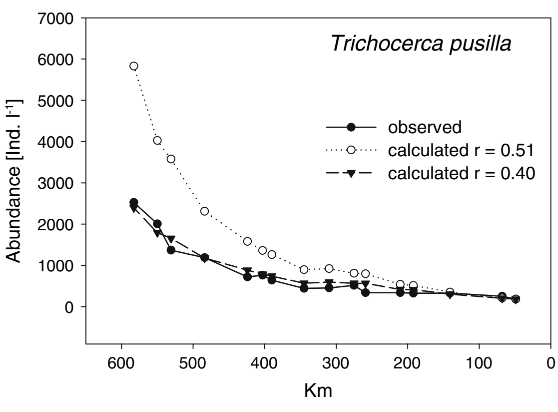

Fig. 2 Observed abundance dynamics of *Trichocerca pusilla* in the main channel during the Lagrangian survey 2000 (black circles, solid lines) and calculated dynamics based on actual discharge data (ARGE Elbe), transport time (BfG, Eidner pers. comm.) and growth rates (r = 0.51 for *T. pusilla*; open circles, dotted lines). Calculations with the best fit (r = 0.40 for *T. pusilla*) are indicated by black triangles and solid lines

Results

Lagrangian survey 2000

In July 2000 a mean discharge of 309 m^3 s^{-1} at km 536 was measured. Compared to other years the water temperatures were relatively low at the end of July 2000 and ranged between 16.2°C at km 192 and 21.0°C at Geesthacht (km 583) (Fig. 3).

Crustaceans in the mid-river stations remained below 1.5 ind. l^{-1} up to km 301 and then increased towards a maximum of 20.6 ind. l^{-1} at station km 550 (Fig. 3). In the upper part of the river, developmental stages of copepods (nauplii and copepodids) dominated but did not increase in abundance during downstream transport. *Bosmina longirostris, Macrothrix laticornis*, and *Alona rectangula* became dominant from km 424 on towards downstream.

Fifty-nine rotifer taxa were detected in the mainstream, *Trichocerca pusilla* dominated the community at almost every station with an average of 55.4% of total abundance, followed by *Keratella cochlearis* (12.6%), *Synchaeta oblonga* (9.5%) and *Keratella*

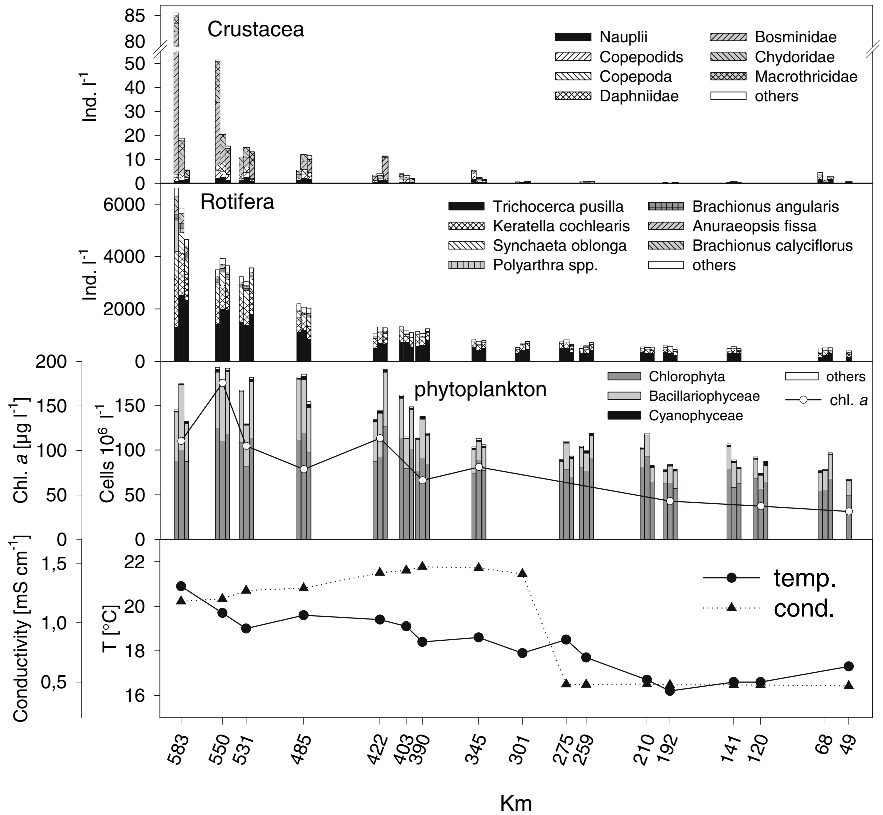

Fig. 3 Longitudinal variation of total abundance and species composition of Crustacea (ind. l^{-1}), Rotifera (ind. l^{-1}) and phytoplankton (Cells*10^6 l^{-1}) and variation of the parameters chl. *a* (µg l^{-1}), water temperature (°C) and conductivity (mS cm^{-1}) on the Lagrangian survey in July 2000. Left, middle and right bar of each group represents the left bank, mainstream and right bank, respectively

cochlearis var. *tecta* (8.1%; Fig. 3). No clear longitudinal shift in community structure was observed, except an increasing relative abundance of brachionids in the lower parts of the river. Up to km 345 rotifer densities remained below 850 ind. l^{-1}, with a minimum (404 ind. l^{-1}) detected at km 49. Maximum abundance of 6,618 ind. l^{-1} was found at the left bank of the lowest station, km 583. With a mean coefficient of variance cv = 9.90% ± 5.41. The tributaries Schwarze Elster and Ohre contained rotifer densities below 20 ind. l^{-1}. In the high saline river Saale (4670 µS cm^{-1}) 112.7 rotifers l^{-1} were detected, most of them were contracted small illoricate individuals, presumably belonging to the order Bdelloidea (Fig. 3). Neither densities (477. 5 ind. l^{-1}) nor community structure (dominated by *T. pusilla* and *K. cochlearis*) of the river Mulde differed remarkably from the Elbe, so that the influence of this tributary was neglectable. With a total abundance of 927.3 ind. l^{-1}, the Havel showed highest rotifer densities within the sampled tributaries, although this value amounts to only 75% of the abundance of the Elbe at km 424. Small synchaetids, mostly *Synchaeta tremula* dominated the community, accounting for over 35% of total abundance.

Rotifer dynamics in the sampled backwaters varied extremely in terms of abundance and species composition. Highest densities were detected in the backwater at km 545 with over 13,000 ind. l^{-1} dominated by *Trichocerca pusilla*. A mean of 19 species were detected in the backwaters. *Polyarthra* spp., *Filinia longiseta*, *Brachionus calyciflorus* and *Pompholyx sulcata*, which are almost absent in the mainstream reached high abundance values in some of the habitats.

Phytoplankton community in the mainstream was dominated by green algae and centric diatoms, which accounted for 70.38% and 27.28%, respectively, over at all stations (Fig. 3). The observed longitudinal increase of total phytoplankton densities was much less pronounced than the dynamics observed for rotifers and crustaceans. Lowest values (67.0*10^6 cells l^{-1}) were detected in Dresden (km 49) and maximum abundance of 192.3*10^6 cells l^{-1} appeared at km 550.

Transverse variation, expressed by the coefficient of variance cv (%) at each longitudinal station showed significant differences ($n = 15$) (Kruskal–Wallis test, $\alpha = 0.1\%$, $H = 18.70$, $\chi^2 = 13.86$).

In situ growth experiments and calculation of main channel development

Only rotifers were considered in the in situ growth experiment. A continuous growth over the duration of the experiment (72 h) was registered, with a mean maximum abundance of 2028.33 (±110.94) ind l^{-1} at the third day. Coefficient of variance in the three treatments at the first, second and third day was 11.23%, 7.94% and 5.47%, respectively. Community structure did not change significantly over the exposition period. *Trichocerca pusilla* dominated in all sampled parallels with a mean of 48.54% (±4.32) and it showed an development with $r = 0.51$ day^{-1} ($F = 88.87$, $F_{0.01} = 11.26$).

Calculation of the mainstream development of *T. pusilla* led to a maximum abundance of 5828.7 ind. l^{-1} at Geesthacht, km 583, which is about twice the observed value of 2527.3 ind. l^{-1} (Fig. 3). Growth rates which fitted best with the observed dynamics (least square principle) were 0.40 day $^{-1}$ for *T. pusilla* (Figs. 2, 3).

Transverse survey

Lateral sampling in Havelberg, km 422, (Fig. 1) from 11th to 12th of August 2000, was performed under similar hydrophysical conditions as the Lagrangian survey, 2 weeks earlier. Discharge rate was 311 m^3 s^{-1} at km 536, mean water temperature was 19.82°C ± 0.48 and measured conductivity ranged between 1270 µS cm^{-1} and 1370 µS cm^{-1} (mean: 1321 µS cm^{-1}). A total of 39 rotifer taxa were detected in the samples (mean: 21 taxa). *Trichocerca pusilla* dominated the community with a mean abundance of 3984.1 ± 451.9 ind. l^{-1}, accounting for over 70% of total rotifers in all samples. Total rotifer densities ranged between 2645.4 ind. l^{-1}, and 4690.9 ind. l^{-1} (mean: 3984.9 ind. l^{-1}). Kruskal–Wallis *H*-test revealed significant lateral differences for *Trichocerca pusilla* ($P = 0.0207$). Compared to the mainstream *T. pusilla* exhibited significant lower abundances in the left groyne field ($P = 0.0030$).

Discussion

Longitudinal dynamics

The hydromorphological characteristic of each river is a major factor determining plankton development (Basu & Pick, 1997). Water transport time and availability of retentive structures differs from river to river rendering comparisons between systems (Viroux, 1997). Even in one river system seasonal variation of discharge, and therefore variation in the hydromorphology, leads to rapid fluctuations in the plankton community (Van Dijk & Van Zanten, 1995; Kim & Joo, 2000; Viroux, 1997, 2002). The Potamal region of the Elbe is characterized by a free flowing stretch of about 600 km and, especially during low flow summer months, reduced availability of retentive lateral structures. A distinct steady increase of plankton abundances, dominated by rotifers, reflects this hydromorphological character, confirming previous studies in other large rivers (De Ruyter van Steveninck et al., 1992; Basu et al., 2000a; Kim & Joo, 2000) and the Elbe (Meister, 1994). The distance of about 50 km from the nearest upstream located navigation dam makes it likely that the plankton community at the most upstream station, km 46, consists of true riverine plankton (Akopain et al., 1999). Considering transport times of about 9 days from Dresden to Geesthacht at low flow conditions, together with a high autotrophic and heterotrophic production (Desertova et al., 1996; Karrasch et al., 2001), it is not surprising that the zooplankton community of the Elbe is dominated by rotifers (10,000 ind l^{-1}) which attain high densities during summer months (Holst et al., 2002).

Abundant rotifer species such as *Keratella cochlearis*, *Brachionus angularis* and *Synchaeta oblonga* have often been described as dominant species in lotic environments (Basu & Pick, 1996; Pourriot et al., 1997; Holst et al., 1998; May & Bass, 1998; Basu et al., 2000a; Kim & Joo, 2000), whereas *Trichocerca pusilla*, which reached high densities in summer has been detected in much fewer rivers (Ferrari et al., 1989; May & Bass, 1998; Walz & Welker, 1998; Lair et al., 1999). This summer species has been described as an indicator of eutrophy (Zankai, 1989; Pejler & Bērzinš, 1993). Filter feeding brachionids (*Keratella* spp., *Brachionus* spp.) and cladocerans generally became abundant in the slower flowing downstream parts of the river, whereas the development of fast growing grasping species, especially the rotifer *Trichocerca pusilla*, appeared far more upstream. The inoculation of the river Havel, with relative high densities of filter feeders (rotifers and cladocerans; Meister 1994; Fig. 4), could be one reason for this phenomenon. In addition to this, higher flow velocities and turbidities in the upstream parts may have inhibited growth of filter feeding generalists, favoring grasping specialists (Kirk & Gilbert, 1990; Kirk, 1991; Miquelis et al., 1998).

Lateral influences

With the exception of the river Havel (and the Mulde concerning rotifers), the major tributaries contained low zooplankton densities confirming the results of Meister (1994). The Havel is characterized by numerous navigation dams and long water transport time allowing zooplankton to grow and therefore can be generally stated as a promoter of plankton densities in the Elbe. With low plankton densities and high relative discharge the Saale must exert a potential diluting influence on the Elbe zooplankton community.

The zooplankton communities of connected backwaters differed remarkably in terms of abundance and species composition from the main channel and between each other. Larger species like *Brachionus calyciflorus* as well as delicate forms like *Filinia longiseta*, which were almost absent in the main channel appeared in high densities in some backwaters. It is well known that abiotic and biotic parameters in these lentic habitats, structuring zooplankton communities differ significantly from mainstream (Van den Brink et al., 1994; Spaink et al., 1998). Generally, the impact of biotic control such as competition and predation increases under lentic conditions and physical parameters like losses due to advection, turbulence and turbidity diminish (Baranyi et al., 2002). The significant positive relationship between rotifer and crustacean abundance in the main channel underlines the abiotic control of both groups mainly due to advection. Nevertheless over 60% of the variation remains unexplained so that additional factors such as selective predation, for example by planktivorous fish (Bass et al., 1997; Spaink et al., 1998; Jack & Thorp, 2002), and overall food availability have to be taken into consideration. However, the importance of these backwaters as an inoculum for the zooplankton community of the main channel has a rather qualitative than quantitative character, because exchange between water bodies is limited due to the singular connection to main channel. Flow through side branches which significantly affect main channel zooplankton communities, as reported from the Danube (Hein et al., 1999), are rare in the middle part of the Elbe, at least at low water levels.

The most numerous retentive structures in the Elbe Potamal are groyne fields, but previous plankton studies (Karrasch et al., 2001; Holst et al., 2002) have shown that retention times of most of these structures are too low to establish detectable gradients between groyne field and Elbe main channel, at least for phytoplankton and rotifers. Spaink et al. (1998) did not detect any differences of plankton

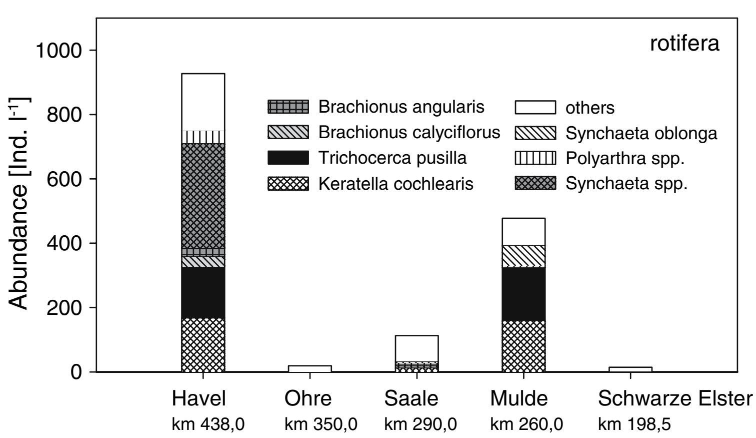

Fig. 4 Mean abundance and species composition of rotifera (ind. l^{-1}) in the major tributaries of the River Elbe sampled on the Lagrangian survey in July 2000

abundances between a groyne field and the main channel of the river Rhine, confirming these results. On the other hand, there is a great hydromorphological variation between the groyne fields in the river Elbe (Sukhodolov et al., 2001), resulting in different retentive capacities, so that the generalization of this result are uncertain.

The calculated abundances for *Trichocerca pusilla*, based on the results of the in situ experiment in Dresden (Fig. 2), exceeded the observed values, which leads to the conclusion that the observed longitudinal development of this species is basically a result of the ability of reproduction within the mainstream. Several explanations, e.g., grazing pressure of *Dreissena polymoropha* or influence of increasing salinity, can be taken into account for the fact that the calculation fitted best with a much lower growth rate of 0.40 day^{-1}.

Finally, the results of the lateral survey in August 2000 support the hypothesis that differences in the utilization of retentive lateral structures exist. Rotifers exhibited a low lateral variation with *T. pusilla* even slightly more abundant in the main channel then in the groyne fields. One has to bare in mind that this species specific utilization of retentive habitats is basically different from the interactions between water age and total zooplankton communities within slow flowing floodplain habitats as described for the River Danube (Baranyi et al., 2002).

Considering the results of this study some general conclusions can be drawn about the characteristics of zooplankton development in the Potamal region of the River Elbe.

With a free flowing section of about 600 km and scarce appreciable lateral retentive structures like slow flowing side branches or macrophyte beds, the Potamal of the River Elbe is dominated by rotifers which have the ability of rapid reproduction within the main channel. Abiotic factors like water transport time and water temperature are the main parameters controlling rotifer abundance since grazing is presumably negligible and food availability is high. Maximum rotifer abundances of over 10,000 ind. l^{-1} observed at low discharge and high water temperatures and comparable low crustacean densities underline the importance of advection for zooplankton development and the channelized character of the Elbe Potamal, at least for passive drifting organisms like zooplankton. Major lateral influences are exerted by the tributaries Havel, contributing detectable amounts of larger filter feeding cladocerans and rotifers to the main channel, and the salt loaded Saale which dilutes Elbe plankton densities. Lateral retentive effects caused by the numerous groyne fields are barely recordable on the microscale of each single groyne field, mainly due to the high exchange rate of water within most of these structures. Nevertheless, the results of this study indicate that the predominant Bosminids seem to be capable of maintaining position in slow flowing habitats from which inoculation of the main channel takes place. This process takes place especially in the downstream parts of the Potamal where lower flow velocities and larger groyne fields promote retention. Further detailed studies are necessary to investigate the biotic processes in groyne fields and to define the overall impact of these structures on the riverine zooplankton community of the Elbe.

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