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Anja Scherwass, Tanja Bergfeld, Andreas Schoel, Markus Weitere, Hartmut Arndt

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Changes in the plankton community along the length of the River Rhine: Lagrangian sampling during a spring situation

Scherwass, A. ^{1*}, Bergfeld, T. ², Schöl, A. ², Weitere, M. ¹ & Arndt, H. ¹

¹ *University of Cologne, Center for Biological Sciences, Institute for Zoology, Department of General Ecology, Otto-Fischer-Str. 6, D-50674 Cologne, Germany*
² *Federal Institute of Hydrology, Department of Ecological Interactions, Am Mainzer Tor 1, D-56068 Koblenz, Germany*

*Corresponding author: Anja Scherwass
E-mail: anja.scherwass@uni-koeln.de, Phone: ++49 221 470 4249
Fax: ++49 221 470 5932

Key words: protozoa, phytoplankton, metazooplankton, bacteria, river, Lagrangian sampling

Abstract:

The development of the planktonic microbial community (bacteria, heterotrophic nanoflagellates (HNF) and ciliates) was investigated along a 660 km stretch of the River Rhine using Lagrangian sampling in May 2000, and by taking the influence of the main tributaries into account. The relative importance of the components of the microbial food web (HNF, ciliates) increased in the course of the German river stretch, whereas the absolute abundance of protozooplankton decreased and phytoplankton abundance increased. Bacterial abundance remained relatively constant throughout the river stretch investigated. The taxonomic composition of phytoplankton changed from a dominance of cryptophytes to a dominance of diatoms, whereas flagellates, ciliates and metazooplankton showed no shift in species composition. Some tributaries had higher abundances of planktonic organisms than the Rhine itself, but only the River Moselle contributed significantly to the plankton load of the Rhine. However, even after its confluence with the River Rhine abundances of the heterotrophic plankton (HNF and ciliates) remained low and decreased further downstream. The shifts in the composition of the pelagic microbial food web along the river stretch are discussed in the context of group-specific growth and loss processes.

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Introduction

During the last two decades research on the microbial food webs of different aquatic habitats has increased, giving insight into the characteristics and interactions of this thus far poorly understood part of the aquatic food web (Weisse *et al.*, 1990; Sanders *et al.*, 1992; Gilbert *et al.*, 1998 etc.). Our understanding of the functions and dynamics of the microbial components in riverine systems is still at an early stage (see Servais *et al.*, 2000; Weitere *et al.*, 2005; Joaquim-Justo *et al.*, 2006; Kiss *et al.*, 2009). Moreover, the longitudinal development of planktonic organisms has only been studied for selected groups, i.e. phytoplankton (Reynolds and Glaister, 1993; Reynolds and Descy, 1996; Ietswaart *et al.*, 1999), metazooplankton (de Ruyter van Steveninck *et al.*, 1992; Welker and Walz, 1998; Viroux, 2002) and heterotrophic nanoflagellates (Weitere and Arndt, 2002 a, b).

However, studies on the components of the microbial loop in rivers have indicated the importance of protozoans, which often make up a high proportion of the planktonic biomass and have a high potential grazing impact on the bacterial biomass (Carlough and Meyer, 1989; Arndt and Mathes, 1991; Sleight *et al.*, 1992; Lair *et al.*, 1999; Servais *et al.*, 2000; Weitere *et al.*, 2005; Joaquim-Justo *et al.*, 2006; Bergfeld *et al.*, 2009). Despite these studies, the dynamics of the microbial plankton community and their regulating factors during downstream transport over longer river stretches remain poorly understood (e.g. Sorokin, 1990).

The present study was conducted to investigate the composition and changes within the different groups of the plankton community, in particular on the components of the microbial food web, during downstream transport in a large river. Due to the canalisation of its bed, the River Rhine is particularly suited for following a water parcel during downstream passage: the influence of back waters is negligible, which facilitates the investigation of the influence of the major tributaries. The abundances of all plankton components were studied along a 660 km stretch of the Rhine.

We hypothesized that the abundances of all constituents of the plankton community (phyto-, proto- and metazooplankton) would increase

downstream due to internal production resulting in a characteristic river plankton community in the potamal region (as has been proposed previously; e.g. Vannote *et al.*, 1980; Allan, 2007). Such a downstream increase in abundance has been shown in the River Rhine on a 660 km stretch in an earlier study of phytoplankton and rotifers (de Ruyter van Steveninck *et al.*, 1992). However, more recent studies at different stations along a river stretch have shown that there can be a significant reduction of some plankton components, probably due to losses to benthic filter feeders (Weitere and Arndt, 2002 a, b; Scherwass and Arndt, 2005).

Method

The development of plankton was investigated on a stretch of the River Rhine in Germany between km- 173.1 and km- 844.9 (Fig. 1; the Rhine km numbers refer to the distance from the outflow at Lake Constance). The investigation took place from May 22nd to 28th 2000 following a water parcel moving downstream. The study was carried out towards the end of the phytoplankton spring bloom, so that we assumed a high productivity of all components of the microbial food web. Twenty-four sampling stations including eight tributaries were investigated (Table I). Between km- 173.1 and km- 334, most of the river flows in an artificial river bed regulated by ten dams; only below 10% of the total discharge (usually between 20 and 150 m³ sec⁻¹) flows in the former river bed. The part of the river which flows in the original bed is hereafter referred to as the “Rest-Rhine”. The Rhine flows in its natural bed with no further dams from km- 334 to the end of the investigated area (km-844.9).

The samples between km-173.1 and km-483.2 were taken at 1 m depth from the research vessel ‘Max Honsell’ (from the ‘LUBW’ - Landesanstalt für Umwelt, Messungen und Naturschutz Baden-Württemberg). At km-590.9, - 684.5 and -844.9, sampling was carried out from pontoons situated in the main stream of the river. To ensure sampling of the same water parcel during downstream transport, water flow time was calculated with the aid of the computer simulation program ‘Alarm’ (Spreafico and Mazijk, 1993). Three samples were generally taken at each sampling site: one each on the

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2 1 left and right side and one in the middle of the river. If this was not possible,
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4 2 three consecutive samples were taken from the middle of the river within
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6 3 30 minutes.
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8 4 Immediately after sampling, temperature as well as chlorophyll *a* and
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10 5 oxygen content were measured using a multi-probe (Yellow Spring
11 6 Instrument Inc.). In order to assess the seston content, 500 mL of river water
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13 7 were filtered through preweighted GF/F glass fibre filters (Whatman). The
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15 8 filters were then dried for 24 h at 100 °C and weighed. As a preparation for
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17 9 determining the bacterial density, water samples were fixed with formalin
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19 10 (2 % final concentration). 1 mL of sample was filtered onto 0.2 µm black
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21 11 polycarbonate filters within 24 hours after sampling, stained with 0.2 mL of
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23 12 DAPI (working solution 0.01 mg mL⁻¹) and then stored at -20 °C until
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25 13 further processing. Bacteria were counted under an epifluorescence
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27 14 microscope (Zeiss Axioskop) under UV-excitation (365 nm; Filter: BP 395-
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29 15 440 BP, beam splitter 460, LP 470). At least 400 bacteria were counted per
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31 16 filter, grouped into size classes according to measurements with an eye-
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33 17 piece micrometer. Because the delicate heterotrophic and autotrophic
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35 18 nanoplankton are often destroyed during fixation, they were live-counted on
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37 19 board. The live-count was conducted directly after sampling under a phase
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39 20 contrast microscope (Zeiss Axiostar) with magnifications of 100 – 400x to
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41 21 determine their abundance and taxonomic composition. At least five
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43 22 subsamples of 5 – 10 µL each were counted until sufficient numbers of
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45 23 protists for statistical analysis were obtained. The lengths and widths of
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47 24 individual nanoplanktonic organisms were measured using video
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49 25 microscopy to calculate biovolumes (based on simple geometrical forms).
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51 26 Unfiltered samples of microplankton (ciliates and larger algae) were fixed
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53 27 with Bouin's fluid (5% final concentration), concentrated in the laboratory
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55 28 and processed as described in Scherwass *et al.* (2002) using a method
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57 29 combining density gradient centrifugation (to exclude inorganic seston
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59 30 particles) and quantitative protargol staining (Skibbe, 1994). The resulting
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31 permanent slides were examined under a microscope (Axiophot 2, Zeiss)
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33 with a magnification of up to 1000x. Biovolumes were estimated based on
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simple geometric forms assuming a shrinkage factor of 30%. This shrinkage
factor refers to observations for several ciliate groups (Pfister *et al.*, 1999).

In addition to the analysis of protozooplankton, 2 or 4 L of water were sieved through a plankton net (10 μm -mesh size) and the metazooplankton was counted at 200x magnification. Metazooplankton lengths, abundance and composition were determined, and published length-weight ratios were used to calculate the biovolume (e.g. Bottrell *et al.*, 1976). These data were collected to estimate the abundance and biomass of metazooplankton organisms for the present study; a more detailed investigation of metazooplankton was conducted at one station (Cologne Rhine-km 684.5) in a parallel study (Weitere *et al.*, 2005).

Statistical analyses were conducted using SPSS for Windows (version 15.0). Spearman rank coefficients were used to analyse correlations between plankton abundances and flow time.

Results

Abiotic parameters and abundances of plankton organisms

Water temperature and oxygen concentration varied only slightly along the length of the river stretch, whereas the chlorophyll *a* concentration increased significantly during downstream transport, resulting in a maximum of $11.8 (\pm 1.6) \mu\text{g L}^{-1}$ measured at Rhine-km-844.9 (Fig. 2a). Seston content and turbidity increased markedly during downstream transport as well (Fig. 2b).

Phytoplankton abundance showed an increase (up to eightfold, Fig. 3a) from the Upper to the Lower Rhine (positively correlated with the increase of the chlorophyll *a*). Most tributaries and the “Rest-Rhine” showed higher abundances of phytoplankton than the Rhine itself. The largest difference between the main stream and the tributaries was found in the middle stretch of the Rhine: in the rivers Moselle and Lahn, phytoplankton abundances were about nine times higher than in the Rhine at this location (Fig. 3a). Particularly the Moselle contributed a significant plankton load to the Rhine (Tab. II).

Bacterial abundances remained constant over the stretch of the Rhine averaging $3.7 \times 10^6 (\pm 5.5 \times 10^5)$ bacteria mL^{-1} (Fig. 3 b) with a slight tendency towards higher values in the upper part of the river. Generally, bacterial abundances were lower in the tributaries and the ‘Rest-Rhine’ than

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2 1 in the River Rhine (where they averaged $2.2 \times 10^6 (\pm 6.9 \times 10^5)$ bacteria
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4 2 mL^{-1}).
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6 3 The abundances of both heterotrophic nanoflagellates and ciliates declined
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8 4 during downstream transport (Fig. 4 a, b). Moreover, abundances of both
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10 5 protozoan groups were significantly negatively correlated with the flow time
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12 6 ($b = -0.385$, $p < 0.01$ for HNF; $b = -0.424$, $p < 0.01$ for ciliates). The
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14 7 average HNF abundance dropped from $407 (\pm 50) \text{ ind. mL}^{-1}$ at km-173.1 to
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16 8 $328 \text{ ind. mL}^{-1} (\pm 10)$ at km-844.9, and did not exceed a value of 400 ind.
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18 9 mL^{-1} in the Middle and Lower Rhine. Tributaries of the middle and lower
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20 10 reaches of the Rhine showed abundances which were significantly higher
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22 11 than in the main stream reaching mean values between 703 and 1,683 ind.
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24 12 mL^{-1} in the Main, Lahn and Moselle.
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26 13 The pattern of downstream development of ciliate abundance was partly
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28 14 similar to that of the HNF (Fig. 4 b). A significant reduction from a mean of
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30 15 $263 \text{ ciliates L}^{-1} (\pm 21)$ at Rhine-km-173.1 to $64 \text{ ind. L}^{-1} (\pm 32)$ at Rhine-km-
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32 16 844.9 was observed. Ciliates showed high numbers in the Lahn, Moselle and
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34 17 “Rest-Rhine” (up to a mean of 838 ind. L^{-1} in the latter), whereas low
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36 18 abundances were recorded for the small tributaries.
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38 19 Though only roughly estimated in the present study, the metazooplankton
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40 20 abundance (mainly rotifers) seem to show the same trend as HNF and
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42 21 ciliates along the river stretch with decreasing abundances during
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44 22 downstream transport from about 70 to about 20 ind. L^{-1} .
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46 23 The plankton load contributed by the largest tributaries in the reach of the
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48 24 Rhine investigated was calculated based on the abundances of organisms
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50 25 (Tab. II). The Moselle contributed a large part to the total plankton
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52 26 community in the Rhine: up to 42% of phytoplankton, 10.1% of bacteria,
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54 27 20% of HNF, and 43.0 % of ciliates. The largest metazooplankton load was
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56 28 contributed by the River Main (57 %).
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Share of different planktonic components in terms of biovolume

Phytoplankton made up the largest proportion of the total plankton biovolume in spring 2000. Its biovolume ranged from $0.36 \text{ mm}^3 \text{ L}^{-1}$ (Rhine-km-173.1) to $1.70 \text{ mm}^3 \text{ L}^{-1}$ (Rhine-km-844.9); up to $3.4 \text{ mm}^3 \text{ L}^{-1}$ (in the Moselle) were observed in the tributaries. The bacterial biovolume ranged

from 0.21 to 0.34 mm³ L⁻¹. Phytoplankton exceeded bacterial biovolume at all stations (Fig. 5 a). Bacteria contributed the most to the total heterotrophic biovolume (comprising bacterial and total zooplankton biovolume, data not shown).

The biovolume of total zooplankton was about one order of magnitude lower than that of phytoplankton (ranging between 0.03 mm³ L⁻¹ and 0.16 mm³ L⁻¹ in the Rhine), being dominated by heterotrophic nanoflagellates (Fig. 5 b), which contributed between 50 and 88% to the total zooplankton biovolume. The absolute biovolume of HNF (between 0.02 and 0.09 mm³ L⁻¹) was much higher than that of metazooplankton. In the tributaries, HNF accounted for up to 86 % ("Rest-Rhine" km-225.5) of total zooplankton biovolume. Ciliates contributed the least to the total zooplankton in the River Rhine as well as in all tributaries; their biovolume reached a maximum of 8 % (km-469.3) in the Rhine and 21 % (River Kinzig) in the tributaries (Fig. 5 b, 0.1 and 4 x 10³ mm³ L⁻¹, respectively). The share of metazooplankton decreased from 43 % at km-173.1 to 13 % at km-844.9 (0.002 – 0.03 mm³ L⁻¹). In the tributaries metazooplankton reached between 9 and 91 % ("Rest-Rhine" at km-291).

Changes in taxonomic composition

The taxonomic composition of phytoplankton on the basis of biovolume (Fig. 6) showed a distinct change during downstream transport. Cryptophytes dominated the plankton community in the Upper Rhine and diminished in importance during downstream transport. The proportion of diatoms increased significantly in parallel to the reduction of the cryptophytes in the River Rhine, whereas the tributaries showed a considerable number of chlorophytes.

In contrast to phytoplankton, protozooplankton did not show a clear change in taxonomic composition during downstream transport (Fig. 6). Among HNF, chrysomonads were the dominant group during the investigation. This was true for the River Rhine itself as well as for all tributaries. Their relative contribution remained comparatively constant throughout downstream transport. For ciliates, oligotrichs (typical planktonic forms) formed the largest component of the biomass, followed by peritrichs (mainly benthic

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forms). Their relative taxonomic composition did not change significantly during downstream transport. Metazooplankton was always dominated by rotifers, other metazooplankton groups were only found in a few cases such as nauplii larvae, mussel larvae and, less frequently, cladocerans.

Discussion

Changes of the planktonic community during downstream transport

The abundance and biovolume of plankton components in the Rhine is generally low throughout the year as has been shown in several long-term studies (ICPR, 2002; Scherwass and Arndt, 2005; Weitere *et al.*, 2005; Bergfeld *et al.*, 2009), especially when compared to other large rivers, e.g. River Loire (e.g. Lair *et al.*, 1999). The season with the highest plankton abundance in the River Rhine is spring (ICPR, 2002; Weitere *et al.*, 2005). As a consequence, the spring situation in May 2000 was chosen for the present Lagrangian investigation in order to be able to observe changes in the plankton community composition along the river stretch.

Within the plankton community of the River Rhine, we found a high proportion of protozooplankton (on average 75% of the total zooplankton biovolume) in the present study. This observation agrees with long-term studies of the River Rhine at Cologne (Rhine-km 684.5, Weitere *et al.*, 2005) and Koblenz (Rhine-km 590, Bergfeld *et al.*, 2009) and thus seems to be a general phenomenon in the middle and lower reaches of the River Rhine. The present study indicates that this is characteristic along almost the total river stretch, at least in spring/early summer. The proportion of protozoans to the total zooplankton in the River Rhine is high in comparison to other large rivers (e.g. in the Loire, Meuse and Elbe; see Lair *et al.*, 1999; Servais *et al.*, 2000; Wörner and Zimmermann-Timm, 2005), despite the fact that their proportion is generally higher in rivers compared to lakes .. A similarly high contribution of protozoans to the total zooplankton biovolume as shown for the River Rhine was only reported for the River Yenisei in Siberia by Sorokin (1990) and for two large rivers belonging to the Rhine River system, the Moselle and its tributary, the Saar (Bergfeld *et al.*, 2009).

Lagrangian sampling allowed further insights into changes of the plankton community during downstream transport within the River Rhine in spring. The development of the abundance of the microbial plankton differed between the groups of organisms. Bacterioplankton remained at a nearly constant low level during downstream transport despite their high potential growth rates. This is in contrast to the results of earlier studies in the River Rhine, where an increase of bacterioplankton over the course of the Rhine was observed during the same season (April and May; de Ruyter van Steveninck *et al.*, 1992; Ietswaart *et al.*, 1999). Also the increase of phytoplankton along the river stretch was much lower during the present study than during earlier studies (de Ruyter van Steveninck *et al.*, 1992; Ietswaart *et al.*, 1999; Friedrich and Pohlmann, 2009). One possible explanation for these changes in plankton dynamics might be the drastic changes of the community structure of invertebrates due to massive growth of invasive species immigrated into the River Rhine within the last two decades (ICPR 1996, 2002, see below).

Potential factors causing losses of plankton during downstream transport in spring

Sedimentation of plankton due to decreasing flow velocities in lower river reaches may be one reason for their decline during downstream transport, as has been shown e.g. in the lowland River Spree (Koehler *et al.*, 2002) and the River Meuse (Marneffe *et al.*, 1996). However, due to the strong canalisation of the River Rhine combined with a high discharge, flow velocity remained high up to the end of the investigated reach (km-844.9) and sedimentation was assumed to play a significant role only in the very low Dutch reaches of the Rhine (de Ruyter van Steveninck *et al.*, 1990). Additionally, turbidity increases with increasing river length and may affect autotrophic as well as heterotrophic plankton (Reynolds and Descy, 1996; Pourriot *et al.*, 1997). However, the light-dependent phytoplankton seems not to be affected by increased turbidity in spring, as its abundance increased along the river stretch. For metazooplankton, a disturbance of feeding due to high concentrations of inorganic particles in combination with high turbulence might negatively affect metazooplankton (Miquelis *et al.*, 1998).

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2 1 This could be the reason for the reduced metazooplankton abundance in the
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4 2 lower reaches of the River Rhine. The abundance of heterotrophic protists
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6 3 also decreased along the river stretch, but protists can be positively affected
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8 4 by inorganic sediment particles as they offer a habitat for colonization
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10 5 (Wörner *et al.*, 2002). This indicates that the dynamics of the different
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12 6 plankton groups cannot be explained by turbidity alone. Regarding
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14 7 mechanical forces potentially affecting plankton organisms it has to be
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16 8 considered that protists and bacteria have much lower Reynolds numbers
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18 9 than metazoans and are unlikely to be physically damaged in their relatively
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20 10 laminar surroundings (cf. Vogel, 1993). Thus turbulence does not seem to
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22 11 directly influence the unicellular organisms, whereas a negative influence on
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24 12 metazoans is possible (Picard and Lair, 2003; Sluss *et al.*, 2008).
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26 13 Another reason for decreasing plankton numbers in the course of the river
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28 14 stretch may be dilution by the tributaries. However, during our
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30 15 investigations tributaries generally had higher abundances of plankton than
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32 16 the River Rhine (see Tab. II). By taking these high plankton loads of the
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34 17 tributaries into account, our present data show that within-stream processes
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36 18 rather than effects of the tributaries might be the reason for the plankton
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38 19 dynamics observed in the Rhine.
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40 20 In an earlier study, we demonstrated with a combination of size fractionation
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42 21 experiments and Lagrangian sampling, that planktonic heterotrophic
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44 22 flagellates showed high losses during the downriver passage in the Lower
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46 23 Rhine (km 685 to 845, Weitere *et al.*, 2002a). The losses strongly depended
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48 24 on temperature (high losses in summer, low losses in winter), indicating
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50 25 biotic interactions. Furthermore, the losses could not be explained by
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52 26 planktonic grazers as derived from size-fractionation experiments. This gave
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54 27 rise to the conclusion that benthic grazers contribute significantly to losses
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56 28 of plankton in the Rhine. This conclusion is in accordance with the
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58 29 application of a water quality model in the Rhine for the year 1990 which
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60 30 revealed that metazooplankton grazing on the algal production was
negligible, but that algae were partly reduced by grazing of the benthic
mussel *Dreissena polymorpha* (Schöl *et al.*, 2002). Studies from other rivers
pointed to the importance of benthic predation on the components of the
planktonic microbial food web of rivers (e.g. Basu and Pick, 1997; Welker

and Walz 1998; Descy *et al.*, 2003). Some efficient benthic filter-feeding macroinvertebrates like *Corbicula* spp., *Dreissena polymorpha* and *Corophium curvispinum* are abundant in the Lower Rhine (e.g. Rajagopal *et al.*, 1995, 1998) and have been shown to capture particles of a wide size range (see e.g. Sprung and Rose, 1988; Scherwass *et al.*, 2001; Viergutz *et al.*, 2007; Weitere *et al.*, 2008). In their study in the River Rhine, Ietswaart *et al.* (1999) calculated a significant loss rate of algae due to predation by the benthic macrofauna community of 0.38 d^{-1} for the warm season for the year 1995. Losses to the benthic grazers may probably be even larger as only a few ‘focus’ grazers were considered in these estimations. The role of other potentially important benthic filter feeders including sponges, bryozoans and ciliates is as yet unknown (Weitere *et al.*, 2003; Kathol *et al.*, 2009; Vohmann *et al.*, 2009).

A possible control of the plankton by benthic filter feeders could explain group-specific patterns observed in the present study. The slow growing groups (metazoans, ciliates) decrease much more than fast growing groups such as heterotrophic flagellates, possibly due to different abilities to compensate for grazing losses (Weitere and Arndt, 2002a; Scherwass and Arndt, 2005). Bacteria probably experience a low grazing pressure by benthic filter feeders due to their small size (Sprung and Rose, 1988), but a strong grazing pressure may affect heterotrophic flagellates within the water column (Weitere *et al.*, 2002b). The loss rates of phytoplankton seem to be governed by factors different to those of protozooplankton. Further detailed longitudinal studies are required to explain these discrepancies in future.

The present case study for a spring scenario is the first that considered the longitudinal dynamics not only of classical components but also of organisms of the microbial food web in a large river. Additional studies at particular locations along the river stretch of the Rhine showed that general patterns such as stable or even decreasing plankton abundance occurs throughout the year despite high potential productivity (Weitere and Arndt, 2002a,b; Weitere *et al.*, 2005; Bergfeld *et al.*, 2009). Despite clear indications of a significant impact of the benthos on the plankton dynamics as found in different studies in the Rhine (see above), the interplay between

the different factors in controlling plankton in the Rhine (e.g. grazing, residence time, turbidity, turbulence, sediment infiltration) is as yet poorly understood. The importance of biotic versus non-biotic factors varies with the river stretch and each plankton group (Strayer *et al.*, 2008). Future empirical studies as well as model approaches need to focus on the interplay of the multiple factors in controlling plankton in rivers. In this context, it has to be pointed out that dynamics of plankton in the River Rhine shown here were observed only for the last ten years. There was still a considerable downstream increase of all plankton components until 1995 (de Ruyter van Steveninck *et al.*, 1992; ICPR, 1996; Friedrich and Pohlmann, 2009). Efforts to reduce the nutrient load (ICPR, 2002) and the massive increase of populations of invasive species (especially the effective plankton filterers such as *Corbicula spp.*, ICPR, 2002) are probably important reasons for the recent shift. Understanding the regulation of the plankton dynamics in changing riverine environments is a major challenge for future studies.

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Table I: List of sampling stations on the Rhine and in the tributaries at the confluence

Table II: Plankton load contributed by the main tributaries Neckar (at Rhine-km-429), Main (at Rhine-km-496) and Moselle (at Rhine-km-592) to the River Rhine on the 25th and 26th of May 2000. The load of the River Rhine before inflow of tributaries close to the river mouth, load of tributaries in absolute values and load of tributaries in % of the Rhine before inflow are shown.

Figure 1: Map of the river stretch investigated from km 173.1 to km 844.9

Figure 2: Values for (a) temperature, oxygen concentration and chlorophyll *a* and (b) seston content and turbidity content during downstream transport between May 22nd and 28th, 2000. Mean values \pm standard deviation are shown.

Figure 3: Abundance of phytoplankton (a) and bacteria (b) along the stretch of the River Rhine investigated (\blacklozenge) and in the tributaries (\square) (mean values \pm standard deviation) (Tributaries are marked with numbers: 1 = “rest-Rhine” at km-225.5, 2 = “rest-Rhin”e at km-291, 3 = Kinzig at km-298, 4 = Ill at km-312, 5 = Neckar at km-429, 6 = Main at km-496, 7 = Lahn at km-585, 8 = Moselle at km-592).

Figure 4: Abundance of heterotrophic protozooplankton (a: HNF, b: ciliates) along the stretch of the River Rhine investigated (\blacklozenge) and in the tributaries (\square); numbers indicate tributaries (s. Fig. 3) (mean values \pm standard deviation).

Figure 5: Biovolume partitioning of (a) bacteria and phytoplankton and (b) of the different groups of heterotrophic plankton along the stretch of the River Rhine investigated and in the tributaries (*no data available).

Figure 6: Relative taxonomic composition of biovolume of phytoplankton, HNF and ciliates along the stretch of the River Rhine investigated.

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1 Table I: River Rhine

<i>Date</i>	<i>Rhine-km</i>	<i>Flow time [h]</i>	<i>Sampling station</i>	<i>Discharge [m³/sec]</i>
22.05.00	173.1	0	Weil am Rhein	1478.6
22.05.00	190.5	4	above Ottmannsheim	
22.05.00	214.6	9	Unterwasser Fessenheim	
23.05.00	267.3	24	Nonnenweier	
23.05.00	279.4	28	Plobsheimer Becken	
23.05.00	296.4	32	Kehl	1500
24.05.00	342.5	48.5	Rastatt	1590
24.05.00	359.2	52	Karlsruhe	1568
24.05.00	395	57	Philippsburg	1633.2
25.05.00	457.9	71	downstream Biblis	1817.6
25.05.00	469.3	76	Gimsheim	
25.05.00	483.2	80	below Nierstein	
26.05.00	571	100.5	Boppard	2037.4
26.05.00	590.9	104	Koblenz	2213.5
27.05.00	684.5	125	Cologne	2256.9
28.05.00	844.9	158	Grietherbusch	2346.9

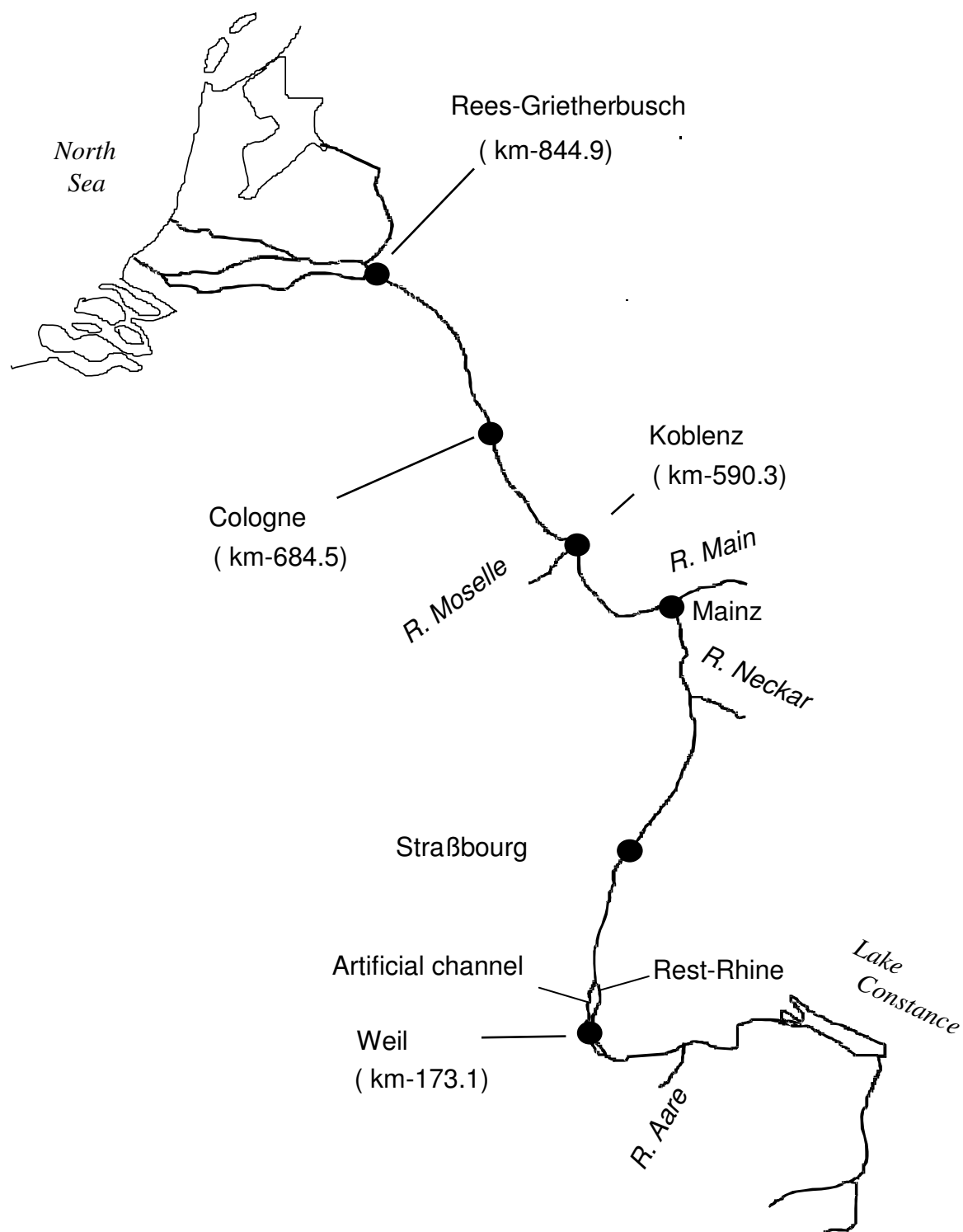
Table I: Tributaries

<i>Date</i>	<i>Inflow at Rhine-km</i>	<i>Tributary</i>	<i>Discharge [m³/sec]</i>			
22.05.00	225.5	“rest- Rhine”				
23.05.00	291	“rest- Rhine”				
23.05.00	298	Kinzig	13.1			
23.05.00	312	Ill				
25.05.00	429	Neckar	169.5			
26.05.00	496	Main	133.5			
26.05.00	585	Lahn	20,6			
26.05.00	592	Moselle	211.5			

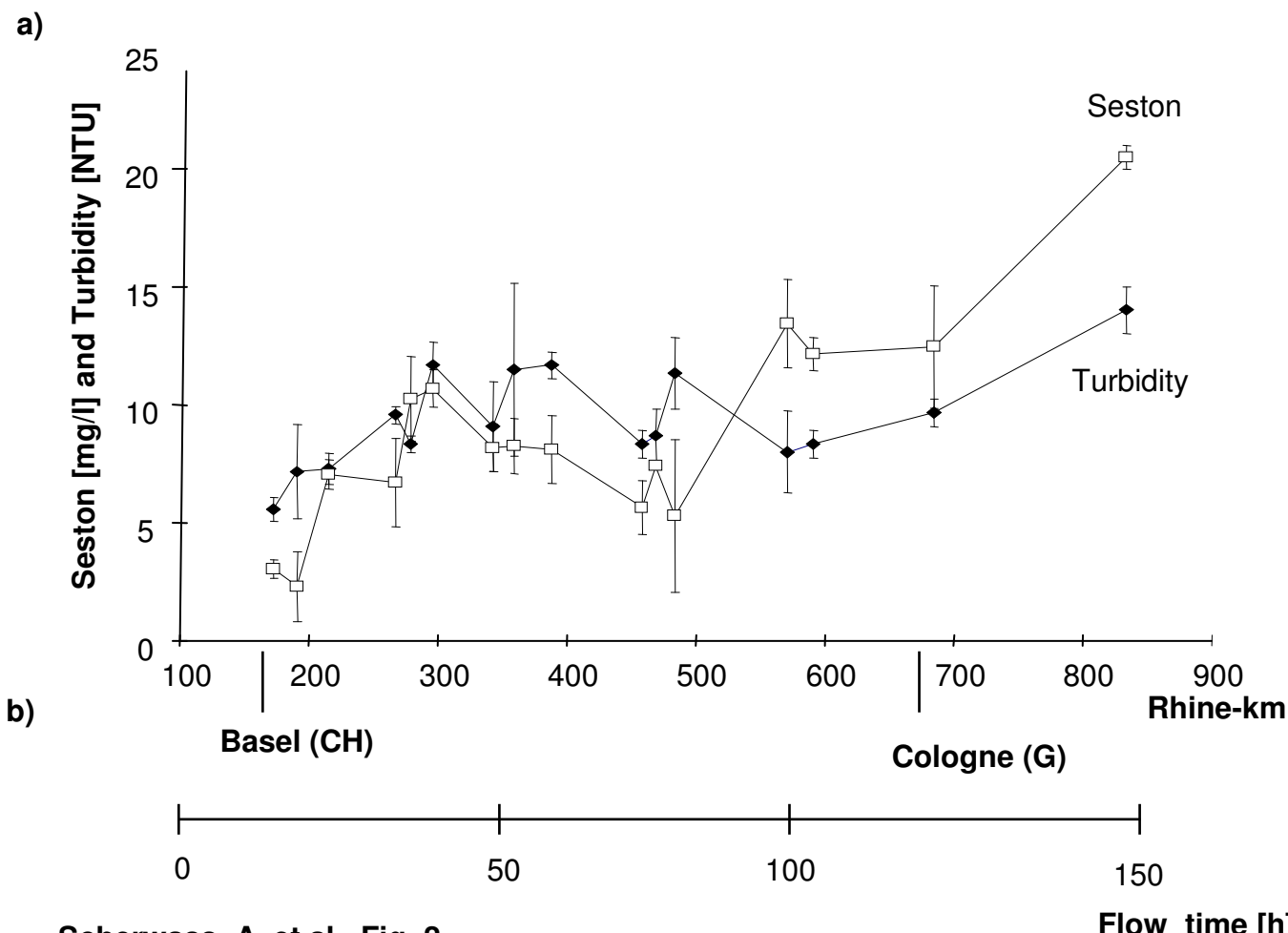
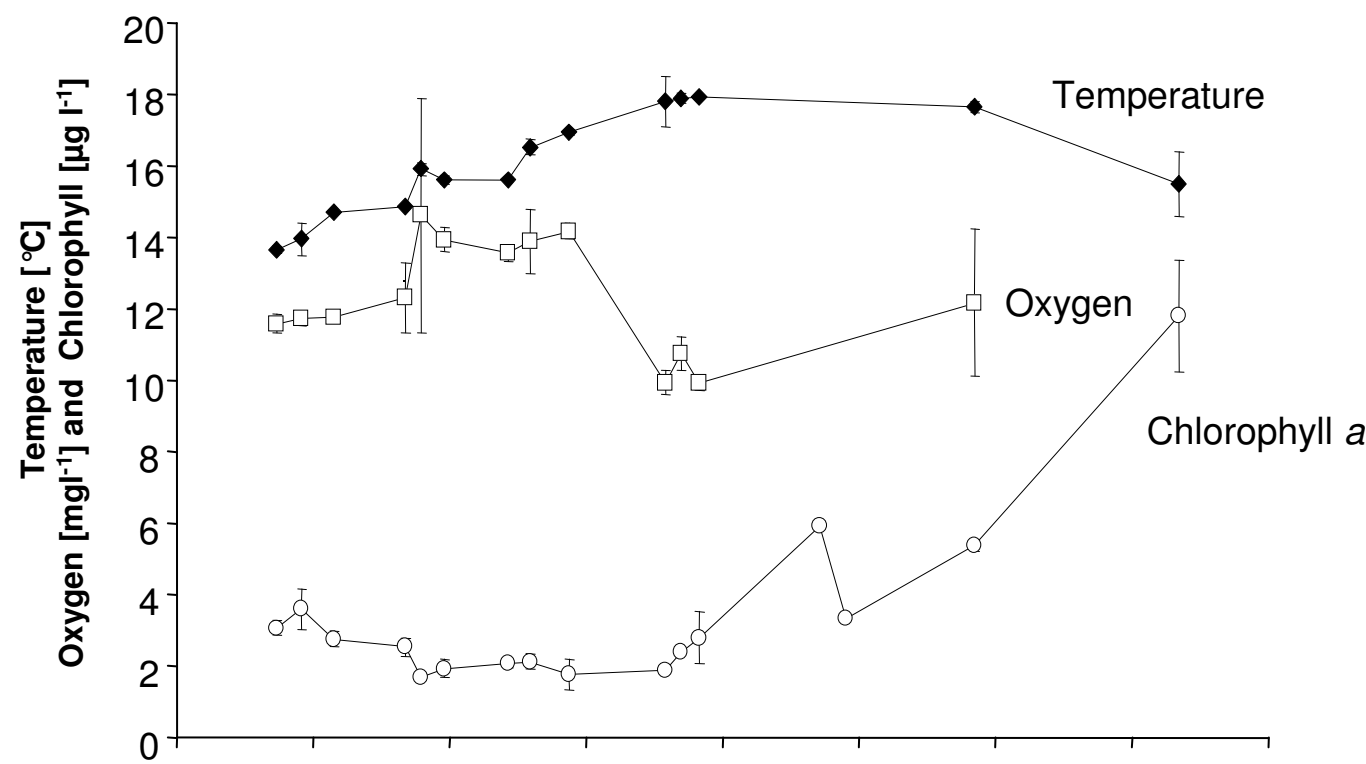
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Table II:

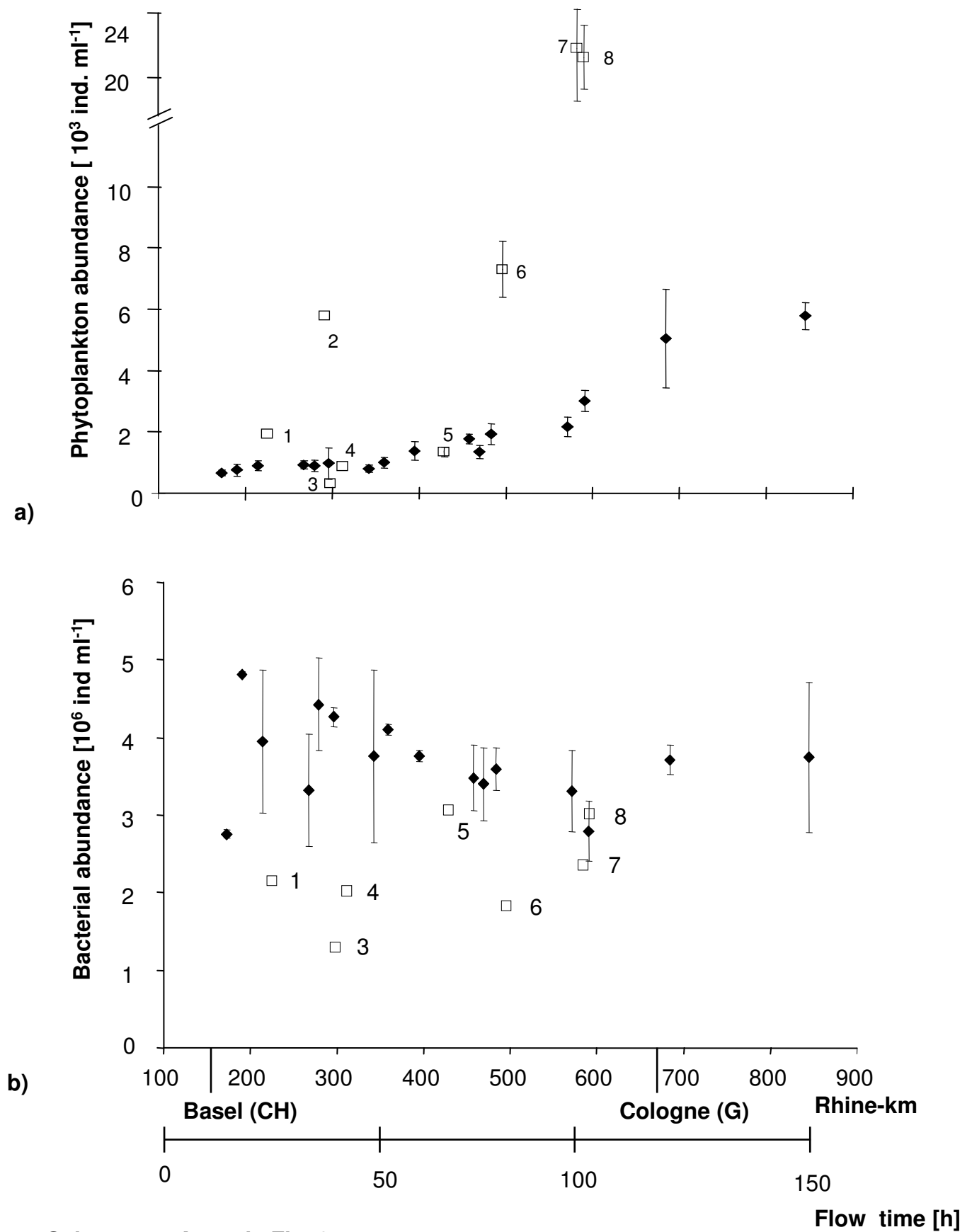
<i>Inflow of Neckar</i>	<i>load Rhine at km-395</i>	<i>load Neckar (inflow at Rhine-km- 429)</i>	<i>% load of main stream</i>
HNF [ind/sec]	8.38 x 10 ¹¹	3.11 x 10 ¹⁰	3.6
Ciliates [ind/sec]	3.64 x 10 ⁸	3.57 x 10 ⁶	1.0
Phytoplankton [ind/sec]	2.26 x 10 ¹²	2.29 x 10 ¹¹	9.2
Bacteria[ind./sec]	6.14 x 10 ¹⁵	5.19 x 10 ¹⁴	7.8
<i>Inflow of Main</i>	<i>load Rhine at km-483.2</i>	<i>load Main (inflow at Rhine-km-496)</i>	<i>% load of main stream</i>
HNF [ind/sec]	9.37 x 10 ¹¹	9.40 x 10 ¹⁰	9.1
Ciliates [ind/sec]	3.76 x 10 ⁸	2.11 x 10 ⁷	5.3
Phytoplankton [ind/sec]	3.94 x 10 ¹²	9.75 x 10 ¹¹	19.9
Bacteria [ind/sec]	6.52 x 10 ¹⁵	2.44 x 10 ¹⁴	3.6
Metazooplankton [ind/sec]	8.2 x 10 ⁷	1.1 x 10 ⁷	57
<i>Inflow of Moselle</i>	<i>load Rhine at km-590.9</i>	<i>load Moselle (inflow at Rhine-km-592)</i>	<i>% load of main stream</i>
HNF [ind/sec]	6.25 x 10 ¹¹	1.66 x 10 ¹¹	20.0
Ciliates [ind/sec]	6.9 x 10 ⁷	5.12 x 10 ⁷	42.6
Phytoplankton [ind/sec]	6.14 x 10 ¹²	4.50 x 10 ¹²	42.3
Bacteria [ind/sec]	6.17 x 10 ¹⁵	6.37 x 10 ¹⁴	10.1
Metazooplankton [ind/sec]	1.7 x 10 ⁷	9 x 10 ⁶	34.8



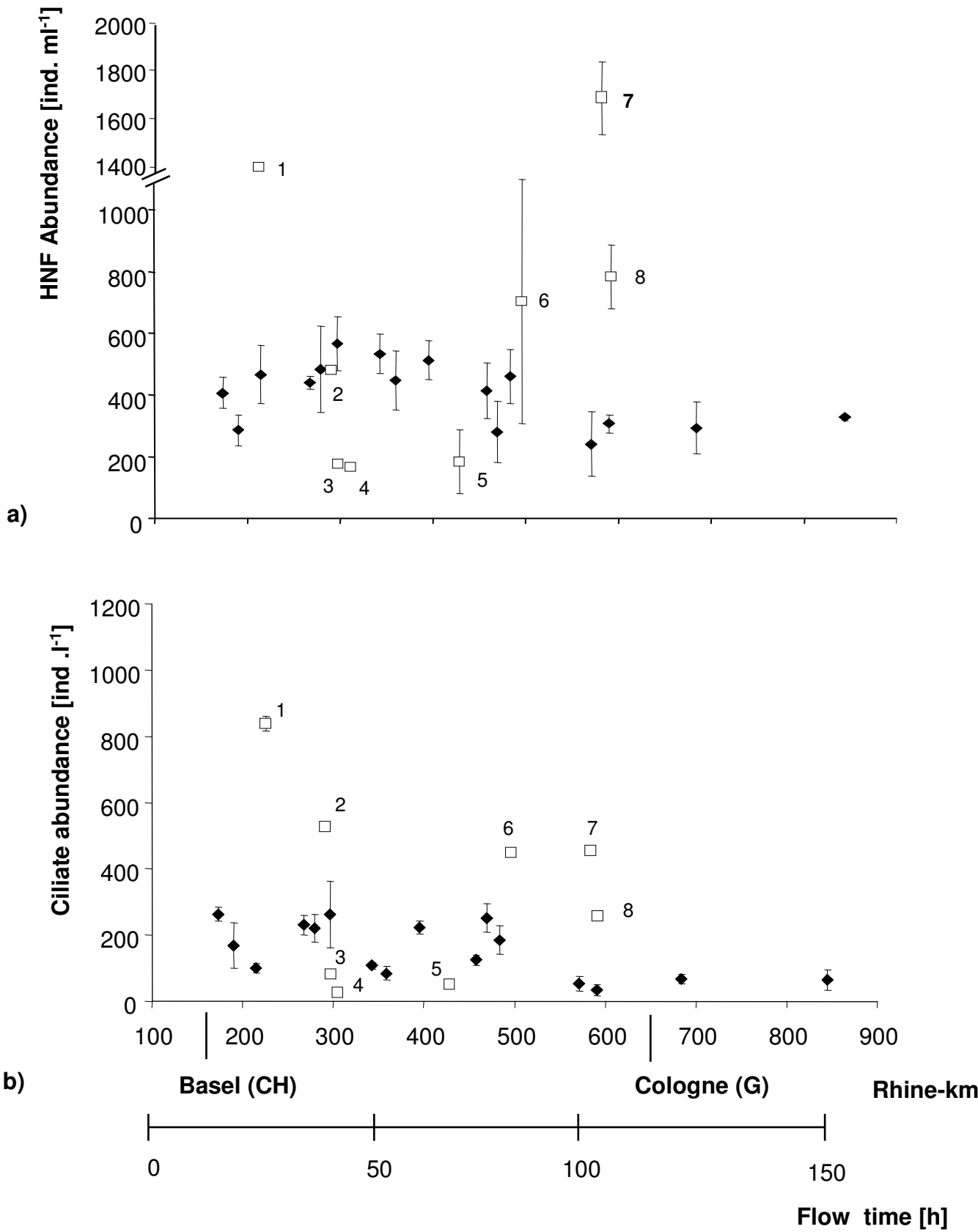
Scherwass, A. et al., Fig. 1



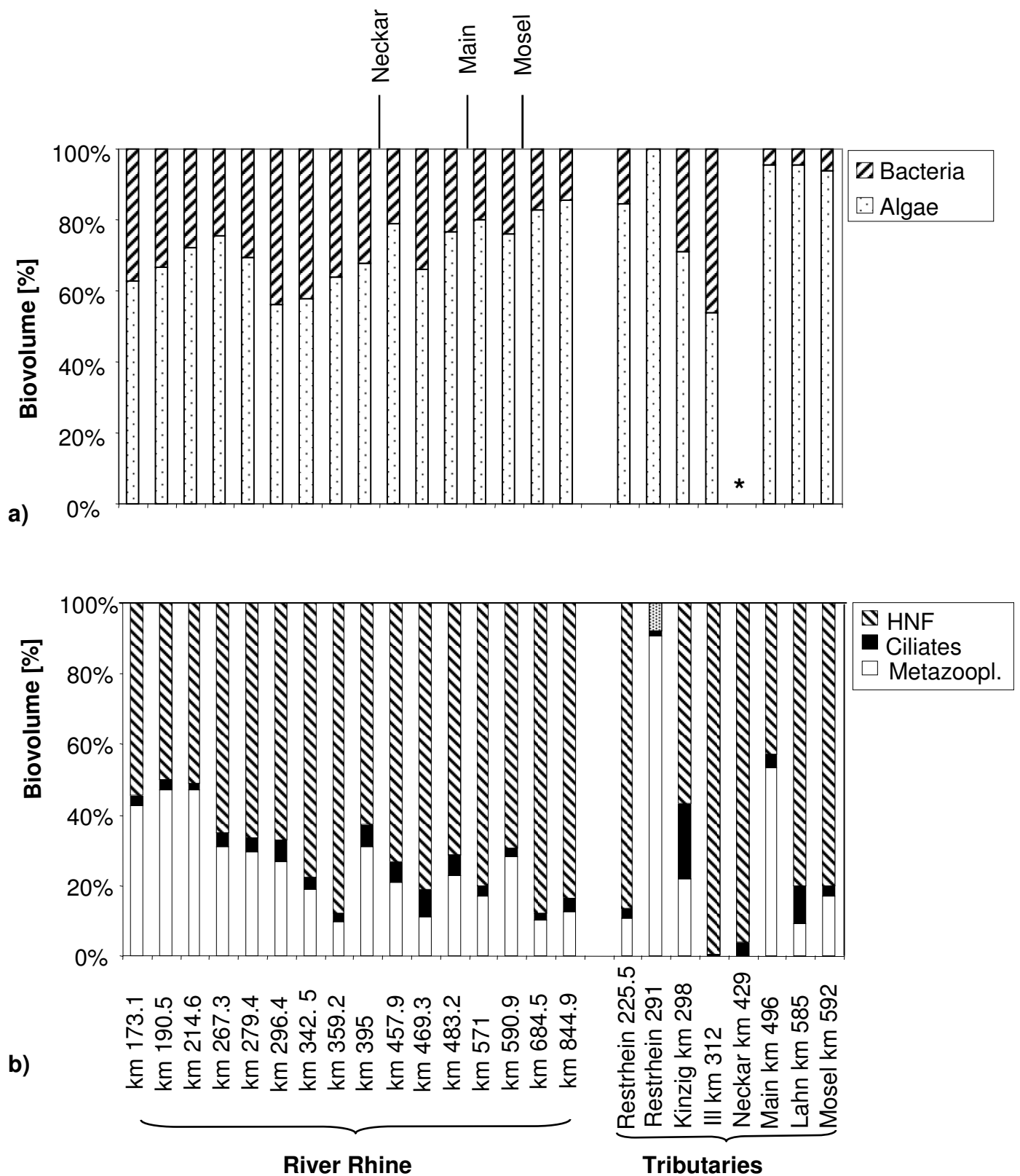
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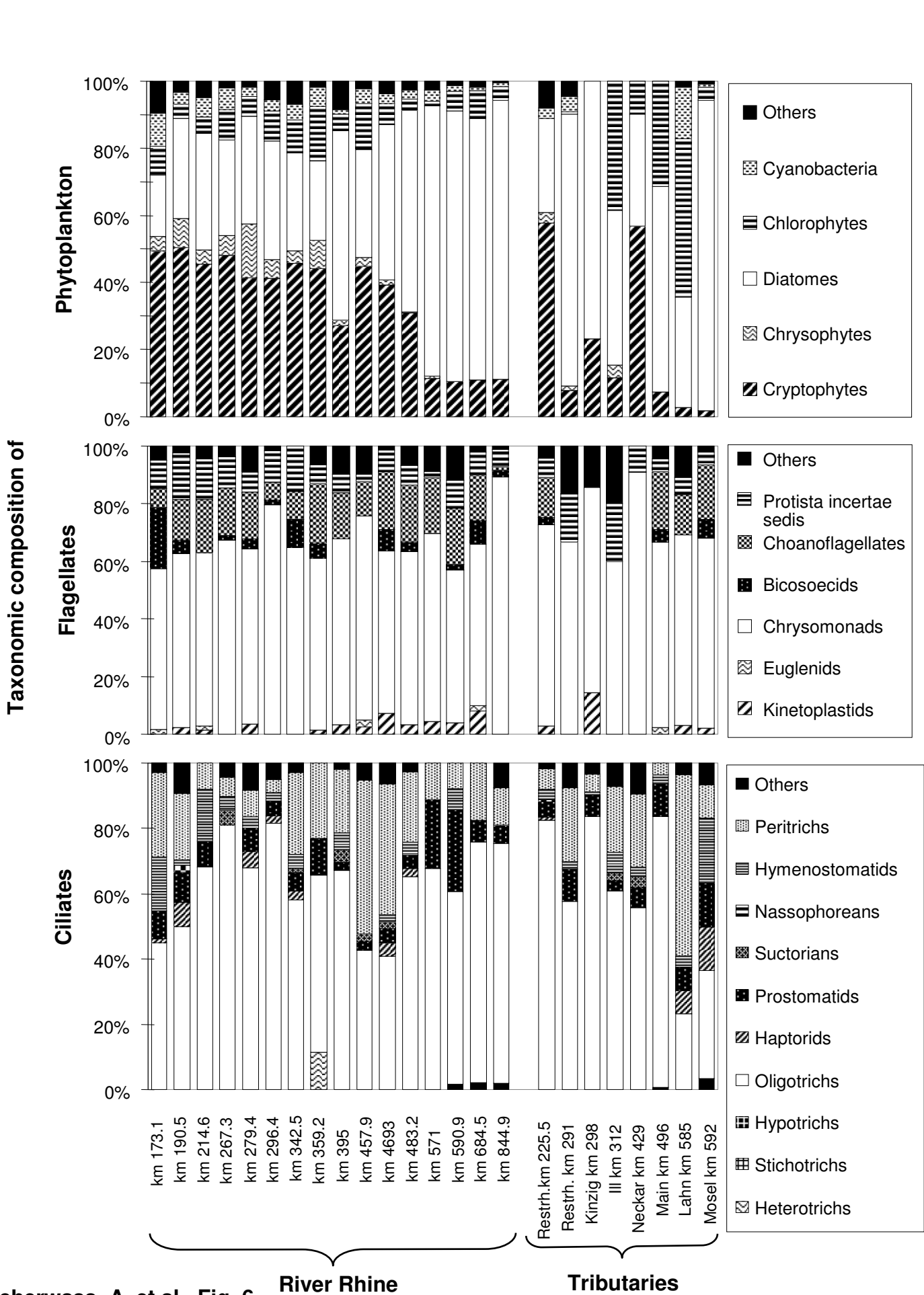
Scherwass, A. et al., Fig. 3



Scherwass, A. et al., Fig. 4



Scherwass, A. et al., Fig. 5



Scherwass, A. et al., Fig. 6