



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

Journal:	<i>Journal of Plankton Research</i>
Manuscript ID:	JPR-2009-076.R2
Manuscript Type:	Original Article
Date Submitted by the Author:	21-Dec-2009
Complete List of Authors:	Scherwass, Anja; University of Cologne, Zoological Institute General Ecology Bergfeld, Tanja; Federal Institute of Hydrology, Department of Ecological Interactions Schoel, Andreas; Federal Institute of Hydrology, Department of Ecological Interactions Weitere, Markus; University of Cologne, Zoological Institute General Ecology Arndt, Hartmut; University of Cologne, General Ecology
Keywords:	protozoa, phytoplankton, metazooplankton, bacteria, river, Lagrangian sampling



1  
2 1  
3  
4 2  
5  
6 3  
7  
8 4  
9  
10 5  
11 6  
12 6  
13 7  
14  
15 8  
16 9  
17 9  
18 10  
19 10  
20 11  
21 11  
22 12  
23  
24 13  
25  
26 14  
27  
28 15  
29  
30 16  
31 17  
32  
33 18  
34  
35 19  
36  
37 20  
38 21  
39 21  
40 22  
41 22  
42 23  
43  
44 24  
45  
46 25  
47 25  
48 26  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

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

Scherwass, A. <sup>1\*</sup>, Bergfeld, T. <sup>2</sup>, Schöl, A. <sup>2</sup>, Weitere, M. <sup>1</sup> & Arndt, H. <sup>1</sup>

<sup>1</sup> *University of Cologne, Center for Biological Sciences, Institute for Zoology, Department of General Ecology, Otto-Fischer-Str. 6, D-50674 Cologne, Germany*

<sup>2</sup> *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](mailto: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.

## 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

1  
2 1 downstream due to internal production resulting in a characteristic river  
3  
4 2 plankton community in the potamal region (as has been proposed  
5  
6 3 previously; e.g. Vannote *et al.*, 1980; Allan, 2007). Such a downstream  
7  
8 4 increase in abundance has been shown in the River Rhine on a 660 km  
9  
10 5 stretch in an earlier study of phytoplankton and rotifers (de Ruyter van  
11  
12 6 Steveninck *et al.*, 1992). However, more recent studies at different stations  
13  
14 7 along a river stretch have shown that there can be a significant reduction of  
15  
16 8 some plankton components, probably due to losses to benthic filter feeders  
17  
18 9 (Weitere and Arndt, 2002 a, b; Scherwass and Arndt, 2005).

## 22 12 **Method**

23  
24 13 The development of plankton was investigated on a stretch of the River  
25  
26 14 Rhine in Germany between km- 173.1 and km- 844.9 (Fig. 1; the Rhine km  
27  
28 15 numbers refer to the distance from the outflow at Lake Constance). The  
29  
30 16 investigation took place from May 22<sup>nd</sup> to 28<sup>th</sup> 2000 following a water  
31  
32 17 parcel moving downstream. The study was carried out towards the end of  
33  
34 18 the phytoplankton spring bloom, so that we assumed a high productivity of  
35  
36 19 all components of the microbial food web. Twenty-four sampling stations  
37  
38 20 including eight tributaries were investigated (Table I). Between km- 173.1  
39  
40 21 and km- 334, most of the river flows in an artificial river bed regulated by  
41  
42 22 ten dams; only below 10% of the total discharge (usually between 20 and  
43  
44 23 150 m<sup>3</sup> sec<sup>-1</sup>) flows in the former river bed. The part of the river which flows  
45  
46 24 in the original bed is hereafter referred to as the “Rest-Rhine”. The Rhine  
47  
48 25 flows in its natural bed with no further dams from km- 334 to the end of the  
49  
50 26 investigated area (km-844.9).

51  
52 27 The samples between km-173.1 and km-483.2 were taken at 1 m depth from  
53  
54 28 the research vessel ‘Max Honsell’ (from the ‘LUBW’ - Landesanstalt für  
55  
56 29 Umwelt, Messungen und Naturschutz Baden-Württemberg). At km-590.9, -  
57  
58 30 684.5 and -844.9, sampling was carried out from pontoons situated in the  
59  
60 31 main stream of the river. To ensure sampling of the same water parcel  
32  
33 during downstream transport, water flow time was calculated with the aid of  
34  
35 the computer simulation program ‘Alarm’ (Spreafico and Mazijk, 1993).  
36  
37 Three samples were generally taken at each sampling site: one each on the

1  
2 1 left and right side and one in the middle of the river. If this was not possible,  
3  
4 2 three consecutive samples were taken from the middle of the river within  
5  
6 3 30 minutes.

7 4 Immediately after sampling, temperature as well as chlorophyll *a* and  
8  
9 5 oxygen content were measured using a multi-probe (Yellow Spring  
10  
11 6 Instrument Inc.). In order to assess the seston content, 500 mL of river water  
12  
13 7 were filtered through preweighted GF/F glass fibre filters (Whatman). The  
14  
15 8 filters were then dried for 24 h at 100 °C and weighed. As a preparation for  
16  
17 9 determining the bacterial density, water samples were fixed with formalin  
18  
19 10 (2 % final concentration). 1 mL of sample was filtered onto 0.2 µm black  
20  
21 11 polycarbonate filters within 24 hours after sampling, stained with 0.2 mL of  
22  
23 12 DAPI (working solution 0.01 mg mL<sup>-1</sup>) and then stored at -20 °C until  
24  
25 13 further processing. Bacteria were counted under an epifluorescence  
26  
27 14 microscope (Zeiss Axioskop) under UV-excitation (365 nm; Filter: BP 395-  
28  
29 15 440 BP, beam splitter 460, LP 470). At least 400 bacteria were counted per  
30  
31 16 filter, grouped into size classes according to measurements with an eye-  
32  
33 17 piece micrometer. Because the delicate heterotrophic and autotrophic  
34  
35 18 nanoplankton are often destroyed during fixation, they were live-counted on  
36  
37 19 board. The live-count was conducted directly after sampling under a phase  
38  
39 20 contrast microscope (Zeiss Axiostar) with magnifications of 100 – 400x to  
40  
41 21 determine their abundance and taxonomic composition. At least five  
42  
43 22 subsamples of 5 – 10 µL each were counted until sufficient numbers of  
44  
45 23 protists for statistical analysis were obtained. The lengths and widths of  
46  
47 24 individual nanoplanktonic organisms were measured using video  
48  
49 25 microscopy to calculate biovolumes (based on simple geometrical forms).  
50  
51 26 Unfiltered samples of microplankton (ciliates and larger algae) were fixed  
52  
53 27 with Bouin's fluid (5% final concentration), concentrated in the laboratory  
54  
55 28 and processed as described in Scherwass *et al.* (2002) using a method  
56  
57 29 combining density gradient centrifugation (to exclude inorganic seston  
58  
59 30 particles) and quantitative protargol staining (Skibbe, 1994). The resulting  
60  
31 permanent slides were examined under a microscope (Axiophot 2, Zeiss)  
32  
33 with a magnification of up to 1000x. Biovolumes were estimated based on  
34  
simple geometric forms assuming a shrinkage factor of 30%. This shrinkage  
factor refers to observations for several ciliate groups (Pfister *et al.*, 1999).

1  
2 1 In addition to the analysis of protozooplankton, 2 or 4 L of water were  
3  
4 2 sieved through a plankton net (10  $\mu\text{m}$ -mesh size) and the metazooplankton  
5  
6 3 was counted at 200x magnification. Metazooplankton lengths, abundance  
7  
8 4 and composition were determined, and published length-weight ratios were  
9  
10 5 used to calculate the biovolume (e.g. Bottrell *et al.*, 1976). These data were  
11  
12 6 collected to estimate the abundance and biomass of metazooplankton  
13  
14 7 organisms for the present study; a more detailed investigation of  
15  
16 8 metazooplankton was conducted at one station (Cologne Rhine-km 684.5) in  
17  
18 9 a parallel study (Weitere *et al.*, 2005).

19 10 Statistical analyses were conducted using SPSS for Windows (version 15.0).  
20  
21 11 Spearman rank coefficients were used to analyse correlations between  
22  
23 12 plankton abundances and flow time.

## 24 13

### 25 14 **Results**

#### 26 14 *Abiotic parameters and abundances of plankton organisms*

27 15  
28 16 Water temperature and oxygen concentration varied only slightly along the  
29  
30 16 length of the river stretch, whereas the chlorophyll *a* concentration increased  
31  
32 17 significantly during downstream transport, resulting in a maximum of  
33  
34 18 11.8 ( $\pm$  1.6)  $\mu\text{g L}^{-1}$  measured at Rhine-km-844.9 (Fig. 2a). Seston content  
35  
36 19 and turbidity increased markedly during downstream transport as well (Fig.  
37  
38 20 2b).

39 21  
40 22 Phytoplankton abundance showed an increase (up to eightfold, Fig. 3a) from  
41  
42 23 the Upper to the Lower Rhine (positively correlated with the increase of the  
43  
44 24 chlorophyll *a*). Most tributaries and the “Rest-Rhine” showed higher  
45  
46 25 abundances of phytoplankton than the Rhine itself. The largest difference  
47  
48 26 between the main stream and the tributaries was found in the middle stretch  
49  
50 27 of the Rhine: in the rivers Moselle and Lahn, phytoplankton abundances  
51  
52 28 were about nine times higher than in the Rhine at this location (Fig. 3a).  
53  
54 29 Particularly the Moselle contributed a significant plankton load to the Rhine  
55  
56 30 (Tab. II).

57 31 Bacterial abundances remained constant over the stretch of the Rhine  
58  
59 32 averaging  $3.7 \times 10^6$  ( $\pm$   $5.5 \times 10^5$ ) bacteria  $\text{mL}^{-1}$  (Fig. 3 b) with a slight  
60  
33 tendency towards higher values in the upper part of the river. Generally,  
34  
34 bacterial abundances were lower in the tributaries and the ‘Rest-Rhine’ than

1  
2 1 in the River Rhine (where they averaged  $2.2 \times 10^6 (\pm 6.9 \times 10^5)$  bacteria  
3  
4 2  $\text{mL}^{-1}$ ).

5 3 The abundances of both heterotrophic nanoflagellates and ciliates declined  
6 4 during downstream transport (Fig. 4 a, b). Moreover, abundances of both  
7 5 protozoan groups were significantly negatively correlated with the flow time  
8 6 ( $b = -0.385$ ,  $p < 0.01$  for HNF;  $b = -0.424$ ,  $p < 0.01$  for ciliates). The  
9 7 average HNF abundance dropped from  $407 (\pm 50) \text{ ind. mL}^{-1}$  at km-173.1 to  
10 8  $328 \text{ ind. mL}^{-1} (\pm 10)$  at km-844.9, and did not exceed a value of  $400 \text{ ind.}$   
11 9  $\text{mL}^{-1}$  in the Middle and Lower Rhine. Tributaries of the middle and lower  
12 10 reaches of the Rhine showed abundances which were significantly higher  
13 11 than in the main stream reaching mean values between 703 and 1,683 ind.  
14 12  $\text{mL}^{-1}$  in the Main, Lahn and Moselle.

15 13 The pattern of downstream development of ciliate abundance was partly  
16 14 similar to that of the HNF (Fig. 4 b). A significant reduction from a mean of  
17 15  $263 \text{ ciliates L}^{-1} (\pm 21)$  at Rhine-km-173.1 to  $64 \text{ ind. L}^{-1} (\pm 32)$  at Rhine-km-  
18 16 844.9 was observed. Ciliates showed high numbers in the Lahn, Moselle and  
19 17 “Rest-Rhine” (up to a mean of  $838 \text{ ind. L}^{-1}$  in the latter), whereas low  
20 18 abundances were recorded for the small tributaries.

21 19 Though only roughly estimated in the present study, the metazooplankton  
22 20 abundance (mainly rotifers) seem to show the same trend as HNF and  
23 21 ciliates along the river stretch with decreasing abundances during  
24 22 downstream transport from about 70 to about  $20 \text{ ind. L}^{-1}$ .

25 23 The plankton load contributed by the largest tributaries in the reach of the  
26 24 Rhine investigated was calculated based on the abundances of organisms  
27 25 (Tab. II). The Moselle contributed a large part to the total plankton  
28 26 community in the Rhine: up to 42% of phytoplankton, 10.1% of bacteria,  
29 27 20% of HNF, and 43.0 % of ciliates. The largest metazooplankton load was  
30 28 contributed by the River Main (57 %).

#### 31 29 *Share of different planktonic components in terms of biovolume*

32 30 Phytoplankton made up the largest proportion of the total plankton  
33 31 biovolume in spring 2000. Its biovolume ranged from  $0.36 \text{ mm}^3 \text{ L}^{-1}$  (Rhine-  
34 32 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  
35 33 Moselle) were observed in the tributaries. The bacterial biovolume ranged



1  
2 1 from 0.21 to 0.34 mm<sup>3</sup> L<sup>-1</sup>. Phytoplankton exceeded bacterial biovolume at  
3  
4 2 all stations (Fig. 5 a). Bacteria contributed the most to the total heterotrophic  
5  
6 3 biovolume (comprising bacterial and total zooplankton biovolume, data not  
7  
8 4 shown).

9  
10 5 The biovolume of total zooplankton was about one order of magnitude  
11 6 lower than that of phytoplankton (ranging between 0.03 mm<sup>3</sup> L<sup>-1</sup> and  
12 7 0.16 mm<sup>3</sup> L<sup>-1</sup> in the Rhine), being dominated by heterotrophic  
13 8 nanoflagellates (Fig. 5 b), which contributed between 50 and 88% to the  
14 9 total zooplankton biovolume. The absolute biovolume of HNF (between  
15 10 0.02 and 0.09 mm<sup>3</sup> L<sup>-1</sup>) was much higher than that of metazooplankton. In  
16 11 the tributaries, HNF accounted for up to 86 % (“Rest-Rhine” km-225.5) of  
17 12 total zooplankton biovolume. Ciliates contributed the least to the total  
18 13 zooplankton in the River Rhine as well as in all tributaries; their biovolume  
19 14 reached a maximum of 8 % (km-469.3) in the Rhine and 21 % (River  
20 15 Kinzig) in the tributaries (Fig. 5 b, 0.1 and 4 x 10<sup>3</sup> mm<sup>3</sup> L<sup>-1</sup>, respectively).  
21 16 The share of metazooplankton decreased from 43 % at km-173.1 to 13 % at  
22 17 km-844.9 (0.002 – 0.03 mm<sup>3</sup> L<sup>-1</sup>). In the tributaries metazooplankton  
23 18 reached between 9 and 91 % (“Rest-Rhine” at km-291).  
24 19  
25 20  
26 21  
27 22  
28 23  
29 24  
30 25  
31 26  
32 27  
33 28  
34 29  
35 30  
36 31  
37 32  
38 33  
39 34  
40 35  
41 36  
42 37  
43 38  
44 39  
45 40  
46 41  
47 42  
48 43  
49 44  
50 45  
51 46  
52 47  
53 48  
54 49  
55 50  
56 51  
57 52  
58 53  
59 54  
60 55

#### Changes in taxonomic composition

38 20 The taxonomic composition of phytoplankton on the basis of biovolume  
39 21 (Fig. 6) showed a distinct change during downstream transport.  
40 22 Cryptophytes dominated the plankton community in the Upper Rhine and  
41 23 diminished in importance during downstream transport. The proportion of  
42 24 diatoms increased significantly in parallel to the reduction of the  
43 25 cryptophytes in the River Rhine, whereas the tributaries showed a  
44 26 considerable number of chlorophytes.  
45 27

51 28 In contrast to phytoplankton, protozooplankton did not show a clear change  
52 29 in taxonomic composition during downstream transport (Fig. 6). Among  
53 30 HNF, chryomonads were the dominant group during the investigation. This  
54 31 was true for the River Rhine itself as well as for all tributaries. Their relative  
55 32 contribution remained comparatively constant throughout downstream  
56 33 transport. For ciliates, oligotrichs (typical planktonic forms) formed the  
57 34 largest component of the biomass, followed by peritrichs (mainly benthic

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).

1  
2 1 Lagrangian sampling allowed further insights into changes of the plankton  
3  
4 2 community during downstream transport within the River Rhine in spring.  
5  
6 3 The development of the abundance of the microbial plankton differed  
7  
8 4 between the groups of organisms. Bacterioplankton remained at a nearly  
9  
10 5 constant low level during downstream transport despite their high potential  
11  
12 6 growth rates. This is in contrast to the results of earlier studies in the River  
13  
14 7 Rhine, where an increase of bacterioplankton over the course of the Rhine  
15  
16 8 was observed during the same season (April and May; de Ruyter van  
17  
18 9 Steveninck *et al.*, 1992; Ietswaart *et al.*, 1999). Also the increase of  
19  
20 10 phytoplankton along the river stretch was much lower during the present  
21  
22 11 study than during earlier studies (de Ruyter van Steveninck *et al.*, 1992;  
23  
24 12 Ietswaart *et al.*, 1999; Friedrich and Pohlmann, 2009). One possible  
25  
26 13 explanation for these changes in plankton dynamics might be the drastic  
27  
28 14 changes of the community structure of invertebrates due to massive growth  
29  
30 15 of invasive species immigrated into the River Rhine within the last two  
31  
32 16 decades (ICPR 1996, 2002, see below).

33 17  
34 18 *Potential factors causing losses of plankton during downstream transport in*  
35 19 *spring*

36 20 Sedimentation of plankton due to decreasing flow velocities in lower river  
37 21 reaches may be one reason for their decline during downstream transport, as  
38 22 has been shown e.g. in the lowland River Spree (Koehler *et al.*, 2002) and  
39 23 the River Meuse (Marneffe *et al.*, 1996). However, due to the strong  
40 24 canalisation of the River Rhine combined with a high discharge, flow  
41 25 velocity remained high up to the end of the investigated reach (km-844.9)  
42 26 and sedimentation was assumed to play a significant role only in the very  
43 27 low Dutch reaches of the Rhine (de Ruyter van Steveninck *et al.*, 1990).  
44 28 Additionally, turbidity increases with increasing river length and may affect  
45 29 autotrophic as well as heterotrophic plankton (Reynolds and Descy, 1996;  
46 30 Pourriot *et al.*, 1997). However, the light-dependent phytoplankton seems  
47 31 not to be affected by increased turbidity in spring, as its abundance increased  
48 32 along the river stretch. For metazooplankton, a disturbance of feeding due to  
49 33 high concentrations of inorganic particles in combination with high  
50 34 turbulence might negatively affect metazooplankton (Miquelis *et al.*, 1998).

1  
2 1 This could be the reason for the reduced metazooplankton abundance in the  
3  
4 2 lower reaches of the River Rhine. The abundance of heterotrophic protists  
5  
6 3 also decreased along the river stretch, but protists can be positively affected  
7  
8 4 by inorganic sediment particles as they offer a habitat for colonization  
9  
10 5 (Wörner *et al.*, 2002). This indicates that the dynamics of the different  
11  
12 6 plankton groups cannot be explained by turbidity alone. Regarding  
13  
14 7 mechanical forces potentially affecting plankton organisms it has to be  
15  
16 8 considered that protists and bacteria have much lower Reynolds numbers  
17  
18 9 than metazoans and are unlikely to be physically damaged in their relatively  
19  
20 10 laminar surroundings (cf. Vogel, 1993). Thus turbulence does not seem to  
21  
22 11 directly influence the unicellular organisms, whereas a negative influence on  
23  
24 12 metazoans is possible (Picard and Lair, 2003; Sluss *et al.*, 2008).

25  
26 13 Another reason for decreasing plankton numbers in the course of the river  
27  
28 14 stretch may be dilution by the tributaries. However, during our  
29  
30 15 investigations tributaries generally had higher abundances of plankton than  
31  
32 16 the River Rhine (see Tab. II). By taking these high plankton loads of the  
33  
34 17 tributaries into account, our present data show that within-stream processes  
35  
36 18 rather than effects of the tributaries might be the reason for the plankton  
37  
38 19 dynamics observed in the Rhine.

39  
40 20 In an earlier study, we demonstrated with a combination of size fractionation  
41  
42 21 experiments and Lagrangian sampling, that planktonic heterotrophic  
43  
44 22 flagellates showed high losses during the downriver passage in the Lower  
45  
46 23 Rhine (km 685 to 845, Weitere *et al.*, 2002a). The losses strongly depended  
47  
48 24 on temperature (high losses in summer, low losses in winter), indicating  
49  
50 25 biotic interactions. Furthermore, the losses could not be explained by  
51  
52 26 planktonic grazers as derived from size-fractionation experiments. This gave  
53  
54 27 rise to the conclusion that benthic grazers contribute significantly to losses  
55  
56 28 of plankton in the Rhine. This conclusion is in accordance with the  
57  
58 29 application of a water quality model in the Rhine for the year 1990 which  
59  
60 30 revealed that metazooplankton grazing on the algal production was  
31  
32 31 negligible, but that algae were partly reduced by grazing of the benthic  
33  
34 32 mussel *Dreissena polymorpha* (Schöl *et al.*, 2002). Studies from other rivers  
35  
36 33 pointed to the importance of benthic predation on the components of the  
37  
38 34 planktonic microbial food web of rivers (e.g. Basu and Pick, 1997; Welker

1  
2 1 and Walz 1998; Descy *et al.*, 2003). Some efficient benthic filter-feeding  
3  
4 2 macroinvertebrates like *Corbicula* spp., *Dreissena polymorpha* and  
5  
6 3 *Corophium curvispinum* are abundant in the Lower Rhine (e.g. Rajagopal *et*  
7  
8 4 *al.*, 1995, 1998) and have been shown to capture particles of a wide size  
9  
10 5 range (see e.g. Sprung and Rose, 1988; Scherwass *et al.*, 2001; Viergutz *et*  
11  
12 6 *al.*, 2007; Weitere *et al.*, 2008). In their study in the River Rhine, Ietswaart  
13  
14 7 *et al.* (1999) calculated a significant loss rate of algae due to predation by  
15  
16 8 the benthic macrofauna community of  $0.38 \text{ d}^{-1}$  for the warm season for the  
17  
18 9 year 1995. Losses to the benthic grazers may probably be even larger as only  
19  
20 10 a few 'focus' grazers were considered in these estimations. The role of other  
21  
22 11 potentially important benthic filter feeders including sponges, bryozoans and  
23  
24 12 ciliates is as yet unknown (Weitere *et al.*, 2003; Kathol *et al.*, 2009;  
25  
26 13 Vohmann *et al.*, 2009).

26 14 A possible control of the plankton by benthic filter feeders could explain  
27  
28 15 group-specific patterns observed in the present study. The slow growing  
29  
30 16 groups (metazoans, ciliates) decrease much more than fast growing groups  
31  
32 17 such as heterotrophic flagellates, possibly due to different abilities to  
33  
34 18 compensate for grazing losses (Weitere and Arndt, 2002a; Scherwass and  
35  
36 19 Arndt, 2005). Bacteria probably experience a low grazing pressure by  
37  
38 20 benthic filter feeders due to their small size (Sprung and Rose, 1988), but a  
39  
40 21 strong grazing pressure may affect heterotrophic flagellates within the water  
41  
42 22 column (Weitere *et al.*, 2002b). The loss rates of phytoplankton seem to be  
43  
44 23 governed by factors different to those of protozooplankton. Further detailed  
45  
46 24 longitudinal studies are required to explain these discrepancies in future.

47 25  
48 26 The present case study for a spring scenario is the first that considered the  
49  
50 27 longitudinal dynamics not only of classical components but also of  
51  
52 28 organisms of the microbial food web in a large river. Additional studies at  
53  
54 29 particular locations along the river stretch of the Rhine showed that general  
55  
56 30 patterns such as stable or even decreasing plankton abundance occurs  
57  
58 31 throughout the year despite high potential productivity (Weitere and Arndt,  
59  
60 32 2002a,b; Weitere *et al.*, 2005; Bergfeld *et al.*, 2009). Despite clear  
33  
34 33 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

1  
2 1 the different factors in controlling plankton in the Rhine (e.g. grazing,  
3 residence time, turbidity, turbulence, sediment infiltration) is as yet poorly  
4 2 understood. The importance of biotic versus non-biotic factors varies with  
5 3 the river stretch and each plankton group (Strayer *et al.*, 2008). Future  
6 4 empirical studies as well as model approaches need to focus on the interplay  
7 5 of the multiple factors in controlling plankton in rivers. In this context, it has  
8 6 to be pointed out that dynamics of plankton in the River Rhine shown here  
9 7 were observed only for the last ten years. There was still a considerable  
10 8 downstream increase of all plankton components until 1995 (de Ruyter van  
11 9 Steveninck *et al.*, 1992; ICPR, 1996; Friedrich and Pohlmann, 2009).  
12 10 Efforts to reduce the nutrient load (ICPR, 2002) and the massive increase of  
13 11 populations of invasive species (especially the effective plankton filterers  
14 12 such as *Corbicula spp.*, ICPR, 2002) are probably important reasons for the  
15 13 recent shift. Understanding the regulation of the plankton dynamics in  
16 14 changing riverine environments is a major challenge for future studies.  
17 15  
18 16  
19 17  
20 18  
21 19  
22 20  
23 21  
24 22  
25 23  
26 24  
27 25  
28 26  
29 27  
30 28  
31 29  
32 30

### 31 17 **Acknowledgements:**

32 18 The study was supported by scholarships from the  
33 19 Landesgraduiertenförderung NRW to A. Scherwass and from the Deutsche  
34 20 Bundesstiftung Umwelt to M. Weitere. We thank Mr. Vobis and his  
35 21 colleagues from the Landesanstalt für Umweltschutz Baden-Württemberg  
36 22 (LUBW) as well as the crew of the R/V 'Max Honsell' for the support  
37 23 during sampling. We are indebted to the scientific and technical assistance  
38 24 by Annick Eimer, Claudia Günster and Walter Krings. We would also like  
39 25 to thank Frederic Bartlett for linguistic comments.  
40 26  
41 27  
42 28  
43 29  
44 30  
45 31  
46 32  
47 33  
48 34  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

### 51 28 **References**

52 29 Allan, J. D. (2007) *Stream Ecology*. Springer: London/New York

53 30  
54 31  
55 32  
56 33  
57 34  
58  
59  
60  
34

57 31 Arndt, H. and Mathes, J. (1991) Large heterotrophic flagellates form a  
58 32 significant part of protozooplankton biomass in lakes and rivers. *Ophelia*,  
59 33 **33**, 225--234.  
60 34

- 1  
2 1 Basu, B. K. and Pick, F. R. (1997) Phytoplankton and zooplankton  
3  
4 2 development in a lowland, temperate river. *J. Plankt. Res.*, **19**, 237—253.  
5  
6 3
- 7 4 Bergfeld, T., Scherwass, A., Ackermann, B., Arndt, H. and Schöl, A. (2009)  
8  
9 5 Comparison of the components of the planktonic food web in three large  
10  
11 6 rivers (Rhine, Moselle and Saar) *Riv. Res Appl.*, **25**, 1232—1250.  
12  
13 7
- 14 8 Bottrell, H. H., Duncan, A., Gliwicz, Z. M., Grygierek, E., Herzig, A.,  
15  
16 9 Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P. and Weglenska, T. A.  
17  
18 10 (1976) A review of some problems in zooplankton production studies.  
19  
20 11 *Norweg. J. Zool.*, **24**, 419--456.  
21  
22 12
- 23 13 Carlough, L. A. and Meyer, J. L. (1989) Protozoans in two southeastern  
24  
25 14 blackwater rivers and their importance to trophic transfer. *Limnol*  
26  
27 15 *Oceanogr.*, **34**, 163--177.  
28  
29 16
- 30 17 De Ruyter van Steveninck, E. D., Admiraal, W., Breebaart, L., Tubbing,  
31  
32 18 G.M.J. and van Zanten, B. (1992) Plankton in the River Rhine: structural  
33  
34 19 and functional changes observed during downstream transport. *J. Plankt.*  
35  
36 20 *Res.*, **14**, 1351--1368.  
37  
38 21
- 39 22 De Ruyter van Steveninck, E. D. de, Admiraal, W. and Zanten, B. van  
40  
41 23 (1990) Changes in plankton communities in regulated reaches of the lower  
42  
43 24 river Rhine. *Regul. Rivers*, **5**, 67—75.  
44  
45 25
- 46 26 Descy, J. P., Everbecq, E., Gosselain, V., Viroux, L. and Smits, J. S. (2003)  
47  
48 27 Modelling the impact of benthic filter-feeders on the composition and  
49  
50 28 biomass of river plankton. *Freshw. Biol.*, **48**, 404--417.  
51  
52 29
- 53 30 Friedrich, G. and Pohlmann, M. (2009) Long-term plankton studies at the  
54  
55 31 Lower Rhine/Germany. *Limnologica*, **39**, 14—39.  
56  
57 32  
58  
59  
60

1  
2 1 Gilbert, D., Amblard, C., Bourdier, G. and Francez, A. J. (1998) The  
3  
4 2 microbial loop at the surface of a peatland: structure, function and impact of  
5  
6 3 nutrient input. *Microb. Ecol.* **35**, 83--93.  
7  
8 4

9  
10 5 ICPR (1996) *Das Makrozoobenthos des Rheins 1990 - 1995*. International  
11 6 Commission for the protection of the Rhine, Koblenz.  
12  
13 7

14  
15 8 ICPR (2002) *Das Makrozoobenthos des Rheins 2000*. International  
16 9 Commission for the protection of the Rhine, Koblenz.  
17  
18 10

19  
20 11 Ietswaart, T., Breebaart, L., van Zanten, B. and Bijkerk, R. (1999) Plankton  
21 12 dynamics in the river Rhine during downstream transport as influenced by  
22 13 biotic interactions and hydrological conditions. *Hydrobiologia*, **410**, 1—20.  
23  
24 14

25  
26 15 Joaquim-Justo, C., Pirlot, S., Viroux, L., Servais, P., Thomé, J. P. and  
27 16 Descy, J. P. (2006) Trophic links in the lowland River Meuse (Belgium):  
28 17 assessing the role of bacteria and protozoans in planktonic food webs. *J.*  
29 18 *Plankt. Res.*, **9**, 857 -- 870.  
30  
31 19

32  
33 20 Kathol, M., Norf, H., Arndt, H. and Weitere, M. (2009) Effects of  
34 21 temperature increase on the grazing of planktonic bacteria by biofilm-  
35 22 associated consumers. *Aquat. Microb. Ecol.*, **55**, 65--79.  
36  
37 23

38  
39 24 Kiss, A. K., Acs, E., Kiss, K. T. and Torok, J. K. (2009) Structure and  
40 25 seasonal dynamics of the protozoan community (heterotrophic flagellates,  
41 26 ciliates, amoeboid protozoa) in the plankton of a large river (River Danube,  
42 27 Hungary). *Europ. J. Protist.*, **45**, 121--138.  
43  
44 28

45  
46 29 Koehler, J., Bahnwart, M. and Ockenfeld, K. (2000) Growth and loss  
47 30 processes of riverine phytoplankton in relation to water depth. *Int. Rev.*  
48 31 *Hydrobiol.*, **87**, 241—254.  
49  
50 32

51  
52 33 Lair, N., Jacquet, V. and Reyes-Marchant, P. (1999) Factors related to  
53 34 autotrophic potamoplankton, heterotrophic protists and micrometazoan



- 1  
2 1 abundance, at two sites in a lowland temperate river. *Hydrobiologia*, **394**,  
3 13--28.  
4 2  
5 3  
6 4  
7 5  
8 6 Marneffe, Y., Descy, J. P. and Thomé, J. P. (1996) The zooplankton of the  
9 7 lower river Meuse, Belgium: seasonal changes and impact of industrial and  
10 8 municipal discharges. *Hydrobiologia*, **319**, 1—13.  
11 9  
12 10  
13 11  
14 12 Miquelis, A., Rougier, C. and Pourriot, R. (1998) Impact of turbulence and  
15 13 turbidity on the grazing rate of the rotifer *Brachionus calyciflorus* (Pallas).  
16 14 *Hydrobiologia*, **386**, 203-211.  
17 15  
18 16  
19 17  
20 18  
21 19 Pfister, G., Sonntag, B. and Posch, T. (1999) Comparison of a direct live  
22 20 count and an improved quantitative protargol stain (QPS) in determining  
23 21 abundance and cell volumes of pelagic freshwater protozoa. *Aquat. Microb.*  
24 22 *Ecol.*, **18**, 95--103.  
25 23  
26 24  
27 25  
28 26  
29 27  
30 28  
31 29  
32 30 Picard, V. and Lair, N. (2003) Laboratory approach of the growth of rotifers  
33 31 sampled in the Middle Loire (France) under turbulence. *Journal de*  
34 32 *Recherche Océanographique*, **28**, 196 – 199.  
35 33  
36 34  
37 35  
38 36  
39 37  
40 38  
41 39  
42 40  
43 41  
44 42  
45 43  
46 44  
47 45  
48 46  
49 47  
50 48  
51 49  
52 50  
53 51  
54 52  
55 53  
56 54  
57 55  
58 56  
59 57  
60 58  
34 59  
34 60

- 1  
2 1 Reynolds, C. S. and Descy, J.-P. (1996) The production, biomass and  
3 structure of phytoplankton in large rivers. *Arch. Hydrobiol. Suppl.*, **113**,  
4 2 'Large Rivers', 61--187.  
5 3  
6 4  
7 5  
8 6  
9 7  
10 8  
11 9  
12 10  
13 11  
14 12  
15 13  
16 14  
17 15  
18 16  
19 17  
20 18  
21 19  
22 20  
23 21  
24 22  
25 23  
26 24  
27 25  
28 26  
29 27  
30 28  
31 29  
32 30  
33 31  
34 32  
35 33  
36 34  
37 35  
38 36  
39 37  
40 38  
41 39  
42 40  
43 41  
44 42  
45 43  
46 44  
47 45  
48 46  
49 47  
50 48  
51 49  
52 50  
53 51  
54 52  
55 53  
56 54  
57 55  
58 56  
59 57  
60 58  
34 59
- Reynolds, C. S. and Glaister, M. S. (1993) Spatial and temporal changes in  
phytoplankton abundance in the upper and middle reaches of the River  
Servan. *Arch. Hydrobiol. Suppl.*, **101**, 1--22.
- Sanders, R. W., Caron, D. A. and Berninger, U. G. (1992) Relationships  
between bacteria and heterotrophic nanoplankton in marine and fresh waters  
– an inter-ecosystem comparison. *Mar. Ecol. Progr. Ser.*, **86**, 1—14.
- Scherwass, A. and Arndt, H. (2005) Structure, dynamics and control of the  
ciliate fauna in the potamoplankton of the river Rhine in Cologne. *Arch.  
Hydrobiol.*, **164**, 287--307.
- Scherwass, A., Wickham, S. A. and Arndt, H. (2002) Determination of the  
abundance of ciliates in highly turbid waters - an improved method tested  
for the River Rhine. *Arch. Hydrobiol.*, **156**, 135--143.
- Scherwass, A., Eimer, A. and Arndt, H. (2001) Selective influence of filter-  
feeding benthic bivalves (*Corbicula spec.*, *Mytilus spec.*) on planktonic  
ciliates. *Verh. Int. Verein. Limnol.*, **17**, 3315 -- 3318.
- Schöl, A. , Kirchesch, V., Bergfeld, T., Schöll, F., Borcharding, J. and  
Müller, D. (2002) Modelling the chlorophyll *a* content of the River Rhine-  
interrelation between riverine algal production and population biomass of  
grazers, rotifers and the zebra mussel *Dreissena polymorpha*. *Internat. Rev.  
Ges. Hydrobiol.*, **87**, 295--317.
- Servais, P., Gosselain, V., Joaquim-Justo, C., Becquevort, S., Thomé, J. P.  
and Descy, J. P. (2000) Trophic relationships between planktonic  
microorganisms in the river Meuse (Belgium): a carbon budget. *Arch.  
Hydrobiol.*, **149**, 625--653.

- 1  
2 1  
3  
4 2 Skibbe, O. (1994) An improved quantitative protargol stain for ciliates and  
5 other planktonic protists. *Arch. Hydrobiol.*, **130**, 339--347.  
6 3  
7 4  
8  
9 5 Sleight, M. A., Baldock, B. M. and Baker, J. H. (1992) Protozoan  
10 communities in chalk streams. *Hydrobiologia*, **248**, 53--64.  
11 6  
12 7  
13  
14 8 Sluss, T. D., Cobbs, G. A. and Thorp, J. H. (2008) Impact of turbulence on  
15 riverine zooplankton: a mesocosm experiment. *Freshw. Biol.*, **53**, 1999 –  
16 2010.  
17 9  
18 10  
19 11  
20 12 Sorokin, Y. I. (1990) Heterotrophic microplankton in plankton successions  
21 and self purification processes along the Yenisei river. *Arch. Hydrobiol.*  
22 *Beih. Ergebn. Limnol.*, **34**, 267--273.  
23 13  
24 14  
25 15 Spreafico, M. and van Mazijk, A. (Red.) (1993): *Alarmmodell Rhein. Ein*  
26 *Modell für die operationelle Vorhersage des Transportes von Schadstoffen*  
27 *im Rhein. Bericht Nr. 1-12.* Kommission für die Hydrologie des Rheins,  
28 Lelystad.  
29 16  
30 17  
31 18 Sprung, M. and Rose, U. (1988) Influence of food size and food quantity on  
32 the feeding of the mussel *Dreissena polymorpha*. *Oecologia*, **77**, 526 -- 532.  
33 19  
34 20  
35 21 Strayer, D. L., Pace, M. L., Caraco, N. F., Cole, J. J., Findlay, S. E. G. and  
36 Stuart, E. G. (2008) Hydrology and grazing jointly control a large-river food  
37 web. *Ecology*, **89**, 12 – 18.  
38 22  
39 23  
40 24 Vannote, R. L., Minshall, G. W., Cummins, K.W., Sedell, J.R. and Cushing,  
41 C.E. (1980) River Continuum Concept. *Can. J. Fish. Aquat. Sci.*, **37**, 130 --  
42 137.  
43 25  
44 26  
45 27  
46 28 Viergutz, C., Kathol, M. and Norf, H. (2007) Control of microbial  
47 communities by the macrofauna: a sensitive interaction in the context of  
48 extreme summer temperatures? *Oecol.*, **151**, 115 – 124.  
49 29  
50 30  
51 31  
52 32  
53 33  
54 34  
55  
56  
57  
58  
59  
60

1  
2 1  
3  
4 2 Viroux , L. (2002) Seasonal and longitudinal aspects of microcrustacean  
5  
6 3 (Cladocera, Copepoda) dynamics in a lowland river. *J. Plankt. Res.*, **24**,  
7  
8 4 281—292.  
9

10 5  
11 6 Vogel, S. (1993) *Life in Moving Fluids: The Physical Biology of Flow*.  
12  
13 7 Princeton University Press: New Jersey.  
14

15 8  
16 9 Vohmann, A., Mutz, M., Arndt, H. and Weitere, M. (2009) Grazing impact  
17  
18 10 and phenology of the freshwater sponge *Ephydatia muelleri* and the  
19 11 bryozoans *Plumatella emarginata* and *Fredericella sultana* under  
20 12 experimental warming. *Freshw. Biol.*, **54**, 1078 – 1092.  
21  
22 13  
23

24 14  
25 15 Weisse, T., Müller, H., Pintocoelho, R.M., Schweizer, A., Springmann, D.  
26 16 and Baldringer, G. (1990) Response of the microbial loop to the  
27 17 phytoplankton spring bloom in a large prealpine lake. *Limnol. Oceanogr.*,  
28 18 **35**, 781--794.  
29  
30  
31  
32

33 19  
34 20 Weitere, M. and Arndt, H. (2002 a) Top-down effects on pelagic  
35 21 heterotrophic nanoflagellates (HNF) in a large river (River Rhine): Do  
36 22 losses to the benthic environment play a role? *Freshw. Biol.* , **46**, 1437--  
37 23 1450.  
38  
39  
40  
41  
42

43 24  
44 25 Weitere, M. and Arndt, H. (2002 b) Water discharge-regulated  
45 26 bacteria/heterotrophic nanoflagellates (HNF) interactions in the water  
46 27 column of the River Rhine. *Microb. Ecol.* **44**, 19--29.  
47  
48  
49  
50

51 28  
52 29 Weitere, M., Schmidt-Denter, K., Auer, B. and Arndt, H. (2003) Laboratory  
53 30 experiments on the impact of biofilms on the plankton of a large river.  
54 31 *Freshw. Biol.*, **48**, 1983--1992.  
55  
56  
57

58 32  
59 33 Weitere, M., Scherwass, A., Sieben, K. T. and Arndt, H. (2005) Planktonic  
60 34 food web structure and potential carbon flow in the lower River Rhine with  
a focus on the role of protozoans. *Riv. Res. and Appl.*, **21**, 535--549.

1  
2 1  
3  
4 2 Weitere, M., Dahlmann, J., Viergutz, C. and Arndt, H. (2008) Differential  
5 grazer-mediated effects of high summer temperatures on pico- and  
6 3  
7 nanoplankton communities. *Limnol. Oceanogr.*, **53**, 477 – 486.  
8 4  
9

10 5  
11 6 Welker, M. and Walz, N. (1998) Can mussels control the plankton in rivers?  
12 - a planktological approach applying a Lagrangian sampling strategy.  
13 7  
14 *Limnol. Oceanogr.* **43**, 753--762.  
15 8  
16

17 9  
18 10 Woerner, U., Zimmermann-Timm, H. and Kausch, H. (2002) Aggregate-  
19 associated bacteria and heterotrophic flagellates in the River Elbe – Their  
20 11  
21 relative significance along the longitudinal profile from km 46 to km 583.  
22 12  
23 *Int. Rev. Hydrobiol.*, **87**, 255 – 266.  
24 13  
25

26 14  
27 15 Wörner, U. and Zimmermann –Timm, H. (2006) *Plankton und benthische*  
28 *Besiedlung in Buhnenfeldern. Aggregate in Buhnenfeldern. In: Stoffdynamik*  
29 16  
30 *und Habitatstruktur in der Elbe*. Ed.: Pusch, M, Fischer, H. Weißensee  
31 17  
32 Verlag: Berlin. pp. 118-146.  
33 18  
34  
35 19  
36  
37 20  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

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 25<sup>th</sup> and 26<sup>th</sup> 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 22<sup>nd</sup> and 28<sup>th</sup>, 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).

1  
2 1 Figure 6: Relative taxonomic composition of biovolume of phytoplankton,  
3  
4 2 HNF and ciliates along the stretch of the River Rhine investigated.  
5  
6 3  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

For Peer Review

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
1 Table I: River Rhine

<i>Date</i>	<i>Rhine-km</i>	<i>Flow time [h]</i>	<i>Sampling station</i>	<i>Discharge [m<sup>3</sup>/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 [m<sup>3</sup>/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			

1

2 1  
3  
4 2 Table II:

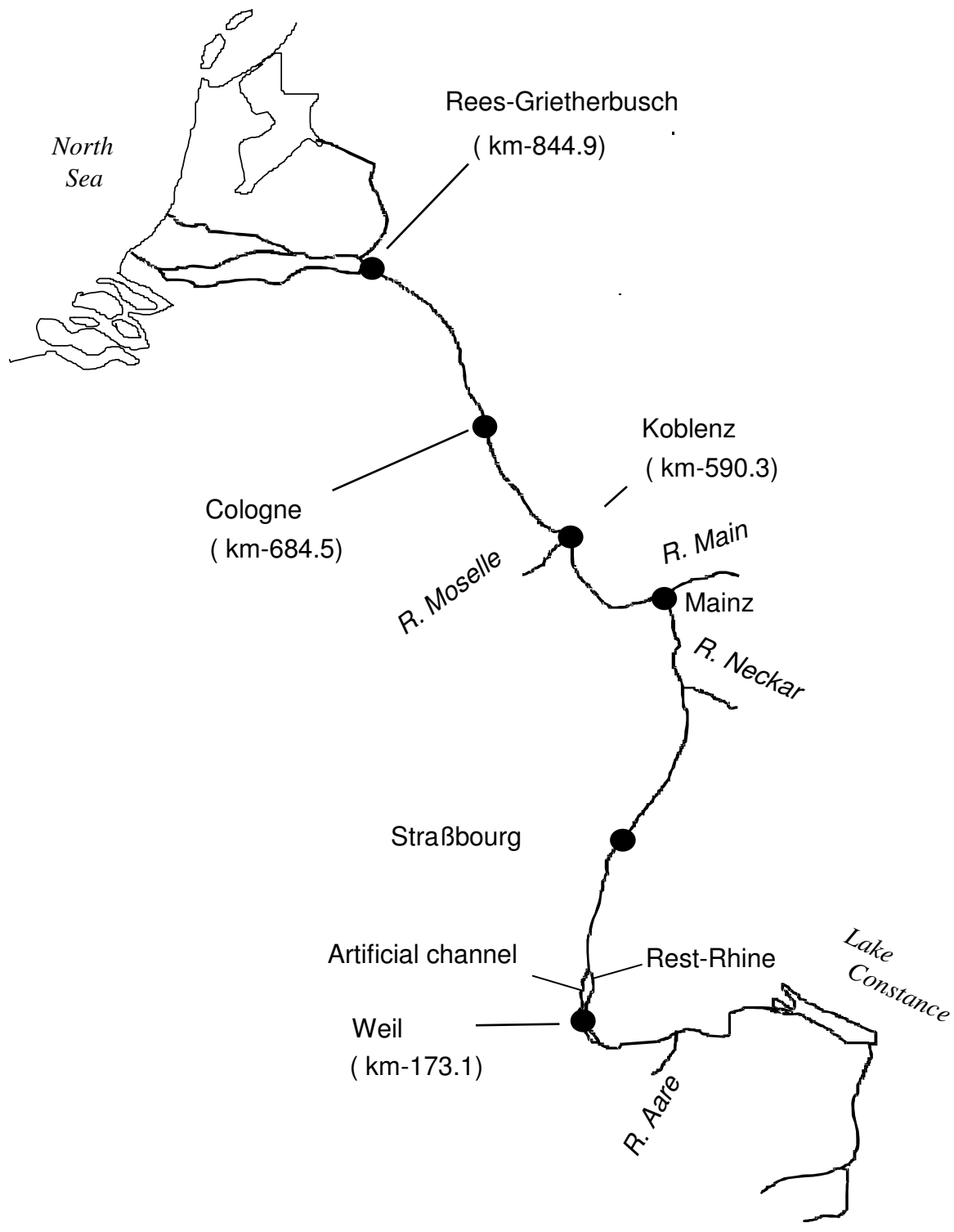
<i>Inflow of Neckar</i>	<i>load Rhine at km-395</i>	<i>load Neckar (inflow at Rhine-km-429)</i>	<i>% load of main stream</i>
HNF [ind/sec]	$8.38 \times 10^{11}$	$3.11 \times 10^{10}$	3.6
Ciliates [ind/sec]	$3.64 \times 10^8$	$3.57 \times 10^6$	1.0
Phytoplankton [ind/sec]	$2.26 \times 10^{12}$	$2.29 \times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

59 3

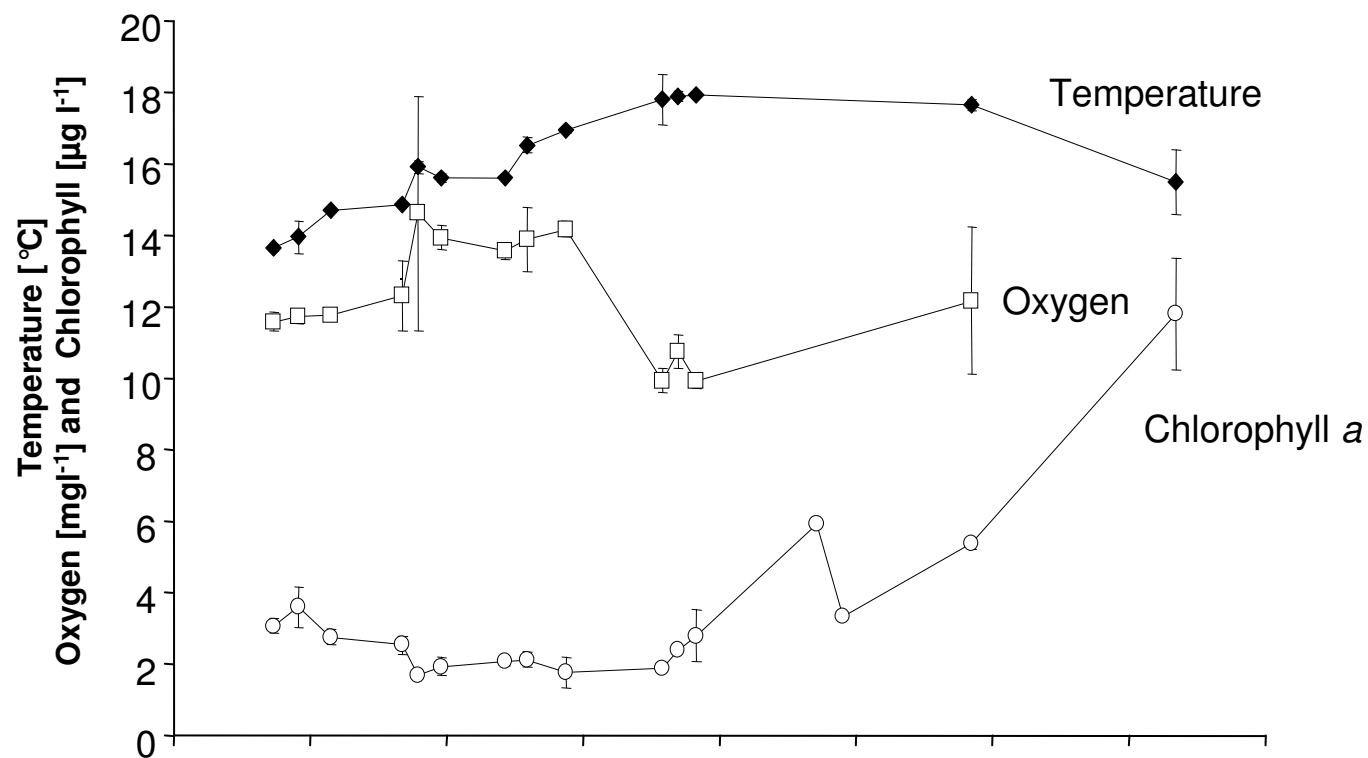
60 4

5

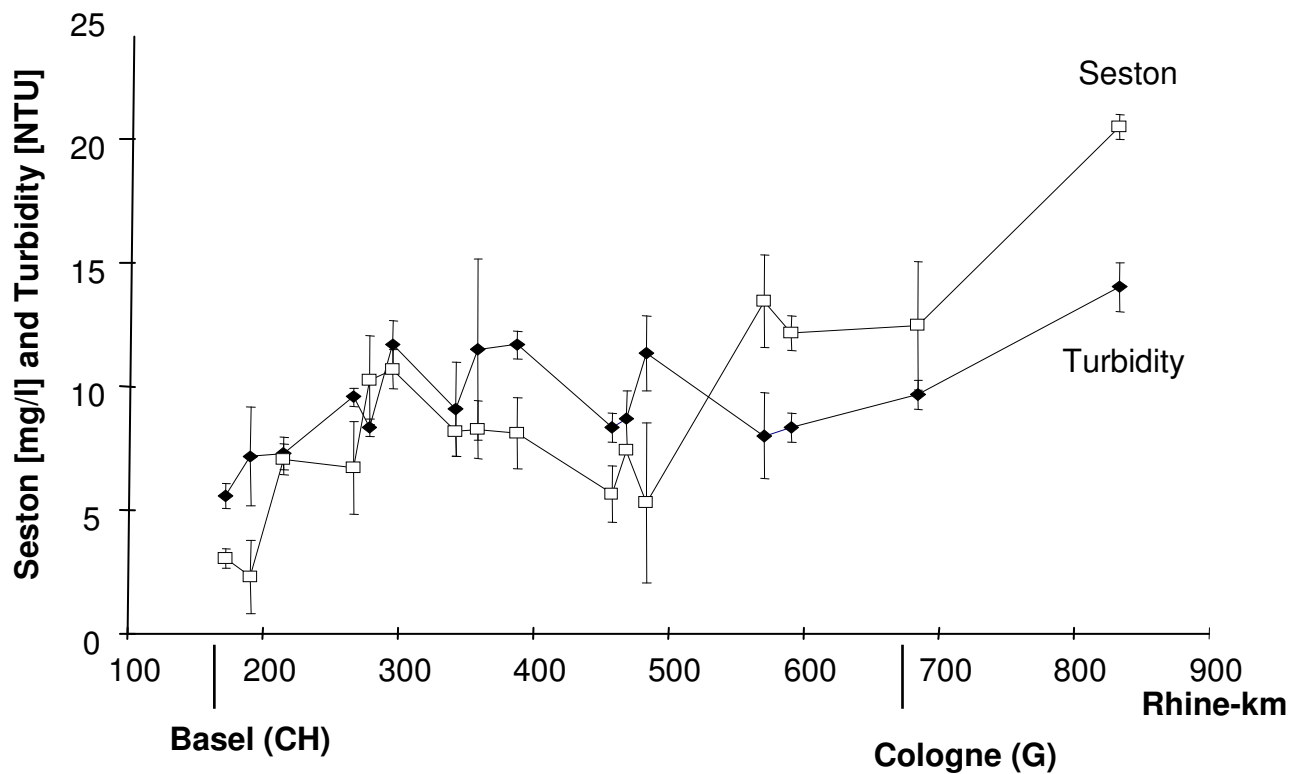
1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60



Scherwass, A. et al., Fig. 1



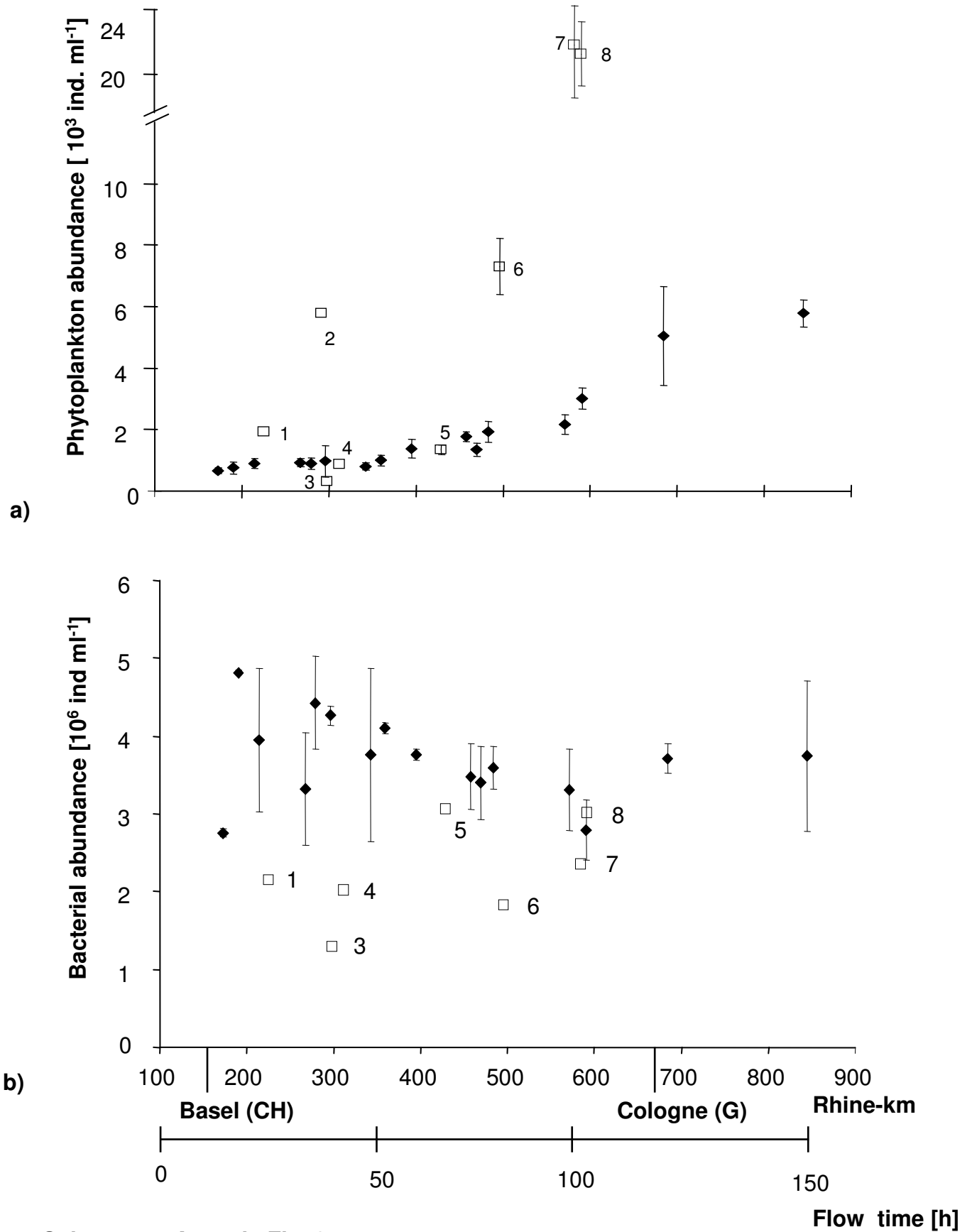
a)



b)

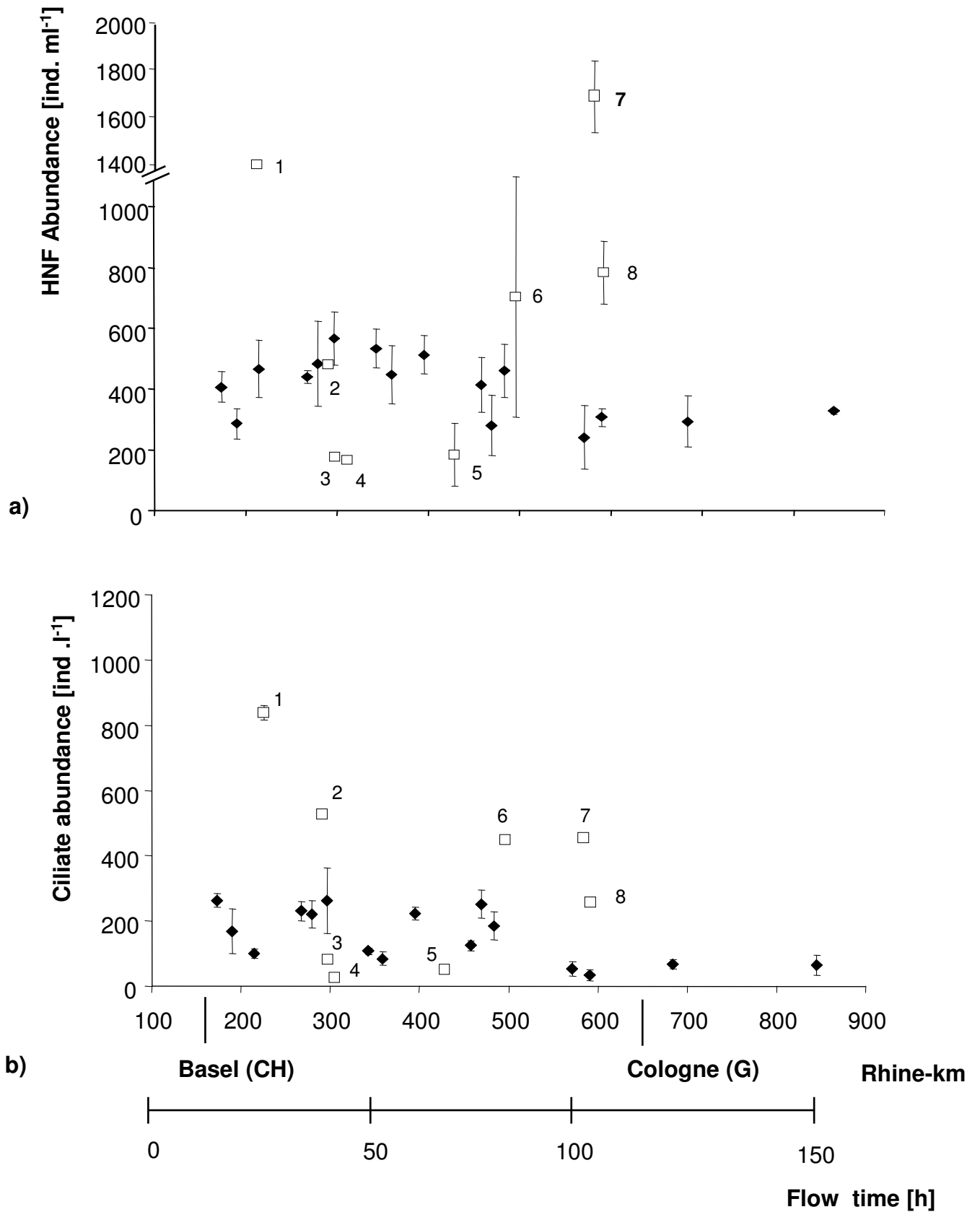
Scherwass, A. et al., Fig. 2

Flow time [h]

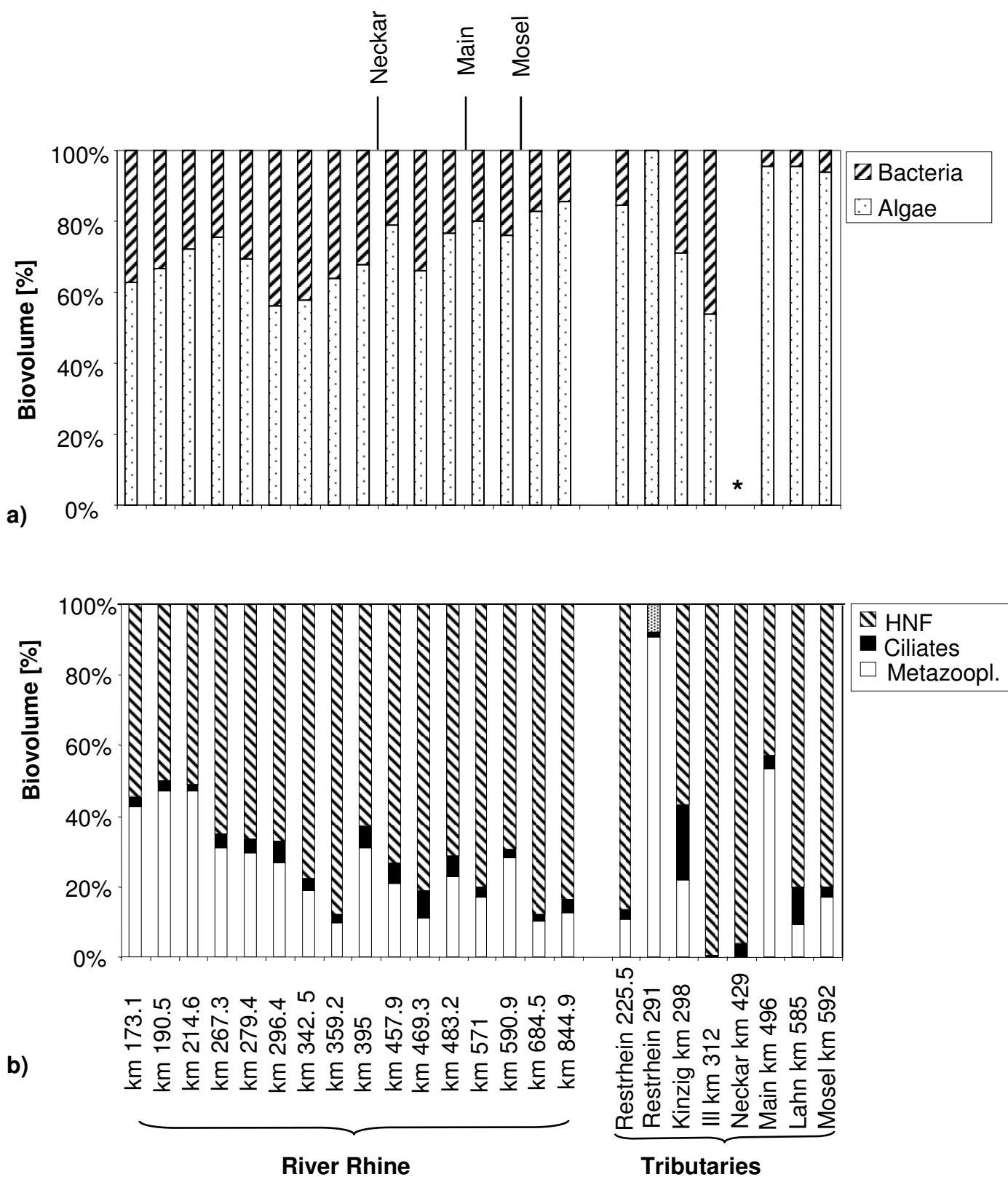


Scherwass, A. et al., Fig. 3

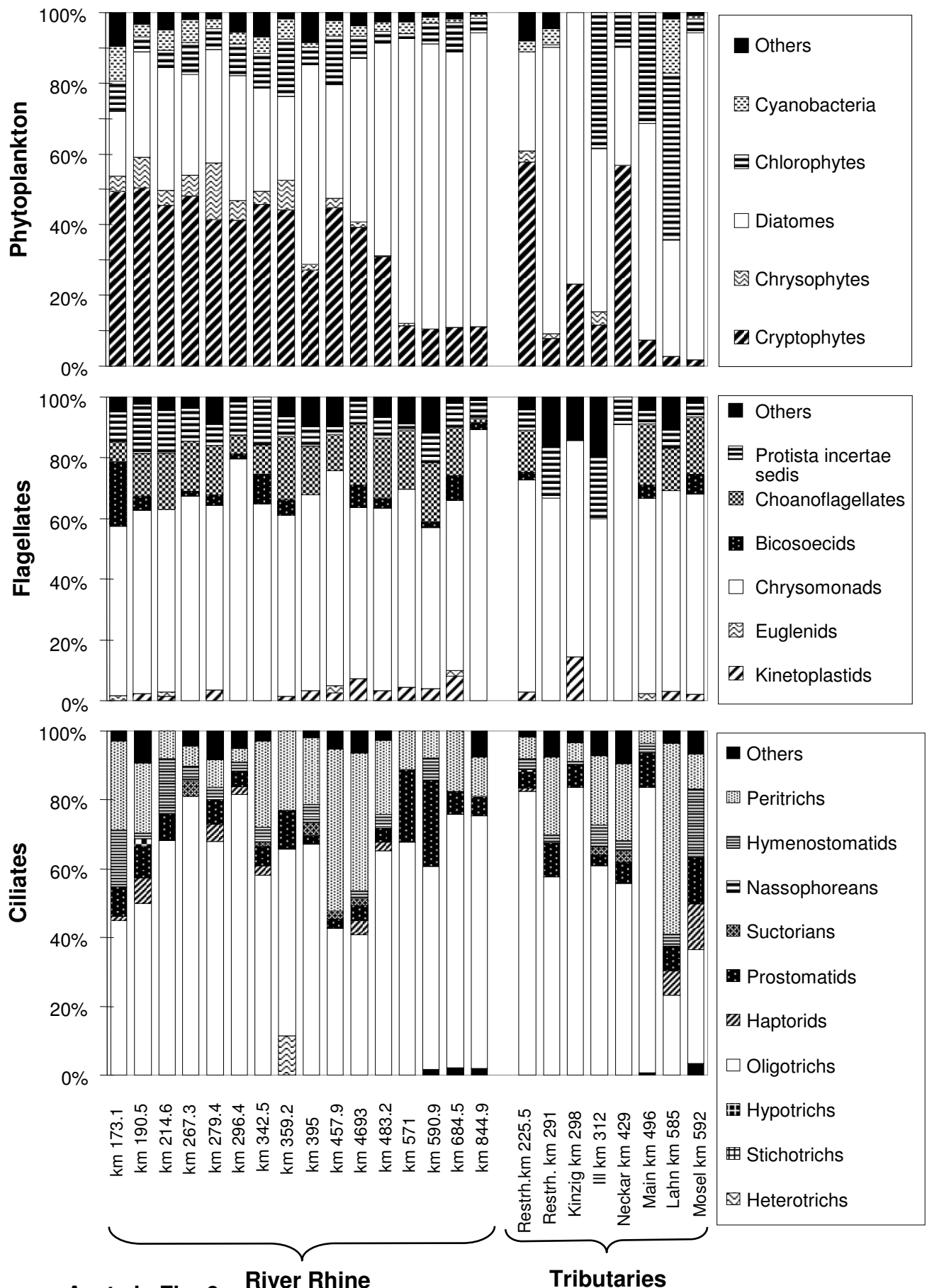
1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60



Scherwass, A. et al., Fig. 4



Scherwass, A. et al., Fig. 5



Scherwass, A. et al., Fig. 6