The following book chapter 11 might be cited as:

Teubner K, Großschartner M, Teubner IE (2018) Response of Zooplankton to Restoration and Climate Warming in Alte Donau. pp 163-212. *In*: Dokulil MT, Donabaum K, Teubner K (eds) The Alte Donau: Successful Restoration and Sustainable Management. Aquatic Ecology Series, vol 10. Springer (doi: 10.1007/978-3-319-93270-5_11)

The final publication is available at Springer via: https://doi.org/10.1007/978-3-319-93270-5_11 **Aquatic Ecology Series**

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The Alte Donau: Successful Restoration and Sustainable Management An Ecosystem Case Study of a Shallow Urban Lake



Chapter 11 Response of Zooplankton to Restoration and Climate Warming in Alte Donau

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Abstract Lake restoration is commonly assessed by changes in water transpar-5 ency, nutrients and biomass of phytoplankton, while information about changes in 6 zooplankton that is triggered by lake management is often missing. In our 19-year 7 study we used rotifers and crustaceans to document the effect of restoration mea-8 sures on zooplankton in the oxbow lake Alte Donau, a former side-arm of the 9 Danube River which is most popular for recreation and angler (cyprinid-dominated 10 shallow water). The record covers four management periods: the period before res-11 toration, the restoration (including years of chemical phosphate precipitation by 12 Riplox treatment), the re-establishment of macrophytes and the sustained 'stable 13 conditions'. We found the highest abundance of all zooplankton in the first Riplox-14 year, with decreasing zooplankton abundance in following periods associated with 15 the decline of phytoplankton. In the long term, the main compositional change 16 related to a shift from a cladoceran-rotifer-rich to a copepod-rotifer-rich zooplank-17 ton assemblage. Thus, the large-bodied zooplankton shifted from a community 18 composed of mainly filter-feeding herbivorous cladocerans under eutrophic algal-19 turbid conditions to mainly selective-feeding omnivorous and herbivorous cope-20 pods under mesotrophic transparent-water conditions. While the carbon ratio 21 between zoo- and phytoplankton increased significantly during the first three peri-22 ods and remained high under 'stable conditions', the mean body size of zooplankton 23 did not exhibit a long-term trend. Short-term increases of large-bodied zooplankton 24 coincided with an intermittent increase of calanoid copepod abundance (Eudiaptomus 25

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[©] Springer International Publishing AG, part of Springer Nature 2018 M. Dokulil et al. (eds.), *The Alte Donau: Successful Restoration and Sustainable Management*, Aquatic Ecology Series 10, https://doi.org/10.1007/978-3-319-93270-5_11

gracilis) during the chemical treatment concomitant with a drastic phytoplankton 26 biomass reduction and the occurrence of large-bodied cladocerans (Simocephalus 27 vetulus and Sida crystallina) in some years with re-established underwater vegeta-28 tion. Besides the main response of zooplankton to the 'bottom up' control that was 29 triggered by the reduction of phytoplankton food supply by one order of magnitude, 30 we studied the zooplankton response to climate change. The impact of climate 31 warming was evident from intra-annual coincidence of the climate signal (NAO_{DIEM}) 32 and water temperature (WT) in winter and early spring, the increase of surface 33 water temperature (SWT) by 1.52 °C per decade in April and the prolongation of the 34 warm period (SWT > 22 $^{\circ}$ C) by 10.5 days per decade in summer. This prolongation 35 of the warm season seemed to support the summer development of the medusa stage 36 of freshwater jellyfish (Craspedacusta sowerbii). During the transition from spring 37 to summer, the progressively earlier clear-water phase followed two trends. The first 38 period with a 33-day earlier clear-water phase per decade coincided with pro-39 nounced ecosystem changes from a high to a low eutrophic state created by chemi-40 cal restoration measures. The second period with a moderate earlier progression of 41 7 days per decade was accompanied by a further, slight TP decrease associated with 42 the re-establishment of macrophytes. When comparing rotifers, cladocerans, cala-43 noid and cyclopoid copepods, the latter group benefits most from seasonal tempera-44 ture increases and climate warming. 45

46 **11.1 Introduction**

Urban lakes are often altered by humans as they are located in densely populated 47 areas. Both open water bodies and banks are affected by pollution and artificial bank 48 stabilisation due to human activities and are thus commonly 'heavily modified' or 49 degraded ecosystems. More recently, however, awareness has increased that urban 50 ecosystems can, in fact, generate valuable services for urban life (Bolund and 51 Hunhammar 1999). This awareness has led to a shift in urban planning from a focus 52 on water exploitation to a focus on ecosystem health, satisfying both nature conser-53 vation and the use of waters for recreational and cultural activities. Concepts in 54 sustainable landscape planning and biomanipulation used as a lake restoration tool 55 indicate that healthy freshwaters gain supra-regional importance by their efficient 56 retention of carbon and other nutrient elements (Ripl 1995; Søndergaard et al. 2001; 57 Reichstein et al. 2013). Lake restoration prevents runoff of nutrients from degraded 58 urban areas through rivers into the ocean, from where it is difficult to get nutrients 59 back into terrestrial ecosystems (Ripl 1995). Accelerated circulation of matter 60 becomes increasingly important during lake restoration, i.e. when a nutrient-rich 61 lake is facing a drastic reduction of the pool size of essential nutrients (Teubner 62 et al. 2003). Zooplankton, which is the focus of this chapter, facilitates rapid cycling 63 of matter in nutrient-poor lakes (Capblancq 1990) and therefore contributes sub-64 stantially to retaining nutrients in a healthy ecosystem (Loreau 1995). 65

Alte Donau in Vienna faced these different aspects of an urban lake mentioned 66 before. The habitat for cold-water fish assemblages in the Danube River shifted to a 67 habitat for warm-water fish assemblages after the cut-off from the main river chan-68 nel in 1870–1875 (see fish in Chap. 15, history in Chap. 2). During the mesotrophic 69 period in the 1980s, the oxbow lake was cyprinid-dominated with extensive dense 70 underwater vegetation (Löffler 1988). In the 1990s, Alte Donau has undergone a 71 strong nutrient enrichment (Dokulil et al. 2010a). This was accompanied by the 72 development of large cyanobacterial blooms and a consequently low water transpar-73 ency. The highest phytoplankton biomass was measured in 1994. The phytoplank-74 ton was dominated by the filamentous cyanobacterium Cylindrospermopsis 75 raciborskii (Dokulil and Mayer 1996) and reached a chlorophyll-a concentration of 76 about 140 μ g L⁻¹. Concomitantly, the water transparency was lowest with a Secchi 77 depth of 0.28 m in September 1994 (see Fig. 6.4 in Chap. 6, phytoplankton compo-78 sition in Chap. 9). The awareness of the value of urban ecosystems led to actions to 79 restore Alte Donau (Chap. 5). The restoration comprised different treatments such 80 as the use of Riplox (1995/1996) to limit the growth of planktonic cyanobacteria 81 and algae (Chap. 9) and the re-establishment of submerged vegetation for the pur-82 pose of sustained restoration by biomanipulation (Chap. 8). The lake restoration 83 included both the open water bodies and the banks (Chap. 18). Furthermore, a mas-84 ter plan of urban planning was elaborated to generate the surrounding recreational 85 area in order to create a better quality of urban life in Vienna (Chap. 19). 86

Besides the impact of eutrophication, the recent climate change and its impact on 87 ecosystems have also led to a growing public awareness of the state of aquatic envi-88 ronments. Early climate change studies have focused on identifying and quantifying 89 the impact of climate change on freshwater and marine ecosystems at local and 90 global scale. More recent follow up studies have led to the development of future 91 management strategies for mitigating the risks posed by climate change (IPCC 92 2014). The vulnerability of ecosystems to climate change is amplified by man-made 93 degradation of landscape that is most relevant for an urban oxbow lake such as Alte 94 Donau. Awareness of the risks associated with climate change is here seen in com-95 bination with the damage done to ecosystem health. The main threat for ecosystems 96 is thus not only the direct impact of temperature increase created by global warm-97 ing, but also the deterioration of the water cycle, soil and vegetation including habi-98 tat loss that are caused and enhanced by anthropogenic eutrophication and landscape 99 alterations (e.g., Blenckner 2005; Ripl et al. 2007; Jeppesen et al. 2010a; Dokulil 100 and Teubner 2011; Reichstein et al. 2013). In this view, rivers and lakes are under-101 stood as sentinels for landscape degradation and for climate change (e.g., Karr 102 1998; Verburg et al. 2003; Adrian et al. 2009; Schindler 2009). This chapter focuses 103 on the change of zooplankton community structure following restoration as well as 104 on the potential impact of global warming. 105

Many limnological aspects were studied to understand the long-term development of biota in Alte Donau. The zooplankton (this chapter) and the phytoplankton (Chap. 9) are the two biological plankton parameters monitored for the longest time in this book. The analysis of the 19-year record of zooplankton aims at describing the long-term dynamics in species composition and comparing the community 110 structure between the two large lake basins. Here, we compare the zooplankton
assemblages between four main periods of the ecosystem-based lake management.
These periods cover the eutrophication period before the first chemical treatment in
April 1995, the 'restoration' period encompassing the first and the second chemical

April 1995, the 'restoration' period encompassing the first and the second chemical treatment including further restoration measures, the period of re-establishment of

treatment including further restoration measures, the period of re-establishment of macrophytes and the period of 'stable conditions'. In addition, we explore if the

117 impact of restoration on the development of zooplankton of Alte Donau was super-

118 imposed by global warming.

119 **11.2 Methods**

120 11.2.1 Sampling During the Four Periods of Lake Treatment

Alte Donau is a polymictic oxbow lake (7 m maximum depth, 2.5 m mean depth), with a water volume of 3.54×10^6 m³ and a surface area of 1.43 km² (Dokulil et al. 2010a, for lake history see also Chap. 2). The water body consists of two main impoundments. The morphology and hydrology of these two basins are described in Chaps. 3 and 4, respectively.

Zooplankton samples were taken at three depths (0.5 m, 2.5 m and near the bot-126 tom at 4.5 m) with a 5 L Schindler sampler in the south basin (AD1) and the north 127 basin (AD4) and were integrated over depth. The samples were filtered through a 128 44 µm mesh size net, resuspended in 50 mL lake water and fixed with formalde-129 hyde. The zooplankton time series presents a consistent data set as determination of 130 species and counting of samples was conducted by the same person (M.G.) for the 131 whole 19-year period. We calculated the biomass of the crustaceans by length to 132 weight regressions according to McCauley (1984) and Bottrell et al. (1976), assum-133 ing a dry to wet weight ratio of 0.15. We derived the biomass of rotifers from mea-134 surements of all three dimensions following Ruttner-Kolisko (1977). To compare 135 the biomass of zooplankton and the biovolume of phytoplankton, we translated the 136 mass related measures of both plankton groups into carbon content by using the 137 volume conversion of Behrendt (1990). 138

Zooplankton samples were taken at biweekly intervals during the observation
period from April 1994 to November 2012. This 19-year time series thus covers the
four main periods of the lake treatment specified in Chap. 6, which are slightly
modified in this chapter: 1 – 'eutrophication' (before April 1995), 2 – 'restoration
including the two years with chemical phosphate precipitation' (April 1995–1999),
a – 'macrophyte re-establishment' (2000–2006) and 4 – 'stable conditions'
(2007–2012).

The restoration period covers the treatment with $FeCl_3$ and limestone for phosphate precipitation followed by addition of $Ca(NO_3)_2$ to enhance nitrate oxidation of the sediment (Ripl 1976; Donabaum et al. 1999). This two-step chemical treatment (Riplox) was applied twice, in April 1995 and April 1996 (Chap. 5). An earlier study 149 on the ecosystem response comparing the ecosystem before the restoration with the 150 situation during the first and the second Riplox-year revealed different pathways of 151 prompt responses by the plankton community. It showed that the short-term impact 152 of chemical treatment in the first year was quite different from that observed during 153 the second year (Teubner et al. 2003). For this reason, we split the restoration period 154 in two, i.e. 2a) April 1995 to March 1996 and 2b) April 1996 to 1999. One main 155 focus of this book chapter is the long-term impact on zooplankton during the five 156 restoration periods (1, 2a, 2b, 3 and 4). 157

11.2.2 Data Treatment, Statistics and Graphical Representations Identifying Development Patterns upon Restoration

Figures 11.1, 11.2, 11.3 and 11.4 are based on the original dataset. However, as 161 phytoplankton and zooplankton were not always sampled by exactly 2-week inter-162 vals, we interpolated the available data at daily resolution (Livingstone 2003; Sapna 163 et al. 2015) and averaged these over a two-week period. These data were then used 164 to calculate the zooplankton to phytoplankton carbon ratios and the net change rates 165 of zooplankton at regular 2-week time intervals (Figs. 11.5 and 11.6). The net 166 change rate of zooplankton biomass (kzoo, hereafter referred to as net growth rate 167 of zooplankton) is calculated as 168

$$kzoo = \left(\ln Zoot2 - \ln Zoot1\right) / \Delta t \tag{11.1}$$

where Zoot2 is the zooplankton biomass at time t = t2, Zoot1 the biomass at time 170 t = t1 and Δt the time span in number of days (e.g., Teubner et al. 2003). The net 171 growth rate of phytoplankton is calculated analogous to Eq. 11.1 (see also Chap. 9). 172 The net growth rates of zooplankton and phytoplankton integrated over time are the 173 cumulative growth rates of the respective plankton group. The timing of the clear-174 water phase was defined by the coincidence of low phytoplankton biovolume after 175 the spring bloom and enhanced Secchi disc depth, indicating high water transpar-176 ency during the spring-summer transition. 177

Prior to the statistical analysis, data were tested for normality. According to the 178 non-parametric Shapiro-test (Dunn and Clark 1974), not all parameters followed a 179 normal distribution, in particular not those of single species. We therefore Intransformed these data (using natural logarithm) to normal distribution. For better 181 graphical illustration, we also plotted data on the LN-scale in Figs. 11.2, 11.3, 11.6a 182 and 11.8A1, B1, C1 and D1. Data that contained the value zero were transformed 183 by $\ln(x + 1)$. 184

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We conducted statistical analyses to identify the differences among sampling 185 sites (AD1, AD4) and restoration periods using R (R i386 Version 2.15.2). We 186 applied Kruskal-Wallis tests to determine differences between annual median values 187 of both time series (indicated by grey bars in Fig. 11.1) and of the five restoration 188 periods (Figs. 11.3 and 11.4). To identify homogeneous subsets when comparing 189 the zooplankton assemblages during the five restoration periods, we further con-190 ducted pairwise Mann-Whitney UT tests with a Bonferroni correction (Figs. 11.3 191 and 11.4). The abundances of single species and of taxonomic zooplankton groups 192 are displayed as notched box-whisker plots using SYSTAT 10 (SPSS Inc.) (Figs. 11.2 193 and 11.3). The boxes are notched at the median; the length of the notches indicates 194 the 95% confidence interval. Additionally, we show the change in zooplankton com-195 munity structure in triangular plots, assuming that the three large taxonomic groups 196 comprise the total zooplankton of large and medium-sized species (Fig. 11.4). The 197 triangular diagrams (Gibbs 1878) depict here the portions among the three zoo-198 plankton groups and have the advantage of graphically displaying the points in one 199 plane, different from a three-dimensional space of a x-y-z Cartesian coordinate sys-200 tem. To avoid overlay of data points, we displayed the results in separate triangles 201 for each restoration period. Application and interpretation of the triangular graphs 202 in limnology are described in detail in Teubner and Teubner (1998), Teubner and 203 Dokulil (2002) and Teubner et al. (2003) for nutrient stoichiometry and phytoplank-204 ton composition. 205

206 11.2.3 Data Treatment, Statistics to Identify Climate Response

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Graphs related to the climate response are displayed in Figs. 11.7, 11.8 and 11.9. 207 The analyses of long-term trends in zooplankton community development, the 208 potential responses of zooplankton to water temperature and climate signals super-209 imposing restoration efforts are based on biweekly data retrieved from linearly 210 interpolated data as described above (Figs. 11.7 and 11.9). All graphs in Fig. 11.7, 211 which are related zooplankton abundance, are analysed for the 19-year period 212 (1994–2012) and then related to the timing of the clear-water phase for 21 years 213 (1994–2014) and to water temperature for 22 years (1993–2014). 214

We used the North Atlantic Oscillation (NAO, Hurrell et al. 2001) Index as cli-215 mate signal since it is a common proxy for studying the climate impact on aquatic 216 ecosystems in the temperate zone (NAO station-based, from Hurrell eds. 2015). 217 We have chosen the NAO signal for the period December – March (NAO_{DIFM}, see 218 Fig. 11.7) as the winter climate signal does not vanish as fast as the NAO signal of 219 later months (see, e.g., Blenckner et al. 2007; Dokulil et al. 2010b); thus, it is suit-220 able for unravelling the climate response in late spring-early summer in Alte Donau. 221 In accordance with this, we analysed if warming occurs during the main season of 222 zooplankton development by selecting two dates in late April and early July to 223

reveal temperature trends during the 19-year period. We further calculated the num-224 ber of 'warm' lake water days (surface water temperature, SWT, above 22 °C) to 225 analyse the length of the warm period in summer (Fig. 11.7b). In order to trace the 226 climate response related to this summer period, we used the annual NAO. Additionally, 227 we analysed the extreme hot summer period by determining the number of days 228 exceeding the threshold of 25 °C, as this temperature was the highest integer of the 229 biweekly averages of SWT (Fig. 11.7b). According to suggestions regarding the 230 optimal growth temperature for the polyp $(19-25 \, ^{\circ}\text{C})$ and the medusa development 231 of Craspedacusta sowerbii derived in culture experiments (Folino-Rorem et al. 232 2016), we calculated the annual periods with 19–25 °C SWT and above 21 °C SWT 233 in number of days per year in Alte Donau. All data in Fig. 11.7 (with the exception 234 of the skewed distribution for the number of extreme hot days above 25 °C SWT) 235 and Fig. 11.9 satisfy normal distribution. Despite the normal distribution for data in 236 Fig. 11.7, the respective trends of the year-to-year variation are calculated as robust 237 lines by non-parametric fitting according to Theil (1950) as described in Helsel and 238 Hirsch (2002). These robust trend lines are applied to calculate the reliable slope of 239 the year-to-year trends, which are robust against outliers of unusual high or low 240 values in the first or last year of observation. The statistical significance of the trends 241 is calculated by Mann-Kendall tests using R (McLeod 2015). Regarding the year-242 to-year variation of the clear-water phase (Fig. 11.7d), a rapid decrease occurred in 243 the beginning and was followed by a slower decrease in later years. For this reason, 244 the time series was tested for breakpoints using Davies-test in R (Muggeo 2008, 245 2015), but the results were not significant (p-value>0.05). Nevertheless, data were 246 separated into two phases based on the a priori assumption of different stages of 247 the lake restoration. The segmented two regression lines are shown in Fig. 11.7d. 248 The first period refers to the rapid phytoplankton biomass decrease occurring in the 249 years prior to treatment initiation and the restoration treatment period including the 250 phosphate precipitation (period 1 and 2), while the second period covers the subse-

phosphate precipitation (period 1 and 2), while the second period covers the subsequence251quent years where only small changes in the phytoplankton yield occurred, i.e. the252periods with macrophyte re-establishment and stable conditions (period 3 and 4;253periods see in methods Sect. 11.2.1 above). In addition, the regression line for the254whole time series is displayed.255

11.3 Results

The long-term development of the zooplankton abundance and biomass is shown in Fig. 11.1a, b for the south (AD1) and the north basin (AD4). This 19-year development comprises the five periods of ecosystem-based management (1, 2a/2b, 3 and 4) covering the periods before, during and after chemical phosphorus precipitation (for a description of these periods see introduction and methods in Sect. 11.2.1). 261

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Fig. 11.1 Long-term series of zooplankton development comprising five periods: before restoration (1), restoration with chemical Riplox treatment (2a, 2b), re-establishment of macrophytes by periodical water level drawdown (3) and 'stable conditions' (4). Abundance (**a**) and biomass (**b**) of total zooplankton are shown for both sampling sites, the south basin (AD1) and the north basin (AD4). The abundance of individual taxonomic groups (**c**: cladocerans, **d**: copepods, **e**: rotifers) and the comparison of species numbers (**f**) represent averages of AD1 and AD4. Years with significant differences between AD1 and AD4 (H-test, p-values. See text) are indicated by dark grey horizontal bars for graphs (**a**–**e**)

11.3.1 Comparison of Zooplankton Abundance and Biomass in the South and North Basin

When comparing the zooplankton structure year by year between the north and the 264 south basin, we only found statistically significant differences in the year 1994 265 (Fig. 11.1a, b; bars indicate years with significant differences between sites; H-test, 266 p < 0.05 for rotifer abundance, all other p < 0.001). The annual average of zooplank-267 ton abundance in the north basin was 2027 individuals per litre in 1994, which cor-268 responds to a zooplankton biomass of 899 μ g L⁻¹. Zooplankton abundance in the 269 south basin was about six times lower than in the north basin with annual mean 270 values of 324 individuals L^{-1} , which corresponds to a biomass of 152 µg L^{-1} . 271 Furthermore, we found significantly lower values in the south basin for the indi-272 vidual taxonomic groups, i.e. cladocerans, copepods and rotifers, in the year 1994 273 (see abundance in Fig. 11.1c, d, e). These statistically significant differences are 274 probably mainly due to the lake treatment by water exchange in 1993 which aimed 275 at improving the water quality in Alte Donau; relatively nutrient-poor water from 276 Neue Donau (New Danube) was introduced to flush the eutrophied water body of 277 Alte Donau. The water from the channel Neue Donau entered Alte Donau in the 278 south end of the south basin (site 'Seestern'). Thus, we assume that the north basin 279 rather than the south basin mirrors the state of the zooplankton community during 280 the eutrophication period in 1994 before the chemical treatment started in 1995. As 281 these site differences correspond to a different magnitude of zooplankton abun-282 dance and biomass, but not to a significantly different species pattern, we did not 283 treat the data for the two basins separately. Moreover, we did not find between-site 284 differences in abundance or biomass for either total zooplankton or for individual 285 zooplankton groups during the subsequent 5-year 'restoration' period from 1995 to 286 1999 (see period 2 in Fig. 11.1). Also, in the next 13 years that included the period 287 of 'macrophyte re-establishment' and 'stable conditions', we did not find any statis-288 tically significant between-site differences for total zooplankton abundance or bio-289 mass. Statistically significant abundances were only detected for some individual 290 zooplankton groups in particular years. These significant differences are indicated 291 by grey bars for years 2000, 2001, 2006, 2009 and 2010 in Fig. 11.1c, d, e (H-test, 292 p < 0.05 for rotifers 2000, p < 0.05 for all others). 293

The water exchange using water of the neighbouring channel, Neue Donau, in 294 1993 aiming at improving the water quality in Alte Donau did not influence the 295 whole water body but only one basin. Furthermore, this water exchange had only a 296 short-term effect on the zooplankton in 1994, waning in the following years. 297 Therefore, we conclude that between-site differences in Alte Donau are of minor 298 importance in describing the main picture of the long-term response of the zoo-299 plankton to the lake restoration. For this reason, results are summarised for the 300 water body as a whole. 301

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302 11.3.2 Species Composition of Zooplankton

The zooplankton abundance is mainly dominated by small-sized rotifers (Fig. 11.1f, 303 see also list of species in Table 11.1). On average, we identified 10 rotifer species 304 with a maximum number of 18 and a minimum number of 3 species during the 305 19-year investigation period. About 29% of the identified rotifers are known to be 306 algivorous, another 29% bacterivorous/algivorous and 26% omnivorous. Another 307 9% of the rotifer species are known to be bacterivorous. Only about 7% of these 308 microzooplankton are classified as carnivorous. The seven most abundant rotifers 309 are Keratella cochlearis, Polyarthra dolichoptera-vulgaris, Kellicottia longispina, 310 Brachionus angularis, Collotheca mutabilis, Gastropus stylifer and Conochilus uni-311 cornis (Fig. 11.2). 312

Larger-sized zooplankton species are cladocerans and copepods which are found at an average of five and four species, respectively (maximum 8 and 6, Fig. 11.1f; see species list in Table 11.1). Most of the cladocerans are classified as omnivorous

2		Taxa
.3	Rotifera	Anuraeopsis fissa Gosse, Ascomorpha ecaudis Perty, A. ovalis Bergendal, A.
.4		saltans BARTSCH, Asplanchna priodonta Gosse, Brachionus angularis Gosse, B.
5		calyciflorus PALLAS, B. diversicornis DADAY, B. quadricornis MEISSNER,
6		Cephalodella sp., Collotheca mutabilis HUDSON, Colurella uncinata MÜLLER,
7		Conochilus unicornis ROUSSELET, Encentrum sp., Euchlanis sp., Filinia longiseta
;		EHRENBERG, F. terminalis PLATE, Gastropus stylifer IMHOF, Hexarthra mira
)		HUDSON, Kellicottia longispina KELLICOTT, Keratella cochlearis Gosse, K.
0		quadrata Müller, Lecane closterocerca SMARDA, L. cornuta Müller, L. elongata
1		HARRING & MYERS, L. luna MÜLLER, L. lunaris EHRENBERG, Lepadella sp.,
2		Lophocharis sp., Macrochaetus subquadratus PERTY, Monommata sp., Mytilina sp.,
3		Notholca acuminata Ehrenberg, N. jugosa Gosse, N. squamala Müller,
1		Pleosoma hudsoni Імноғ, Polyarthra dolichoptera-vulgaris Idelson/Carlin,
5		Pompholyx solcata Hudson, Squatinella sp., Synchaeta pectinata Ehrenberg, S.
6		tremula-oblonga Ehrenberg, Testudinella patina Hermann, Trichocerca birostris
7		MINKIEWICZ, T. capucina WIERZEJSKI ET ZACHARIAS, T. cilindrica Imhof, T.
В		insignis Herrick, T. pusilla LAUTERBORN, T. similis WIERZEJSKI, Trichotria
9		pocillum Müller, T. tetractis Ehrenberg
)	Cladocera	Acroperus harpae BAIRD, Alona affinis LEYDIG, Alonella nana BAIRD, Bosmina
1		longirostris O.F. MÜLLER, Camptocercus rectirostris SCHOEDLER; Ceriodaphnia
2		quadrangular O.F. Müller, Chydorus sphaericus O.F. Müller, Daphnia cucullat
3		SARS, D. hyalina LEYDIG, Diaphanosoma brachyurum LIEVIN, D. orghidani
4		NEGREA, Disparalona rostrata KOCH, Eubosmina coregoni BAIRD, Eurycercus
5		lamellatus O.F. MÜLLER, Graptoleberis testudinaria FISHER, Leptodora kindtii
6		FOCKE, Pleuroxus truncatus O.F. MÜLLER, Polyphemus pediculus LINNE,
7		Pseudochydorus globosus BAIRD, Scapholeberis mucronata O.F. MÜLLER, Sida
3		crystallina O.F. Müller, Simocephalus vetulus O.F. Müller
)	Copepoda	Calanoida: Eudiaptomus gracilis SARS
)		Cyclopoida: Cyclops vicinus ULYANIN, Eucyclops serrulatus FISCHER, Megacyclops
1		viridis JURINE, Mesocyclops leuckarti CLAUS, Thermocyclops oithonoides
2		G.O. SARS, <i>T. crassus</i> FISCHER

t1.1 **Table 11.1** List of zooplankton species found from 1993 to 2012



Fig. 11.2 Box-whisker plots of the abundance of individual species of cladocerans, copepods and rotifers during the five treatment periods. Cladocerans: Eubo core – *Eubosmina coregoni*, Diap brac – *Diaphanosoma brachyurum*, Chyd spha – *Chydorus sphaericus*, Ceri quad – *Ceriodaphnia quadrangular*, Lept kind – *Leptodora kindtii*, Daph cucu – *Daphnia cucullata*, Bosm long – *Bosmina longirostris*, Calanoid copepods: Eudi grac – *Eudiaptomus gracilis*, Cyclopoid copepods: Ther cras – *Thermocyclops crassus*, Cycl vici – *Cyclops vicinus*; Meso leuc – *Mesocyclops leuck-arti*, Ther oith – *Thermocyclops oithonoides*, Rotifers: Brac angu – *Brachionus angularis*, Aspl prio – *Asplanchna priodonta*, Coll muta – *Collotheca mutabilis*, Gast styl – *Gastropus stylifer*, Kera cochl – *Keratella cochlearis*, Kell long – *Kellicottia longispina*, Poly doli – *Polyarthra dolichoptera-vulgaris*, Trich capu – *Trichocerca capucina*, Leca luna – *Lecane luna*, Trich pusi – *Trichocerca pusilla*, Cono unic – *Conochilus unicornis*, Trich nisi – *Trichocerca insignis*. Black boxes indicate the highest median abundance of a species; 1, 2a, 2b, 3 and 4 refer to the treatment periods (see Fig. 11.1)

(45%). Also, high percentages of primarily bacterivorous (25%) or rather bacterivo-316 rous/algivorous (21%) cladocerans are found. Carnivorous species only constitute 317 8%. The most abundant cladocerans are Eubosmina coregoni, Ceriodaphnia quad-318 rangular, Daphnia cucullata, Bosmina longirostris, Diaphanosoma brachvurum 319 and *Chydorus sphaericus* (Fig. 11.2). The adult stages of copepods are mainly 320 omnivorous (67%). The remaining recorded species are classified as algivorous 321 (33%). The main copepod species are Eudiaptomus gracilis, Thermocyclops 322 crassus, T. oithonoides and Mesocyclops leuckarti, while Cyclops vicinus is less 323 abundant (Fig. 11.2). In addition to the more common species displayed in Fig. 11.2, 324 the relatively rare littoral cladocerans, Simocephalus vetulus, Sida crystallina and 325 Acroperus harpae, were found. 326

32711.3.3Comparison of Zooplankton Composition328Between the Five Treatment Periods

In addition to the time series on the 19-year development displayed in Fig. 11.1, the 329 comparison of zooplankton structure during the five periods of lake management (1, 330 2a, b, 3 and 4) is shown in Figs. 11.2, 11.3 and 11.4. Fig. 11.2 depicts the distribu-331 tion pattern of the most abundant rotifers and crustaceans. None of these species 332 revealed a quasi-evenly distributed occurrence across all treatment periods. The cla-333 doceran Eubosmina coregoni and the rotifer Brachionus angularis were the two 334 most abundant species during the eutrophic period before the Riplox treatment 335 (period 1). Furthermore, Eubosmina coregoni, which had the highest peak abun-336 dance during the 19-year study, were only dominant in the eutrophic period 337 (Fig. 11.2) and did not occur from late autumn 2003 until the end of the study. The 338 rotifer Keratella cochlearis was the only species showing the highest abundance 339 during the first year of the chemical phosphorus precipitation (Fig. 11.2, period 2a). 340 For many other rotifers, median abundances increased within the restoration period, 341 from the first to the second year of the Riplox treatment in 1995/1996 and the fol-342 lowing years of restoration until 1999, reaching the highest abundances in period 343 2b. The cladocerans which were also most abundant in period 2b were Diaphanosoma 344 brachvurum, Chydorus sphaericus, Daphnia cucullata, Eudiaptomus gracilis, 345 Cyclops vicinus and Mesocyclops leuckarti. Only few crustacean species reached 346 peak abundances in the subsequent periods, i.e. the period of 'macrophyte re-347 establishment' (Fig. 11.2, period 3, Bosmina longirostris) and in the successive 348 years of 'stable conditions' (Fig. 11.2, period 4, Ceriodaphnia quadrangular, 349 Thermocyclops oithonoides). It is worth noting that also some rarely found cladoc-350 erans, such as Simocephalus vetulus and Sida crystallina, occurred during the re-351 establishment of macrophytes (not shown in Fig. 11.2). These cladocerans are very 352 large-sized species such as with a body length of about 2000 and 2500 µm for 353 Simocephalus vetulus and Sida crystallina, respectively (for size comparison, the 354 length of Daphnia cucullata varies between 300 and 1200 µm). These species were 355

very low in abundance and were only found in the late period of re-establishment of 356 macrophytes and under stable conditions (from April 2005 and onwards). 357 Simocephalus vetulus reached a maximum abundance of 0.75 individuals L^{-1} and a 358 biomass of 5.6 μ g L⁻¹, and *Sida crystallina* an abundance of 0.5 individuals L⁻¹ and 359 a biomass of 2 μ g L⁻¹. Both species were only found in 1–2.5% of the plankton 360 samples taken during period 3 and 4. Another littoral but smaller bodied cladocer-361 ean species, Acroperus harpae with a body length of 700 µm, was also found from 362 the period of macrophyte re-establishment onwards. A. harpae occurred more regu-363 larly during periods 3 and 4 than the above-mentioned two littoral, large-bodied 364 cladocerans (first occurrence of A. harpae recorded in April 2003, present in about 365 10% of the samples taken in period 3 and 4). 366

The rotifer Kellicottia longispina seemed to be the only rotifer exhibiting a similar 367 distribution pattern as that of the abundant crustacean zooplankton. Unlike the crus-368 taceans, many rotifer species showed their highest abundance in the long-term period 369 after chemical restoration (13 years from 2000 to 2012). The rotifer species with the 370 highest abundance in period 3 were Collotheca mutabilis, Polyarthra dolichoptera-371 vulgaris and Lecane luna, and in period 4 Gastropus stylifer, Trichocerca capucina, 372 Trichocerca pusilla, Conochilus unicornis and Trichocerca insignis (Fig. 11.2). 373 When looking at the individual species (see Fig. 11.2), we found at least one rotifer 374 and one crustacean species with peak abundances in each of the five periods. For 375 some species, the peak abundance was far from being statistically significant. 376 Nevertheless, the species-specific comparison provides a rough overview of the per-377 sistence pattern of the individual species during this long-term period. 378

The statistical difference between the five periods of ecosystem-based lake res-379 toration management is shown in Fig. 11.3 for the abundances of all zooplankton 380 species and for the four taxonomic zooplankton groups. For 'all zooplankton', we 381 found significant differences between the median abundance of the five periods 382 (Kruskal-Wallis test, H = 64.76, df = 4, p < 0.001). The highest abundance of all 383 zooplankton occurred in the first year of the Riplox treatment (period 2a). At the end 384 of the 'restoration' (period 2b), total zooplankton abundance decreased significantly 385 (subgroup 'b'). The period of macrophyte re-establishment seemed to be accompa-386 nied by a recovery of zooplankton abundance (overlap of subgroups a and b). 387 Finally, during the latter part of lake restoration (period 4 of 'stable conditions'), 388 total zooplankton abundance demonstrated a further significant decrease (homoge-389 nous subgroup 'c') and the lowest abundance in a comparison between all periods 390 (1, 2a, 2b, and 3). 391

The four taxonomic groups revealed a different pattern of succession during the 392 periods of lake restoration. The abundance of calanoids (Kruskal-Wallis test, 393 H = 17.28, df = 4, p < 0.01) did not differ statistically when comparing the eutrophic 394 period with the periods of 'macrophyte re-establishment' and 'stable conditions' 395 (all three periods belong to subgroup 'b'). The abundance of calanoids increased 396 only shortly during the first year of Riplox treatment (overlap between subgroups a 397 and b) and reached an intermediate peak in the second year of the chemical treat-398 ment (subgroup 'a'). During these 2 years, median calanoid copepod contributions 399 relative to copepods were 21% and 23%: the long-term median wasonly shortly 400



Fig. 11.3 Box-whisker plot of the abundance of all zooplankton, copepods (cyclopoids and calanoids), cladocerans and rotifers during the five treatment periods. According to Kruskal-Wallis tests, statistical differences among lake treatment periods were found for all zooplankton groups (p < 0.01) with the exception of cyclopoids (p = 0.814). Furthermore, statistically significant differences between homogeneous data subsets for calanoids, cladocerans, rotifers and all zooplankton are represented by letters above each box as determined by pairwise Mann-Whitney U tests with Bonferroni correction. 2a, 2b, 3 and 4 indicate the treatment periods as in Fig. 11.1

during the first year of Riplox treatment (overlap between subgroups a and b) and
reached an intermediate peak in the second year of the chemical treatment (subgroup 'a'). During these 2 years, median calanoid copepod contributions relative to
copepods were 21% and 23%: the long-term median was 19%. For cyclopoids, the
main group of copepods, no statistically significant differences were observed



Fig. 11.4 Zooplankton structure displayed as the relative contribution of copepods (Cop), cladocerans (Clad) and rotifers (Rot) to total zooplankton for the five treatment periods by triangular diagrams. Filled blue circles denote abundance, open circles biomass. 1, 2a, 2b, 3 and 4 are the treatment periods as depicted in Fig. 11.1. The top left triangle is a scheme illustrating how to read the zooplankton graphs. All points in the sector 'Cop' indicate a contribution of at least 50% copepods to the total zooplankton. Analogously, the sector 'Clad' represents \geq 50% cladocerans and sector 'Rot' \geq 50% rotifers. Points in the middle area indicate that no single zooplankton group exceeded 50% of total zooplankton (more information on triangular diagrams in limnology can be found in the Methods Sect. 11.2.2). According to the Kruskal-Wallis tests, the relative abundance and the relative biomass of all three zooplankton groups were statistically different between the five lake treatment periods (see text)



Fig. 11.5 Time series of net change rates of zooplankton (A, 1994–2012), cumulative net change rates of zooplankton and phytoplankton (B, period for zooplankton as in A, for phytoplankton 1993–2014), annual averages of zooplankton body size (C, calculated as the ratio of zooplankton biomass [μ g L⁻¹] to zooplankton abundance [number of individuals L⁻¹], 1994–2012), and annual averages of total phosphorus concentrations (TP, molar) and Secchi depth (Secchi) (D, 1993–2014). A and B show net change rates at biweekly intervals (see method); 1, 2a, 2b, 3 and 4 are treatment periods as in Fig. 11.1

between the five periods (Kruskal-Wallis test, H = 1.57, df = 4, p = 0.814). The 406 abundance of cladocerans showed pronounced differences among lake treatment 407 periods (Kruskal-Wallis test, H = 60.87, df = 4, p < 0.001). These crustaceans were 408 mainly abundant in the eutrophication period (1) with a strong intermediate decrease 409 in the first year of the Riplox treatment (2a), with a rising abundance during period 410 2b and a decrease in the subsequent periods. The low abundance during the final 411 'stable' period of restoration management is similar to the low abundance achieved 412 after the abrupt decrease with the first Riplox-treatment. Rotifer abundance showed 413 also significant differences (Kruskal-Wallis test, H = 69.97, df = 4, p < 0.001) and 414 tended to increase in the first year of the Riplox treatment (2a), reaching peak abun-415 dance compared with all other periods. In the following years, the abundance of 416 rotifers decreased again. The lowest rotifer abundance, found in the last period, i.e. 417 'stable conditions' (subgroup c), was similar to the initial abundance under eutro-418 phic conditions before application of chemical restoration. 419

Figure 11.4 shows the proportional shifts of the zooplankton groups over the five 420 periods of ecosystem-based management. The triangle graphs illustrate the relative 421 contribution of the three main zooplankton groups, the two crustaceans and the 422 rotifers. All three zooplankton groups revealed highly significant differences 423 (Kruskal-Wallis test, df = 4, p < 0.001; copepods: H = 129.7, cladocerans: H = 62.65, 424 rotifers: H = 60.77) when comparing abundances among the five treatment periods 425 (see filled blue circles in Fig. 11.4). The most pronounced shift of relative abun-426 dance during the treatment periods was found for cladocerans vs copepods and the 427 least pronounced, but still highly significant change, emerged for rotifers (see also 428 Sect. 11.3.5 about the climate impact). Cladocerans and rotifers each contributed at 429 least 50% to the total zooplankton abundance during the eutrophic period (Fig. 11.4 430 1) and were thus the two most abundant groups before the restoration was initiated. 431 In later periods of the lake restoration treatment, the cladocerans did not reach an 432 abundance larger than 50% again (Fig. 11.4 2–4). Instead, copepods became abun-433 dant and reached more than 50% in period 3 and 4 (Fig. 11.4 3-4). In contrast, the 434 relative contribution of rotifers was high in all periods and peaked in period 3 when 435 macrophytes were re-established (Fig. 11.43). In the final period of stable conditions, 436 relative rotifer abundance slightly declined and copepod abundance further 437 increased. During the 19-year investigation period, an abundance shift occurred 438 from a rotifer-cladoceran-rich community during the eutrophication period to a 439 rotifer-copepod-rich community in the later periods of lake restoration. 440

The relative contribution of the three main taxonomic groups to total zooplank-441 ton biomass demonstrated significant differences (Kruskal-Wallis test, df = 4, 442 p < 0.001, copepods: H = 75.26, cladocerans: H = 52.60; p < 0.01, rotifers: H = 17.02, 443 see open circles in Fig. 11.4). Again, the change of rotifers during the treatments 444 was less pronounced when compared to copepods and cladocerans. Nevertheless, 445 the contribution of the relative biomass reveals a different perspective, as the here 446 investigated zooplankton covers a larger size-spectrum of animals from small-447 bodied rotifers to large-bodied copepods and cladocerans. Even rotifers, which 448 often contributed much more than 50% to total abundance, never exceeded a bio-449 mass contribution of 50% during any time of the 19-year investigation (Fig. 11.4 450 1-4). The zooplankton biomass was mainly dominated by cladocerans during the 451

eutrophic period. In the later years of the lake management, in particular during
macrophyte re-establishment and stable conditions (period 3 and 4 in Fig. 11.4
3–4), copepods contributed at least 50% to the zooplankton biomass. Thus, we can
conclude that in terms of biomass proportion the zooplankton is dominated by crustaceans and shifted from a cladoceran-rich community in the eutrophic period to a
copepod-rich community throughout the periods of the ecosystem-based lake
restoration.

459 11.3.4 Long-Term Development in Net Growth Rate 460 of Zooplankton Biomass, Size Structure and the Carbon 461 Ratio of Zooplankton to Phytoplankton

The time series of the net growth rate of zooplankton, the zooplankton size and 462 related measures are shown in Fig. 11.5. The net growth rate of zooplankton bio-463 mass is depicted in Fig. 11.5 a. Positive rates (n = 219, mean positive rate is 464 0.0185 day^{-1}) were less common than negative rates (n = 227, mean negative rate is 465 -0.0182 day^{-1}). The total sum of the positive rates over the whole study period from 466 1994 to 2012 was 4.05 day⁻¹ and -4.13 day⁻¹ for the negative rates. Thus, the zoo-467 plankton biomass decrease was nearly compensated by the zooplankton biomass 468 increase over the 19 years. As to the net growth rate of zooplankton abundance, the 469 numbers differed only slightly (positive changes: n = 205, mean = 0.0191 day⁻¹, 470 total sum = 3.92 day^{-1} ; negative changes n = 241, mean = -0.0165, total 471 sum = -3.97 day^{-1}) and thus do not describe a substantially different situation than 472 that for the long-term dynamics of the net growth rates of zooplankton biomass 473 (graph for the net growth rate of zooplankton abundance is not shown). In accor-474 dance with this, the cumulative net growth of zooplankton biomass was relatively 475 balanced throughout the five periods of ecosystem-based management. The only 476 period with clearly limited zooplankton development in the growing season occurred 477 in 1996, i.e. the year of the second chemical treatment (period 2b). In the successive 478 2 years within the 2b restoration period, zooplankton biomass recovered to the orig-479 inal level and then remained stable following a rather regular seasonal pattern with 480 intra-annual fluctuations (Fig. 11.5b). The fairly balanced long-term dynamic of the 481 net growth rates of zooplankton biomass was, however, quite different from the 482 dynamics of the net growth rates of phytoplankton (Fig. 11.5b). In the year of the 483 first chemical phosphate precipitation (period 2a), the phytoplankton biomass 484 decreased as a response to the reduced concentration of the main nutrient, phospho-485 rus (Fig. 11.5b, d). The drastic loss of phytoplankton biomass could not be compen-486 sated by positive net growth rates afterwards due to the persistence of low phosphorus 487 availability. In turn, this led to a stabilised high water transparency (Fig. 11.5d, 488 transparency is displayed as Secchi depth; for long-term dynamics of nutrients, phy-489 toplankton and related measures see also Chaps. 6 and 9). 490

Annual average of mean zooplankton body size over the 19-year study is depicted in Fig. 11.5c. The long-term development did not show a particular trend during the



Fig. 11.6 Relationship between the carbon of zooplankton and phytoplankton for the five treatment periods from 1994 to 2012. (a) carbon ratio (molar) versus total phosphorus concentration (TP, molar) displayed on a logarithmic scale (LN), (b) carbon ratio for individual treatment periods as Box-whisker plot. 1, 2a, 2b, 3 and 4 indicate the treatment periods as in Fig. 11.1

treatment periods but displayed two distinct increases, namely in the successive 493 years 1998/1999 and in year 2004. The first peak coincided with the naturally recovered underwater vegetation after the second chemical phosphate precipitation. 495 The second short-term increase of animal size occurred during the re-planting of submerged vegetation (macrophyte biomass in Fig. 8.7 in Chap. 8). 497

According to the large phytoplankton blooms seen before the restoration (period 498 1), the carbon ratio of zooplankton to phytoplankton was significantly low when 499 concentrations of total phosphorus were high (Fig. 11.6a, b). The remarkable 500 increase of this carbon ratio in the following three periods of lake management 501 (periods 2a, b and 3) was mainly due to the reduced phytoplankton biomass and not 502 enhanced zooplankton biomass. However, during the final period, the 'stable condi-503 tions', the carbon ratio of zooplankton to phytoplankton decreased compared with 504 the period of macrophyte re-establishment. This significant decrease of the ratio 505 coincided with the decline in total zooplankton abundance and biomass (Figs. 11.1a, 506 b and 11.3; see here the statistical significance of reduced abundance for total zoo-507 plankton in period 4), while phytoplankton biomass remained the same. 508

11.3.5Impact of Climate Warming on Seasonality and Long-
Term Development of Zooplankton509510

The response to climate driven water warming is illustrated in Fig. 11.7. Figure 11.7a 511 displays the correlation between the North Atlantic Oscillation index for the winter 512 period from December to March (NAO_{DJFM}, see method) and the water temperature 513 integrated over depth (WT). The winter climate index significantly correlates with 514



Fig. 11.7 Impact of climate warming. A: Correlation between the climate index NAO_{DJFM} and the water temperature integrated over the water column (WT) for all biweekly intervals from January (J) to December (D) during 21 years (1994–2014). Lines in the correlogram indicate the threshold

Fig. 11.8 Freshwater jellyfish (*Craspedacusta sowerbii*) is a commonly appearing species during hot summer periods in Alte Donau. The photo shows its size compared with the water plant Spiked Water-milfoil (*Myriophyllum spicatum*). (Photo taken on August 15, 2015)



water temperature in the beginning of year, from late January to early March. The 515 impact of this climate signal then abates from late March and onwards. 516

The surface water temperature (SWT) measured in late April significantly 517 increased by 1.52 °C per decade (p-value <0.05, Fig. 11.8b). The SWT increase in 518 early July was much lower (0.9 °C per decade with p-value >0.05, Fig. 11.8b) and 519 thus indicates less pronounced warming in summer than in spring. During the inves-520 tigation period 1993 to 2014, the number of days when SWT exceeded 22 °C varied 521 between 31 and 87 days (Fig. 11.8c), the number of days significantly increasing 522 during the investigation period, by 10.5 days per decade (p-value <0.05, Fig. 11.8c). 523 This lengthening of the warm period is mainly due to a progressively earlier onset 524 of the warm period (slope = -0.76, p-value < 0.05; not shown in graphs). The first 525 day in the year on which the temperature exceeded the threshold of 22 °C thus 526 shifted by about 7 days to an earlier date per decade (6.84 days per decade, varying 527

Fig. 11.7 (continued) of the coefficient of correlation (R) with statistical significance (p-value<0.05) B: Year-to-year variation of surface water temperature (SWT) measured in spring (biweekly means of the second half of April, 1994–2014) and summer (biweekly means of the first half of July, 1993–2014). The lines refer to robust trends with a slope of 0.17 for SWT (tau = 0.39, p-value = 0.014) in April and of 0.1 in July (tau = 0.27, p-value = 0.08). These trends refer to an increase of SWT of 1.52 °C per decade in late April and 0.9 °C per decade in early July. C: Year-to-year variation of the number of days when SWT is above 22 °C and above 25 °C (1994–2014). The slope of the robust trend line for the number of days with SWT > 22 °C is 1.17 (tau = 0.31, p-value = 0.049), indicating an increase in the number of hot days in summer (10.5 days per decade with a SWT higher than 22 °C). Stars denote years of abundant freshwater jellyfish in summer reported by local newspapers or observed by the authors. D: Year-to-year variation of the timing of the clear-water phase. The single robust trend (line 1), covering all years from 1994–2014, has a slope of -10.2, indicating a time shift by about 11-day advance in the occurrence of the clear-water phase per decade (10.8 days; tau = -0.26, p-value = 0.1). The robust trend line for the 6-year time segment from 1994 to 1999 (line 2, slope = -3.67, tau = -0.47, p-value = 0.25) refers to treatment periods 1 and 2 and the 15 years from 2000 to 2014 (line 3, slope = -0.8, tau = -0.14, p-value = 0.5) for treatment periods 3 and 4

between end of May to end of June). In contrast, the lengthening of the warm summer period was less pronounced (slope = 0.20, p-value >0.05) and resulted in a later offset of about 2 days per decade only (1.8 days per decade, varying from the end of August to mid-September). While the progressively earlier onset is significantly negatively correlated with the annual NAO index (r = -0.49, p-value <0.05), the delayed trend of the offset is positively, but not significantly, correlated with the climate signal (r = 0.31, p-value >0.05, not shown in graphs).

When considering the extremely warm days with SWT above 25 °C (see Methods Sect. 11.2.3), we found that this threshold was exceeded for at least 10 days in 7 years (1994, 1998, 2002, 2003, 2006, 2012 and 2013), while in the remaining years the extremely hot summer period only lasted less than 1 week (5 years) or did not appear at all (9 years, Fig. 11.8c).

During summer periods of extreme warm water, the medusa stage of 540 Craspedacusta sowerbii Lankester was observed in Alte Donau as documented 541 in local reports (Fig. 11.7c). This freshwater jellyfish had been sporadically observed 542 from July to August as from the 1970s in Neue Donau (Waidbacher, personal com-543 munication), and repeatedly mentioned in the local news (e.g., 28 July 2006: 544 'Süsswasser-Quallen wieder da') and observed by the authors (2014 and 2015). The 545 medusa of this freshwater jellyfish is often observed macroscopically in Alte Donau 546 (Fig. 11.8) but may easily be overlooked in regular samplings as they often emerge 547 for only a few days in small areas in the elongated lake basin (spatial patchiness). 548 The abundance of this freshwater jellyfish is therefore not included in the regular 549 zooplankton estimations in Figs. 11.1a, b. The number of days with a water tem-550 perature range from 19 to 25 °C, offering optimal growth conditions for the polyp 551 stage of C. sowerbii (see method), varies between 58 and 137 in Alte Donau and 552 exhibits an increasing trend (the slope of robust trendline is 0.4, p-value>0.05, data 553 not shown). Counting only the number of days where the seasonal threshold of 554 25 °C was reached, the period varied between 20 and 104 days, which is, on aver-555 age, 62% of total length in the period with temperatures between 19 and 25 °C 556 period. The period with SWT above 21 °C, assuming to promote the development 557 of mature medusa (see method), varies between 60 and 108 days in Alte Donau 558 (starting at Julian Day 140 to 180, i.e. late May to the end of June; ends at Julian 559 Day 232 to 261, i.e. late August to mid-September). Again, the duration of this 560 period demonstrated an increasing trend (slope of robust trendline is 0.71, 561 p-value>0.05, data not shown). Thus, the prolongation of the period with an opti-562 mum temperature range supporting the medusa stage was more pronounced than for 563 the polyp development in Alte Donau. 564

The seasonally low phytoplankton development in spring indicated presence of a clear-water phase in Alte Donau. The timing of this phase varied between the 95th (early April) and 145th day (late May) in a year during the 21-year investigation period (Fig. 11.7d). The robust trend line covering the whole period from 1994 to 2014 has a slope of -10.2, suggesting an earlier occurrence of the clear-water phase of about 11 days per decade (Fig. 11.7d, p-value >0.05). Considering the two main treatment periods of different orders of phytoplankton yield separately (see Method 571 Sect. 11.2.3), the year-to-year variation still showed earlier timing for both time 572 segments. The robust trend line for 1994–1999, covering the 2 years before restora-573 tion and the 'restoration period' (period 1 and 2), exhibited a 33-day earlier onset 574 per decade of the clear-water phase. This shift is much more pronounced towards 575 early spring than the shift indicated by the second robust line for 2000-2014. The 576 second robust line is describing only a shift of 7 days earlier per decade ('re-577 established macrophytes' and 'stable conditions', period 3 and 4). 578

The seasonality of the four taxonomic groups of zooplankton (cyclopoid and 579 calanoid copepods, cladocerans and rotifers) and the relationship between these 580 zooplankton groups and WT are shown in Fig. 11.9. Considering the long-term 581 average of the biweekly abundances throughout the seasons, the seasonal distribu-582 tion pattern of cyclopoid copepods closely resembled a unimodal distribution. 583 The abundance peaks occurred in May and an even higher peak appeared in July, 584 with a temporary short-time depression in June (Fig. 11.9a3). Due to the weak 585 summer depression, the annual cycle of cyclopoid abundances coincided closely 586 with the temperature peak in Alte Donau. When displaying these long-term data 587 as a scatter plot in Fig. 11.9a1, the statistically significant relationship between 588 the abundance of cyclopoids and WT becomes obvious (Fig. 11.9a1, P = 0.83, 589 p0 < 0.001). Fig. 11.9a2 again shows the correlation between the abundance of the 590 cyclopoids and WT but for each biweekly interval throughout the year in a 591 correlogram. 592

The cyclopoids were positively related with temperature at almost all times of 593 the year (Fig. 11.9a2). The relationship was strongest during the cold season and 594 culminated in a statistically significant relationship during four biweekly intervals 595 from December (R = 0.67 and 0.66, p-value<0.05) to January (R = 0.62 and 0.69, 596 p-value<0.05, Fig. 11.9a2). Thus, cyclopoids, which commonly show peak abun-597 dance during the summer season, generated particularly high abundances when WT 598 was unusually high during winter. In contrast to the cyclopoid copepods, the less 599 dominant calanoid copepods exhibited a pronounced bimodal seasonal develop-600 ment pattern (Fig. 11.9b3) and an inverse relationship with seasonal WT in late 601 summer to autumn (Fig. 11.9b2). During the autumn peak from September to early 602 October, the abundance of calanoids seemed to be stimulated in years with rela-603 tively low temperatures compared with the situation in warm years (p-value>0.05, 604 Fig. 11.9b2). This inverse relationship between abundance and warming in autumn 605 on the one hand and the general suppression of calanoid development for months 606 during the growing season on the other (midsummer decline from June to August in 607 Fig. 11.9b3) weakened the long-term relationship between calanoid abundance and 608 water temperature as shown in Fig. 11.9b1 (P = 0.22, p-value < 0.001). In case of the 609 cladocerans (Fig. 11.9d), the seasonal abundance was suppressed again from June 610 to August (Fig. 11.9d3). In contrast to the copepods, no significant inverse relation-611 ship was found between the long-term warming trend and the long-term develop-612 ment of the cladocerans (Fig. 11.9d2). The relationship traced in the long-term data 613



Fig. 11.9 Relationship between water temperature (WT) and the abundance of the four main taxonomic zooplankton groups (a-d). a1: Correlation between WT and the abundance of cyclopoid copepods reflected by long-term data (P = Pearson correlation coefficient, n = 449).

between WT and the abundance of cladocerans thus primarily owe to seasonality 614 (high abundance in summer, low in winter). Both parameters corresponded well 615 with each other (P = 0.61, p-value<0.001, Fig. 11.9d1). Rotifers, the most abundant 616 zooplankton group, showed a maximum peak in spring (April to May in Fig. 11.9c3), 617 their seasonal depression during the peak season being less pronounced (Fig. 11.9c3) 618 than those of calanoids and cladocerans. The relationship between zooplankton 619 warming trends was, however, not uniform throughout the year. The rotifers seemed 620 to be benefit from mild winters and their abundance was evidently suppressed in 621 autumn (Fig. 11.9c2). The relationship between long-term temperature and rotifer 622 abundance was almost as strong as for cladocerans (Fig. 11.9c1, P = 0.58, 623 p-value <0.001). 624

The long-term seasonal patterns of the four main zooplankton groups all show 625 spring peak abundances in the beginning to mid-May (calanoids, rotifers and cla-626 docerans) or from the middle to the end of May (cyclopoids). In contrast, the degree 627 of summer suppression varied significantly between groups; thus, an early second 628 peak was observed in July for cyclopoids and rotifers and in September for cala-629 noids and cladocerans. Moreover, the intra-annual variations in abundance of all 630 four groups were directly linked with WT in winter or spring, i.e. abundance was 631 higher in years with a mild winter and vice versa. According to long-term averages, 632 the two zooplankton groups exhibiting a pronounced midsummer decline, i.e. cala-633 noids and cladocerans, were moderately inversely related to WT in summer. In con-634 trast, the two zooplankton groups showing a short-term summer depression after the 635 spring peak, i.e. cyclopoids and rotifers, tended to be directly related to summer 636 WT. Furthermore, cyclopoids, which show the strongest coherence with the sea-637 sonal cycle of WT in the long-term averages (Fig. 11.9a3) and which are positively 638 related to WT throughout the seasons (Fig. 11.9a2), were the zooplankton group 639 demonstrating the strongest relationship between WT and abundance (r = 0.83 in 640 Fig. 11.9a1) in Alte Donau. In turn, the long-term abundance of calanoids, which 641 exhibit a pronounced spring peak, a strong and long-lasting summer depression 642 (Fig. 11.9b3) and a positive relationship to WT in spring and a negative relationship 643 in summer (Fig. 11.9b2), corresponds to the lowest statistical relationship between 644 WT and abundance. 645

Fig. 11.9 (continued) **a**2: Correlogram displaying the correlation coefficient (R, Spearman rank) for the relationship between WT and the abundance of cyclopoids every second week throughout a year (n = 19 for each bar, covering the 19-year period from 1994–2012, for details see Method Sect. 11.2.3). Lines indicate the statistical significance of R (p-value<0.05). **a**3: Seasonal distribution pattern of WT (bars) and the abundance of cyclopoids (line) displayed as long-term means at biweekly intervals from January to December (**j**–**d**, averages over the19-year study period). Graphs for rotifers (**c**1–**c**3), calanoid copepods (**b**1–**b**3), and cladocerans (**d**1–**d**3) are similar to that of cyclopoids (**a**1–**a**3)

646 11.4 Discussion

Despite the large spatial heterogeneity of the banks and basins of the former river 647 branch (Table 3.1 and Fig. 3.1 in Chap. 3; Chaps. 18 and 19), the total biomass of 648 zooplankton does not differ statistically significantly when comparing the two 649 impoundments. The only exception during the 19-year study is the year 1994 (as 650 demonstrated by statistical results in this study and plankton description for 1994 in 651 Mayer et al. 1997). Also, the biomasses of all three zooplankton groups, rotifers, 652 cladocerans and copepods, differed significantly between the two basins in 1994 653 (large between-site differences were also found for the abundance of ciliates, as 654 shown in Table 12.1 in Chap. 12). The reason for the differences in zooplankton 655 biomass in this particular year might be the partial water exchange with Neue Donau 656 (inflow at the south end of the south basin, at 'Seestern', see Chap. 5), undertaken 657 with the aim to temporarily improve the water quality in Alte Donau (Mayer et al. 658 1997). The year 1994 thus exemplifies that disturbance by water management 659 impacts the zooplankton since the abundance in the south basin was obviously 660 lower than in the north basin. It is, however, beyond the scope of this study to anal-661 yse the impacts of short-term water exchanges (washout effect to enhance water 662 transparency, Chap. 5) and of water drawdown in spring (stimulating the vernal 663 growth of macrophytes, details in Fig. 8.7 in Chap. 8) on zooplankton structure. 664

The species composition of the zooplankton community found in Alte Donau is 665 similar to that found in other shallow lakes. About 78% of the rotifer species, 64% 666 of the cladocerans and 43% of the copepod species found in Alte Donau also occur 667 in, for example, large and shallow Lake Võrtsjärv, Estonia (surface area 270 km²) 668 (Haberman and Virro 2004). Likewise, the main species of rotifers, cladocerans and 669 copepods observed in Alte Donau were found in lakes with a similar surface area, 670 for instance riverine lake Großer Müggelsee (Eckert and Walz 1998). All zooplank-671 ton species listed by Baranyi et al. (2002) for the hydrologically dynamic waters of 672 the Danube River floodplain (Regelsbrunn near Vienna) were also common in Alte 673 Donau. The mean zooplankton abundance (March to October) of these floodplain 674 waters, characterised by a short water age ranging from hours to 39 days, is 1495 675 individuals L^{-1} , which is, however, much higher than the number in the oxbow lake 676 Alte Donau (mean abundance from March to October over the 19-year study 677 period = 632 individuals L^{-1} , the long-term annual mean being even lower, namely 678 494 individuals L^{-1} including 352 rotifers L^{-1} , 83 copepods L^{-1} and 59 cladocerans 679 L^{-1}). About 30% of the rotifer species described by Lair (2005) for a river ecosys-680 tem, the Middle Loire, were also observed in our study in Alte Donau. It underpins 681 that some planktonic rotifers can adapt well to a habitat of an elevated current 682 despite their small size (hydrology see Chap. 4). The annual peak abundance of the 683 rotifers agrees well with those of the long-term observations in Middle Loire despite 684 the lower abundance in our study, which is ranging between 1000 to 2000 individu-685 als per L during the 18 years of ongoing restoration in Alte Donau (1995-2012, cf. 686 decline of TP and phytoplankton in Chaps. 1, 6, 10 and 20). 687

11.4.1 Response of Zooplankton to Lake Restoration: What Are the Specifics of the Oxbow Lake Alte Donau?

11.4.1.1 Main Picture of Altered Crustacean Composition Following the Trophic Change

In particular, large-bodied cladocerans are found to be efficient grazers on phyto-692 plankton when considering that the size of food particles increases with animal size 693 (e.g., Brooks and Dodson 1965; Burns 1968, 1969; Arndt et al. 1993; Shapiro and 694 Wright 1984; Lampert et al. 1986; Gulati and Van Donk 2002; Gudimova et al. 695 2011). In Alte Donau, cladocerans such as Daphnia cucullata and Chydorus 696 sphaericus were found to be the dominant grazers when filamentous cyanobacteria 697 (Cylindrospermopsis raciborskii, Limnothrix redekei) bloomed in spring and sum-698 mer in the year 1994 (Dokulil and Mayer 1996; Mayer et al. 1997; Dokulil 2015) 699 and macrophyte biomass was low (2 tons dry weight of macrophytes for the whole 700 water basin, see Chap. 8). The cladocerans were the only zooplankton group attain-701 ing highest abundance before the chemical treatment (Fig. 11.3). When comparing 702 the relative contribution in the eutrophication period with later restoration periods, 703 zooplankton biomass was composed of high portions of cladocerans (Fig. 11.4-1). 704 In terms of biomass, this period hosted a cladoceran-dominated zooplankton assem-705 blage (cladoceran-rotifer-rich), and in terms of abundance it was a rotifer-cladoceran-706 rich community (Fig. 11.4-1). After restoration, the zooplankton biomass shifted 707 towards a copepod-rotifer-rich community and in terms of abundance to a rotifer-708 copepod-rich community. The crustacean zooplankton therefore shifted from 709 mainly filter-feeding herbivorous cladocerans in the eutrophic algal-turbid state to 710 mainly selective-feeding omnivorous and herbivorous copepods in the mesotrophic 711 transparent-water (trophic states are illustrated Fig. 20.3 in Chap. 20). Such species 712 shifts from cladocerans to copepods are commonly described along trophic gradi-713 ents from high to low total phosphorus in lakes (Pace 1986; Jeppesen et al. 2000; 714 Kasprzak and Koschel 2001; Köhler et al. 2005). In Alte Donau, the majority of the 715 copepod species consisted of cyclopoids (6 species in Table 11.1), calanoids only 716 being represented by one species (*Eudiaptomus gracilis*), as also found in other 717 studies (Anneville et al. 2007a). The dominance of the omnivorous cyclopoid cope-718 pods indicates moderate food availability under eutrophic to mesotrophic condi-719 tions (Kasprzak and Koschel 2000; Anneville et al. 2007b; Mehner et al. 2008). The 720 herbivorous calanoid copepods, constituting 19% of the copepods in a long-term 721 perspective, typically indicate a nutrient state lower than mesotrophic, i.e. it is gen-722 erally assumed that the calanoid copepods are adjusted to lower food thresholds 723 than cyclopoid copepods (Adrian 1997; Kasprzak and Koschel 2000; Mehner et al. 724 2008). The suggestion that calanoids have a low demand for algal food agrees with 725 our observations in Alte Donau where an intermediate increase in calanoid abun-726 dance occurred during the two Riplox-years (restoration periods 2a and 2b), i.e. 727 peak abundances of calanoids coincided with extremely low phytoplankton bio-728 masses after phosphate precipitation (Fig. 11.3). According to Sommer and Stibor 729 (2002), large-bodied calanoid copepods and cladocerans might not be mutually 730

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exclusive as calanoids feed on large-sized algae, while the remaining small-sized 731 algae might be still suitable as food for filter-feeding cladocerans. This finding is 732 supported by the results of our study showing coherent occurrence pattern of indi-733 vidual species during the Riplox-year; thus, the peak abundance of the calanoid 734 Eudiaptomus gracilis coincided with the peak abundance of Daphnia cucullata in 735 Alte Donau (Fig. 11.2). Other aspects regarding the food quality for zooplankton 736 relative to the trophic state are described in Geller and Müller (1981), Capblance 737 (1990), Jeppesen et al. (2000), Kurmayer et al. (2003), Kainz et al. (2004), Ferrão 738 Filho et al. (2005) and Brett et al. (2009), and these are all relevant for the zooplank-739 ton shift in Alte Donau, which will be described in more detail in the following Sect. 740 11.4.1.2 for the years in which a drastic P reduction occurred. 741

11.4.1.2 Short-Term Zooplankton Response to Strong Phosphorus Reduction During Riplox-Years

Benndorf (1987) stated that top-down control by zooplankton only efficiently con-744 tributes to enhancing water transparency if the internal load of phosphorus has been 745 reduced a priori, thereby ensuring limited growth of algae through bottom-up 746 control. The Riplox-treatment (Ripl 1976), i.e. the chemical phosphate precipitation 747 and stabilisation of the oxidized sediment in April 1995 and April 1996, aimed at 748 creating a prompt phosphorus reduction in the water column and a long-term reduc-749 tion of the internal phosphorus load at the sediment-water interphase (treatment 750 described in Chap. 5 and in Donabaum et al. (1999); for a review of the retention of 751 internal phosphorus load see, for instance, Søndergaard et al. 2001). Phosphorus is 752 the main limiting nutrient element for phytoplankton growth in freshwaters (Hecky 753 and Kilham 1988). The relationship between total phosphorus and phytoplankton 754 vield (estimated chlorophyll-a or phytoplankton biovolume) is depicted in Fig. 9.10 755 (Chap. 9) and Fig. 20.3 (Chap. 20), showing the strong phosphorus reduction lead-756 ing to lower phytoplankton biomass in 1995 and 1996 (see also time series in 757 Fig. 11.5). 758

The total phosphorus concentration of 2.37 μ mol L⁻¹ before the restoration 759 decreased to 0.89 µmol L⁻¹ in 1995 and 0.6 µmol L⁻¹ in 1996 after the Riplox treat-760 ment in Alte Donau (median values derived from Teubner et al. 2003). Triggered by 761 phosphorus precipitation, the planktonic community adjusted to efficiently utilising 762 the remaining phosphorus sources. Planktonic biota acted here as a sink for phos-763 phorus under P-limitation which was seen in two ways: (a) with the tighter coupling 764 between food and consumer organisms, a larger portion of phosphorus was bound 765 by biota at the expense of the dissolved P-fractions, and (b) with the compositional 766 shifts from N-rich cyanobacteria to P-rich eukaryotic algae, the increase in the rela-767 tive importance of P-rich bacteria and the increase of the zooplankton portion rela-768 tive to phytoplankton, the stoichiometry of biota shifted towards a P-rich plankton 769 community (Teubner et al. 2003). The zooplankton played an important role in 770 accomplishing the higher phosphorus utilisation efficiency of the plankton 771 community. A tight coupling at both the producer-consumer and the nutrient-772

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producer interface was achieved mirroring higher phosphorus turnover rates under 773 phosphorus limiting growth conditions (e.g., Capblancq 1990; Teubner et al. 2003). 774 The carbon ratio between zooplankton and phytoplankton (C_{zoo}:C_{phyto}) increased 775 clearly after the Riplox treatment and is indicating the coupling of zooplankton and 776 food but from a standing crop perspective (Fig. 11.6; see also Teubner et al. 2003). 777 This increase was mainly due to the low biovolume of phytoplankton under P-limited 778 conditions as many short-lived primary producers often respond promptly to drastic 779 nutrient reduction (e.g., Jeppesen 2000; Ibelings et al. 2007). In Alte Donau, her-780 bivorous zooplankton was suppressed by the absence of large-sized phytoplankton 781 blooms. Instead, the small zooplankton mainly feeding on bacteria and small algae 782 such as rotifers (e.g., Fig. 11.3) and ciliates (Chap. 12) became increasingly abun-783 dant in the Riplox-years when total phosphorus levels were low (Teubner et al. 784 2003). The existence of two alternate zooplankton assemblages dominated by either 785 small rotifers or large cladocerans is commonly found and discussed in the study of 786 fish stocks and top-down control on zooplankton in lakes (e.g., Gilbert 1988; 787 Järvinen and Salonen 1998; Jeppesen et al. 2000; Lehtovaara et al. 2014), as fish 788 primarily feed on large-bodied zooplankton, allowing growth of small-sized zoo-789 plankton species. Lower abundances of Eudiaptomus gracilis and Daphnia cucul-790 lata were observed in the small basin 'Kaiserwasser'. This decrease was related to 791 the fish stocking experiment in 1998 (see Sect. 11.4.1.4). In contrast, the zooplank-792 ton community in the two main basins was not affected by the stocking in 1995/96 793 as the fish community did not change remarkably. In addition, macrophyte canopies 794 were still missing during this early restoration period and thus could not serve as 795 spawning and feeding grounds for predatory fish species. Therefore, we assume that 796 the high abundance of rotifers and ciliates at low cladoceran levels, occurring in 797 particular in the first Riplox-year, was rather mainly due to the bottom-up control of 798 the large herbivorous zooplankton than to the top-down control by fish. 799

The food quality for zooplankton during both Riplox-years has rapidly changed. 800 While the phytoplankton biovolume significantly decreased year for year with 801 P-precipitation, bacterial biomass remained almost the same (Teubner et al. 2003). 802 With a significantly higher bacterial enzyme activity mobilising the P source from 803 the dissolved organic phosphorus fraction in Alte Donau, the planktonic bacteria 804 further gained relative importance over phytoplankton for P acquisition under 805 reduced phosphorus availability. The loss rates of bacterioplankton (not the stand-806 ing crop) were in the same order of magnitude as those of phytoplankton. With the 807 reduction of total phosphorus, they even became slightly higher than those of phy-808 toplankton (Teubner et al. 2003). These increased relative loss rates have been 809 regarded as indirect evidence of enhanced grazing on bacteria (e.g. by rotifers and 810 ciliates) which has been observed in other ecosystems (e.g., Berman 1990). 811 According to other studies (e.g., Jones and Cannon 1986; Capblancq 1990; Elser 812 and Goldman 1991; Loreau 1995; Gismervik et al. 1996; Queimaliños et al. 1998; 813 Vadstein 2000; Tadonléké et al. 2009), the planktonic bacteria in Alte Donau, the 814 eukaryotic phytoplankton and the small-bodied zooplankton (rotifers and ciliates), 815 seemed to be the most important factors for accelerating the circulation of matter 816 under reduced phosphorus availability in both Riplox-years 1995/96. After the 817 Riplox-years, total phosphorus concentrations slightly increased again (Fig. 11.5)
indicating a resilience phase which has been observed together with hysteresis patterns discussed for trophic changes in other lakes including shallow to deep water
bodies (e.g. Carpenter et al. 1985; Beisner et al. 2003; Dokulil and Teubner 2005;
Jeppesen et al. 2005; Morabito et al. 2005; Ibelings et al. 2007; Anneville et al.
2007a; Schindler 2012, see also hysteresis for re-establishment for macrophytes in
Alte Donau in Fig. 20.4. in Chap. 20).

825 11.4.1.3 Impact of Macrophyte Re-establishment on Habitat Change

The time series of the annual mean body size in Alte Donau mirrored alternate shifts 826 between micro- and mesozooplankton, i.e. between small rotifers and large crusta-827 ceans. During the 19-year development period, an increase in annual mean zoo-828 plankton body size was observed two times, which could be both linked to an 829 increase of underwater vegetation cover. In 1998/1999, when the first intermediate 830 increase of mean body size was detected (see time series in Fig. 11.5c), seven of the 831 12 main crustacean species, but only 1 of the 12 main rotifer species, reached peak 832 abundances (see restoration period 2b in Fig. 11.2). The seven crustaceans were the 833 cladocerans Diaphanosoma brachvurum, Chydorus sphaericus, and Daphnia 834 cucullata and the copepods Eudiaptomus gracilis, Thermocyclops crassus, Cyclops 835 vicinus, and Mesocyclops leuckarti, and the rotifer Kellicottia longispina. The 836 increase of mean zooplankton size coincided with the spontaneous growth of mac-837 rophytes in response to the chemical treatment in 1998, after macrophytes had 838 almost disappeared in the first year of the Riplox treatment (0.5 tons of dry weight 839 for macrophytes only in the whole lake). In 1998/1999, the submerged macrophytes 840 already yielded 12–14 tons of total dry weight (all macrophyte biomass from Fig. 841 8.7 in Chap. 8). The most dominant submerged vegetation species was Myriophyllum 842 spicatum. Nitellopsis obtusa together with five other charophytes as well as Najas 843 marina further gained remarkable yields (Table 8.2, Fig. 8.7 and 8.8 in Chap. 8). 844 Other studies confirm that even small increases of underwater vegetation can have a 845 large impact on the zooplankton community (Schriver et al. 1995; Burks et al. 846 2002). Although Secchi depth increased further and the standing crop of macro-847 phytes resulted in a 30 times higher biomass yield (Chap. 8), the mean size of zoo-848 plankton decreased again (Fig. 11.5c, d). A second increase of mean zooplankton 849 body size, observed in 2004, was in the beginning of re-planting of macrophytes 850 (period of 'macrophyte re-establishment'). This coincided with a remarkable mac-851 rophyte development (about 360 tons dry weight for the whole lake, details in Chap. 852 8). During this period, in particular Myriophyllum spicatum had high biomass. This 853 water plant typically builds up a canopy formation in the top water layer by profuse 854 branching of shoots near the surface. Other underwater vegetation, such as 855 Nitellopsis and Najas already mentioned before, were found again in 2004 but 856 reached only relatively low biomass yield (cf. Fig. 20.5 in Chap. 20). The small- to 857 medium-sized canopies of these 'stoneworts' and other 'slow growing species' 858 (Chap. 20) are rather far from the surface. Different from the zooplankton situation 859

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in 1998/1999, extremely large-sized cladocerans, such as Simocephalus vetulus and 860 Sida crystallina, commonly occurred in 2004 but contributed only low abundances. 861 Exceptionally large-sized crustaceans are well known from other macrophyte-862 dominated habitats (e.g., Timms and Moss 1984; Jeppesen et al. 2000). Even though 863 these two cladoceran species were sporadically observed until 2012 in Alte Donau, 864 the mean size of zooplankton species declined again. The further increase of mac-865 rophyte vegetation during our study was thus not mirrored by uniform dominance 866 of large zooplankton species. Nevertheless, the increased abundance of macro-867 phytes coincided with the dynamics of the carbon ratio between zooplankton and 868 phytoplankton, which remained high until the end of the zooplankton investigation 869 period. Such an increase in the biomass ratio between zooplankton and phytoplank-870 ton is commonly found at declining nutrient levels (e.g. Padisák 1993; Teubner et al. 871 2003; Jeppesen et al. 2000, 2005; He et al. 2017). 872

In shallow lakes, the canopy of underwater macrophyte serves as a daytime ref-873 uge for zooplankton against visual predators such as planktivorous fish (e.g., Burks 874 et al. 2002). Macrophyte beds, however, may provide further benefits for zooplank-875 ton than just acting as a spatial refuge. Depending on the macrophyte canopy struc-876 ture (Carpenter and Lodge 1986, see 'open' and 'closed' canopy type in Sand-Jensen 877 and Pedersen 1999 for stream habitats) and on the strength of macrophyte allelopa-878 thy to inhibit epiphyton and phytoplankton growth (e.g. Van Donk and van de Bund 879 2002; Berger and Schagerl 2004; Hilt and Gross 2008), submerged macrophytes 880 can serve as a valuable habitat for zooplankton development. The macrophyte 881 stands offer an environment of moderate flow velocity and abundant food supply for 882 zooplankton by stimulating the growth of epiphytic and planktonic algae. Even 883 though it is commonly noted that the allelopathy of submerged macrophytes con-884 tributes to stabilising the clear-water state in shallow lakes (e.g., Hilt and Gross 885 2008), submerged macrophyte stands in lakes and rivers are not 'algal free zone' but 886 inhabit epiphytic algae and cyanobacteria (e.g., Carpenter and Lodge 1986; 887 Hofmann 1993; Schaumburg et al. 2004). As underwater vegetation utilises dis-888 solved nutrients and as their life span (several months) exceeds the short life period 889 of algae and cyanobacteria (1 day to a few weeks), submerged macrophytes might 890 contribute to stabilising both the ecosystems state (Scheffer and van Nes 2007) and 891 the zooplankton habitat structure. 892

In the case of Alte Donau, Myriophyllum spicatum serves as the most common 893 refuge simply because it is the dominant macrophyte. The canopy formation of M. 894 spicatum at the water surface, however, might be less beneficial as a daytime refuge 895 for zooplankton compared with medium-high Charophyte-species, which have 896 evenly distributed branches along the water column. Underwater mowing in Alte 897 Donau removes the dense branches of the Myriophyllum spicatum canopy near the 898 surface. This mowing frequently applied in recent years on the one hand and the still 899 low presence of medium-sized macrophytes with abundant branching shoots (e.g., 900 Charophyte-species) on the other hand seem to hamper the refuge effect for zoo-901 plankton in Alte Donau (see also Sect. 15.2.3 in Chap. 15 on losses of young fish by 902 mowing of macrophytes). A more patchy underwater vegetation might further 903 enhance the refuge heterogeneity for zooplankton. The heterogeneity of ambient 904

habitat structure for zooplankton is difficult to describe with regular sampling (e.g.,
Van Donk and Van de Bund 2002) and is not analysed here because appropriate
high-resolution measurements of the patchy zooplankton habitat structure were
beyond the scope of this study.

909 11.4.1.4 Top-Down Control by Fish

Top-down control of zooplankton by fish can be of decisive importance in a lake. It 910 is commonly observed that large-bodied zooplankton (mainly Daphnia) becomes 911 predominant in shallow lakes when the number of planktivorous fish decreases and 912 vice versa (e.g., Brooks and Dodson 1965; Carpenter et al. 1985; Gilbert 1988; 913 Järvinen and Salonen 1998; Jeppesen et al. 2000; Benndorf et al. 2001; Mehner et al. 914 2008; He et al. 2017). In accordance with this, an increase of large zooplankton such 915 as Daphnia pulex has been observed to occur in years after natural fish mortality 916 under ice in winter (e.g., Rücker et al. 2003). In contrast, small-sized zooplankton 917 species have been recorded to benefit from fish stocking in high-altitude lakes, natu-918 rally fishless mountainous freshwater basins (Schabetsberger et al. 2009). 919

Fish stock experiments with top predators indicate that a lower grazing pressure 920 due to loss of piscivorous fish triggers the establishment of large-bodied crustaceans 921 (Shapiro and Wright 1984; Lazzaro 1987; Ronneberger et al. 1993; Pace et al. 922 1999). In Alte Donau, such biomanipulation experiments were conducted in the 923 impoundment 'Kaiserwasser' in 1998. In the presence of piscivorous fish, the bio-924 mass of crustaceans such as Eudiaptomus gracilis and Daphnia cucullata increased 925 (Fig. 15.15 in Chap. 15), confirming the findings mentioned before. The cladocer-926 ans seem to be easier to capture than copepods by planktivorous fish (Drenner et al. 927 1978; Lazzaro 1987; Schriver et al. 1995; Mehner et al. 2008). During the 19-year 928 development period in Alte Donau, the zooplankton biomass exhibited a significant 929 shift from a cladoceran-rich towards a copepod-rich community (Fig. 11.4). 930 Therefore, our results suggest that the grazing pressure of fish on zooplankton still 931 remained high at the end of the 19-year period. 932

The species composition of the fish assemblages in Alte Donau did not change 933 significantly during the study period (fish surveys in Table 15.2, Chap. 15), which is 934 different from common internal-lake biomanipulation treatment aimed at removing 935 planktivorous and benthivorous fish (Søndergaard et al. 2007). Fish assemblage in 936 Alte Donau is still dominated by cyprinids, from the 1980s over the whole zoo-937 plankton study period. Alte Donau is traditionally popular for angling, where the 938 most common stocking fish was the common carp over decades (Chap. 15, see also 939 about Löffler 1988 in the introduction in this chapter). With the reduction of total 940 phosphorus and the associated drastic reduction of phytoplankton (Fig. 11.5 in this 941 Chapter, further Chap. 9 and Fig. 20.3 in Chapter 20), fish catches declined in Alte 942 Donau (time series in Fig. 15.1, Chap. 15) as commonly described for other lakes 943 that undergo re-oligotrophication (e.g., Jeppesen et al. 2000, 2002; Gerdeaux et al. 944 2006). Before restoration, the mean chlorophyll-concentration was 35 μ g L⁻¹ and 945 the mean fish catch was 6157 kg biomass (period 1). At 'stable conditions' (period 4), 946

both declined to 4 µg L⁻¹ and 4314 kg, respectively. A significant linear response 947 between lowering chlorophyll-a and decreasing fish catches is found for 1998 to 948 2012 (Fig. 20.7 in Chap. 20) and covers the last 15 years of observation. Furthermore, 949 fish catches were inversely associated with water transparency measured as Secchi 950 depth over the last 21 years (from 1992 to 2012, Spearman rank correlation, 951 r = -0.73, p < 0.001, not shown in graphs). This relationship indicates an over-952 whelming control by fish on the plankton community. It seems that the grazing 953 pressure by fish on zooplankton in Alte Donau could not be dampened by a refuge 954 effect of re-established macrophyte stands as described from other studies (Schriver 955 et al. 1995; Tátrai et al. 2009), with the exception of a short-term increase in the 956 abundance of large zooplankton species in 2004 as discussed in Sect. 11.4.1.3. It 957 can be therefore concluded that fish populations have consistently controlled the 958 food web structure in Alte Donau for the whole study period and thus cannot explain 959 the large shift in zooplankton composition. The main change in zooplankton assem-960 blages thus responded primarily to a bottom up control, i.e. to the strong reduction 961 of the phytoplankton food supply by one order of magnitude and associated effects 962 of water transparency increase as discussed in Sects. 11.4.1.1 and 11.4.1.2. 963

11.4.2 Response of Zooplankton to Global Warming: What Are964the Specifics of Urban Shallow Alte Donau?965

11.4.2.1 Climate Signal and Warming of Surface Water

The oxbow lake Alte Donau is located in the Vienna Basin belonging to the 967 Pannonian Plain. The Vienna Basin is one of the most vulnerable areas of climate 968 impact in Austria (Dokulil and Herzig 2009; Dokulil et al. 2010b; Olesen et al. 969 2011) alongside the Austrian Alps (e.g., Thies et al. 2007; Nickus et al. 2010; 970 Füreder et al. 2012; Tolotti et al. 2012). Alte Donau is located in the city of Vienna, 971 which has about 1.8 mill. residents and, thus, warming might be further strength-972 ened locally by the effect of urban heat islands (UHI, IPCC 2014). The area of 973 Vienna is 41,487 km² comprising 35.6% urban residential areas, 14.3% traffic areas, 974 45.5% parks and green space, and 4.6% covered by surface waters (MA23 2015). 975 According to the proximity to the urban area of Vienna, it could be assumed that 976 UHIs (e.g., Peterson 2003) have a potential impact on the microclimate of Alte 977 Donau. Böhm (1998) compared time series of air temperature and urban heat excess 978 temperatures of urban and suburban sites with those of rural reference sites in 979 Vienna for the study period 1991 to 1995. While heat excess temperatures were 980 pronounced in the urban areas of Vienna during the study period (mainly during 981 winter for the measuring site 'city centre' distant from parks), low values of heat 982 excess were measured at the suburban site 'Donauinsel', which is in a close distance 983 to Alte Donau. Böhm (1998) concluded that urban effects on air temperature are 984 more influenced by local surroundings than by the city Vienna itself. The significant 985 warming trend detected for the 22-year period in our investigation might thus be 986

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less influenced locally by UHI, i.e. the city of Vienna; rather large-scale effects such 987 as climate warming may be of strong importance. Evidence for the response to 988 global warming by Alte Donau was derived from the significant correlation between 989 the climate signal NAO and SWT. The NAO index is commonly used as climate 990 signal in the Northern Hemisphere and Europe to detect year-to-year variability 991 driven by global climate change mediated by 'local' weather and subsequent filtered 992 by lake processes (Straile et al. 2003; Blenckner 2005; Adrian et al. 2009) through 993 physical conditions affecting lake biology (e.g., George and Hewitt 1999, 994 Weyhenmeyer et al. 1999, Gerten and Adrian 2000, Winder and Schindler 2004a, b, 995 Shatwell et al. 2008). In Vienna, NAO positive years are typically associated with 996 high total incoming shortwave radiation (long sunshine duration), low cloud cover 997 and low precipitation and thus relate to hot, dry years. In turn, NAO negative years 998 refer to cold wet years (unpublished results by KT; for other observations between 999 NAO and weather at specific sites in Europe; see George and Hewitt 1999, and 1000 Blenckner 2005). Thus, NAO-associated phenomena mirror meteorological forcing 1001 (examples given in Jennings et al. 2000, George et al. 2004). According to a long-1002 term study of a stratified alpine lake in Central Europe by Schmid and Köster (2016), 1003 warming trends of the lake surface in spring and summer are caused by advection of 1004 warm air (60%) and direct heating (40%) due to the incoming solar radiation. 1005

In Alte Donau, the seasonally strongest correlation was found between the NAO 1006 index of the winter period December to March (NAO_{DIFM}) and early year WT, from 1007 late January to early March. This result is consistent with those of other studies, 1008 which have reported a high impact of winter NAO on lake properties (Jennings et al. 1009 2000; Gerten and Adrian 2000; Blenckner 2005; George and Hewitt 1999; 1010 Weyhenmeyer et al. 1999; George et al. 2004; Blenckner et al. 2007; Adrian et al. 1011 2009; Dokulil and Herzig 2009). Furthermore, the significant SWT increase with 1012 1.52 °C per decade in late April together with a weakening of warming trends in 1013 July in Alte Donau confirm the findings in other lakes studies of a pronounced 1014 response to warming in early spring (e.g., Weyhenmeyer et al. 1999; Gerten and 1015 Adrian 2000; Blenckner 2005; Dokulil et al. 2010b; Winder and Schindler 2004a; 1016 Kainz et al. 2017). This result also holds true when comparing the response to the 1017 climate signal during the seasonal hysteresis observed in the first and the second 1018 half of the year in Alte Donau. While seasonal warming above 22 °C follows the 1019 annual climate signal, seasonal cooling below 22 °C is not statistically significantly 1020 related to annual NAO. In accordance with this, seasonal warming follows a pro-1021 nounced trend of an earlier onset of the threshold temperature of 22 °C. Seasonal 1022 cooling below 22 °C is only slightly delayed. Such seasonal hysteresis of climate 1023 response patterns, strengthening the time shifts in spring but weakening those later 1024 in the year, as for instance the vernal onset and autumnal offset of thermal stratifica-1025 tion and associated development of phytoplankton described e.g., by Winder and 1026 Schindler (2004a) and Deng et al. (2014), are also well-known from other pheno-1027 logical studies. 1028

Besides the generally pronounced climate impact in winter and spring, Austria –
together with Switzerland and Poland – experiences the strongest warming anomalies in summer in central Europe (O'Reilly et al. 2015; Woolway et al. 2016). From

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a lake perspective and in addition to the persistence of climate signals passing lake 1032 filters (Blenckner 2005) in winter and spring (e.g., Blenckner et al. 2007; Adrian 1033 et al. 2009), the impact of climate warming in summer is also a topic of discussion 1034 with particular focus on plankton dynamics (e.g., Wilhelm and Adrian 2008; Adrian 1035 et al. 2009). A significant trend of summer warming has been verified for Alte 1036 Donau where the period with SWT above 22 °C has increased by 10.5 days per 1037 decade. This further confirms the importance of lake surface summer warming as 1038 found also in other studies in this region (see Neusiedlersee in Sapna et al. 2015; 1039 O'Reilly et al. 2015; Woolway et al. 2016), often promoting the proliferation of 1040 cyanobacteria directly by temperature increase and also by associated early stratifi-1041 cation and/or reduced thermal turbulences in stratifying deep but also polymictic 1042 shallow lakes (e.g., Joehnk et al. 2008; Pearl and Huisman 2008; Shatwell et al. 1043 2008; Dupuis and Hann (2009); Wagner and Adrian 2009; Markensten et al. 2010; 1044 Kosten et al. 2012; Posch et al. 2012; Dokulil and Teubner 2012; Dokulil 2014; 1045 Rigosi et al. 2014). 1046

11.4.2.2 Warming and the Most Spectacular Zooplankton Species: Freshwater Jellyfish

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In Alte Donau, the most spectacular zooplankton species occurring in hot summer 1049 periods is Craspedacusta sowerbii (Fritz et al. 2007). While many studies from the 1050 1980s and onwards emphasise the increasing geographical spreading of this neobi-1051 otic species among freshwater habitats, including the Danube catchment in Germany 1052 and Austria (e.g., Tittizer et al. 2000; Fritz et al. 2007), other studies focus on the 1053 dates of the seasonal observations of the medusa stage from mid-June to July/ 1054 August or early September (Kronfelder 1989; Grohs 1998; Jankowski et al. 2005; 1055 Peukert 2009). The seasonal development of the medusa stage of C. sowerbii 1056 described in these studies matches the duration of the warm period above 21 °C in 1057 Alte Donau (from late May to mid-September). This confirms the optimal tempera-1058 ture range for the development of the medusa stage suggested by Folino-Rorem 1059 et al. (2016) from culture studies. More recent studies discuss the sporadic develop-1060 ment between years, as in the year after occurrence of the medusa stage it is absent 1061 in the following year (e.g., Jankowski et al. 2005; Folino-Rorem et al. 2016). Folino-1062 Rorem et al. (2016) give their culture observations an eco-physiological perspective 1063 by including the full life cycle of C. sowerbii. They conclude that warm tempera-1064 tures besides high food availability (feeding frequency and/or amount of food) are 1065 of decisive importance for the optimal development of this freshwater jellyfish. The 1066 significant trend recorded of prolonged summer periods with SWT exceeding 22 °C 1067 supports the more frequent reports of the medusa stage of C. sowerbii in Alte Donau. 1068 Our temperature trend analysis for the period 1993 to 2014 further illustrated that 1069 the prolongation of the period with SWT above 21 °C is more pronounced than the 1070 prolongation of the period with temperatures within the range of 19 to 25 °C, favour-1071 ing the medusa stage relative to the polyp stage given that the development is con-1072 trolled by temperature. Moreover, our estimate of 60 and 108 days with SWT > 21 °C 1073

in Alte Donau exceeds the minimum life cycle (22 days) and life expectation of the 1074 medusa form (21 to 77 days) proposed from culture work by Folino-Rorem et al. 1075 (2016). However, the lack of data about the different life stages of C. sowerbii over 1076 consecutive years (abundances or presence/absence data) in Alte Donau does not 1077 allow us to draw any firm conclusions about whether the growth of this freshwater 1078 jellyfish is primarily controlled by temperature or by food availability or by a com-1079 bination of both. According to mesocosm and enclosure experiments by Jankowski 1080 et al. (2005), the medusa stage feeds in particular on small herbivorous crustaceans 1081 (Bosmina longirostris and juvenile cyclopoid copepods) and may thus play an 1082 important role as top invertebrate predator on zooplankton community. 1083

1084 11.4.2.3 Phenology of the Clear-Water Phase in Two Distinct Periods with Regard to the P Decline

Lake phenology of the clear-water phase, i.e. the timing of short-term control of 1086 phytoplankton by zooplankton grazing during the spring-summer transition, was of 1087 early interest in the study of the impact of global warming on lake biology (Müller-1088 Navarra et al. 1997; Gerten and Adrian 2000; Jeppesen et al. 2003; Shatwell et al. 1089 2008; De Senerpont Domis 2013; Berger et al. 2007; Huber et al. 2008; Berger et al. 1090 2014). The relative robustness of the timing of the clear-water phase associated with 1091 other physico-biological lake events led to a description of the general seasonal suc-1092 cession pattern found in many lakes in the temperate zone. The pattern mainly indi-1093 cates regime shifts between the two principal seasons of phytoplankton development 1094 in a year, i.e. from winter/spring to summer/autumn (Teubner 2000, see also sea-1095 sonal pattern in Chap. 9) along the seasonal cycle (Lampert et al. 1986, Sommer 1096 et al. 1986; De Senerpont Domis 2013). The timing of the clear-water phase between 1097 early April to late May in our 21-year study is closer to the timing in other shallow 1098 polymictic to dimictic lakes (early May to mid-June for shallow polymictic Großer 1099 Müggelsee in Teubner et al. 1999; Straile and Adrian 2000; Huber et al. 2010; mid-1100 May to early June for stratifying lakes such as Plußsee in Müller-Navarra et al. 1997 1101 and Lake Washington in Winder and Schindler 2004a, b) than in many other large 1102 deep, mainly pre-alpine or alpine lakes in Central Europe (Straile and Adrian 2000; 1103 Straile 2002). The trend towards an earlier clear-water phase in Alte Donau con-1104 firms general findings about an earlier onset of the spring clear-water phase in many 1105 other lakes in recent decades (Müller-Navarra et al. 1997; Straile and Adrian 2000; 1106 Straile 2002; Shatwell et al. 2008). The reason for the earlier timing of this spring to 1107 summer event is partly due to the stronger warming at the beginning of the year as 1108 discussed by seasonal hysteresis in Sect. 11.4.2.1. Another reason is the temperature 1109 dependence of organism growth. Empirical data revealed that an increase in tem-1110 1111 perature and an increase in food availability led to a shortening of the life span and life cycles but to an increase of the reproduction rate for rotifers, cladocerans and 1112 copepod species (e.g., Gophen 1976; Herzig 1983a, b; Orcutt and Porter 1983, 1113 Sarma et al. 2002). Contemplating the climate change scenarios for lakes, it is 1114 expected that the trophic structure might change from a simple but elongated food 1115

web in a cold climate to a more complex (with a higher degree of omnivory) but 1116 shortened food web in a warm climate (Jeppesen et al. 2010a; see also shifts in 1117 dietary composition of (zoo)planktivorous fish which prey alternatively on (zoo) 1118 benthic organisms in Alte Donau described in Chap. 15). Therefore, the effect of a 1119 warmer climate relates to different and connected parts of the bottom-up and topdown control in lakes, which includes also an enhanced probability of a clear-water 1121 phase according to theoretical simulation models by Scheffer et al. (2001). 1122

Early studies on the intra-annual variation of the clear-water phase without 1123 including the climate aspect revealed that the probability of this short-term spring 1124 event depends on the resource control of phytoplankton growth, on the one hand, 1125 and the predation pressure on phytoplankton by zooplankton and fish, on the other 1126 hand (e.g., Brett and Goldman 1997; Teubner et al. 1999). It is commonly known 1127 that biomass yields are mainly highly dependent on the trophic status of a lake (e.g., 1128 Carlson 1977; Vollenweider 1968, not least shallow lakes e.g., Teubner et al. 1999; 1129 Jeppesen et al. 2000; Teubner and Dokulil 2002), but it is assumed that the timing 1130 of seasonal minima and maxima, including the timing of the clear water phase, is 1131 less sensitive to trophic changes but responds to global warming (e.g., Straile and 1132 Adrian 2000; Müller-Navarra et al. 1997; Winder and Schindler 2004a, b). 1133

The long-term phenological shifts of the clear-water phase in Alte Donau pre-1134 sumably reflect the interference of two trends pointing in the same direction, the 1135 trend of re-oligotrophication superimposed by the trend of global climate change. 1136 The two periods with different trends for progressive earlier clear-water phase in 1137 Alte Donau (earlier time shift of 33 days per decade for 1994–1998 and 7 days per 1138 decade for 2000-2014) thus contradict the general robustness of the clear-water 1139 phenology mentioned above. The pronounced earlier clear-water phase from 1994 1140 to 1999 occurred concomitantly with the drastic reduction of the mean spring total 1141 phosphorus pool from 1.4 to 0.7 µmol L⁻¹ (spring mean value) and the associated 1142 reduction of phytoplankton chlorophyll-a spring peak, decreasing from 29.2 μ g L⁻¹ 1143 to 10.7 μ g L⁻¹ (spring maximum value, mean values are 9.0 and 7.2 μ g L⁻¹). We did 1144 not estimate the extents to which the earlier timing of the clear-water phase relates 1145 to the re-oligotrophication and the superimposed climate forcing. A common 1146 method to disentangle the two trends is the analysis of the residuals from the regres-1147 sion line of the detrended data (George and Hewitt 1999; Weyhenmeyer et al. 1999; 1148 George et al. 2004; Seebens et al. 2007; Adrian et al. 2009). According to our expe-1149 rience, detrending of biological lake data responding to different nutrient levels 1150 should be done with caution unless the ecosystem changes can be confirmed to be 1151 only moderate. Alte Donau has undergone drastic changes in trophic state within a 1152 short period. Detrending would here primarily satisfy statistics and thereby mathe-1153 matically eliminate the response to high nutrients levels in biological time series 1154 rather than mirroring lake ecology responding to a complex regime shift passing the 1155 transition from a nutrient-rich to a nutrient-poor ecosystem. Biological systems 1156 respond to different levels of, for instance, phosphorus in different ways because the 1157 absolute value of phosphorus (total pool size) is here of high importance (Teubner 1158 et al. 2003). The drastic short-term reduction of the phosphorus pool with phosphate 1159 precipitation enhances phosphorus utilisation efficiency of the planktonic community, 1160 which was achieved by an increase of microbial activity and alterations in phytoplankton and zooplankton traits (Teubner et al. 2003, see also Sect. 11.4.1.2).
Therefore, we chose not to apply detrending.

An empirical analysis of a large number of Danish lakes by Jeppesen et al. (2003) 1164 showed that phenological shifts of the clear-water phase toward an earlier date 1165 occur when the spring phytoplankton peak declines from year to year in response to 1166 reduced external loading. Alte Donau supports the findings by Jeppesen et al. (2003) 1167 that bottom-up control affects the clear-water phase phenology. Van Donk et al. 1168 (2003) also argued, based on a Danish lake survey, that shifts towards an earlier 1169 clear-water phase could mainly be attributed to changing lake management prac-1170 tises aimed at improving water quality than to lake warming by climate change. 1171

In Alte Donau, after the years with an initial strong reduction of phosphorus availability (1994–1999), a moderate phenological shift of the clear-water phase towards earlier onset in 2000–2014 coincided with the balanced intra-annual variations in spring chlorophyll-a concentration, which may be primarily attributed to a climate change response as found in many of the above-mentioned studies.

1177 11.4.2.4 Impact of Temperature Increase on Zooplankton Development

Seasonal differences in the relation between WT and individual micro- and meso-1178 zooplankton groups were assessed with correlograms, generated for biweekly inter-1179 vals in the 19-year period. The correlograms typically show a close temporal 1180 coherence pattern between WT and all four zooplankton groups in winter and 1181 spring. Extraordinarily high abundances of zooplankton early in the year corre-1182 spond with warm winters and springs, while the opposite is true for cold winters. 1183 1184 The closest relationship between year-to-year variations of temperature and zooplankton development was found for cyclopoids and rotifers. In case of calanoids 1185 and cladocerans, the positive relationship between abundances and WT is still pre-1186 dominant but much weaker. This general positive relationship between temperature 1187 and zooplankton abundance early in the year confirms observations by George and 1188 Hewitt (1999) for other lakes in the temperate zone, where small changes in the cold 1189 seasons have significant effects on the development of zooplankton. During the 1190 transition from the cold to the warm season, three aspects of temperature enhancing 1191 the zooplankton development point in the same direction: (1) growth stimulation by 1192 temperature dependent on the ontogenetic zooplankton development (see tempera-1193 ture dependent embryonic and postembryonic zooplankton development shortening 1194 the life cycles and thus promoting faster growth rates at sufficient food availability 1195 as discussed in Sect. 11.4.2.3), and (2) the vernal warming and (3) the climate driven 1196 intra-annual temperature increase. The progressive growth of many organisms in 1197 1198 spring is linked to the excess of nutrient availability after winter stagnation, the vernal increase of day length and water temperature, which is most beneficial for 1199 fast-growing small primary producers. With the onset of the growing season for 1200 1201 phytoplankton and related plankton organisms, vernal warming thus stimulates the increase of food availability for zooplankton (e.g., Adrian et al. 2006; Berger et al. 1202

2014). In addition, the intra-annual temperature increase driven by climate warming 1203 affects lake phenology mainly in winter and spring in Central Europe (Gerten and Adrian 2002, Blenckner 2005, Huber et al. 2010; example for the subtropics see e.g., Deng et al. 2014), as mentioned before in Sect. 11.4.2.1, and thus superimposes 1206 ontogenetic and seasonal temperature effects. The coherent vernal temperature response of all four zooplankton groups culminates in a narrow time window for their peak abundance in Alte Donau.

The cyclopoids were most closely linked to water temperature (Fig. 11.9a1), i.e. 1210 they mirrored a consistently positive response to temperature increase for all sea-1211 sons over the 19-year study period (Fig. 11.9a2) and did not built up a pronounced 1212 early summer depression (Fig. 11.9a3) which was different than for the other crus-1213 taceans or the rotifers in our study. Their development thus seemed to be triggered 1214 by different temperature effects pointing in the same direction. The temperature 1215 increase, which is linked to both the seasonal warming (Fig. 11.9a3) and the year-1216 to-year warming trend by climate change (Fig. 11.9a2), led to an overall success of 1217 these crustaceans in Alte Donau (Fig. 11.9a1). Mesocyclops leuckarti, Thermocyclops 1218 crassus and T. oithonoides (Fig. 11.2, Table 11.1) are known for their tolerance of 1219 high temperature during their embryonic development (e.g., Gophen 1976; Herzig 1220 1983b; Wagner and Adrian 2011) and occurrence at maximum temperatures in sum-1221 mer (e.g., Tackx et al. 2004). Together, these three thermophilic species became 1222 increasingly dominant after the phosphate precipitation in Alte Donau when com-1223 pared with the abundances of the remaining cyclopoids, which are known for a 1224 rather temperature-indifferent development (Megacyclops viridis, Eucyclops ser-1225 rulatus) or for being adapted to relatively low temperatures (Cyclops vicinus). 1226 Adrian and co-workers disentangled the seasonal temperature effects from global 1227 warming by looking at the phenology response of individual cyclopoid species and 1228 found evidence that the mentioned thermophilic 'summer' species benefit from 1229 global warming trends. According to their results (Gerten and Adrian 2002; Adrian 1230 et al. 2006), enhanced annual peak abundances of Mesocyclops leuckarti and 1231 Thermocyclops oithonoides relate to the climate driven warm years. In case of the 1232 latter species, a higher summer peak abundance was found to be accomplished by 1233 an earlier start of growth in the beginning of the year (Gerten and Adrian 2002), 1234 which corresponded to an earlier ice break up and an associated earlier spring peak 1235 of phytoplankton in the studied shallow polymictic lake (Adrian et al. 2006). The 1236 persistence of cyclopoids in our study could be accomplished by species alterations 1237 among these crustaceans towards thermophilic species. The cyclopoid copepods as 1238 a whole took advantage of seasonal and global warming on the one hand (Fig. 11.9a) 1239 and were robust against trophic changes on the other hand (Fig. 11.3). The dynamic 1240 of the calanoid copepods, which were less abundant and were represented by only 1241 one species (Eudiaptomus gracilis), was different. They accomplished higher yields 1242 for short periods during intermitted treatment years of extreme low phosphorus 1243 availability (Fig. 11.3, see also discussion in Sect. 11.4.1.1) but benefited the least 1244 from warming in general, which was indicated by seasonal decreases during par-1245 ticularly hot summer periods (Fig. 11.9b). The latter agrees with other studies show-1246 ing that E. gracilis is taking advantage from a relatively short embryonic development 1247 at low temperatures, but fails at high temperatures (e.g., Herzig 1983b). In accordance, unlike cyclopoid copepods, calanoid copepods can even reveal a negative response to elevated annual mean temperatures as found by other long-term field studies (Carter and Schindler 2012).

In Alte Donau, the second strongest response to the overall water temperature 1252 increase was found for cladoceran crustaceans (Fig. 11.9d1). The suppression of 1253 daphnids by climate warming, as discussed by Jeppesen et al. (2010b), Wagner et al. 1254 (2013) and Taysanoğlu et al. (2017), agrees with our finding that the pronounced 1255 summer decline of cladocerans refers to the long-term increase of WT in summer 1256 (Fig. 11.9d2, see also calanoids above). A further climate response most relevant for 1257 all zooplankton from rotifers to crustaceans in Alte Donau was the predominant 1258 positive response to intra-annual temperature variation in winter and spring in con-1259 cert with the common phenology of the close timing of their spring peak (Fig. 11.9, 1260 cf. Adrian et al. 2006, Gerten and Adrian 2000, 2002). The responses of individual 1261 zooplankton key species, which alternate between warm and cold year scenarios 1262 1263 and which also may alter the foodweb, are discussed in other climate studies (Adrian 1997; Benndorf et al. 2001; Winder and Schindler 2004b; Wagner and Benndorf 1264 2007; Berger et al. 2014). 1265

1266 11.5 Conclusions

The main compositional shift from a cladoceran-rotifer-rich to a copepod-rotifer-1267 rich zooplankton assemblage seems to be driven by bottom-up control and thus 1268 1269 relates to drastic reductions of phytoplankton yield after initial phosphorus precipitation and sustained low phosphorus availability during the subsequent years of 1270 biomanipulation. With the suppression of filter-feeding herbivorous cladocerans 1271 through reduced food supply, mainly selective-feeding omnivorous and herbivorous 1272 copepods survived under mesotrophic transparent-water conditions. Rotifers and 1273 1274 calanoid copepods became particularly abundant during the two Riplox-years when food availability drastically declined. Large-bodied crustaceans did not seem to 1275 consistently benefit from predator avoidance by re-grown submerged vegetation as 1276 assessed by the mean body-size of zooplankton community. The grazing pressure of 1277 mainly cyprinid fish thus could not be dampened by the refuge effect of re-1278 1279 established macrophyte stands in Alte Donau. During the long-term restoration period, significant climate warming trends were detected such as an increase in 1280 surface water temperatures in spring and a prolongation of the warm period in sum-1281 mer. Cyclopoid copepods seemed to benefit most from a warmed-up environment, 1282 as it was the only zooplankton group with a robust positive long-term response to 1283 1284 climate warming throughout all seasons. In addition, the prolonged summer periods linked to global warming may have supported the medusa stage of C. sowerbii in 1285 Alte Donau. 1286

Acknowledgments We thank David Livingstone and Susanne Wilhelm for valuable comments 1287 on methods of climate research during European Union projects REFLECT (http://www.ife.ac.uk/ 1288 reflect/) and CLIME (http://clime.tkk.fi/) that were useful for analysing the climate impact in Alte 1289 Donau. We are grateful to Thorsten Blenckner, Rita Adrian, Alois Herzig and two other colleagues 1290 for critical comments improving the manuscript. We also thank Anne Mette Poulsen for improving 1291 the language style. We would like to thank all of the numerous collaborators and the Municipal 1292 Department for permission of publication. We further thank the 'Wiener Fischereiausschuss' 1293 (Austrian Fishery Association) for providing long-term fish catch records. The long-term lake 1294 measurements were financially supported by Municipal Department - 45 (Water Management -1295 Vienna). 'Österreichisches Komitee Donauforschung, Internationale Arbeitsgemeinschaft 1296 Donauforschung' partly funded data assessment (K.T.). Further data evaluation (I.T.) was partly 1297 funded by the TU Wien Science award 2015 received by Wouter Dorigo (EOWAVE). 1298

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