

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 transparency, nutrients and biomass of phytoplankton, while information about changes in zooplankton that is triggered by lake management is often missing. In our 19-year study we used rotifers and crustaceans to document the effect of restoration measures on zooplankton in the oxbow lake Alte Donau, a former side-arm of the Danube River which is most popular for recreation and angler (cyprinid-dominated shallow water). The record covers four management periods: the period before restoration, the restoration (including years of chemical phosphate precipitation by Riplox treatment), the re-establishment of macrophytes and the sustained ‘stable conditions’. We found the highest abundance of all zooplankton in the first Riplox-year, with decreasing zooplankton abundance in following periods associated with the decline of phytoplankton. In the long term, the main compositional change related to a shift from a cladoceran-rotifer-rich to a copepod-rotifer-rich zooplankton assemblage. Thus, the large-bodied zooplankton shifted from a community composed of mainly filter-feeding herbivorous cladocerans under eutrophic algal-turbid conditions to mainly selective-feeding omnivorous and herbivorous copepods under mesotrophic transparent-water conditions. While the carbon ratio between zoo- and phytoplankton increased significantly during the first three periods and remained high under ‘stable conditions’, the mean body size of zooplankton did not exhibit a long-term trend. Short-term increases of large-bodied zooplankton coincided with an intermittent increase of calanoid copepod abundance (*Eudiaptomus*

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gracilis) during the chemical treatment concomitant with a drastic phytoplankton biomass reduction and the occurrence of large-bodied cladocerans (*Simocephalus vetulus* and *Sida crystallina*) in some years with re-established underwater vegetation. Besides the main response of zooplankton to the 'bottom up' control that was triggered by the reduction of phytoplankton food supply by one order of magnitude, we studied the zooplankton response to climate change. The impact of climate warming was evident from intra-annual coincidence of the climate signal (NAO_{DJFM}) and water temperature (WT) in winter and early spring, the increase of surface water temperature (SWT) by 1.52 °C per decade in April and the prolongation of the warm period (SWT > 22 °C) by 10.5 days per decade in summer. This prolongation of the warm season seemed to support the summer development of the medusa stage of freshwater jellyfish (*Craspedacusta sowerbii*). During the transition from spring to summer, the progressively earlier clear-water phase followed two trends. The first period with a 33-day earlier clear-water phase per decade coincided with pronounced ecosystem changes from a high to a low eutrophic state created by chemical restoration measures. The second period with a moderate earlier progression of 7 days per decade was accompanied by a further, slight TP decrease associated with the re-establishment of macrophytes. When comparing rotifers, cladocerans, calanoid and cyclopoid copepods, the latter group benefits most from seasonal temperature increases and climate warming.

11.1 Introduction

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

Alte Donau in Vienna faced these different aspects of an urban lake mentioned before. The habitat for cold-water fish assemblages in the Danube River shifted to a habitat for warm-water fish assemblages after the cut-off from the main river channel in 1870–1875 (see fish in Chap. 15, history in Chap. 2). During the mesotrophic period in the 1980s, the oxbow lake was cyprinid-dominated with extensive dense underwater vegetation (Löffler 1988). In the 1990s, Alte Donau has undergone a strong nutrient enrichment (Dokulil et al. 2010a). This was accompanied by the development of large cyanobacterial blooms and a consequently low water transparency. The highest phytoplankton biomass was measured in 1994. The phytoplankton was dominated by the filamentous cyanobacterium *Cylindrospermopsis raciborskii* (Dokulil and Mayer 1996) and reached a chlorophyll-a concentration of about $140 \mu\text{g L}^{-1}$. Concomitantly, the water transparency was lowest with a Secchi depth of 0.28 m in September 1994 (see Fig. 6.4 in Chap. 6, phytoplankton composition in Chap. 9). The awareness of the value of urban ecosystems led to actions to restore Alte Donau (Chap. 5). The restoration comprised different treatments such as the use of Riplox (1995/1996) to limit the growth of planktonic cyanobacteria and algae (Chap. 9) and the re-establishment of submerged vegetation for the purpose of sustained restoration by biomanipulation (Chap. 8). The lake restoration included both the open water bodies and the banks (Chap. 18). Furthermore, a master plan of urban planning was elaborated to generate the surrounding recreational area in order to create a better quality of urban life in Vienna (Chap. 19).

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

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

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 treatment including further restoration measures, the period of re-establishment of macrophytes and the period of 'stable conditions'. In addition, we explore if the impact of restoration on the development of zooplankton of Alte Donau was superimposed by global warming.

11.2 Methods

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 $3.54 \times 10^6 \text{ m}^3$ and a surface area of 1.43 km^2 (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 bottom at 4.5 m) with a 5 L Schindler sampler in the south basin (AD1) and the north basin (AD4) and were integrated over depth. The samples were filtered through a $44 \mu\text{m}$ mesh size net, resuspended in 50 mL lake water and fixed with formaldehyde. The zooplankton time series presents a consistent data set as determination of species and counting of samples was conducted by the same person (M.G.) for the whole 19-year period. We calculated the biomass of the crustaceans by length to weight regressions according to McCauley (1984) and Bottrell et al. (1976), assuming a dry to wet weight ratio of 0.15. We derived the biomass of rotifers from measurements of all three dimensions following Ruttner-Kolisko (1977). To compare the biomass of zooplankton and the biovolume of phytoplankton, we translated the mass related measures of both plankton groups into carbon content by using the volume conversion of Behrendt (1990).

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), 3 – '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 $\text{Ca}(\text{NO}_3)_2$ 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 on the ecosystem response comparing the ecosystem before the restoration with the situation during the first and the second Riplox-year revealed different pathways of prompt responses by the plankton community. It showed that the short-term impact of chemical treatment in the first year was quite different from that observed during the second year (Teubner et al. 2003). For this reason, we split the restoration period in two, i.e. 2a) April 1995 to March 1996 and 2b) April 1996 to 1999. One main focus of this book chapter is the long-term impact on zooplankton during the five restoration periods (1, 2a, 2b, 3 and 4).

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 phytoplankton and zooplankton were not always sampled by exactly 2-week intervals, we interpolated the available data at daily resolution (Livingstone 2003; Sapna et al. 2015) and averaged these over a two-week period. These data were then used to calculate the zooplankton to phytoplankton carbon ratios and the net change rates of zooplankton at regular 2-week time intervals (Figs. 11.5 and 11.6). The net change rate of zooplankton biomass (k_{zoo} , hereafter referred to as net growth rate of zooplankton) is calculated as

$$k_{zoo} = (\ln Zoot2 - \ln Zoot1) / \Delta t \quad (11.1)$$

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

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

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

11.2.3 Data Treatment, Statistics to Identify Climate Response

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

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

reveal temperature trends during the 19-year period. We further calculated the number of 'warm' lake water days (surface water temperature, SWT, above 22 °C) to analyse the length of the warm period in summer (Fig. 11.7b). In order to trace the climate response related to this summer period, we used the annual NAO. Additionally, we analysed the extreme hot summer period by determining the number of days exceeding the threshold of 25 °C, as this temperature was the highest integer of the biweekly averages of SWT (Fig. 11.7b). According to suggestions regarding the optimal growth temperature for the polyp (19–25 °C) and the medusa development of *Craspedacusta sowerbii* derived in culture experiments (Folino-Rorem et al. 2016), we calculated the annual periods with 19–25 °C SWT and above 21 °C SWT in number of days per year in Alte Donau. All data in Fig. 11.7 (with the exception of the skewed distribution for the number of extreme hot days above 25 °C SWT) and Fig. 11.9 satisfy normal distribution. Despite the normal distribution for data in Fig. 11.7, the respective trends of the year-to-year variation are calculated as robust lines by non-parametric fitting according to Theil (1950) as described in Helsel and Hirsch (2002). These robust trend lines are applied to calculate the reliable slope of the year-to-year trends, which are robust against outliers of unusual high or low values in the first or last year of observation. The statistical significance of the trends is calculated by Mann-Kendall tests using R (McLeod 2015). Regarding the year-to-year variation of the clear-water phase (Fig. 11.7d), a rapid decrease occurred in the beginning and was followed by a slower decrease in later years. For this reason, the time series was tested for breakpoints using Davies-test in R (Mugge 2008, 2015), but the results were not significant (p -value>0.05). Nevertheless, data were separated into two phases based on the *a priori* assumption of different stages of the lake restoration. The segmented two regression lines are shown in Fig. 11.7d. The first period refers to the rapid phytoplankton biomass decrease occurring in the years prior to treatment initiation and the restoration treatment period including the phosphate precipitation (period 1 and 2), while the second period covers the subsequent years where only small changes in the phytoplankton yield occurred, i.e. the periods with macrophyte re-establishment and stable conditions (period 3 and 4; periods see in methods Sect. 11.2.1 above). In addition, the regression line for the whole time series is displayed.

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).

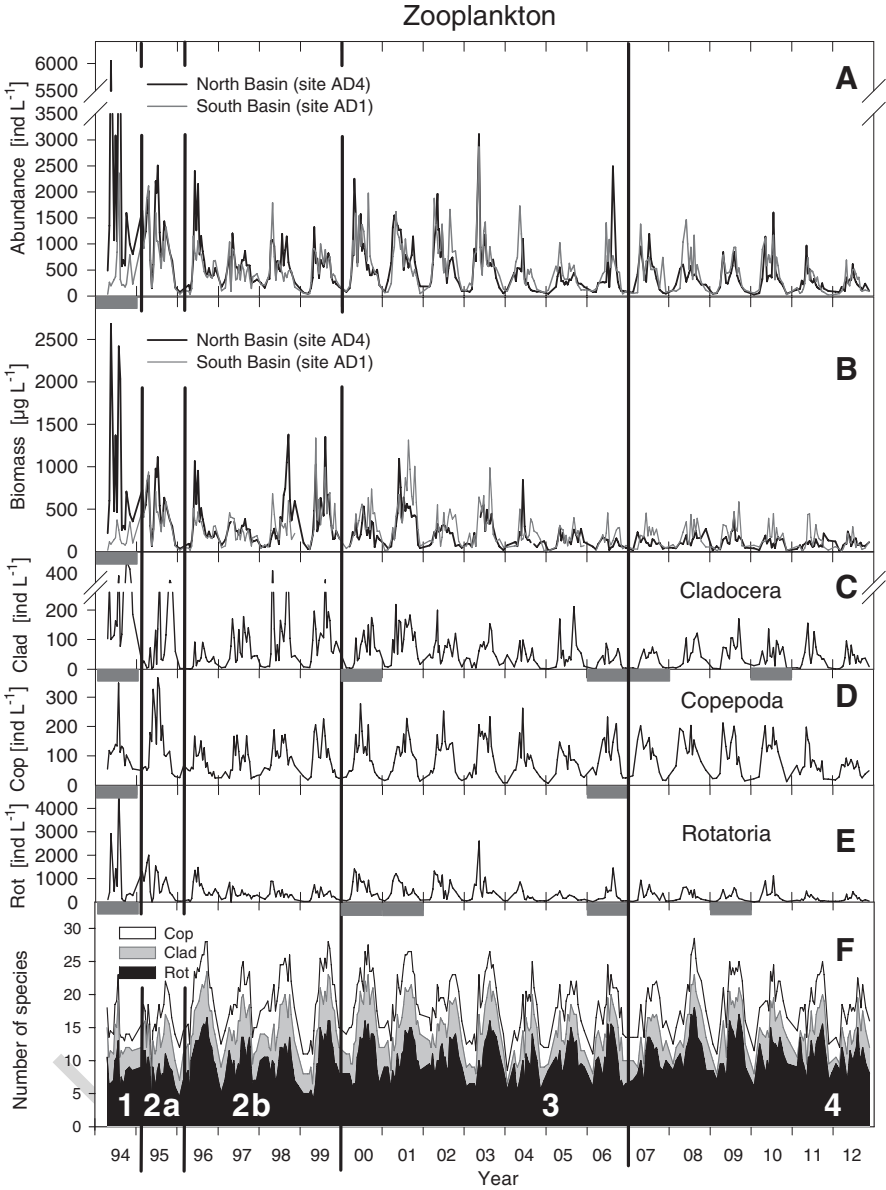


Fig. 11.1 Long-term series of zooplankton development comprising five periods: before restoration (1), restoration with chemical Riplox treatment (2a, 2b), re-establishment of macrophytes by periodical water level drawdown (3) and ‘stable conditions’ (4). Abundance (a) and biomass (b) of total zooplankton 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 south basin, we only found statistically significant differences in the year 1994 (Fig. 11.1a, b; bars indicate years with significant differences between sites; H-test, $p < 0.05$ for rotifer abundance, all other $p < 0.001$). The annual average of zooplankton abundance in the north basin was 2027 individuals per litre in 1994, which corresponds to a zooplankton biomass of 899 $\mu\text{g L}^{-1}$. Zooplankton abundance in the south basin was about six times lower than in the north basin with annual mean values of 324 individuals L^{-1} , which corresponds to a biomass of 152 $\mu\text{g L}^{-1}$. Furthermore, we found significantly lower values in the south basin for the individual taxonomic groups, i.e. cladocerans, copepods and rotifers, in the year 1994 (see abundance in Fig. 11.1c, d, e). These statistically significant differences are probably mainly due to the lake treatment by water exchange in 1993 which aimed at improving the water quality in Alte Donau; relatively nutrient-poor water from Neue Donau (New Danube) was introduced to flush the eutrophied water body of Alte Donau. The water from the channel Neue Donau entered Alte Donau in the south end of the south basin (site 'Seestern'). Thus, we assume that the north basin rather than the south basin mirrors the state of the zooplankton community during the eutrophication period in 1994 before the chemical treatment started in 1995. As these site differences correspond to a different magnitude of zooplankton abundance and biomass, but not to a significantly different species pattern, we did not treat the data for the two basins separately. Moreover, we did not find between-site differences in abundance or biomass for either total zooplankton or for individual zooplankton groups during the subsequent 5-year 'restoration' period from 1995 to 1999 (see period 2 in Fig. 11.1). Also, in the next 13 years that included the period of 'macrophyte re-establishment' and 'stable conditions', we did not find any statistically significant between-site differences for total zooplankton abundance or biomass. Statistically significant abundances were only detected for some individual zooplankton groups in particular years. These significant differences are indicated by grey bars for years 2000, 2001, 2006, 2009 and 2010 in Fig. 11.1c, d, e (H-test, $p < 0.05$ for rotifers 2000, $p < 0.05$ for all others).

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

11.3.2 Species Composition of Zooplankton

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

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

Table 11.1 List of zooplankton species found from 1993 to 2012

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

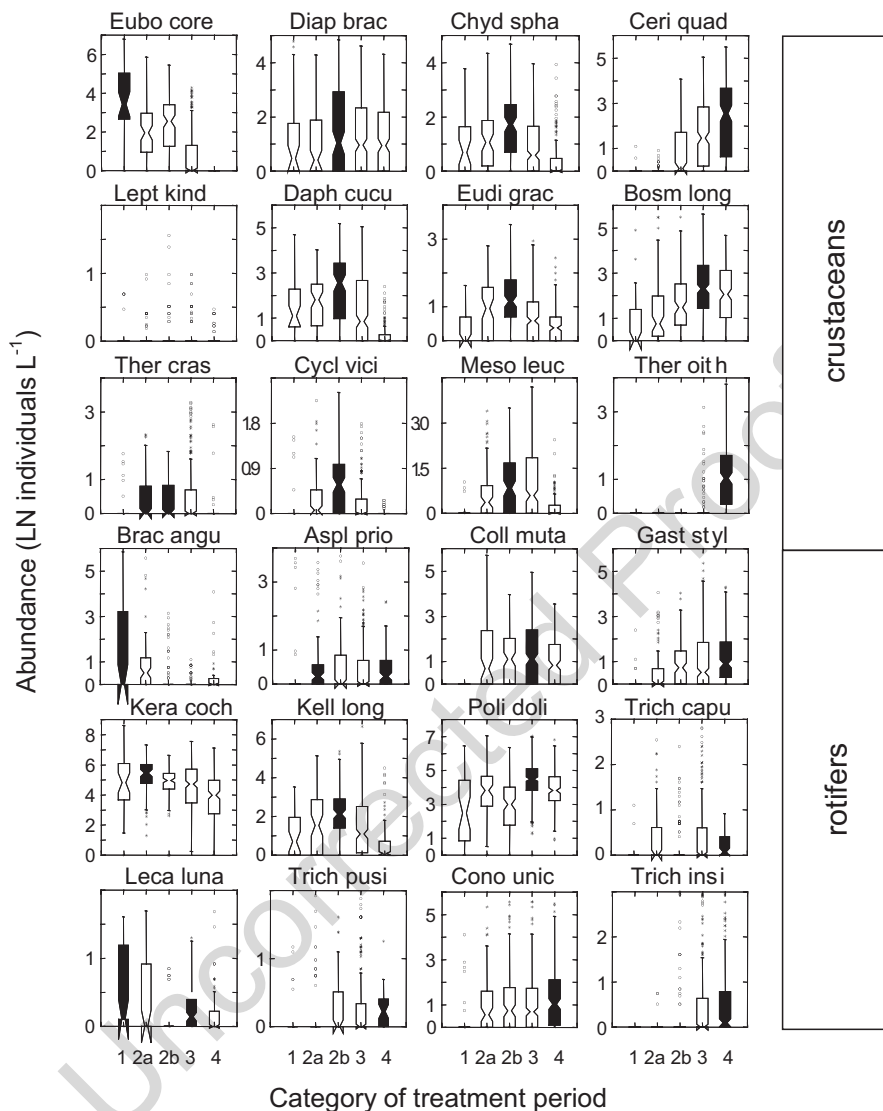


Fig. 11.2 Box-whisker plots of the abundance of individual species of cladocerans, copepods and rotifers during the five treatment periods. Cladocerans: Eubo core – *Eubosmina coregoni*, Diap brac – *Diaphanosoma brachyurum*, Chyd spha – *Chydorus sphaericus*, Ceri quad – *Ceriodaphnia quadrangular*, 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 leuckarti*, 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*, Poli doli – *Polyarthra dolichoptera-vulgaris*, Trich capu – *Trichocerca capucina*, Leca luna – *Lecane luna*, Trich pusi – *Trichocerca pusilla*, Cono unic – *Conochilus unicornis*, Trich insi – *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 bacterivorous/algivorous (21%) cladocerans are found. Carnivorous species only constitute 8%. The most abundant cladocerans are *Eubosmina coregoni*, *Ceriodaphnia quadrangular*, *Daphnia cucullata*, *Bosmina longirostris*, *Diaphanosoma brachyurum* and *Chydorus sphaericus* (Fig. 11.2). The adult stages of copepods are mainly omnivorous (67%). The remaining recorded species are classified as algivorous (33%). The main copepod species are *Eudiaptomus gracilis*, *Thermocyclops crassus*, *T. oithonoides* and *Mesocyclops leuckarti*, while *Cyclops vicinus* is less abundant (Fig. 11.2). In addition to the more common species displayed in Fig. 11.2, the relatively rare littoral cladocerans, *Simocephalus vetulus*, *Sida crystallina* and *Acroperus harpae*, were found.

11.3.3 Comparison of Zooplankton Composition Between the Five Treatment Periods

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

very low in abundance and were only found in the late period of re-establishment of macrophytes and under stable conditions (from April 2005 and onwards). *Simocephalus vetulus* reached a maximum abundance of 0.75 individuals L⁻¹ and a biomass of 5.6 µg L⁻¹, and *Sida crystallina* an abundance of 0.5 individuals L⁻¹ and a biomass of 2 µg L⁻¹. Both species were only found in 1–2.5% of the plankton samples taken during period 3 and 4. Another littoral but smaller bodied cladoceran species, *Acroperus harpae* with a body length of 700 µm, was also found from the period of macrophyte re-establishment onwards. *A. harpae* occurred more regularly during periods 3 and 4 than the above-mentioned two littoral, large-bodied cladocerans (first occurrence of *A. harpae* recorded in April 2003, present in about 10% of the samples taken in period 3 and 4).

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

The statistical difference between the five periods of ecosystem-based lake restoration management is shown in Fig. 11.3 for the abundances of all zooplankton species and for the four taxonomic zooplankton groups. For ‘all zooplankton’, we found significant differences between the median abundance of the five periods (Kruskal-Wallis test, $H = 64.76$, $df = 4$, $p < 0.001$). The highest abundance of all zooplankton occurred in the first year of the Riplox treatment (period 2a). At the end of the ‘restoration’ (period 2b), total zooplankton abundance decreased significantly (subgroup ‘b’). The period of macrophyte re-establishment seemed to be accompanied by a recovery of zooplankton abundance (overlap of subgroups a and b). Finally, during the latter part of lake restoration (period 4 of ‘stable conditions’), total zooplankton abundance demonstrated a further significant decrease (homogeneous subgroup ‘c’) and the lowest abundance in a comparison between all periods (1, 2a, 2b, and 3).

The four taxonomic groups revealed a different pattern of succession during the periods of lake restoration. The abundance of calanoids (Kruskal-Wallis test, $H = 17.28$, $df = 4$, $p < 0.01$) did not differ statistically when comparing the eutrophic period with the periods of ‘macrophyte re-establishment’ and ‘stable conditions’ (all three periods belong to subgroup ‘b’). The abundance of calanoids increased only shortly 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 only shortly

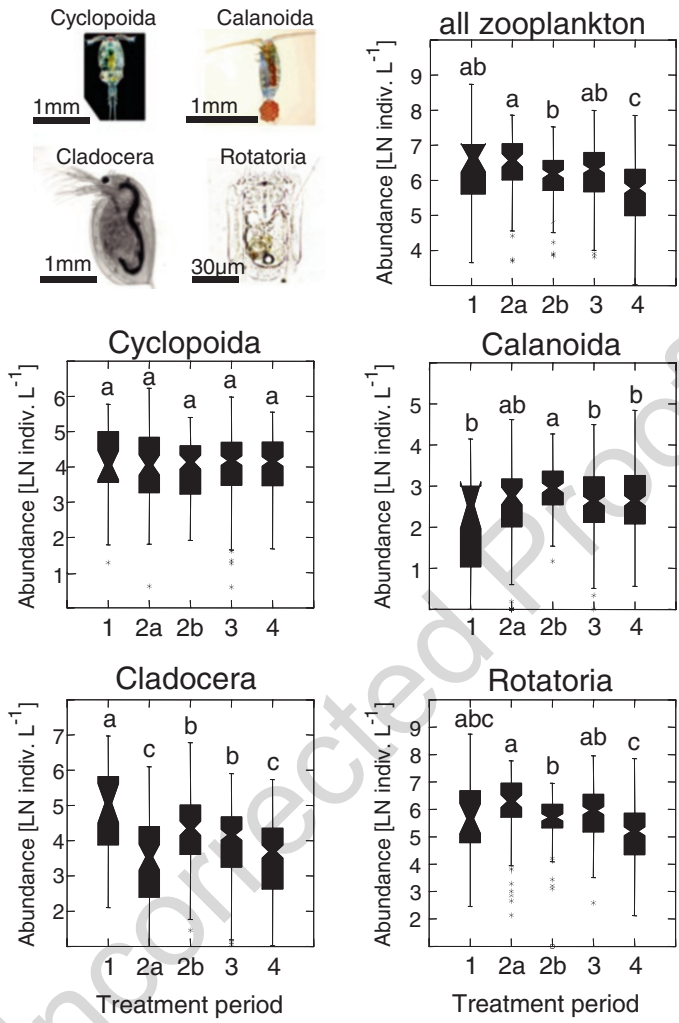


Fig. 11.3 Box-whisker plot of the abundance of all zooplankton, copepods (cyclopoids and calanoids), cladocerans and rotifers during the five treatment periods. According to Kruskal-Wallis tests, statistical differences among lake treatment periods were found for all zooplankton groups ($p < 0.01$) with 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

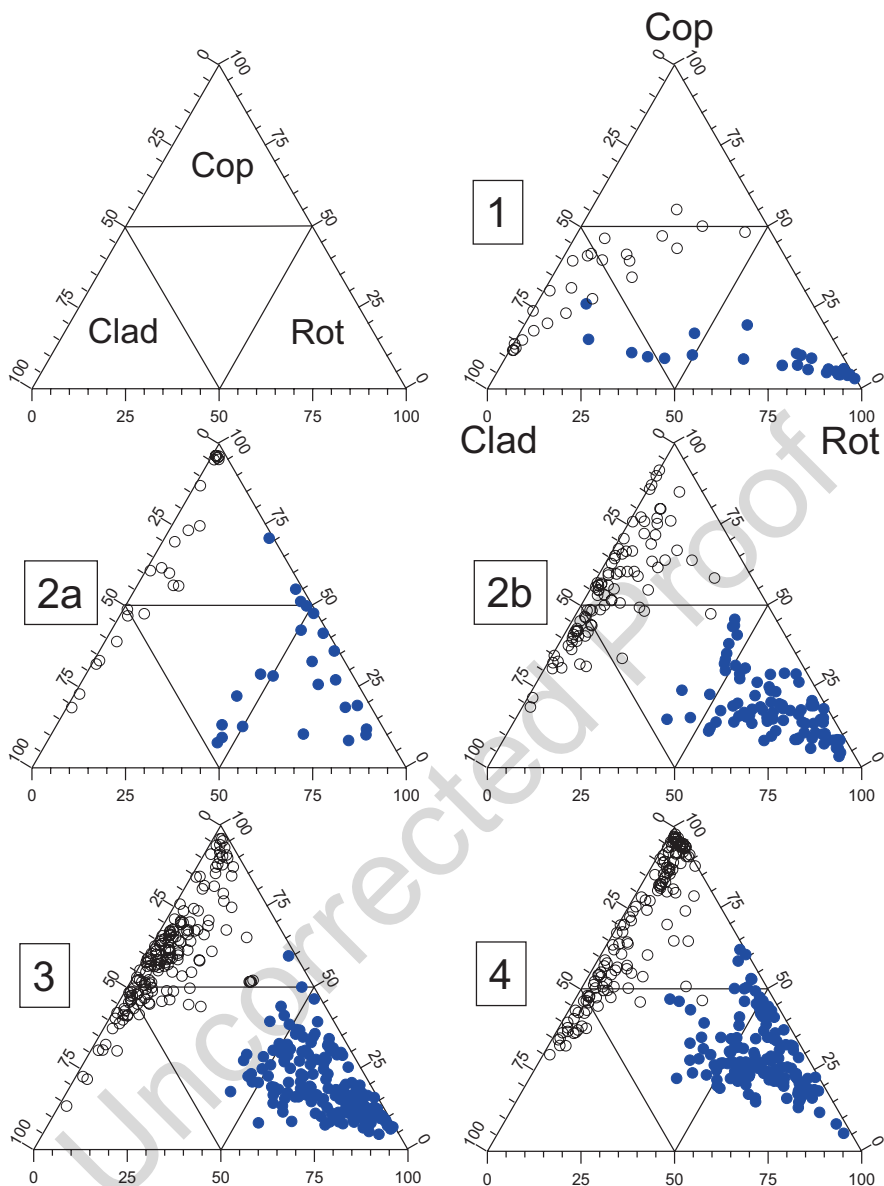


Fig. 11.4 Zooplankton structure displayed as the relative contribution of copepods (Cop), cladocerans (Clad) and rotifers (Rot) to total zooplankton for the five treatment periods by triangular diagrams. Filled blue circles denote abundance, open circles biomass. 1, 2a, 2b, 3 and 4 are the treatment 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)

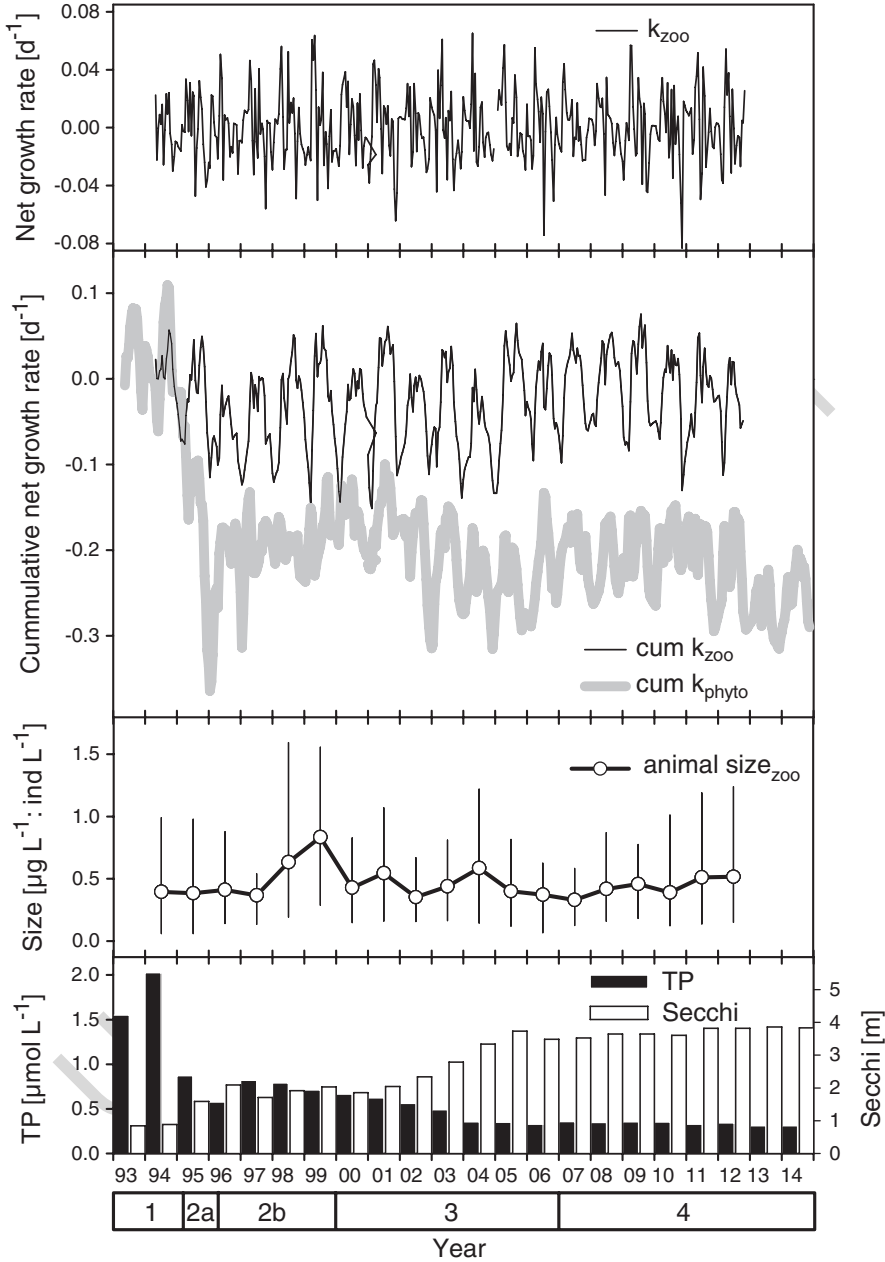


Fig. 11.5 Time series of net change rates of zooplankton (A, 1994–2012), cumulative net change rates of zooplankton and phytoplankton (B, period for zooplankton as in A, for phytoplankton 1993–2014), annual averages of zooplankton body size (C, calculated as the ratio of zooplankton biomass [$\mu g\ L^{-1}$] 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 abundance of cladocerans showed pronounced differences among lake treatment periods (Kruskal-Wallis test, $H = 60.87$, $df = 4$, $p < 0.001$). These crustaceans were mainly abundant in the eutrophication period (1) with a strong intermediate decrease in the first year of the Riplox treatment (2a), with a rising abundance during period 2b and a decrease in the subsequent periods. The low abundance during the final 'stable' period of restoration management is similar to the low abundance achieved after the abrupt decrease with the first Riplox-treatment. Rotifer abundance showed also significant differences (Kruskal-Wallis test, $H = 69.97$, $df = 4$, $p < 0.001$) and tended to increase in the first year of the Riplox treatment (2a), reaching peak abundance compared with all other periods. In the following years, the abundance of rotifers decreased again. The lowest rotifer abundance, found in the last period, i.e. 'stable conditions' (subgroup c), was similar to the initial abundance under eutrophic conditions before application of chemical restoration.

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

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

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.

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

The time series of the net growth rate of zooplankton, the zooplankton size and related measures are shown in Fig. 11.5. The net growth rate of zooplankton biomass is depicted in Fig. 11.5 a. Positive rates ($n = 219$, mean positive rate is 0.0185 day^{-1}) were less common than negative rates ($n = 227$, mean negative rate is -0.0182 day^{-1}). The total sum of the positive rates over the whole study period from 1994 to 2012 was 4.05 day^{-1} and -4.13 day^{-1} for the negative rates. Thus, the zooplankton biomass decrease was nearly compensated by the zooplankton biomass increase over the 19 years. As to the net growth rate of zooplankton abundance, the numbers differed only slightly (positive changes: $n = 205$, mean = 0.0191 day^{-1} , total sum = 3.92 day^{-1} ; negative changes $n = 241$, mean = -0.0165 , total sum = -3.97 day^{-1}) and thus do not describe a substantially different situation than that for the long-term dynamics of the net growth rates of zooplankton biomass (graph for the net growth rate of zooplankton abundance is not shown). In accordance with this, the cumulative net growth of zooplankton biomass was relatively balanced throughout the five periods of ecosystem-based management. The only period with clearly limited zooplankton development in the growing season occurred in 1996, i.e. the year of the second chemical treatment (period 2b). In the successive 2 years within the 2b restoration period, zooplankton biomass recovered to the original level and then remained stable following a rather regular seasonal pattern with intra-annual fluctuations (Fig. 11.5b). The fairly balanced long-term dynamic of the net growth rates of zooplankton biomass was, however, quite different from the dynamics of the net growth rates of phytoplankton (Fig. 11.5b). In the year of the first chemical phosphate precipitation (period 2a), the phytoplankton biomass decreased as a response to the reduced concentration of the main nutrient, phosphorus (Fig. 11.5b, d). The drastic loss of phytoplankton biomass could not be compensated by positive net growth rates afterwards due to the persistence of low phosphorus availability. In turn, this led to a stabilised high water transparency (Fig. 11.5d, transparency is displayed as Secchi depth; for long-term dynamics of nutrients, phytoplankton and related measures see also Chaps. 6 and 9).

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

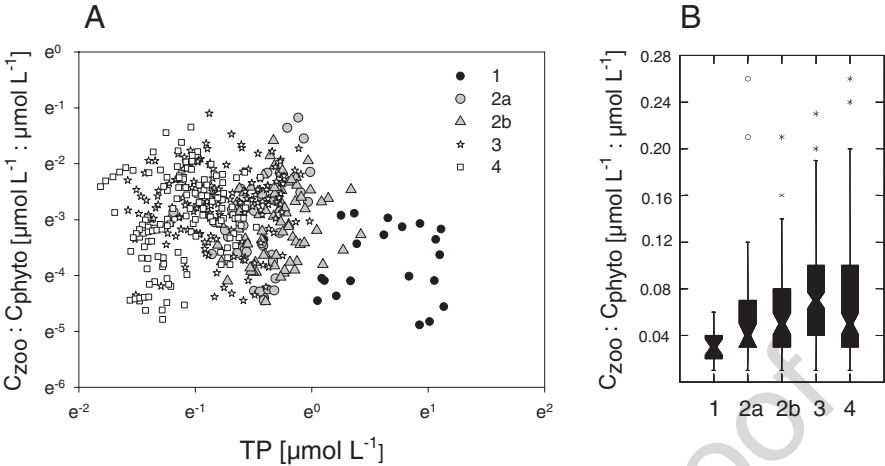


Fig. 11.6 Relationship between the carbon of zooplankton and phytoplankton for the five treatment periods from 1994 to 2012. (a) carbon ratio (molar) versus total phosphorus concentration (TP, molar) displayed on a logarithmic scale (LN), (b) carbon ratio for individual treatment periods as Box-whisker 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 years 1998/1999 and in year 2004. The first peak coincided with the naturally recovered underwater vegetation after the second chemical phosphate precipitation. 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).

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

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

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

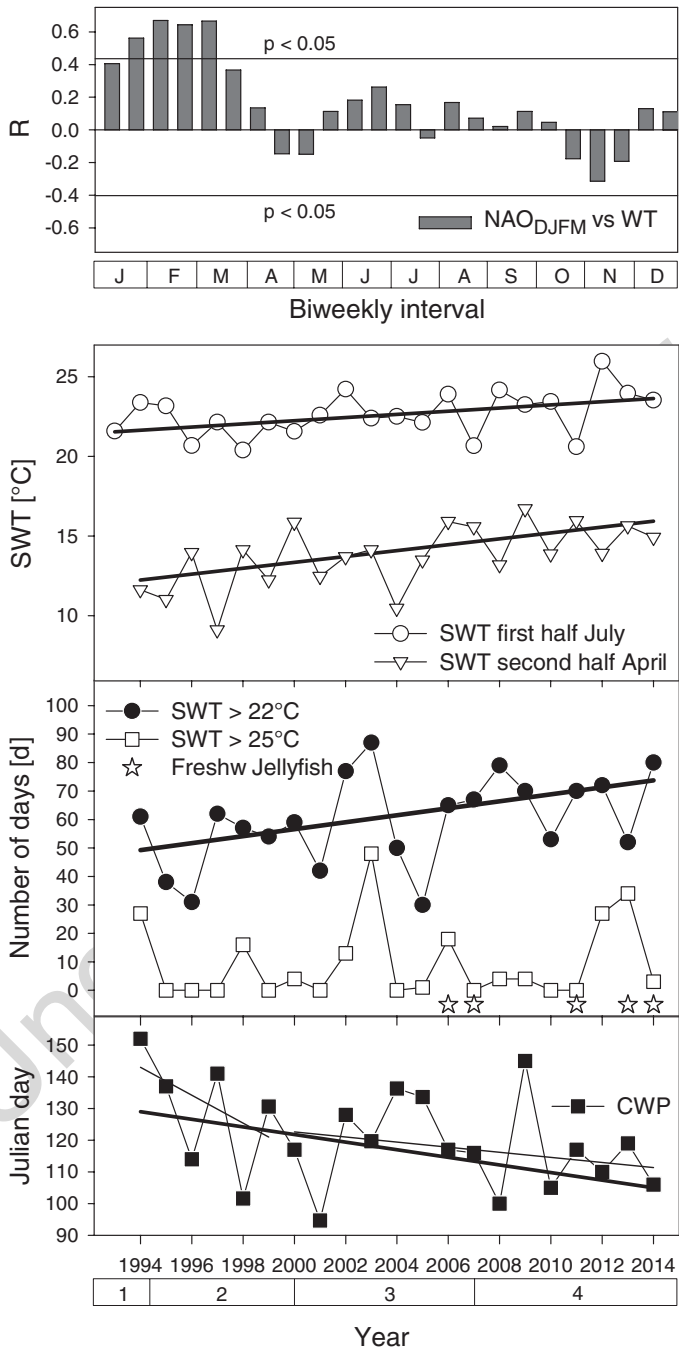


Fig. 11.7 Impact of climate warming. A: Correlation between the climate index NAO_{DJFM} and the water temperature integrated over the water column (WT) for all biweekly intervals from January (J) to December (D) during 21 years (1994–2014). Lines in the correlogram indicate the threshold

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 impact of this climate signal then abates from late March and onwards.

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

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

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 Sect. 11.2.3), the year-to-year variation still showed earlier timing for both time segments. The robust trend line for 1994–1999, covering the 2 years before restoration and the ‘restoration period’ (period 1 and 2), exhibited a 33-day earlier onset per decade of the clear-water phase. This shift is much more pronounced towards early spring than the shift indicated by the second robust line for 2000–2014. The second robust line is describing only a shift of 7 days earlier per decade (‘re-established macrophytes’ and ‘stable conditions’, period 3 and 4).

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

The cyclopoids were positively related with temperature at almost all times of the year (Fig. 11.9a2). The relationship was strongest during the cold season and culminated in a statistically significant relationship during four biweekly intervals from December ($R = 0.67$ and 0.66 , $p\text{-value} < 0.05$) to January ($R = 0.62$ and 0.69 , $p\text{-value} < 0.05$, Fig. 11.9a2). Thus, cyclopoids, which commonly show peak abundance during the summer season, generated particularly high abundances when WT was unusually high during winter. In contrast to the cyclopoid copepods, the less dominant calanoid copepods exhibited a pronounced bimodal seasonal development pattern (Fig. 11.9b3) and an inverse relationship with seasonal WT in late summer to autumn (Fig. 11.9b2). During the autumn peak from September to early October, the abundance of calanoids seemed to be stimulated in years with relatively low temperatures compared with the situation in warm years ($p\text{-value} > 0.05$, Fig. 11.9b2). This inverse relationship between abundance and warming in autumn on the one hand and the general suppression of calanoid development for months during the growing season on the other (midsummer decline from June to August in Fig. 11.9b3) weakened the long-term relationship between calanoid abundance and water temperature as shown in Fig. 11.9b1 ($P = 0.22$, $p\text{-value} < 0.001$). In case of the cladocerans (Fig. 11.9d), the seasonal abundance was suppressed again from June to August (Fig. 11.9d3). In contrast to the copepods, no significant inverse relationship was found between the long-term warming trend and the long-term development of the cladocerans (Fig. 11.9d2). The relationship traced in the long-term data

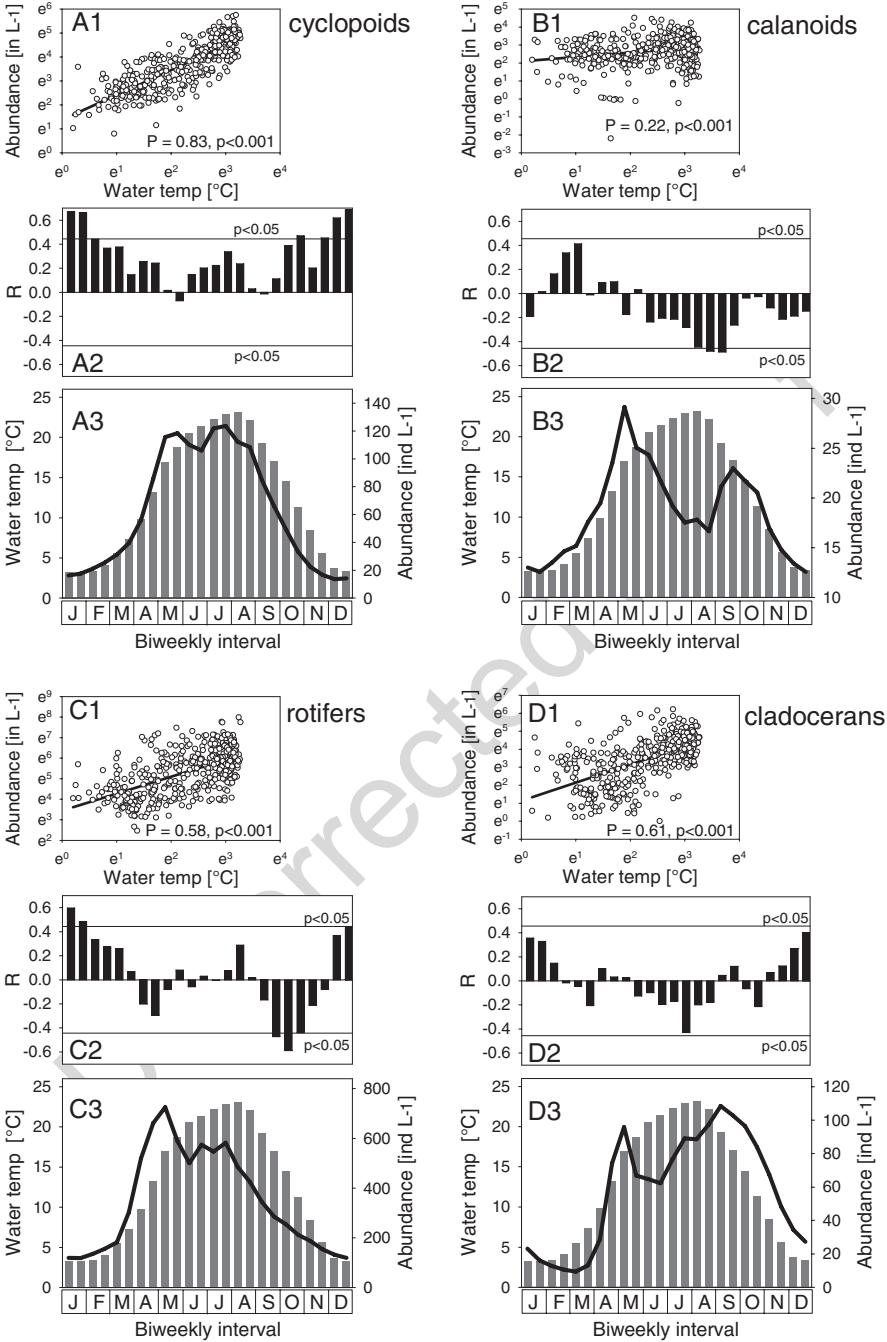


Fig. 11.9 Relationship between water temperature (WT) and the abundance of the four main taxonomic zooplankton groups (a–d). **a1**: Correlation between WT and the abundance of cyclopoid copepods reflected by long-term data (P = Pearson correlation coefficient, n = 449).

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

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

Fig. 11.9 (continued) **a2**: 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 ($p\text{-value} < 0.05$). **a3**: 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 the 19-year study period). Graphs for rotifers (**c1–c3**), calanoid copepods (**b1–b3**), and cladocerans (**d1–d3**) are similar to that of cyclopoids (**a1–a3**)

11.4 Discussion

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

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

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 phytoplankton when considering that the size of food particles increases with animal size (e.g., Brooks and Dodson 1965; Burns 1968, 1969; Arndt et al. 1993; Shapiro and Wright 1984; Lampert et al. 1986; Gulati and Van Donk 2002; Gudimova et al. 2011). In Alte Donau, cladocerans such as *Daphnia cucullata* and *Chydorus sphaericus* were found to be the dominant grazers when filamentous cyanobacteria (*Cylindrospermopsis raciborskii*, *Limnothrix redekei*) bloomed in spring and summer in the year 1994 (Dokulil and Mayer 1996; Mayer et al. 1997; Dokulil 2015) and macrophyte biomass was low (2 tons dry weight of macrophytes for the whole water basin, see Chap. 8). The cladocerans were the only zooplankton group attaining highest abundance before the chemical treatment (Fig. 11.3). When comparing the relative contribution in the eutrophication period with later restoration periods, zooplankton biomass was composed of high portions of cladocerans (Fig. 11.4-1). In terms of biomass, this period hosted a cladoceran-dominated zooplankton assemblage (cladoceran-rotifer-rich), and in terms of abundance it was a rotifer-cladoceran-rich community (Fig. 11.4-1). After restoration, the zooplankton biomass shifted towards a copepod-rotifer-rich community and in terms of abundance to a rotifer-copepod-rich community. The crustacean zooplankton therefore shifted from mainly filter-feeding herbivorous cladocerans in the eutrophic algal-turbid state to mainly selective-feeding omnivorous and herbivorous copepods in the mesotrophic transparent-water (trophic states are illustrated Fig. 20.3 in Chap. 20). Such species shifts from cladocerans to copepods are commonly described along trophic gradients from high to low total phosphorus in lakes (Pace 1986; Jeppesen et al. 2000; Kasprzak and Koschel 2001; Köhler et al. 2005). In Alte Donau, the majority of the copepod species consisted of cyclopoids (6 species in Table 11.1), calanoids only being represented by one species (*Eudiaptomus gracilis*), as also found in other studies (Anneville et al. 2007a). The dominance of the omnivorous cyclopoid copepods indicates moderate food availability under eutrophic to mesotrophic conditions (Kasprzak and Koschel 2000; Anneville et al. 2007b; Mehner et al. 2008). The herbivorous calanoid copepods, constituting 19% of the copepods in a long-term perspective, typically indicate a nutrient state lower than mesotrophic, i.e. it is generally assumed that the calanoid copepods are adjusted to lower food thresholds than cyclopoid copepods (Adrian 1997; Kasprzak and Koschel 2000; Mehner et al. 2008). The suggestion that calanoids have a low demand for algal food agrees with our observations in Alte Donau where an intermediate increase in calanoid abundance occurred during the two Riplox-years (restoration periods 2a and 2b), i.e. peak abundances of calanoids coincided with extremely low phytoplankton biomasses after phosphate precipitation (Fig. 11.3). According to Sommer and Stibor (2002), large-bodied calanoid copepods and cladocerans might not be mutually

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

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 contributes to enhancing water transparency if the internal load of phosphorus has been reduced a priori, thereby ensuring limited growth of algae through bottom-up control. The Riplox-treatment (Ripl 1976), i.e. the chemical phosphate precipitation and stabilisation of the oxidized sediment in April 1995 and April 1996, aimed at creating a prompt phosphorus reduction in the water column and a long-term reduction of the internal phosphorus load at the sediment-water interphase (treatment described in Chap. 5 and in Donabaum et al. (1999); for a review of the retention of internal phosphorus load see, for instance, Søndergaard et al. 2001). Phosphorus is the main limiting nutrient element for phytoplankton growth in freshwaters (Hecky and Kilham 1988). The relationship between total phosphorus and phytoplankton yield (estimated chlorophyll-a or phytoplankton biovolume) is depicted in Fig. 9.10 (Chap. 9) and Fig. 20.3 (Chap. 20), showing the strong phosphorus reduction leading to lower phytoplankton biomass in 1995 and 1996 (see also time series in Fig. 11.5).

The total phosphorus concentration of $2.37 \mu\text{mol L}^{-1}$ before the restoration decreased to $0.89 \mu\text{mol L}^{-1}$ in 1995 and $0.6 \mu\text{mol L}^{-1}$ in 1996 after the Riplox treatment in Alte Donau (median values derived from Teubner et al. 2003). Triggered by phosphorus precipitation, the planktonic community adjusted to efficiently utilising the remaining phosphorus sources. Planktonic biota acted here as a sink for phosphorus under P-limitation which was seen in two ways: (a) with the tighter coupling between food and consumer organisms, a larger portion of phosphorus was bound by biota at the expense of the dissolved P-fractions, and (b) with the compositional shifts from N-rich cyanobacteria to P-rich eukaryotic algae, the increase in the relative importance of P-rich bacteria and the increase of the zooplankton portion relative to phytoplankton, the stoichiometry of biota shifted towards a P-rich plankton community (Teubner et al. 2003). The zooplankton played an important role in accomplishing the higher phosphorus utilisation efficiency of the plankton community. A tight coupling at both the producer-consumer and the nutrient-

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

The food quality for zooplankton during both Riplox-years has rapidly changed. While the phytoplankton biovolume significantly decreased year for year with P-precipitation, bacterial biomass remained almost the same (Teubner et al. 2003). With a significantly higher bacterial enzyme activity mobilising the P source from the dissolved organic phosphorus fraction in Alte Donau, the planktonic bacteria further gained relative importance over phytoplankton for P acquisition under reduced phosphorus availability. The loss rates of bacterioplankton (not the standing crop) were in the same order of magnitude as those of phytoplankton. With the reduction of total phosphorus, they even became slightly higher than those of phytoplankton (Teubner et al. 2003). These increased relative loss rates have been regarded as indirect evidence of enhanced grazing on bacteria (e.g. by rotifers and ciliates) which has been observed in other ecosystems (e.g., Berman 1990). According to other studies (e.g., Jones and Cannon 1986; Capblancq 1990; Elser and Goldman 1991; Loreau 1995; Gismervik et al. 1996; Queimaliños et al. 1998; Vadstein 2000; Tadonlélé et al. 2009), the planktonic bacteria in Alte Donau, the eukaryotic phytoplankton and the small-bodied zooplankton (rotifers and ciliates), seemed to be the most important factors for accelerating the circulation of matter under reduced phosphorus availability in both Riplox-years 1995/96. After the

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).

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

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

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

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

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.

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 is commonly observed that large-bodied zooplankton (mainly *Daphnia*) becomes predominant in shallow lakes when the number of planktivorous fish decreases and vice versa (e.g., Brooks and Dodson 1965; Carpenter et al. 1985; Gilbert 1988; Järvinen and Salonen 1998; Jeppesen et al. 2000; Benndorf et al. 2001; Mehner et al. 2008; He et al. 2017). In accordance with this, an increase of large zooplankton such as *Daphnia pulex* has been observed to occur in years after natural fish mortality under ice in winter (e.g., Rucker et al. 2003). In contrast, small-sized zooplankton species have been recorded to benefit from fish stocking in high-altitude lakes, naturally fishless mountainous freshwater basins (Schabetsberger et al. 2009).

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

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

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

11.4.2 Response of Zooplankton to Global Warming: What Are the Specifics of Urban Shallow Alte Donau?

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

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

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

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

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

11.4.2.2 Warming and the Most Spectacular Zooplankton Species: Freshwater Jellyfish

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

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

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 phytoplankton by zooplankton grazing during the spring-summer transition, was of early interest in the study of the impact of global warming on lake biology (Müller-Navarra et al. 1997; Gerten and Adrian 2000; Jeppesen et al. 2003; Shatwell et al. 2008; De Senerpont Domis 2013; Berger et al. 2007; Huber et al. 2008; Berger et al. 2014). The relative robustness of the timing of the clear-water phase associated with other physico-biological lake events led to a description of the general seasonal succession pattern found in many lakes in the temperate zone. The pattern mainly indicates regime shifts between the two principal seasons of phytoplankton development in a year, i.e. from winter/spring to summer/autumn (Teubner 2000, see also seasonal pattern in Chap. 9) along the seasonal cycle (Lampert et al. 1986, Sommer et al. 1986; De Senerpont Domis 2013). The timing of the clear-water phase between early April to late May in our 21-year study is closer to the timing in other shallow polymictic to dimictic lakes (early May to mid-June for shallow polymictic Großer Müggelsee in Teubner et al. 1999; Straile and Adrian 2000; Huber et al. 2010; mid-May to early June for stratifying lakes such as Plußsee in Müller-Navarra et al. 1997 and Lake Washington in Winder and Schindler 2004a, b) than in many other large deep, mainly pre-alpine or alpine lakes in Central Europe (Straile and Adrian 2000; Straile 2002). The trend towards an earlier clear-water phase in Alte Donau confirms general findings about an earlier onset of the spring clear-water phase in many other lakes in recent decades (Müller-Navarra et al. 1997; Straile and Adrian 2000; Straile 2002; Shatwell et al. 2008). The reason for the earlier timing of this spring to summer event is partly due to the stronger warming at the beginning of the year as discussed by seasonal hysteresis in Sect. 11.4.2.1. Another reason is the temperature dependence of organism growth. Empirical data revealed that an increase in temperature 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 copepod species (e.g., Gophen 1976; Herzig 1983a, b; Orcutt and Porter 1983, Sarma et al. 2002). Contemplating the climate change scenarios for lakes, it is expected that the trophic structure might change from a simple but elongated food

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

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

The long-term phenological shifts of the clear-water phase in Alte Donau presumably reflect the interference of two trends pointing in the same direction, the trend of re-oligotrophication superimposed by the trend of global climate change. The two periods with different trends for progressive earlier clear-water phase in Alte Donau (earlier time shift of 33 days per decade for 1994–1998 and 7 days per decade for 2000–2014) thus contradict the general robustness of the clear-water phenology mentioned above. The pronounced earlier clear-water phase from 1994 to 1999 occurred concomitantly with the drastic reduction of the mean spring total phosphorus pool from 1.4 to 0.7 $\mu\text{mol L}^{-1}$ (spring mean value) and the associated reduction of phytoplankton chlorophyll-a spring peak, decreasing from 29.2 $\mu\text{g L}^{-1}$ to 10.7 $\mu\text{g L}^{-1}$ (spring maximum value, mean values are 9.0 and 7.2 $\mu\text{g L}^{-1}$). We did not estimate the extents to which the earlier timing of the clear-water phase relates to the re-oligotrophication and the superimposed climate forcing. A common method to disentangle the two trends is the analysis of the residuals from the regression line of the detrended data (George and Hewitt 1999; Weyhenmeyer et al. 1999; George et al. 2004; Seebens et al. 2007; Adrian et al. 2009). According to our experience, detrending of biological lake data responding to different nutrient levels should be done with caution unless the ecosystem changes can be confirmed to be only moderate. Alte Donau has undergone drastic changes in trophic state within a short period. Detrending would here primarily satisfy statistics and thereby mathematically eliminate the response to high nutrients levels in biological time series rather than mirroring lake ecology responding to a complex regime shift passing the transition from a nutrient-rich to a nutrient-poor ecosystem. Biological systems respond to different levels of, for instance, phosphorus in different ways because the absolute value of phosphorus (total pool size) is here of high importance (Teubner et al. 2003). The drastic short-term reduction of the phosphorus pool with phosphate precipitation enhances phosphorus utilisation efficiency of the planktonic community,

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

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.

11.4.2.4 Impact of Temperature Increase on Zooplankton Development

Seasonal differences in the relation between WT and individual micro- and mesozooplankton groups were assessed with correlograms, generated for biweekly intervals in the 19-year period. The correlograms typically show a close temporal coherence pattern between WT and all four zooplankton groups in winter and spring. Extraordinarily high abundances of zooplankton early in the year correspond with warm winters and springs, while the opposite is true for cold winters. The closest relationship between year-to-year variations of temperature and zooplankton development was found for cyclopoids and rotifers. In case of calanoids and cladocerans, the positive relationship between abundances and WT is still predominant but much weaker. This general positive relationship between temperature and zooplankton abundance early in the year confirms observations by George and Hewitt (1999) for other lakes in the temperate zone, where small changes in the cold seasons have significant effects on the development of zooplankton. During the transition from the cold to the warm season, three aspects of temperature enhancing the zooplankton development point in the same direction: (1) growth stimulation by temperature dependent on the ontogenetic zooplankton development (see temperature dependent embryonic and postembryonic zooplankton development shortening the life cycles and thus promoting faster growth rates at sufficient food availability as discussed in Sect. 11.4.2.3), and (2) the vernal warming and (3) the climate driven intra-annual temperature increase. The progressive growth of many organisms in 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 fast-growing small primary producers. With the onset of the growing season for 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.

2014). In addition, the intra-annual temperature increase driven by climate warming 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 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. they mirrored a consistently positive response to temperature increase for all seasons over the 19-year study period (Fig. 11.9a2) and did not built up a pronounced early summer depression (Fig. 11.9a3) which was different than for the other crustaceans or the rotifers in our study. Their development thus seemed to be triggered by different temperature effects pointing in the same direction. The temperature increase, which is linked to both the seasonal warming (Fig. 11.9a3) and the year-to-year warming trend by climate change (Fig. 11.9a2), led to an overall success of these crustaceans in Alte Donau (Fig. 11.9a1). *Mesocyclops leuckarti*, *Thermocyclops crassus* and *T. oithonoides* (Fig. 11.2, Table 11.1) are known for their tolerance of high temperature during their embryonic development (e.g., Gophen 1976; Herzig 1983b; Wagner and Adrian 2011) and occurrence at maximum temperatures in summer (e.g., Tackx et al. 2004). Together, these three thermophilic species became increasingly dominant after the phosphate precipitation in Alte Donau when compared with the abundances of the remaining cyclopoids, which are known for a rather temperature-indifferent development (*Megacyclops viridis*, *Eucyclops serrulatus*) or for being adapted to relatively low temperatures (*Cyclops vicinus*). Adrian and co-workers disentangled the seasonal temperature effects from global warming by looking at the phenology response of individual cyclopoid species and found evidence that the mentioned thermophilic ‘summer’ species benefit from global warming trends. According to their results (Gerten and Adrian 2002; Adrian et al. 2006), enhanced annual peak abundances of *Mesocyclops leuckarti* and *Thermocyclops oithonoides* relate to the climate driven warm years. In case of the latter species, a higher summer peak abundance was found to be accomplished by an earlier start of growth in the beginning of the year (Gerten and Adrian 2002), which corresponded to an earlier ice break up and an associated earlier spring peak of phytoplankton in the studied shallow polymictic lake (Adrian et al. 2006). The persistence of cyclopoids in our study could be accomplished by species alterations among these crustaceans towards thermophilic species. The cyclopoid copepods as a whole took advantage of seasonal and global warming on the one hand (Fig. 11.9a) and were robust against trophic changes on the other hand (Fig. 11.3). The dynamic of the calanoid copepods, which were less abundant and were represented by only one species (*Eudiaptomus gracilis*), was different. They accomplished higher yields for short periods during intermitted treatment years of extreme low phosphorus availability (Fig. 11.3, see also discussion in Sect. 11.4.1.1) but benefited the least from warming in general, which was indicated by seasonal decreases during particularly hot summer periods (Fig. 11.9b). The latter agrees with other studies showing that *E. gracilis* is taking advantage from a relatively short embryonic development

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 increase was found for cladoceran crustaceans (Fig. 11.9d1). The suppression of daphnids by climate warming, as discussed by Jeppesen et al. (2010b), Wagner et al. (2013) and Tavşanoğlu et al. (2017), agrees with our finding that the pronounced summer decline of cladocerans refers to the long-term increase of WT in summer (Fig. 11.9d2, see also calanoids above). A further climate response most relevant for all zooplankton from rotifers to crustaceans in Alte Donau was the predominant positive response to intra-annual temperature variation in winter and spring in concert with the common phenology of the close timing of their spring peak (Fig. 11.9, cf. Adrian et al. 2006, Gerten and Adrian 2000, 2002). The responses of individual zooplankton key species, which alternate between warm and cold year scenarios 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 2007; Berger et al. 2014).

11.5 Conclusions

The main compositional shift from a cladoceran-rotifer-rich to a copepod-rotifer-rich zooplankton assemblage seems to be driven by bottom-up control and thus relates to drastic reductions of phytoplankton yield after initial phosphorus precipitation and sustained low phosphorus availability during the subsequent years of biomanipulation. With the suppression of filter-feeding herbivorous cladocerans through reduced food supply, mainly selective-feeding omnivorous and herbivorous copepods survived under mesotrophic transparent-water conditions. Rotifers and calanoid copepods became particularly abundant during the two Riplox-years when food availability drastically declined. Large-bodied crustaceans did not seem to consistently benefit from predator avoidance by re-grown submerged vegetation as assessed by the mean body-size of zooplankton community. The grazing pressure of mainly cyprinid fish thus could not be dampened by the refuge effect of re-established macrophyte stands in Alte Donau. During the long-term restoration period, significant climate warming trends were detected such as an increase in surface water temperatures in spring and a prolongation of the warm period in summer. Cyclopoid copepods seemed to benefit most from a warmed-up environment, as it was the only zooplankton group with a robust positive long-term response to 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 Alte Donau.

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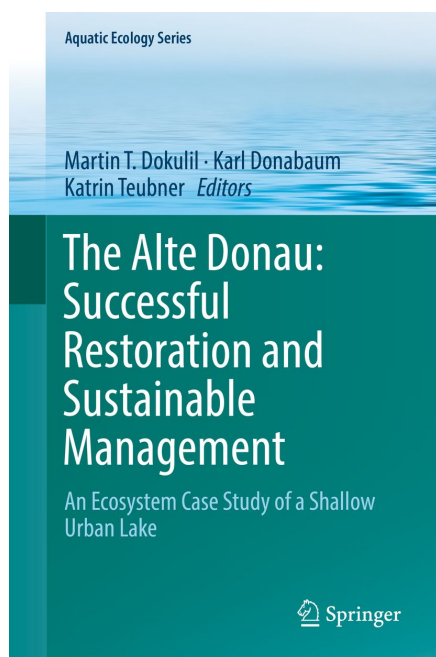
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