Martin T. Dokulil · Karl Donabaum
Katrin Teubner *Editors*

# The Alte Donau: Successful Restoration and Sustainable Management

## An Ecosystem Case Study of a Shallow Urban Lake

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# Chapter 9
# Phytoplankton in Alte Donau: Response to Trophic Change from Hypertrophic to Mesotrophic Over 22 Years

**Katrin Teubner, Wilfried Kabas, and Irene Teubner**

**Abstract** The long-term phytoplankton study in groundwater-seepage lake Alte Donau, a former side-arm of the Danube River in Vienna, covers four main lake treatment periods (1–4) from 1993 to 2014. During hypertrophic conditions with annual total phosphorus (TP) concentrations of 50–70 µg $L^{-1}$ and mean summer phytoplankton biovolume of 18–24 mm³ $L^{-1}$ before restoration (1), the filamentous cyanobacterium *Cylindrospermopsis raciborskii* was the main taxon in association with *Limnothrix redekei*. The drastic phosphorus reduction by chemical RIPLOX-precipitation was repeated twice (2a/b, 1995 and 1996) and resulted in a prompt drop of summer phytoplankton to 4.6 mm³ $L^{-1}$ in 1995 and 1.7 mm³ $L^{-1}$ in 1996. Non-filamentous cyanobacteria contributed here only moderately while relative high peak contributions of chlorophytes occurred. After years of re-establishment of macrophytes (3), the summer phytoplankton biovolume remained low during the period of sustained 'stable conditions' (4) with values between 0.5 and 1.5 mm³ $L^{-1}$. In the long-term, phytoplankton was responding to low annual total phosphorus (10–11 µg $L^{-1}$) which finally indicated a mesotrophic state close to oligotrophic conditions according to the lake classification scheme. The long-term median of chlorophyll-a (chl-a) content was 0.50% of wet weight phytoplankton biomass. As the phytoplankton composition shifted from a cyanobacteria dominated assemblage to a phytoplankton assemblage that was composed of taxa of various taxonomic affiliations, the chl-a content varied considerably. Chl-a content reached its lowest median value of 0.19% when cyanobacteria formed blooms contributing 77% to

K. Teubner (✉)
Department of Limnology & Biological Oceanography, Faculty of Life Sciences,
University of Vienna, Vienna, Austria
e-mail: katrin.teubner@univie.ac.at

W. Kabas (✉)
Vienna, Austria

I. Teubner
Department of Geodesy and Geoinformation, Faculty of Mathematics and Geoinformation,
Vienna University of Technology, Vienna, Austria
e-mail: irene.teubner@geo.tuwien.ac.at

total phytoplankton (period 1) and was highest with 0.83% during the peak development of chlorophytes which contributed 18% to total biovolume (period 2b). The relationship between phytoplankton chl-a and TP is more robust than between phytoplankton biovolume and TP for indicating the lake's trophic state, although both response curves are statistically significant and provide roughly the same main picture of an ecosystem shift from hypertrophic in 1993 to mesotrophic in 2000 and the persistence of mesotrophic conditions for the 15 recent years. Trophic shifts were also indicated by the phytoplankton assemblage metric when comparing phytoplankton species composition between the lake treatment periods. The main picture of seasonal development of phytoplankton taxa and functional phytoplankton groups indicated that assemblages either prevailed in winter to spring or summer to autumn. Annual phytoplankton development thus seems primarily distinctive between the two half-year-cycles, namely the winter-spring and the summer-autumn period, rather than between the four seasons. While the seasonal development of phytoplankton follows the lake phenology commonly observed in temperate lakes, long-term compositional shifts of phytoplankton especially responded to the sustained reduction of TP forced by lake treatment measures in Alte Donau.

**Keywords** Oxbow lake · Lake restoration · Lake recover · Lake biomanipulation · Riplox · Algae · Cyanobacteria · Cylindrospermopsis raciborskii · Seasonality · Trophic classification · Phosphorus · Chlorophyll-a · Chlorophyll:TP · Biovolume:TP · Phytoplankton assemblage metric

## 9.1 Introduction

Rising awareness of eutrophication and advances in the management of eutrophied aquatic systems have been made since the late 1960s. The OECD study (OECD 1982) in the 1980s and the initiative by the EU Water Framework Directive (2000) in the 2000s provided the two milestones in the scientific understanding of the mechanisms of eutrophication and consequently launched the search for aquatic biota, which indicate the specific reference status of each lake type. Since massive phytoplankton growth corresponds most notably to nutrient enrichment in lakes and as these primary producers play a key role in the food chain, phytoplankton is a key biotic parameter assessing lakes. Among the biotic parameters monitored in the oxbow lake Alte Donau, phytoplankton (this chapter) and zooplankton (Chap. 9) provide with 22 and 19 years, respectively, the longest records.

Alte Donau is popular for recreation including swimming and fishing (Teubner et al. 2015). During the 22-year lake restoration, fish were only removed by angler sport. The number of fish catches and fish stocking, however, decreased with years of phosphorus reduction towards a lower trophic level (time series of fish see Fig. 15.1 in Chap. 15, fish biomass versus chl-a in Fig. 20.3 in Chap. 20). During all years, both mainly carp and predatory fish were added. In the long term, the local

fishery increasingly forced the stocking of predatory fish. Some aspects of both bottom-up and top-down control on plankton development are discussed in view of main compositional shifts from a cladoceran-rotifer-rich to a copepod-rotifer-rich of zooplankton assemblage along the lake management periods in Chap. 11. Phytoplankton development in this chapter focuses on the bottom-up control with main emphasis on phosphorus. This main nutrient element is commonly known to limit phytoplankton growth in freshwaters. Accordingly, the main target of restoration and lake management in Alte Donau was to reduce phosphorus availability for phytoplankton growth and aimed at increasing water transparency and thus to enhance water quality. The emphasis of phosphorus-resource control on phytoplankton is the cause for plotting the trophy classification scheme applying Austrian standards ÖNORM M6231 (2001) or using a phytoplankton metric based on an Austrian Trophic State Index (see Sect. 9.2.4) in this chapter. The phosphorus-phytoplankton response also remains relevant when applying functional phytoplankton groups (Reynolds et al. 2002; Padisák et al. 2009), as was done for Alte Donau, since these groups describe the co-occurrence of algae not only along seasons but also along spatio-temporal gradients of nutrient source availability. Freshwater phytoplankton surveys with a focus on eutrophication commonly describe the phytoplankton shifts in view of resource-driven control. These studies describe a unique phytoplankton signature along a trophic gradient across lakes from shallow to deep water bodies (Rojo and Alvarez-Cobelas 1994; Teubner 1996; Teubner et al. 1999, 2003a, 2004; Naselli-Flores and Barone 2003; Stefaniak et al. 2005; Nixdorf and Deneke 1997; Søndergaard et al. 2005), from flushed riverine to stratified systems (Krienitz et al. 1996; Teubner 1996; Teubner et al. 1999; Köhler et al. 2000) or from tropical to temperate climate zone (Chen et al. 2003; Bouvy et al. 2006; Burford et al. 2006, 2016; Liu et al. 2011, 2016; Deng et al. 2016). In all these field surveys, the changes in phytoplankton assemblages associated with eutrophication or restoration are mainly discussed by species alterations among or within four predominant taxonomic affiliations: cyanobacteria, diatoms, golden algae and green algae.

The aim of this chapter is to track the impact of lake restoration measures on compositional shifts of phytoplankton described for four main lake treatment periods (1–4) including the chemical phosphorus flocculation and the re-establishment of submerged vegetation. We further distinguish two sub-periods 2a and 2b concerning the first and second chemical phosphate precipitation by RIPLOX-treatment (Ripl 1976; Donabaum et al. 1999). The comparison of these four main periods by other biota is described for zooplankton in Chap. 11 and for macrozoobenthos in Chap. 14. Besides the compositional shift of phytoplankton due to phosphorus reduction along restoration and management measures in Alte Donau, we analysed the general phytoplankton pattern of seasonal cycles and pigment relationships and its impact on the assessment by trophic classification.

## 9.2 Methods

### 9.2.1 Phytoplankton Sampling During Four Treatment Periods

Alte Donau, a former stretch of the Danube River, is an urban polymictic lake with a maximum depth of 7 m and mean depth of 2.5 m (relative depth 0.52 calculated according to Kõiv et al. 2011) and a surface area of 1.43 km². The shallow oxbow lake consists of two main impoundments, the south basin (in other chapters of this book also called lower basin, 'Untere Alte Donau' or UAD) and the north basin (also called upper basin, 'Obere Alte Donau' or OAD) with their main sampling sites 'AD1' and 'AD4', respectively. According to Löffler (1988) and Mayer et al. (1997), the retention time in the 1980s was roughly estimated by about 20 days to a few months. With the construction of the impoundment Neue Donau (1970) and a hydro power plant in the river Danube (1997) the water level fluctuations markedly decreased step by step as the ground water fluxes changed dramatically (Chap. 2, Fig. 5.1 in Chap. 5; see also Donabaum et al. 2004). A more detailed calculation for the recent years revealed a much longer hydrological retention time fluctuating from 98 days to about 900 days, with a mean of 365 days for south and 175 days for north basin (Chap. 4). The morphology and hydrology of these two basins are further described in Chaps. 3 and 4, respectively.

Samples of phytoplankton and chlorophyll-a (chl-a) were taken with a 5 L-Schindler sampler at 0.2 m depth in the two main impoundments at biweekly (to monthly) intervals from April 1993 to December 2014.

Phytoplankton biovolume was estimated from phytoplankton abundance and size measurements using the sedimentation technique and light microscopy. Biovolume was calculated for individual phytoplankton species according to the basic geometric shape of the cell bodies or the aggregation of cells (Rott 1981). Different from the 19-year record of zooplankton samples, which were analysed by a single person, the microscopical phytoplankton counting over the 22 years was conducted by a number of colleagues. The authors of this chapter (K.T., W.K.) contributed to the phytoplankton counting for several years before and during the restoration period. Taxonomic references reported in AlgaeBase [http://www.algaebase.org; searched on 9 August 2017] were used for determining the phytoplankton taxa.

The 22-year time series covers all periods of the lake treatment described in Chap. 5. For this phytoplankton chapter, the periods were slightly modified analogous to zooplankton in Chap. 11. The periods are as follows: 1 – 'eutrophication' (before April 1995), 2 – 'restoration including the first RIPLOX-treatment in April 1995 and the second RIPLOX-treatment in April 1996 (chemical phosphate precipitation see Fig. 5.3 in Chap. 5, further Chap. 6, methods Chap. 11; details in Ripl 1976; Donabaum et al. 1999) and further restoration measures (April 1995–1999), 3 – 'macrophyte re-establishment' (2000–2006) and 4 – 'stable conditions' (2007–2014). An earlier study comparing the pelagic community in the first and second RIPLOX-year revealed different pathways of prompt responses of plankton organisms to phosphorus reduction (Teubner et al. 2003b). Accordingly, we split the

restoration period in two sub-periods, i.e. (2a) April 1995 to March 1996 and (2b) April 1996 to 1999.

## 9.2.2 Data Treatment and Statistics

Phytoplankton shown separately for the two impoundments is based on the original data set (Fig. 9.5). As phytoplankton, chl-a and total phosphorus (TP), however, were not consistently sampled at exactly 2-week intervals, we interpolated the observations at daily resolution (Livingstone 2003; Sapna et al. 2015) and averaged these over 2 weeks, a month, a summer season or a year (Figs. 9.2, 9.3, 9.4 and 9.6, 9.7, 9.8, 9.9, 9.10, 9.11.). This data treatment is analogous to the data preparation for the zooplankton analysis in Chap. 11.

We calculated net change rates of chl-a (*kchl-a*, hereafter referred to as net growth rate of chl-a) at monthly time intervals as:

$$k_{chl\ a} = \left( \ln chl\ a2 - \ln chl\ a1 \right) / \Delta t \tag{9.1}$$

where *chl-a*2 is the chl-a concentration at time $t = t2$, *chl-a*1 the chl-a at time $t = t1$ and $\Delta t$ the time span in number of days (e.g. Teubner et al. 2003b). Likewise, we analysed the persistence of phytoplankton composition at monthly time intervals expressed by the standardised Bray-Curtis similarity index (0–100) using the software package PRIMER 5. The higher this index, the higher is the resemblance of the phytoplankton composition between successive samples as indicated by species or functional phytoplankton groups. The seasonal variability of this Bray-Curtis index and of chl-a and biovolume data was estimated using the coefficient of variation (CV = standard deviation/mean).

Prior to the statistical analysis, we tested data for normal distribution. According to the non-parametric Shapiro-test (Dunn and Clark 1974), not all parameters followed a normal distribution, in particular not those of single phytoplankton taxa, which were rare in at least one lake treatment period. Also, chl-a and biovolume data for whole study period did not follow normal distribution. 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 H-tests to determine differences between annual median values for both impoundments and for the five restoration periods (Figs 9.7 and 9.8). To identify homogeneous subsets when comparing the phytoplankton assemblages between the two impoundments (see text for difference between site in Fig. 9.5) and during the five restoration periods, we further conducted pairwise Mann-Whitney U-tests with a Bonferroni correction (Figs 9.7 and 9.8). The temporal agreement between chl-a and biovolume was assessed using the non-parametric Spearman rank correlation. The biovolume of higher ranks of phytoplankton taxa are displayed as notched box-whisker plots using SYSTAT 10 (SPSS Inc.) (Figs 9.7 and 9.8). The boxes are

notched at the median; the length of the notches indicates the 95% confidence interval.

### 9.2.3 Assessment by Functional Groups

Phytoplankton species were categorised by their co-occurrence during seasonal succession in similar habitats as 'functional associations' according to Reynolds et al. (2002) modified by Padisák et al. (2009). We tried to avoid using taxa on genus level instead of species level as suggested by Padisák et al. (2009) and further made sure that the functional group categories comprise more than one species. For this reason, we allocated *Melosira varians* C.AGARDH to 'P' and not as a single species to template 'T$_B$' as nominated in Padisák et al. (2009). The individual taxa were allocated to 20 functional groups as follows: cyanobacterial Chroococcales and Synechococcales of the genera *Woronichinia naegeliana* (Unger) Elenkin and *Microcystis aeruginosa f. aeruginosa* KÜTZING, *M*. *viridis* (A.BRAUN) LEMMERMANN, *M wesenbergii* (KOMÁREK) KOMÁREK ex KOMÁREK (Lm), *Aphanocapsa* and *Aphanothece* (K), filamentous nitrogen fixing genera of Nostocales as *Dolichospermum* and *Aphanizomenon* (H1) and *Cylindrospermopsis* (SN) and of non-nitrogen fixing Oscillatoriales as *Limnothrix*, *Planktolyngbya*, *Planktothrix* and *Pseudanabaena* (S1), unicellular centric diatoms (A), pennate diatoms as mainly *Diatoma* and *Tabellaria* (B) and *Asterionella*, *Navicula* and *Nitzschia* (C), *Aulacoseira granulata* (EHRENBERG) SIMONSEN, *Fragilaria* cf. *construens*, *F. crotonensis* KITTON, *Melosira varians* C.AGARDH (P), cyanobacteria and dinoflagellates of the genera *Ceratium*, *Gomphosphaeria*, *Gymnodinium*, *Merismopedia*, *Snowella*, *Woronichinia*, and *Peridinium* (Lo), cryptophytes mainly of the species *Cryptomonas curvata* Ehrenberg *C. erosa Ehrenberg, C*. *marssonii Skuja* (Y), small-cell taxa of Chlorophyta, Euglenophyta and Charophyta as e.g., *Ankyra*, *Carteria*, *Crucigenia*, *Elakatothrix*, *Koliella*, *Monoraphidium*, *Schroederia*, *Tetraedron*, *Tetraselmis*, *Tetrastrum* and *Trachelomonas* (X1), mainly colonial Trebouxiophyceae and Chlorophyceae of the genera *Botryococcus, Coelastrum*, *Dictyosphaerium*, *Lagerheimia*, *Oocystis*, *Quadricoccus*, *Radiococcus* and *Tetrachlorella; Radiocystis* (F) and *Pediastrum* and *Scenedesmus* (J), large cell bodies or filaments mainly of Charophyta and Chlorophyta as *Closterium*, *Cosmarium*, *Mougeotia*, *Planktonema*, *Staurastrum* and *Zygnema* (N), flagellates mainly of Ochrophyta and Cryptophytes as *Chrysomonas*, *Ochromonas* and *Rhodomonas* (X2) and of other species of Ochrophyta of the genera *Dinobryon*, *Mallomonas* and *Synura* (E) and *Uroglena* and two further groups of lower biovolume (U; names for the functional groups are given in brackets and are based on the nomenclature of Reynolds et al. (2002) and Padisák et al. (2009)).

### 9.2.4   Assessment of Trophic State by ÖNORM and Phytoplankton Assemblage Metric Modified from Brettum Index

The assessment of phytoplankton and chl-a along the TP gradient in the water column follows the lake's trophic classification recommended by the ÖNORM M6231 (2001). According to this description of Austrian standards, we display the annual concentration of TP versus summer chl-a and summer phytoplankton biovolume, respectively. TP ranges are described for five trophic levels from oligotrophic to hypertrophic including a sub-category for the eutrophic state with moderately eutrophic and highly eutrophic. For chl-a, the sub-categories for the eutrophic state are missing in the ÖNORM M6231 (2001) and, therefore, we used an empirical value calculated from the chl-a-TP response curve plotted for Alte Donau. Furthermore, although rough numbers of phytoplankton biomass for some trophic levels are provided in the ÖNORM M6231 (2001), we used a more detailed calculation for phytoplankton biovolume for describing the five trophic levels. We calculated the class limits for phytoplankton biovolume by converting the chl-a thresholds to biovolume using a constant ratio that was empirically determined for Alte Donau (median value, 0.50% chl-a of wet weight biomass of phytoplankton assuming a density of 1 mg biomass per 1 mm$^3$ biovolume, 515 observations, details in Fig. 9.9). All numbers for the class limits describing the five trophic levels are displayed in Fig. 9.10.

In addition to the trophic states by ÖNORM M6231 (2001), we applied a phytoplankton assemblage metric to infer the ecological integrity of Alte Donau without referring to the individual species again. The Austrian phytoplankton assemblage metric is modified from the Brettum index (Brettum 1989), which was originally developed for lakes in Norway and refers to a calibration data set over seven ranks. The Austrian metric is based on a multi-year calibration data set of 167 phytoplankton taxa observed in 29 lakes (2429 phytoplankton samples including TP measures, Dokulil et al. 2005), which are mainly deep, oligo- to mesotrophic lakes and predominantly from the pre-alpine and alpine regions in Austria. To cover the full range of trophic states as suggested by ÖNORM, ten mainly shallow and eutrophied lakes in Germany were included in the data set (data of 8 meso- to hypertrophic lakes from Teubner 1996 and of mesotrophic pre-alpine Ammersee from Teubner et al. 2004; Teubner 2006 in Dokulil et al. 2005). The Austrian phytoplankton assemblage metric displays five ranks according to the five states recommended by ÖNORM M6231 (2001).

1. oligotrophic
2. mesotrophic
3. moderately eutrophic
4. highly eutrophic
5. hypertrophic

In the calibration data set, the weighted species scores reflect the frequency distribution of individual phytoplankton species along these five ranks. The weighting among species, which may differ in their biovolume yield by more than one order of magnitude, counterbalances the contribution of many less abundant phytoplankton species against few highly abundant, blooming species, thus giving a reliable lake assessment. The advantage of the Austrian phytoplankton assemblage metric described in Dokulil et al. (2005) is that it includes all species observed in a phytoplankton sample regardless of the species-specific phosphorus range. Thus, biased interpretation using few, a priori selected single indicator species is avoided. Assessing an actual phytoplankton lake sample by the Austrian assemblage metric, the biovolume of each phytoplankton species is multiplied by its species-specific weighted score from the calibration data set. Finally, the scores over all observed lake species are summed up and weighted among the five TP ranks. The rank with the highest total score indicates the highest probability of the trophic state. Phytoplankton assessment methods to identify ecological integrity differ among countries and regions as for example recently summarized by Pasztaleniec (2016). Habitat scores in general, however, have a long tradition in ecology and are commonly retrieved from a meta-analysis of empirical observations of various biotic community structure or other phenomena discovered across individual habitats (Karr 1998; Hofmann 1993; Moog and Chovanec 2000; Moog 2002; Henderson 2003; Crossetti and Bicudo 2008, see also chironomid score in Chap. 14). In case of phytoplankton, such methods are used to assess lake ecology in accordance with the European Framework Directive (e.g., Padisák et al. 2006; Dokulil and Teubner 2006; Solimini et al. 2008; Nõges et al. 2009; Poikane et al. 2011; Pasztaleniec 2016).

## 9.3 Results

### 9.3.1 Phytoplankton Species Composition, Functional Groups and Their Seasonal Pattern

Photographs of some cyanobacteria and algae which were observed in Alte Donau are shown in Fig. 9.1. These photosynthetic organisms vary in their size from small-celled pico-plankton as e.g. *Aphanocapsa* spp. (Fig. 9.1b) to macroscopically visible, large cells as e.g. *Cosmarium botrytis* (Fig. 9.1i) or may form large aggregates, such as *Microcystis aeruginosa*, *M. flos-aquae*, *M. novacekii*, *M. viridis*, *M. wesenbergii* (Fig. 9.1a), *Uroglena volvox* (Fig. 9.1c), *Dinobryon divergens* (Fig. 9.1d), *Botryococcus braunii* (Fig. 9.1g) and *Coenochloris* spec. (Fig. 9.1h). In terms of taxonomy, common freshwater species of all taxonomic groups were observed with the exception of the generally rare freshwater Rhodophyta. Considering the 17 main
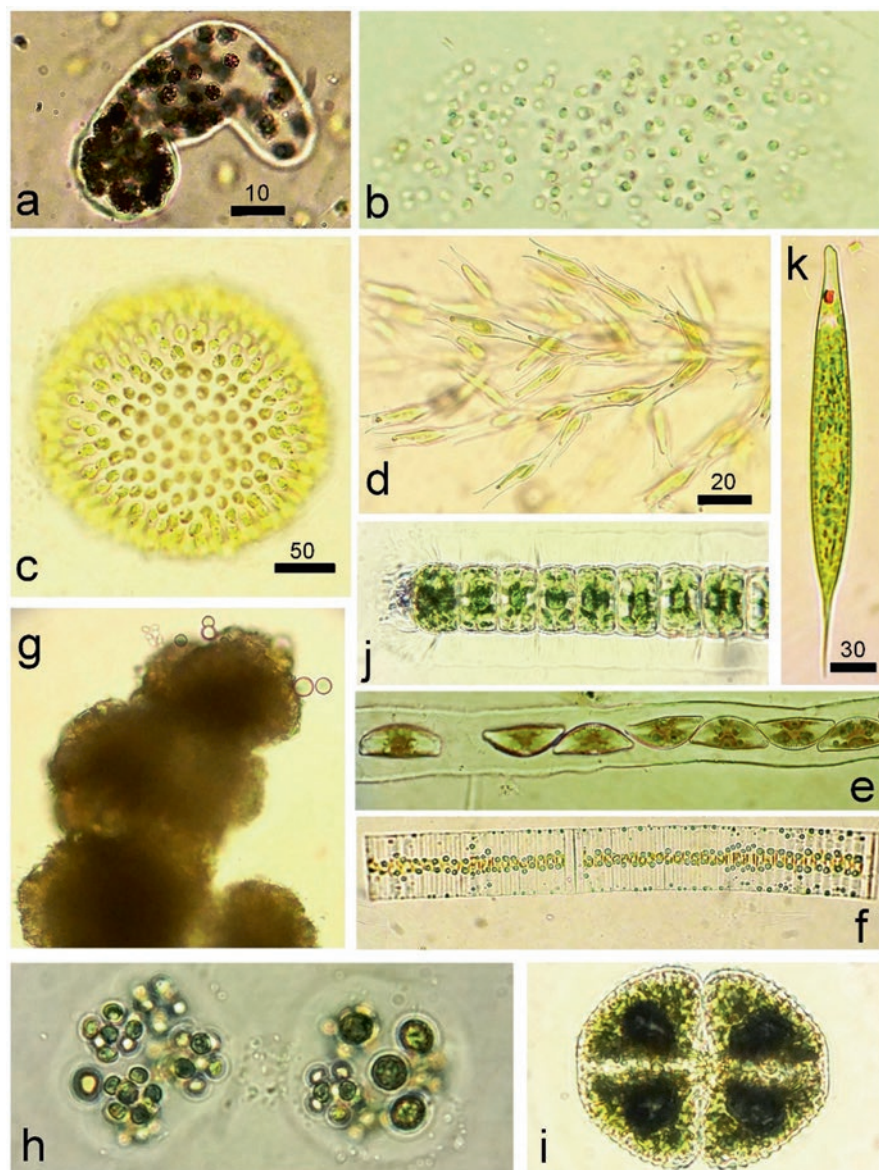
**Fig. 9.1** Phytoplankton species from small-sized picoplankton (b) to large netplankton species (e.g., c) in Alte Donau; (**a** and **b**) Cyanobacteria, (**a**) – *Microcystis wesenbergii*, (**b**) – *Aphanoscapsa* spec.; (**c** and **d**) Ochrophyta, Chysophyceae, **c** – *Uroglena volvox* EHRENBERG, (**d**) – *Dinobryon divergens* O.E.IMHOF; (**e** and **f**) Bacillariophyta, Bacillariophyceae, (**e**) – *Encyonema triangulum* (EHRENBERG) KÜTZING, (**f**) – *Fragilaria* spec.; (**g** and **h**) Chlorophyta, (**g**) – Trebouxiophyceae, *Botryococcus braunii* KÜTZING, (**h**) – Chlorophyceae, *Coenochloris* spec., (**i** and **j**) Charophyta, (**i**) – Conjugatophyceae, *Cosmarium botrytis* MENEGHINI EX RALFS, (**j**) – *Hyalotheca dissiliens* BRÉBISSON EX RALFS, k Euglenophyta, Euglenophyceae, *Euglena acus* (O.F.MÜLLER) EHRENBERG. Scale bar for (**a**, **b**, **h**): 10 μm; for (**d**, **e**, **g**, **i**, **j**): 20 μm; for (**f**, **k**): 30 μm; for (**c**): 50 μm
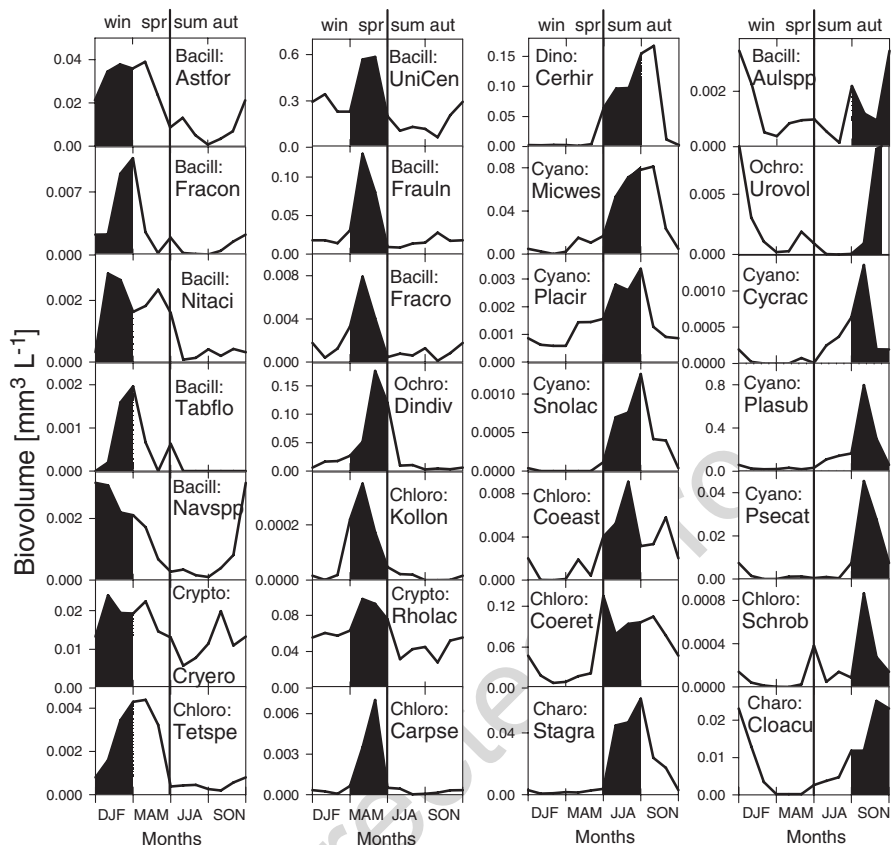
**Fig. 9.2** Seasonal development of 28 phytoplankton taxa as long-term monthly averages from 1993–2014. Black areas indicate the season with the highest mean seasonal biovolume. The vertical line separates biovolumes of winter-spring from summer-autumn

Abbr: winter (DJF): Astfor – *Asterionella formosa* HASSAL, Fracon – *Fragilaria construens* (EHRENB) GRUNOW, Nitaci – *Nitzschia acicularis* W.SMITH, Tabflo – *Tabellaria flocculosa* (ROTH) KÜTZ., Navspp – *Navicula* spp., Cryero – *Cryptomonas erosa* EHRENB., Tetspe – *Testraselmis* spec, spring (MAM): UniCen-unicellular centric diatoms, Frauln – *Fragilaria ulna* (KÜTZ.) LANGE-BERTALOT, Fracro – *Fragilaria crotonensis* KITTON, Dindiv – *Dinobryon divergens* O.E.IMHOF, Kollon – *Koliella longiseta* (VISCH.) HIND., Rholac – *Rhodomonas lacustris* PASCHER et RUTTNER, Carpse – *Carteria pseudomultifilis* PETERFL L., summer (JJA): Cerhir – *Ceratium hirundinella* (O.F.MÜLLER) DUJARDIN, Micwes – *Microcystis wesenbergii* (KOM.) KOM., Placir – *Planktolyngbya circumcreta*, Snolac – *Snowella lacustris* (CHOD.) KOM. et HIND., Coeast – *Coelastrum astroideum* DE-NOT., Coeret – *Coelastrum reticulatum* (DANG.) SENN, Stagra – *Staurastrum gracile* RALFS, autumn (SON): Aulspp – *Aulacoseira* spp., Urovol – *Uroglena volvox* EHRENBERG, Cylrac – *Cylindrospermopsis raciborskii*, Plasub – *Planktolyngbya subtilis* (W.WEST) ANAGN. Et KOM., Psecat – *Pseudanabaena catenata* LAUTERB., Schrob – *Schroederia robusta* KORS., Cloacu – *Closterium acutum* (LEMM) W. KRIEG; Bacill – Bacillariophyta, Crypt – Cryptophyta, Chloro – Chlorophyta, Ochro – Ochrophyta, Dino – Dinoflagellata, Cyano – Cyanobacteria, Charo – Charophyta

functional phytoplankton groups for Alte Donau (see method), five groups refer to 300
cyanobacteria, four to chlorophyte and three to diatom taxa. 301

The monthly development of single species in Alte Donau is given in Fig. 9.2. 302
Most species with pronounced development in winter and spring were bacillario- 303
phytes (diatoms) of Tabellariales, Bacillariales and Fragilariales (needle-shaped 304
diatoms, such as e.g., *Asterionella formosa*, *Nitzschia acicularis*, *Fragilaria con-* 305
*struens*) and Stephanodiscales (a number of species categorised as unicellular cen- 306
tric diatoms). Some cryptophytes as *Cryptomonas erosa* and *Rhodomonas lacustris* 307
and few ochrophytes (e.g. *Dinobryon divergens*) and chlorophytes (*Tetraselmis* 308
spec. and *Carteria pseudomultifilis*) also developed their main biovolume in winter 309
to spring. Many species, such as e.g., *Asterionella formosa*, *Cryptomonas erosa*, 310
*Rhodomonas lacustris* and *Tetraselmis* spec., established large biovolumes through- 311
out these both seasons with the main peak or main seasonal average neither in win- 312
ter or spring. Typical phytoplankton species blooming in summer (Fig. 9.2) were 313
cyanobacteria (*Microcystis wesenbergii*, *Planktolyngbya circumcreta*), chloro- 314
phytes (*Coelastrum astroideum*, *C. reticulatum*), dinoflagellates (*Ceratium hirundi-* 315
*nella*) and charophytes (*Staurastrum gracile*) with high biovolumes lasting to 316
autumn. Other species with a biovolume peak in autumn reached already had high 317
yields in summer (e.g., cyanobacteria *Cylindrospermopsis raciborskii*, 318
*Planktolyngbya subtilis*). The majority of species developed their main yield either 319
in winter and spring or in summer and autumn. Hence, annual phytoplankton devel- 320
opment seems primarily distinctive between the two half-year-cycles, namely the 321
winter-spring and the summer-autumn period, rather than between the four 322
seasons. 323

Analogous to Fig. 9.2., the seasonality of biovolume of four phytoplankton asso- 324
ciations is shown in Fig. 9.3. As found for single species, functional phytoplankton 325
groups built pronounced biovolumes lasting either in winter and spring (functional 326
group 'Y' with species of *Cryptomonas* and 'P' of mainly pennate diatom species) 327
or in summer and autumn (functional group 'Lo' with species of cyanobacteria of 328
Genera *Woronichinia*, *Snowella*, *Gomphosphaeria*, *Merismopedia* and dinoflagel- 329
lates and 'Lm' of Cyanobacteria, e.g. the genus *Microcystis*). The monthly net 330
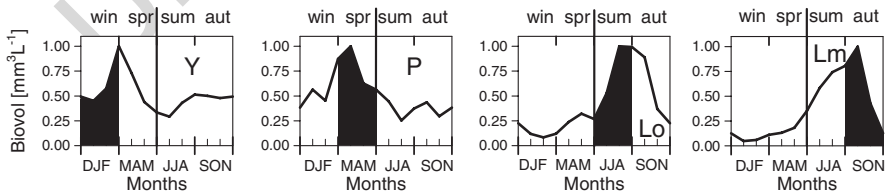growth rate of chl-a (Fig. 9.4a) and changes of phytoplankton composition 331



**Fig. 9.3** Seasonal development of biovolume for four functional phytoplankton groups (Y, P, Lo, and Lm; species allocation see method) as long-term monthly averages from 1993–2014
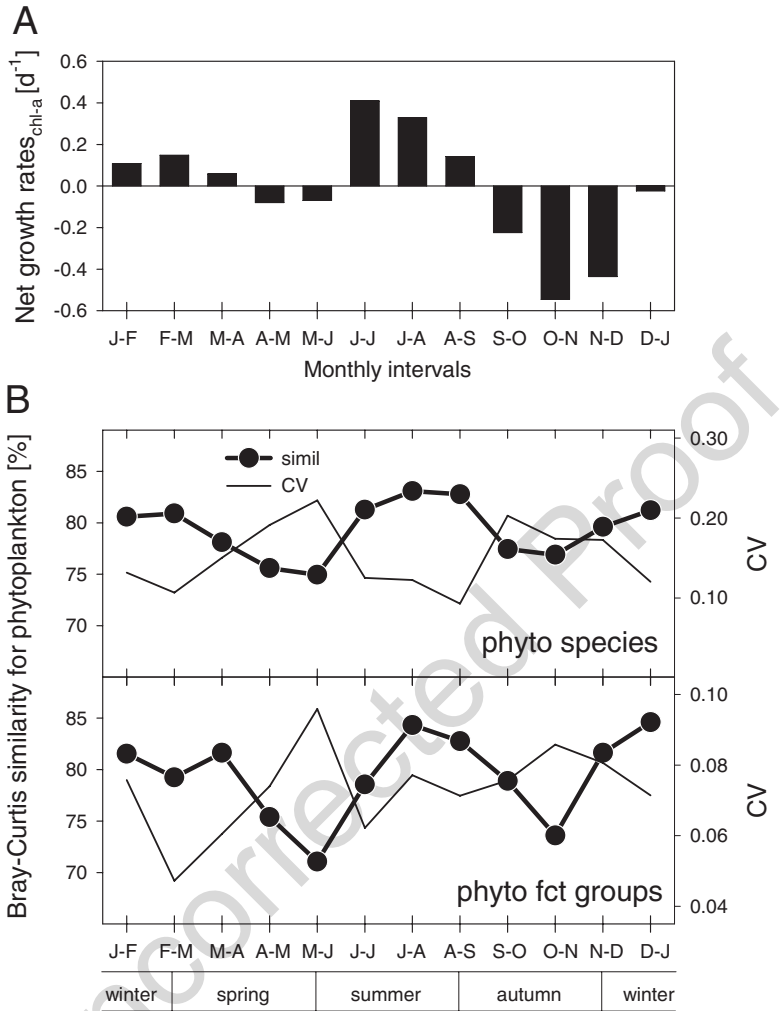
**Fig. 9.4** Seasonal distribution pattern (**a**) of net growth rates of chl-a and (**b**) of compositional shifts of phytoplankton (standardised Bray-Curtis similarity) for 28 phytoplankton species (phyto species) shown in Fig. 9.3 and 13 dominant phytoplankton functional groups (phyto fct groups) displayed as long-term mean (1993–2014) at monthly intervals from January to December. A similarity value of 100% indicates an identical composition of two successive phytoplankton samples, 0% a totally different composition. The coefficient of variation (CV) illustrates the variability of the Bray-Curtis similarity

(Fig. 9.4b) illustrate the seasonal pattern of phytoplankton development. In the long-term average, the net growth rates of chl-a are positive in the first three monthly intervals in the year revealing an increase of phytoplankton biovolume. From April to May and May to June these net growth rates are slightly negative indicating the break down of the spring phytoplankton bloom during the transition from spring to

summer. According to the long-term lake phenology analysed in Chap. 11, the clear-water phase varied between the 95th (early April) and the 145th (late May) day in the year (1994–2014, Fig. 11.7). The following strong increase of net growth rates of chl-a in June to July stands for a rapidly progressive development of summer phytoplankton. Later in summer, the net growth rates of chl-a become moderate positive and are weakest then successively decreasing to lowest and negative values from October to November, i.e. from autumn to winter. With the winter season, net-growth rates of chl-a increase again. The long-term seasonal change of phytoplankton composition is expressed by the Bray-Curtis similarity between two successive monthly samples (Fig. 9.1b). As indicated by the CV, the similarity index varies most at particularly low values during the transition from spring to summer (from April to May and May to June, respectively), which coincides with low net growth rates of chl-a. It corresponds to a most pronounced species shift after the break down of spring bloom and a new growth of summer plankton. A second but less pronounced shift is found from October to November. Both species shifts during the transition from spring to summer and autumn to winter reflect the development in winter-spring or summer-autumn for many single species described before in Fig. 9.2. This general pattern of seasonal phytoplankton phenology is also seen when assessing compositional shifts by biovolume of phytoplankton functional groups (Fig. 9.4b).

### 9.3.2 Long-Term Development of Taxonomic Phytoplankton Groups

Time series of taxonomic groups are shown in Fig. 9.5 for both basins. When comparing the phytoplankton development year by year between the south (AD1) and the north basin (AD4) (Fig. 9.5), we found statistically higher total biovolumes in AD1 only in 2004 (H-test, $p < 0.001$) and 2010 (H-test, $p < 0.05$), while higher total biovolumes in AD4 occurred in 2011 (H-test, $p < 0.005$) and 2012 (H-test, $p < 0.05$). The biovolume of chlorophytes never differed between sites and built relatively high biovolumes before chemical phosphorus precipitation and modest biovolumes in years following the chemical treatment (Fig. 9.5). Analogous, the biovolume of cyanobacteria stayed similar between both basins with the exception of 3 years with peak biovolumes of more than 40 mm$^2$ L$^{-1}$ in the eutrophied years 1993 and 1994 before chemical restoration. Large differences between sites were observed for bacillariophytes (H-test; $p < 0.05$) with statistically higher values in the south basin from 2003 to 2010 and statistically lower values in 2011, both during the lake treatment of re-establishment of macrophytes and stable conditions. Bacillariophytes reached highest yields of 15 mm$^3$ L$^{-1}$ in years 1993 and 1994 before the chemical phosphorus precipitation. In later years of lake treatment periods, biovolumes did not exceed 3 mm$^3$ L$^{-1}$. Similar to the bacillariophytes, the ochrophytes were significantly higher in the south basin from 2004 to 2006 (late years of the macrophyte

re-establishment) but higher in the north basin from 2011 to 2013 (during 'stable conditions'). Their biovolume was relatively low and did not exceed 2 mm³ L⁻¹ biovolume (Fig. 9.5). Cryptophytes and euglenophytes developed only modest biovolumes (Fig. 9.5), but often had statistically significant higher biovolumes in the north basin than in the south basin in some years from 2006 onwards. These differences in phytoplankton structure, mainly from 2004 onwards only, mirror the spatial patchiness of submerged vegetation but are of minor importance when describing the main picture of the long-term response of phytoplankton to lake restoration. For this reason, results in the following graphs are shown as averages for both lake basins of Alte Donau summarizing aspects in the water body as a whole.
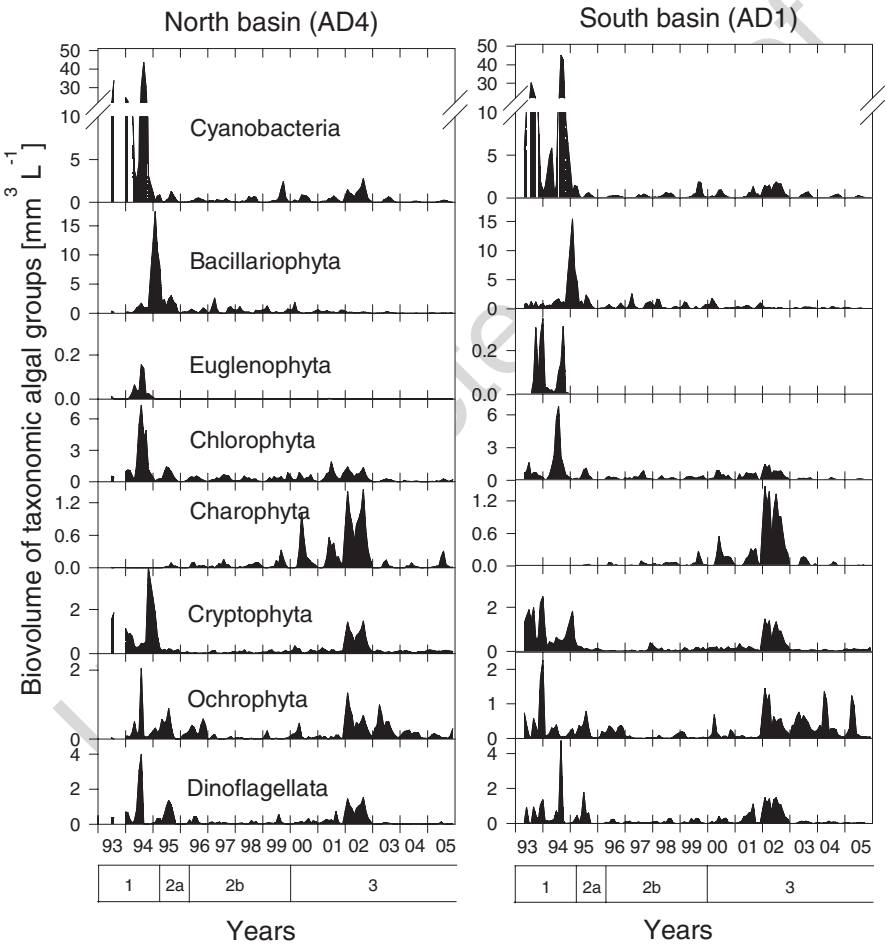


**Fig. 9.5** Time series of original data for monthly phytoplankton development at the sampling sites AD1 (south basin) and AD4 (north basin) from 1993 to 2005 comprising the first three periods of lake treatment: before restoration (*1*), restoration with chemical RIPLOX treatment (*2a*, *2b*) and re-establishment of macrophytes by periodical water level drawdown (*3*)
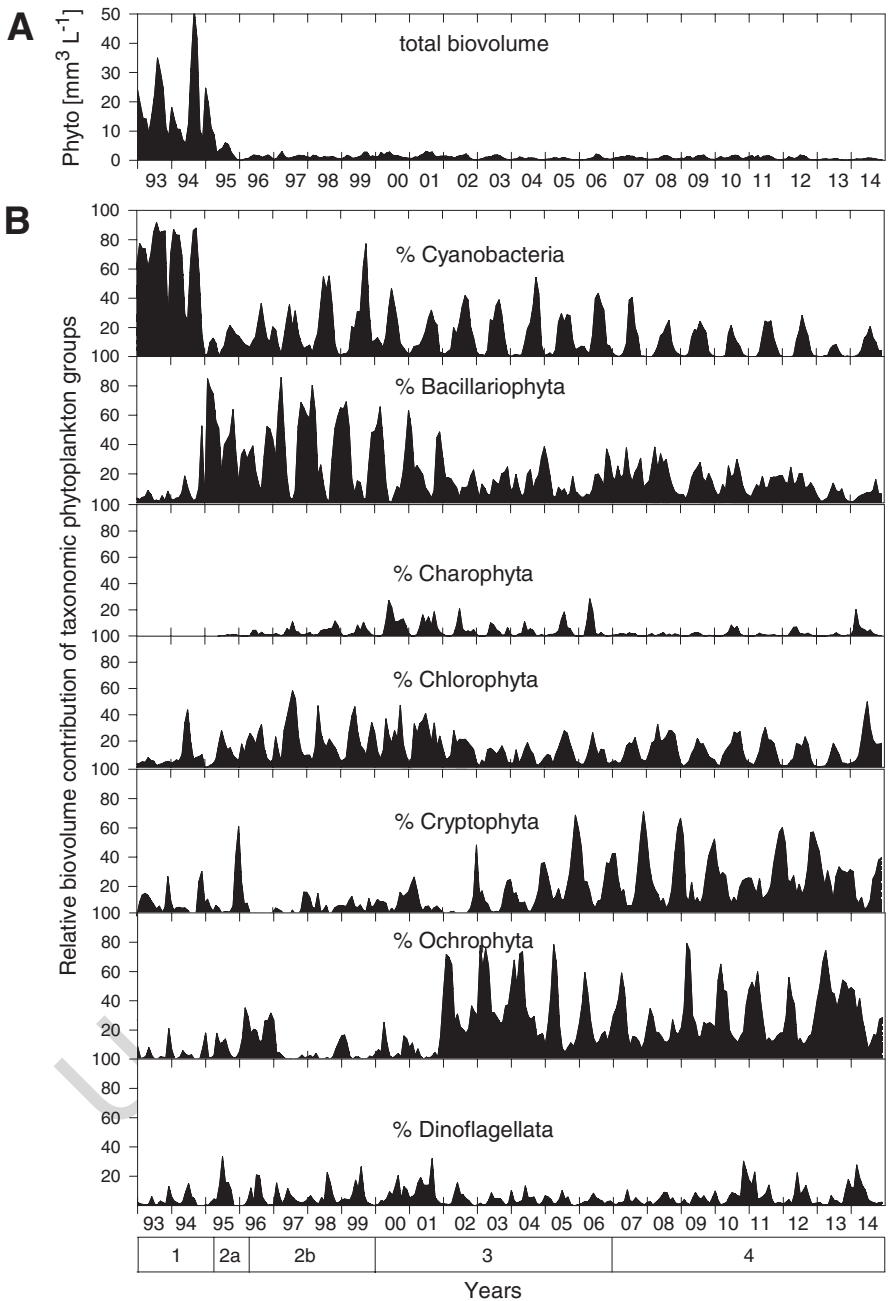
**Fig. 9.6** 22-year time series of phytoplankton development for total biovolume (**a**) and the contribution of higher ranks of phytoplankton taxa (**b**) comprising five treatment periods: before restoration (*1*), restoration with chemical RIPLOX treatment (*2a*, *2b*), re-establishment of macrophytes by periodical water level drawdown (*3*) and 'stable conditions' (*4*). Data are displayed as averages of the two main impoundments shown in Fig. 9.5

387    The total biovolume as average for both basins was peaking during the eutro-
388 phied years 1993 and 1993 with peak values more than $50 \text{mm}^3 \text{ L}^{-1}$ before chemical
389 precipitation by RIPLOX-treatment was carried out (Fig. 9.6a). Under these nutri-
390 ent rich conditions, filamentous cyanobacteria contributed up to 98% to phytoplank-
391 ton (Fig. 9.6b). As described in detail in former studies, *Cylindrospermopsis*
392 *raciborskii*, a taxon of the Nostocales, was the main cyanobacterium at that time and
393 occurred in association with *Limnothrix redekei* (Dokulil and Mayer 1996; Mayer
394 et al. 1997). With various measures of lake treatment, the biovolume contribution of
395 cyanobacteria decreased successively but still could contribute remarkable biovol-
396 umes with peak summer values from 20 to 50% (Fig. 9.6b). The cyanobacterial
397 composition, however, changed considerably when RIPLOX-treatment was con-
398 ducted in 1996 and 1997 and further lake treatment measures were carried out in
399 onward years. *C. raciborskii* almost disappeared and was replaced by various other
400 cyanobacterial taxa such as Chrococcales and Synechococcales (genera
401 *Chroococcus*, *Gomphosphaeria*, *Limnothrix*, *Microcystis*, *Pseudanabaena*,
402 *Radiocystis*, *Snowella*, *Woronichinia*). Bacillariophytes and chlorophytes reached
403 an intermediate importance in building up phytoplankton biovolume during chemi-
404 cal restoration (period 2), charophytes during the re-establishment of macrophytes
405 (period 3). Ochrophytes and cryptophytes contributed most to biovolume during
406 re-establishment of macrophytes and stable conditions (period 3 and 4).

### 9.3.3   Comparison of Phytoplankton Composition and Chl-a Content Between the Five Lake Treatment Periods

409 Besides the time series of the 22-year phytoplankton development, the box-plots in
410 Fig. 9.7 depict the distribution pattern of total biovolume and the chl-a concentra-
411 tion during the five periods of lake management (1, 2a & b, 3 and 4). For reference
412 of the trophic situation, the total phosphorus is displayed in this figure accordingly.
413 With the first chemical phosphorus precipitation in the RIPLOX-treatment year
414 1995, the average concentration during the eutrophied period (1, Fig. 9.7) dropped
415 to less than a half for TP (45% mean, 38% median), to about 20% for chl-a and to
416 about 15% for phytoplankton biovolume. This drastic reduction of phosphorus
417 availability for phytoplankton growth led to statistically significant differences in
418 the median value between the treatment periods (Fig. 9.7 Kruskal-Wallis test, a:
419 $H = 305.15$, $df = 4$, $p < 0.001$, b: $H = 149.78$, $df = 4$, $p < 0.001$, c: $H = 143.38$, $df = 4$,
420 $p < 0.001$) with a significant reduction of all three parameters from period 1 (sub-
421 group 'a') to 2a. The subsequent decrease of TP seems to be very closely associated
422 with chl-a as both these parameters follow almost the same statistically relevant
423 allocation of subgroups displayed by boxes, namely a less distinct phase in the first
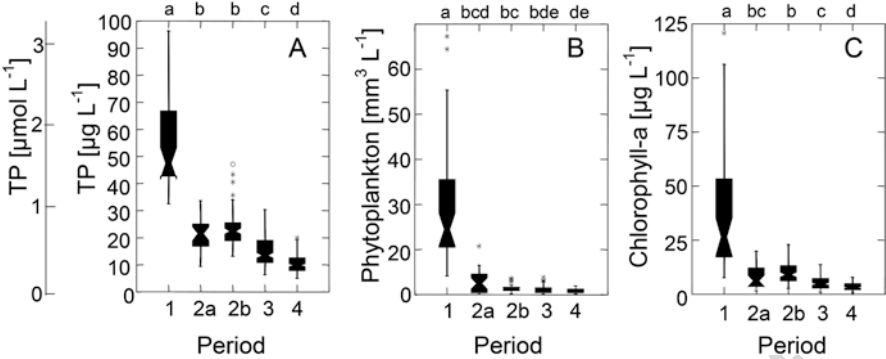424 RIPLOX-year followed by a slight recovery of the trophic level from the first to the

**Fig. 9.7** Box-whisker plots of (**a**) TP concentration (in μmol L$^{-1}$ and μg L$^{-1}$), (**b**) phytoplankton biovolume (mm$^3$ L$^{-1}$) and (**c**) chl-a concentration (μg L$^{-1}$) during the five treatment periods. All data are averages of AD1 and AD4. Statistically significant differences between homogeneous data subsets 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. 9.6 (see methods)

second RIPLOX-year and a further reduction during the re-establishment of macro- 425
phytes (period 3, subgroup 'c') and the period of stable conditions (period 4, sub- 426
group 'd'). Different to chl-a, the biovolume decreased gradually as subgroups were 427
statistically less distinctive during periods 2a to 4. The response of single phyto- 428
plankton groups to lowered TP is described in more detail for phytoplankton chl-a 429
and biovolume in Figs 9.8 and 9.9. 430

Analogous to the time series in Fig. 9.6, the compositional changes of phyto- 431
plankton can be described by shifted proportions among taxa of various taxonomic 432
affiliations (Fig. 9.8). The distribution pattern of chlorophyll content (Fig. 9.8a) and 433
phytoplankton groups (Fig. 9.8b–h) is displayed for the five lake treatment periods. 434
The most significant compositional change is caused by the reduction of cyanobac- 435
teria (Fig. 9.8b). The eutrophied period 1 ('subgroup a') does not overlap with later 436
lake treatment periods. After a strong reduction in the first RIPLOX-treatment 437
(period 2a), the biovolume contribution of cyanobacteria slightly increased in the 438
second RIPLOX-treatment (period 2b) before decreasing in onward periods showing 439
the lowest contribution in the period of stable conditions (period 4, subgroup 'c'). An 440
almost opposite pattern is found for ochrophytes and cryptophytes (Fig. 9.8c, d). A 441
prompt increase of their relative biovolume contribution was observed in the period 442
of the first RIPLOX-year of phosphorus precipitation (period 2a) followed by a 443
slight decrease during the second RIPLOX-treatment and a subsequent increase in 444
phytoplankton biovolume in periods of macrophyte re-establishment (period 3) and 445
stable conditions (period 4). The biovolume contribution of chlorophytes and bacil- 446
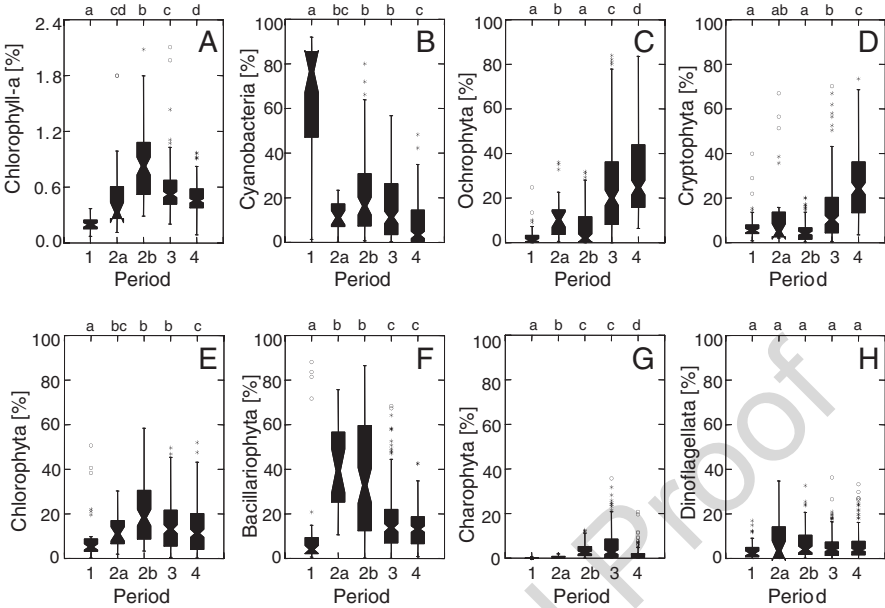lariophytes (Fig. 9.8e, f) revealed an intermediate increase during both RIPLOX- 447

**Fig. 9.8** Box-whisker plots of (**a**) chl-a content of phytoplankton as % of wet weight phytoplankton biomass (see method 9.2.4) and (**b–h**) relative contribution of taxonomic phytoplankton groups. All data are averages of AD1 and AD4. Statistically significant differences between homogeneous data subsets for each parameter 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. 9.6 (see methods)

years, but a successive decline in onward periods. The contribution of charophytes and dinoflagellates (Fig. 9.8g, h) remained low during all five periods. Charophytes reached their highest relative biovolume in the period of macrophyte re-establishment. For dinoflagellates, no significant differences between the treatment periods were observed (Kruskal-Wallis test, H = 9.18, df = 4, p = 0.057). The chl-a content of total phytoplankton (Fig. 9.7a) varied also among lake treatment periods. Its median value was lowest with 0.19% (mean 0.20%) for period 1 when cyanobacteria were mainly contributing to total phytoplankton (median 77%, mean 64%). The chl-a content is highest for period 2b (median 0.83%, mean 0.84%) and coincides with a high contribution of chlorophytes during period 2b (median 18%, mean 21%) and a large contribution of bacillariophytes (median 33%, mean 35%) while the contribution of cyanobacteria was moderate (median 16%, mean 21%).

When looking at biweekly data over the whole study period, phytoplankton chl-a concentration and biovolume shows a high temporal agreement (Spearman rank, r = 0.85 with p < 0.01; Fig. 9.9). The range of variation, however, is different for both parameters. With a CV of 1.5 for phytoplankton chl-a but of 2.4 for phytoplankton biovolume, the chl-a values are less variable than those of phytoplankton biovolume estimating the biweekly phytoplankton yields. The median percentage of chl-a is 0.50% of wet weight phytoplankton biomass (see methods). All data points
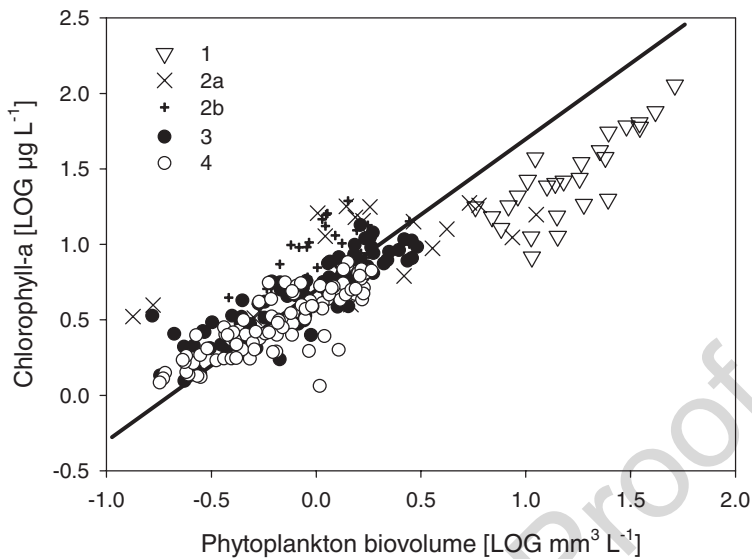
**Fig. 9.9** Relationship between phytoplankton chl-a concentration and phytoplankton biovolume, both displayed on a logarithmic scale ($LOG_{10}$). The solid line indicates 0.50% chlorophyll of phytoplankton biomass wet weight (median of biweekly averages of AD1 and AD4 over 22 years, see methods); Spearman rank correlation, r = 0.85, p < 0.001, n = 513; *1*, *2a*, *2b*, *3* and *4* indicate the lake treatment periods as in Fig. 9.6

describing the eutrophied period before the first chemical phosphate precipitation in   467
April 1995 are below the 0.50% line while most data points of period 2b are above   468
this value.   469

### 9.3.4   Assessment of Trophic State and Phytoplankton Habitat   470
         Score Index   471

The trophic classification according to Austrian standards is described by the rela-   472
tionship of summer phytoplankton chl-a concentration (Fig. 9.10a) or summer phy-   473
toplankton biovolume (Fig. 9.10b) versus annual TP concentration. As shown by   474
22 years passing five lake treatment periods, Alte Donau went through an ecosystem   475
shift from hypertrophic to mesotrophic, and finally reached a relative poor nutrient   476
status close to oligotrophic under 'stable conditions'. This main picture is observed   477
regardless of assessing chl-a or phytoplankton biovolume versus TP. The equivalent   478
assessment by chl-a and biovolume, however, is not valid throughout all five lake   479
treatment periods. Large differences in the assessment of lake nutrient status by   480
chl-a or biovolume were found for period 1 and 2b. During years before chemical   481
restoration (period 1, 1993 and 1994), summer chl-a values and annual TP concen-   482
trations indicate a hypertrophic situation (Fig. 9.10a). The values of chl-a and TP   483
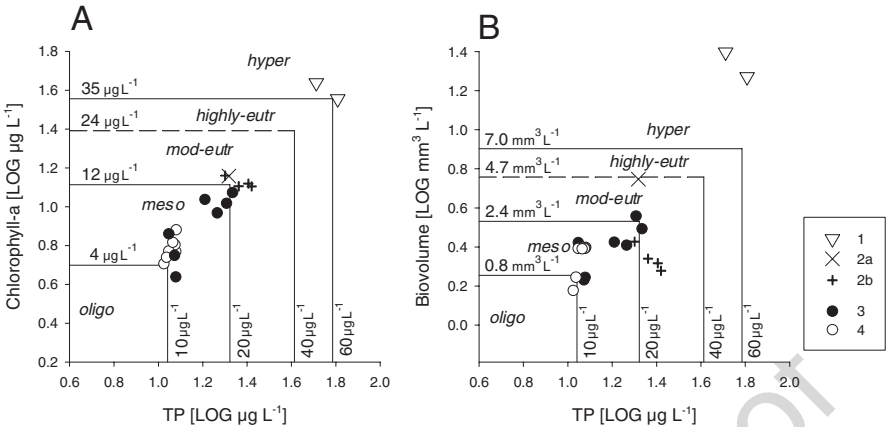
**Fig. 9.10** Scheme of trophic lake classification: trophy classes (*oligo* oligotrophic, *meso* mesotrophic, *mod-eutr* moderately eutrophic, *highly-eutr* highly eutrophic, *hyper* hypertrophic) are shown as response curve of summer phytoplankton chl-a concentration (**a**) and summer phytoplankton biovolume (**b**) to annual TP concentration displayed on a logarithmic scale ($LOG_{10}$); Solid lines and respective numbers of class limits refer to Austrian standards (ÖNORM M6231 2001). Dashed lines and numbers for class limits between highly and moderately eutrophic for chl-a and biovolume are calculated to distinguish the five TP classes accordingly (see methods); data are averages of AD1 and AD4; *1*, *2a*, *2b*, *3* and *4* indicate the lake treatment periods as in Fig. 9.6 (see methods)

484　are both close to the limit between hypertrophic and highly eutrophic. When assess-
485　ing the trophic classification by summer phytoplankton biovolume and annual TP
486　concentration, the biovolume exceeds the class limit of biovolume towards hyper-
487　trophic conditions much more than those of TP (Fig. 9.10b). In addition, trophic
488　class assignment differs for the period with repeated RIPLOX-treatment and fol-
489　lowing years of restoration (period 2b), i.e. summer chl-a still demonstrates a mod-
490　erately eutrophic level while summer biovolume already indicates a mesotrophic
491　level. According to the compositional shifts of phytoplankton, the chl-a content
492　changed during the treatment periods as described for Figs. 9.8 and 9.9. The pre-
493　dominance of cyanobacteria during hypertrophic summer phytoplankton develop-
494　ment was associated with a relatively low chl-a content per phytoplankton biomass.
495　In turn, the chl-a content in period 2b was particularly high when the contribution
496　of cyanobacteria was low but that of chlorophytes considerably high. Comparing
497　the trophic classification scheme of Fig. 9.10a, b, double logarithmic scaled data
498　points for chl-a versus TP follow a linear relation more closely (Spearman rank,
499　r = 0.86 with p < 0.01; Fig. 9.10a) than those of biovolume versus TP (Spearman
500　rank, r = 0.51 with p < 0.05; Fig. 9.10b).

501　The trophic classification assessed by the Austrian phytoplankton assemblage
502　metric are displayed for the five lake treatment periods separately Fig. 9.11. The
503　bars mirror the distribution pattern of species in assemblages occurring from oligo-
504　to hypertrophic. The black bars indicate the most probable trophic classification
505　during each lake treatment period. According to this metric, Alte Donau shifts from

**Fig. 9.11** Phytoplankton habitat quality index for the five lake treatment periods. The phytoplankton assemblage metric refers to five trophic states: 1-oligotrophic (TP < 10 μg L$^{-1}$), 2-mesotrophic (TP 10–20 μg L$^{-1}$), 3-moderately eutrophic (TP 20–40 μg L$^{-1}$), 4-highly eutrophic (TP 40–60 μg L$^{-1}$), and 5-hypertrophic state (TP >60 μg L$^{-1}$), The black bar indicates the highest probability of trophic state; *1*, *2a*, *2b*, *3* and *4* indicate the lake treatment periods as in Fig. 9.6 (see methods)
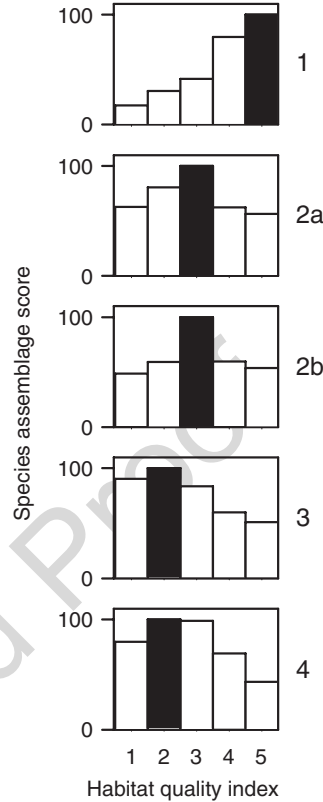
hypertrophic to mesotrophic along the five lake treatment periods which is in agreement with the main picture of the trophic classification shown in Fig. 9.10. With the first RIPLOX-treatment, the metric indicates the pronounced step by prompt species response from an assemblage typically found in hypertrophic lakes (mainly built up by the cyanobacterium *Cylindrospermopsis raciborskii*) to an assemblage shared by species of various taxonomic affiliations commonly found in moderately eutrophic environments. This result thus mirrors the drastic change indicated by the relationship of chl-a versus TP more closely than by phytoplankton biovolume versus TP. According to this metric, the second RIPLOX treatment and the measures during this period 2b manifest this species composition of a moderately eutrophic lake. With period 3 and 4 more species are referring to a mesotrophic reference, which is mainly due to cyanobacteria taxa other than *C. raciborskii* and a further mixture of species allocated to the ochrophytes and cryptophytes (see results for Fig. 9.8 before) commonly observed in mesotrophic lakes.

## 9.4  Discussion

Total biovolume of phytoplankton did not significantly differ for the two impoundments with the exception of 4 years in the 22-year time series. The similar phytoplankton development in the two impoundments is found despite the large spatial heterogeneity of the banks and basins of the former Danube river branch (Table 3.1 and Fig. 3.1 in Chap. 3; see also Chaps. 18 and 19). For example, macrophyte standing crop was about 30% lower in the south basin than in the north basin during the period from 2005 to 2008, while it was 20% higher in the south basin from 2009 to 2012; in onward years the distribution was more even (Karin Pall, pers. comm.). In addition, annual phosphorus loading was more than twice as high in the south than in the north basin in the recent years 2008–2014 (Fig. 6.6 in Chap. 6) which is associated with a longer retention time (Chap. 3). The even distribution of total phytoplankton in both basins, however, is in line with the strong consistency of zooplankton (Chap. 11) and ciliate biomass (Chap. 12) in both impoundments. When looking at particular taxonomic affiliations of phytoplankton, such as bacillariophytes, ochrophytes, cryptophytes and euglenophytes, no statistically significant differences were found before 2002, i.e. the 10 years before underwater vegetation was re-established. In onward years, a frequent alternation of low and high biovolume of different taxonomic affiliations was observed for the two impoundments which arose from the strong re-growth of underwater vegetation (mainly built of *Myriophyllum spicatum*, Fig. 8.9 and Table 8.2 in Chap. 8, Fig. 20.5 in Chap. 20). During that period underwater vegetation strongly increased from a very low biomass in 2002 to a 6-fold higher yield of 125 t dry mass in 2003 and then remained stable at about 300–500 t dry weight (see time series of macrophyte development Figs. 8.7 and 8.11 in Chap. 8). As total phytoplankton biovolume did not significantly differ in years with massive underwater vegetation yield, it can be assumed that biovolume among taxa of different taxonomic affiliations was counterbalanced as e.g. statistically higher biovolumes were found for bacillariophytes in the north basin and for cryptophytes in the south basin. This might display the substitution of benthic-pelagic species versus exclusively pelagic species, as many bacillariophytes are benthic species and might have been additionally found as phytoplankton in water column samples near patchy underwater vegetation, while areas with less underwater vegetation might have stimulated the growth of exclusively planktonic species, such as e.g. the cryptophytes. The shift of mainly tychoplanktonic pennate diatoms towards mainly planktonic solitary centric diatoms and the further shift towards e.g. cryptophytes is commonly described for ecosystems along the transition from lentic to lotic habitats in association with modified light and nutrient exposure (e.g., Bahnwart et al. 1998; Nicklisch 1998; Nicklisch et al. 2007; Centis et al. 2010; Wu et al. 2010; Zohary et al. 2010; Naselli-Flores and Barone 2011; Abonyi et al. 2012; Shatwell et al. 2012).

The species composition of the phytoplankton community found in Alte Donau is similar to that found in the river-floodplain system of the River Danube (e.g., Kiss 1987; Schmidt 1994; Schagerl and Riedler 2000; Mihaljević et al. 2010; Dokulil

and Donabaum 2014). All species reported for Alte Donau were further common in shallow lakes as, e.g., documented for North Germany by Täuscher (2014).

### 9.4.1 The Success of Filamentous Cyanobacteria Cylindrospermopsis raciborskii *in the Nutrient Rich Oxbow Lake*

The awareness of the unhealthy state of the ecosystem Alte Donau increased with the ongoing eutrophication in 1993 and 1994, when progressive turbidity of the water body was mirrored by a Secchi depth of approximately 0.5–1.5 m which was caused by cyanobacterial blooming (Chap. 6, see also Mayer et al. 1997; Donabaum et al. 1999; Dokulil and Teubner 2003). Effective lake restoration and management measures were deemed necessary in this urban lake when realising that the main planktonic cyanobacterium was *Cylindrospermopsis raciborskii* since strains of this cyanobacterium can potentially produce several cyanobacterial toxins, saxitoxins and cylindrospermopsin (e.g., Fastner et al. 2003, 2007; Kurmayer and Christiansen 2009). During the mass development in Alte Donau, however, no evidence of such substances was recorded by symptoms of bathing people, which confirms other field studies of non-toxic strains building up *C. raciborskii* blooms (Alster et al. 2010). Although no measurements of toxins were carried out in Alte Donau and hence no chemical information is available on the presence of toxins attributed to strains of *C. raciborskii*, it can be assumed that such toxic substances were not a major issue in this popular bathing lake in 1993 and 1994 even though being aware of the scientific challenge in predicting toxic cyanobacterial blooms (e.g. Bukowska et al. 2017). This cyanobacterium was originally commonly observed in the subtropical and tropical region (e.g., Bouvy et al. 2006; Figueredo and Giani 2009). It is now more increasingly found as an invasive species in the temperate zone and often seen to be growth stimulated by global warming in nutrient rich shallow lakes (Dokulil and Mayer 1996; Padisák 1997; Isvánovics et al. 2000; Mischke 2003; Nixdorf et al. 2003; Stüken et al. 2006; Fastner et al. 2007; Kling 2009; Kaštovský et al. 2010; Aubriot and Bonilla 2012; Bonilla et al. 2012; Paerl and Otten 2013; Burford et al. 2016; Dokulil 2016; Kokociński et al. 2017). *C. raciborskii* belongs to the Nostocales among the Cyanobacteria which are known to be able to fix $N_2$ in heterocytes during periods of nitrogen limitation (e.g. see trait description for this taxon in the phytoplankton functional group by Mantzouki et al. 2016). $N_2$-fixation by nostocale cyanobacteria, however, is not necessarily a dogma for acquiring nitrogen, even if among vegetative cells also heterocytes are grown by these prokaryotic species (Teubner 1996; Teubner et al. 1999). The preferred and hence more likely sources for utilising nitrogen are ammonium and further nitrate if these N-fractions are available for cyanobacteria (e.g., Dudel and Kohl 1991; Burford et al. 2006). The cyanobacterial filaments of *C. raciborskii* were the most important for building up phytoplankton in 1993 and 1994 when total biovolume yielded a summer maximum

of more than 50 mm³ L⁻¹ (original description in Dokulil and Mayer 1996 and Mayer et al. 1997, reinforced analysis of this dataset in Dokulil 2016). *C. racibor-skii* developed highest biovolumes at a water surface temperature of 21.4 °C under well-mixed, hypertrophic conditions in the polymictic Alte Donau (Dokulil and Teubner 2000; hydrological retention time and hydrological aspects including the ground-water flow attributed to the oxbow and groundwater-seepage lake see meth-ods and Chaps. 3 and 4). Nixdorf and Deneke (1997) compared a variety of eutro-phied lakes in North Germany with deep stratified and shallow well mixed water columns during summer and stated that at least 'very shallow' lakes were the most efficient systems in utilising phosphorus due to the favourable proportion between euphotic depth and mixing depth. An example for this category is Lebbiner See with a maximum depth of 4 m, a contribution of summer cyanobacteria by more than 90% to total biovolume, an occurrence of *C. raciborskii* among other filamentous cyanobacteria, and a summer chlorophyll peak value of 71 µg L⁻¹, indicating three aspects of a phytoplankton situation that is comparable to the condition of Alte Donau before restoration. According to a field survey in The Netherlands referring to more than 400 'lake years' from 80 lakes, which were mainly shallow and eutro-phied, cyanobacteria contributed with 46% the most to phytoplankton (Schreurs 1992). Schreurs emphasized that the comparison of annual yields in '*Oscillatoria*', '*Aphanizomenon*' and '*Microcystis*'-dominated lakes shows that the highest con-centrations of chlorophyll-a occurred in the '*Oscillatoria* lakes' with a long-lasting dominance especially of e.g. *Planktothrix agardhii*. The success of building up an extremely high phytoplankton yield in 'typical' Oscillatoria- years could be verified by the flushed riverine lake 'Langer See' in the early 1990s in Germany (Teubner 1996; Teubner et al. 1999), which built up blooms with solitary filaments of *Planktothrix agardhii* in association with solitary filaments of *Limnothrix redekei* as opposed to alternatively blooming associations forming scum mainly composed of two colonial forms of cyanobacteria, *Aphanizomenon flos-aquae* (bundles of fila-ments) and *Microcystis* spp. (coccal cell aggregates). In Alte Donau, the massive bloom of *C. raciborskii* was associated with *L. redekei* (Dokulil and Mayer 1996; Mayer et al. 1997; Dokulil 2016), which would support the finding by Schreurs (1992) that in particular solitary filaments of cyanobacteria are successfully build-ing up high yields in nutrient-rich shallow lakes.

One aspect in describing the successful development of cyanobacteria in a highly fluctuating environment in terms of light and nutrient availability is analysing the maximum growth rate for optimal growth in comparison to modulated nutrient and light conditions. Such experiments under different light and nutrient exposure are aimed at mimicking a regime of a turbulent turbid water column and could show that cyanobacteria forming solitary filaments (Nicklisch 1998; Nicklisch and Fietz 2001; Nicklisch et al. 2007; Shatwell et al. 2012; Deng et al. 2016) can cope well with continuous or fluctuating light and nutrient availability. Lab experiments and field assays specifically with *Cylindrospermopsis raciborskii* underpin the finding on the successful growth in well mixed turbid environments for this solitary fila-mentous cyanobacterium (Isvánovics et al. 2000; Aubriot and Bonilla 2012; Bonilla

et al. 2012; Amaral et al. 2014; Dokulil 2016). Other aspects for prosperous development of cyanobacteria in general or of *C. raciborskii* in the specific case indicated by long-lasting blooms in particular in summer are a higher temperature optimum for growth (Nicklisch et al. 2007; Joehnk et al. 2008; Kokociński et al. 2017), a highly adaptive strategy of phosphorus acquisition even of ephemeral nutrient-source patches (e.g., Falkner and Falkner 2003; Aubriot and Bonilla 2012; Amaral et al. 2014) and storage behaviour (e.g. Isvánovics et al. 2000).

As maximization of phosphorus uptake is a function of cell surface (in addition to enzyme activity and related capacity of transport incorporating phosphorus, see e.g. Finkel et al. 2009), the long thin filaments of solitary trichoms, as e.g. found for *Cylindrospermopsis raciborskii* and *Limnothrix redekei* (their filament diameter is only 1.8–2.4 μm and 3.05–3.8 μm, respectively; unpublished data Teubner), might provide a further aspect of ecological relevance mirrored by field studies. Comparing surface to volume ratios of species of various taxonomic affiliations in meso- to hypertrophic lakes, the Oscillatoriales together with filaments of Synechococcales (former Oscillatoriales) represent the second highest surface to volume ratios (median 1507 mm$^2$ L$^{-1}$ per mm$^3$ L$^{-1}$, n = 259), while those of filamentous Ulotrichales were much higher (4071 mm$^2$ L$^{-1}$ per mm$^3$ L$^{-1}$, n = 126) and of pennate diatoms slightly lower (1374 mm$^2$ L$^{-1}$ per mm$^3$ L$^{-1}$, n = 357, dimensions measured by Interference reflection microscopy, data from Fig. 23 in Teubner 1996; empirical measures of surface and volume for algae of various taxonomic affiliations see also Morabito et al. 2007).

During the ecosystem shift from the hypertrophic to mesotrophic, the relative contribution of cyanobacteria to total biovolume in summer remained relatively high with about 20% although the TP concentration and total phytoplankton dropped drastically. A closer look at the species shift within the cyanobacteria, however, reveals that cyanobacteria, such as blooming *Cylindrospermopsis raciborskii* disappeared while other cyanobacteria such as *Microcystis*, *Aphanocapsa* taxa became typical cyanobacterial summer taxa even in the period of 'stable conditions' (period 4). Many cyanobacteria found in period 4, however, were already documented for mesotrophic conditions in 1986 and 1987. In a multi-site phytoplankton field survey during that time, Donabaum (1988) reported cyanobacterial taxa (Chroococcales and Synechococcales) such as *Microcystis aeruginosa*, *M. flos-aquae* and *Planktolyngbya limnetica* in addition to ochrophyte and charophyte taxa (*Uroglena* spp., *Closterium aciculare* T.West).

The growth of cyanobacteria is described for a variety of ecotypes from oligo- to hypertrophic and occurs under particular underwater light climate at surface water or deep metalimnetic layers from mixed to stratified water columns, from shallow to deep lakes, from lakes of the tropical and subtropical to the temperate zone (e.g., Jewson 1977; Schreurs 1992; Mur et al. 1993; Dokulil and Teubner 2000; Teubner et al. 2004; Teubner 2006; Paerl and Otten 2013; Qin et al. 2013). The maximum of about 20% peak contribution of cyanobacteria in summer is thus not critical for our conclusion of successful restoration in mesotrophic Alte Donau as (1) cyanobacterial taxa mirror a high ecological plasticity and (2) their portion in phytoplankton is in the same range as for diatoms and green algae, while only those for cryptophytes

and ochrophytes are a bit higher. The success of restoration in view of phytoplankton composition thus might be seen in the balanced mixture of taxa of many taxonomic affiliations (e.g. Bouvy et al. 2006) and points in the direction of enhanced biotic diversity and richness stabilising a healthy ecosystem (e.g., Costanza and Mageau 1999; Dokulil and Teubner 2010). This is also in agreement with the phytoplankton assemblage metric applied for Alte Donau (Dokulil et al. 2005), which indicates a shift from phytoplankton taxa commonly found in hypertrophic lakes observed before restoration to taxa commonly occurring in mesotrophic lakes described for the 'stable' condition of the restored Alte Donau. This result verifies that phytoplankton assemblage metrics are useful tools for analysing the trophic status of lakes and rivers, which is often used to assess the ecological status of an aquatic ecosystem (e.g., Dokulil et al. 2005; Dokulil and Teubner 2006; Padisák et al. 2006; Lepistö et al. 2006; Crossetti and Bicudo 2008; Solimini et al. 2008; Nõges et al. 2009, 2010; Marchetto et al. 2009; Rimet et al. 2009; Poikane et al. 2011; Napiórkowska-Krzebietke et al. 2012; Katsiapi et al. 2016; Lobo et al. 2016; Pasztaleniec 2016; Vadrucci et al. 2017).

## 9.4.2   *The Seasonal Pattern of Phytoplankton Development*

The bloom of *Cylindrospermopsis raciborskii* and *Limnothrix redekei* is not only observed for summer periods (it is commonly agreed that cyanobacteria are typically blooming during the hot season; e.g., Dokulil and Teubner 2000; Cao et al. 2008; Liu et al. 2011; Paerl and Otten 2013), but is lasting also until autumn (Dokulil and Mayer 1996; Mayer et al. 1997; Dokulil 2016). Such a 'warm assemblage' lasting during summer and autumn (Komárková et al. 2003) is dedicated to the growing season established after spring overturn and lasting to autumnal mixing and are commonly studied when describing phytoplankton succession. The importance of 'cold assemblages' lasting from winter to spring (Komárková et al. 2003) became more relevant in recent years with increasing awareness of over-wintering phytoplankton (e.g., Rodhe 1955; Adrian et al. 1999; Weyhenmeyer et al. 1999; Teubner 2000; Morabito et al. 2002; Barone and Naselli-Flores 2003; Naselli-Flores and Barone 2003; Anneville et al. 2005; Dokulil and Herzig 2009; Hampton et al. 2017). It's impact on vernal bloom is most relevant for lake assessment and climate research. This pattern of main compositional shifts that occur only twice a year, i.e. first during the transition from spring to summer establishing a 'warm assemblage' lasting from summer to autumn, and secondly during the transition from autumn to winter building up a 'cold assemblage' lasting from winter to spring, was also found in Alte Donau and verifies earlier studies from shallow to deep lakes (using discriminant function analysis in Teubner 2000 and Bray-Curtis similarity in Teubner et al. 2003a). This seasonal pattern is a cornerstone of understanding phytoplankton development in view of lake phenology in the temperate climate zone, whether in view of the succession of phytoplankton species (e.g. plankton groups ecology by

Sommer et al. 1986, 2012; De Senerpont Domis et al. 2013) or the description of seasonally co-occurring taxa of various affiliations by functional groups (e.g., Reynolds et al. 2002; Padisák et al. 2009; Crossetti and Bicudo 2008; Nõges et al. 2010; Vadrucci et al. 2017). The transition from spring to summer, i.e. 'clear-water phase', is a key parameter when studying lake phenology (Sommer et al. 1986; De Senerpont Domis et al. 2013). In Alte Donau this short period of increased water transparency occurred from early April to late May (Chap. 11) stimulating the vernal growth of submerged plants (see Sect. 8.3.1 in Chap. 8) which is most important for the recovery of aquatic vegetation (e.g. Scheffer et al. 2001; Wu et al. 2014). The timing of the clear-water phase is in accordance with phenology for other shallow polymictic lakes (Teubner et al. 1999; Straile and Adrian 2000; Huber et al. 2010; Shatwell et al. 2008) and different from an often later timing for deeper lakes (Müller-Navarra et al. 1997; Winder and Schindler 2004; Straile 2002). The trend analysis revealed a time shift by about 11 days advance per decade and is associated with climate change (details in Sect. 11.3.5 of Chap. 11). According to our analysis, the phenology of the vernal clear-water phase can be described for two distinct periods with regard to the phosphorus decline, i.e. a more pronounced shift of 33 days per decade earlier during the rapid decline of TP from 1994–1999 (period 1 and 2) and a shift of only 7 days earlier per decade for years of moderately low TP (period 3 and 4). According to empirical analysis including lakes with long-term external reduction of phosphorus loading, the phenology of the vernal clear-water phase should be interpreted with caution as time-shifts cannot be attributed to climate change only but are a result of the interplay of climate forcing and trophic changes in the ecosystem (e.g. Jeppesen et al. 2003).

### 9.4.3 The Success of Restoration in Terms of Controlling Phytoplankton Yield, Assessed by Chl-a And Biovolume

During the late 1980s large water level fluctuations in Alte Donau (Fig. 5 in Chap. 5, see further Chap. 6, Donabaum et al. 2004) were associated with a considerable nutrient input from contaminated groundwater and sewage. During this period, high nutrient concentrations were observed in the Danube River (TP 238 µg L$^{-1}$, total nitrogen 2.53 mg L$^{-1}$) which is in the close vicinity of Neue Donau and Alte Donau (Dokulil and Janauer 1990). The small lake surface, the low 'relative depth' and large inputs of contaminated groundwater characterize Alte Donau as groundwater-seepage fed ecosystem acting similar to those of riverine lakes as highly productive lakes under hypertrophic conditions (Teubner 1996; Teubner et al. 1999). Such lakes are known for their low phosphorus retention (Brett and Benjamin 2008; Kõiv et al. 2011). As reported in detail in the eutrophication history in Chap. 5, an integrated lake management plan included external (e.g. completion of remediation wells and sewage network for allotment gardens and other arrears in close neighbourhood in 1995) and internal measures (e.g., initial chemical RIPLOX-treatment

772 in 1995 and 1996, Fig. 5.3 in Chap. 5) to reduce phosphorus loading from external
773 and internal sources.

774     According to a multi-lake study by Jeppesen et al. (2005), the internal phospho-
775 rus load recovery is about 10–15 years when internal abiotic and biotic lake pro-
776 cesses are shifting towards an efficient phosphorus cycling system and at the same
777 time are diminishing the phosphorus availability for phytoplankton growth. The
778 phytoplankton composition analysed from another long-term multi-lake recovery
779 survey shifted after 15 years from an assemblage mirroring a phosphorus enriched
780 environment to an assemblage occurring in an environment of low phosphorus pool
781 (Anneville et al. 2005). Although the phosphorus pool has already decreased the
782 phytoplankton yield response is often delayed by a few years during internal lake
783 recovery (Dokulil and Teubner 2005, see also hysteresis in Fig. 20.4 in Chap. 20).

784     In Alte Donau, mainly two in-lake treatment measures, the chemical phosphorus
785 flocculation associated with nitrate oxidation of the sediment by RIPLOX-treatment
786 (RIPLOX-scheme see Fig. 5.3 in Chap. 5, sediment analysis in Chap. 7) and the re-
787 establishment of the reed-belt and submerged vegetation (Chaps. 8 and 18), were
788 aimed at accelerating the internal load recovery in Alte Donau, which shifted this
789 urban lake from a hypertrophic state in year 1994 to a moderately eutrophic state in
790 years 1995/96, and to a mesotrophic state in year 2000 (total phosphorus loading as
791 function of the hydraulic load see Fig. 1.1 in Chap. 1). After this five-year in-lake
792 management (1995–1999), the lake remained mesotrophic and reached even lower
793 levels of moderate mesotrophic conditions.

794     Triggered by chemical phosphorus precipitation, the total phosphorus concentra-
795 tion of about 70 μg L$^{-1}$ (2.37 μmol L$^{-1}$) before the restoration (hypertrophic)
796 decreased to about 30 μg L$^{-1}$ (0.89 μmol L$^{-1}$) in 1995 and 20 μg L$^{-1}$ (0.6 μmol L$^{-1}$)
797 in 1996 (moderately eutrophic). Forced by this drastic decline of TP, the planktonic
798 community adjusted promptly to efficiently utilising the remaining phosphorus
799 sources. According to an earlier study by Teubner et al. (2003b) for the years 1994–
800 1996, planktonic biota acted as a sink for phosphorus at lowered TP pool in two
801 ways: a) with the tighter coupling between planktonic food and consumer organ-
802 isms, a larger portion of phosphorus was bound by biota at the expense of the dis-
803 solved P-fractions, and b) with the compositional shifts from an N-rich towards a
804 P-rich biota when assessing stoichiometry of plankton community (Teubner et al.
805 2003b). The zooplankton to phytoplankton ratio markedly increased after the
806 RIPLOX treatment and stands for a close coupling of zooplankton and their food
807 (Fig. 11.6 in Chap. 11, see also Teubner et al. 2003b). The increase of this ratio was
808 mainly due to the low biovolume of phytoplankton under P-limited conditions as
809 many short-lived primary producers often respond promptly to drastic nutrient
810 reduction (e.g., Jeppesen et al. 2000; Ibelings et al. 2007). Such an increase of zoo-
811 plankton relative to phytoplankton is commonly observed in lakes or particular lake
812 sites at declining nutrient levels (e.g., Padisák 1993; Teubner et al. 2003b, Jeppesen
813 et al. 2000, 2005; Moustaka-Gouni et al. 2006; Wu et al. 2007; He et al. 2017).

814     A spontaneous growth of submerged macrophytes was stimulated by enhanced
815 light availability at low phytoplankton yield after past RIPLOX treatment (see time
816 series of phytoplankton and macrophyte yield in Fig. 20.2 in Chap. 20). In addition,
817 the successful re-planting of the reed belt and submerged macrophytes (Chaps. 8

and 18) contributed further to reduce the phosphorus availability for phytoplankton growth from year 2000 onwards. According to the monograph on Alte Donau 1986/87 by Löffler (ed, 1988), the TP plant tissue content varied between submerged species and sampling sites and ranged for individual measurements from 0.52 to 3.6 mg FW $g^{-1}$ (mean values: 1.54 mg FW $g^{-1}$ for *Myriophyllum spicatum*, 1.51 mg FW $g^{-1}$ for species of Characeae). The long stems of *M. spicatum*, that are close to the water surface, are removed by moving which is necessary in some recreational areas used for swimming and boating. Mowing thus further contributes to some extent to eliminate phosphorus from Alte Donau. The impact of accidentally removing fish through mowing is described in Chap. 15. In a longer perspective, the aim is to further increase the standing crop of macrophytes while successively replacing tall-growing macrophyte species (e.g. *Myriophyllum*, Figs. 11.8 and 8.8, plant biomass in Fig. 8.10) by short-growing macrophytes inhabiting deeper layers (species of Characeae, Fig. 8.8) (see Chaps. 8, 18 and 20). The recovery of macrophytes, whether by exclosures or cage planting or by whole-lake stimulated growth due increased underwater light availability forced by biomanipulation, is seen as a successful restoration tool in addition to or instead of common fish manipulation for stabilising a high water quality in shallow to deep lakes (e.g., Ozimek et al. 1990; Jeppesen et al. 2000; Qiu et al. 2001; Ibelings et al. 2007; Hilt et al. 2010; Wu et al. 2014; Phillips et al. 2016). Beside the discussed two main in-lake management measures, the more balanced water fluctuation and the longer retention time (methods, see also Chaps. 2, 3, 5 and 6) might have contributed to stabilizing the low phosphorus availability and subsequently the successful re-establishment of macrophytes in recent years. The persistence of mesotrophic conditions for the 15 recent years of our long-term study Alte Donau stands for the sustained shifting towards a healthy ecosystem (Costanza and Mageau 1999; Dokulil and Teubner 2010).

The dimensionality of ecosystem response is often reduced to the relationship between phytoplankton yield and concentration of the total pool of phosphorus, the most limiting nutrient element in freshwaters. This relationship is commonly used to develop a trophic classification scheme for identifying the overall success of restoration measures or the trophic state in lakes (e.g., Vollenweider 1968; Carlson 1977; Forsberg and Ryding 1980; McCauley et al. 1989; Reynolds 1992; Watson et al. 1992; Teubner and Dokulil 2002; Dokulil and Teubner 2003; Lepistö et al. 2006; Søndergaard et al. 2011; Qin et al. 2013). TP vs Chl-a graphs are also shown in other chapters to introduce (Chap. 1) or summarize the main idea of restoration (Chap. 20) in Alte Donau although data were treated differently than in this phytoplankton chapter (see methods). According to our analysis, the relationship between phytoplankton chl-a or phytoplankton biovolume versus TP roughly provides the same main picture of ecosystem shift from a hypertrophic state in 1993 to a mesotrophic state in 2014. Taking into account the high variability of chl-a content in phytoplankton biomass, it might be a rather counterintuitive result that both the chl-a:TP relationship ($p < 0.01$) and biovolume:TP relationship ($p < 0.05$) are statistically significant when analysing the empirical data on a double logarithmic scale. Chl-a is a ubiquitous photosynthetic pigment occurring in phytoplankton of all taxonomic affiliations (e.g., Tolstoy 1979; Bricaud et al. 1995; Richardson et al. 1983; Donabaum 1992) and is thus used as a proxy for phytoplankton yield. The median

of chl-a wet weight phytoplankton biomass for the whole data record in Alte Donau confirms the average chlorophyll content of 0.50% wet weight phytoplankton biomass reported for a large data set across trophic gradient by Kasprzak et al. (2008) and a large number of cultures including cyanobacteria and eukaryotic taxa (chlorophytes, cryptophytes, bacillariophytes and ochrophytes) by Donabaum (1992). Fluctuations in the chl-a content per biomass or biovolume occur along different time scales of acclimation and adaptation (Geider and MacIntyre 2002). Photoacclimation often results in a relative increase of chl-a yield per cell or per carbon (also measured by an increase of both the size and number of photosynthetic units) for algae that are adjusted to a low light environment while light saturation commonly leads to the opposite (e.g., Geider et al. 1997; Felip and Catalan 2000; Teubner et al. 2001; Schagerl and Müller 2006; Grant and Louda 2010; McKew et al. 2013). Furthermore, chl-a content and light absorption by chl-a increase in response to fluctuating light when compared with constant light (e.g. for cyanobacteria see Nicklisch 1998; Nicklisch and Fietz 2001; Shatwell et al. 2012). According to allometric rules, the cellular chl-a content per biomass is relatively high for small cell dominated assemblages compared to large cells (e.g., Richardson et al. 1983; Bricaud et al. 1995; Vörös and Padisák 1991; Kalchev et al. 1996; Woitke et al. 1996; Felip and Catalan 2000; Teubner et al. 2001). The impact of adaptation is most relevant when species composition changes as the chl-a content per phytoplankton biomass depends on the photosynthetic apparatus that is different among taxa of various affiliations. The elevated chl-a content during periods of relative high contribution of chlorophytes (0.83% wet weight phytoplankton biomass) in Alte Donau relies on the especially high contribution of this photosynthetic pigment in chlorophyte species (e.g., Donabaum 1992; Greisberger and Teubner 2007). In turn, cyanobacteria with photosynthetic phycobilines, which are contributing to light harvesting in addition to chl-a, are well known to rely on low chl-a content per biomass or biovolume yield (Feuillade and Davies 1994; Donabaum 1992; Schagerl and Müller 2006; Schagerl and Donabaum 2003; Greisberger and Teubner 2007), which thus corresponds to lowest chl-a content (0.19% wet weight phytoplankton biomass) during cyanobacterial blooms in Alte Donau (time series of chl-a content per wet weight of phytoplankton see also Dokulil et al. 2007). In this view, biomass phytoplankton yields that are composed of large-celled cyanobacteria and exposed to saturating light conditions might tend to be underestimated by chl-a measurements. Likewise, the biomass yield of small-sized chlorophytes inhabiting depth layers of low light availability might usually be over estimated by chl-a. Facing the different time scales effecting alterations of chl-a (Geider and MacIntyre 2002), namely rather short-term acclimation due to an adjustment within minutes to hours lasting for hours to days or long-term adaptation by species shift due to growth within larger time-sales from 1 day to weeks, a change of chl-a might not be necessarily linked to biovolume increase of phytoplankton. Felip and Catalan (2000) describe the decoupling between the peak chl-a concentration and the peak biovolume during seasonal succession of phytoplankton. When plotting the compositional shift between phytoplankton species (e.g. expressed by a similarity index as shown in Fig. 9.4b) versus the net growth of chl-a (see Fig. 9.4a), the data points follow a dome-shaped frequency distribution. The common pattern is that the high persis-

tence of species in planktonic assemblages is related to almost zero net changes of biomass yield, while pronounced changes in species composition are associated with high values of positive or negative net growth rates (see Fig. 7 in Teubner et al. 2003b, Fig. 2d in Sonntag et al. 2006, the same is valid for Alte Donau but is not graphically shown). Furthermore, highest stability of phytoplankton species composition is often associated with chl-a net change rates ranging between zero and slightly positive values and thus indicate that small growth success best secure the stability of species composition (multi-lake study by Teubner, unpublished). Both examples illustrate that chl-a and phytoplankton biovolume emphasize different aspects of organism behavior. While the yield of biomass or biovolume stands for growth, the chl-a concentration mirrors both the phytoplankton yield and the adjustment of primary producers to their environment via photoacclimation. In this view, chl-a might mirror a more complex response of biota adjusting to their environment than just phytoplankton biovolume. These arguments are in agreement with our empirical results from Alte Donau suggesting that the chl-a vs TP relationship seems more robust than biovolume vs TP (see different levels of significance of both correlations). This finding might be confirmed by other studies that commonly choose phytoplankton chl-a (Vollenweider 1968; Carlson 1977; Forsberg and Ryding 1980; McCauley et al. 1989; Reynolds 1992; Watson et al. 1992; Teubner and Dokulil 2002; Chen et al. 2003; Dokulil and Teubner 2003; Lepistö et al. 2006; Søndergaard et al. 2011; Qin et al. 2013) over phytoplankton biovolume (e.g. Dokulil and Teubner 2005) for the response variable to the total phosphorus pool. Many studies emphasize the logistic shape of the Chl-a to TP relationship (e.g., McCauley et al. 1989; Watson et al. 1992; Dokulil and Teubner 2003; Donabaum et al. 2004). This sigmoid curve is mirroring an exponential growth at low TP concentrations but saturates at high TP. The latter is often discussed in view of a co-limitation, i.e. that an environmental stimulus other than phosphorus such as light or further macronutrient elements (nitrogen and silica) are not sufficiently available for enabling further growth at relatively high TP levels (e.g., Vollenweider 1968; Forsberg and Ryding 1980; McCauley et al. 1989; Teubner and Dokulil 2002). In case of Alte Donau, the log-log-transformed Chl-a:TP or biovolume:TP relationship does not follow the shape of a sigmoid curve and is thus different from multi-lake studies covering a much wider range of trophic levels (McCauley et al. 1989; Watson et al. 1992; Dokulil and Teubner 2003).

## 9.5 Conclusions

The main compositional shift from cyanobacterial dominance under hypertrophic conditions to a balanced mixture of cyanobacteria, diatoms, green algae, golden algae and cryptophytes under mesotrophic conditions seems to be mainly driven by bottom-up control (see integrated lake management plan including external and and internal measures; Chaps. 5, 8 and 18, 19, 20). The drastic decline in phytoplankton yield responded to a sustainable reduction of the total phosphorus pool stimulated by (1) the initial phosphorus precipitation in association with sediment oxidation by

RIPLOX-treatment and (2) the persistent low phosphorus availability in subsequent years due to the successful re-establishment of underwater vegetation. The hypertrophic situation in 1994 was characterised by 35 μg L$^{-1}$ mean phytoplankton chl-a in summer, 63 μg L$^{-1}$ annual mean for TP, 0.85 m annual mean for Secchi depth (0.69 m summer Secchi depth), about 3 t dry weight of submerged macrophytes (Fig. 8.1 in Chap. 8), 6157 kg total fish stocking (40% predatory fish) and 5599 kg total fish catch (37% predatory fish, fish data see further Chap. 15). The period of sustained lake management is mirrored by the stabilised situation during the last 8 years of observation (2007–2014) with 5 μg L$^{-1}$ mean phytoplankton chl-a in summer, 10 μg L$^{-1}$annual mean for TP, 3.7 m annual mean Secchi depth (3.0 m mean summer Secchi depth), about 365 t annual dry weight of submerged macrophytes (Fig. 8.11 in Chap. 8), 4347 kg annual fish stocking (21% predatory fish) and 4314 kg annual fish catch (31% predatory fish, fish data see further Chap. 15 and Fig. 20.7 in Chap. 20). The control of phytoplankton yields effected biota from bacteria to macrozoobenthos as described in other chapters of this book. The suppression of filter-feeding herbivorous cladocerans after reduced algal food supply and the dominance of mainly selective-feeding omnivorous and herbivorous copepods, which survived under mesotrophic transparent-water conditions, is one example of how strongly declined phytoplankton yields impacted planktonic assemblage (Chap. 11). Different from many other lake restoration projects described in literature, fish was not removed as cyprinid-fishing is most popular in this urban lake. Alte Donau thus provides an example of successful and sustained lake restoration mainly accomplished by bottom up (resource-driven) control rather than by top down (consumer-driven) control.

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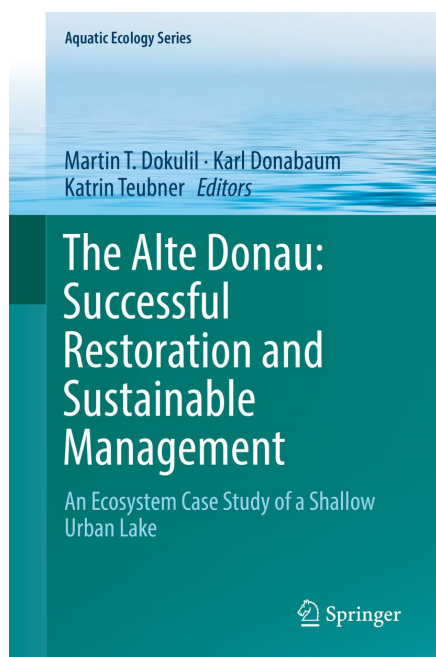
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